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Errata

Page 241, line 10, for "created" read "reached."
Page 271, line 8, for "*Cyas*" read "*Cycas.*"
Page 383, line 3, for "Law or" read "Lawn on."

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BULLETIN

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1918

Studies in the genus Lupinus—II. The Microcarpi, exclusive of Lupinus densiflorus

Charles Piper Smith

(WITH SIXTEEN TEXT FIGURES)

Introduction

The subgenus *Platycarpos* of Watson readily permits separation into two groups, the *Pusilli* of Heller (Muhlenbergia **8**: 87. 1912), or the loosely-flowered small species of the interior of western North America; and the *Microcarpi* (Bull. Torrey Club **44**: 405. 1917), or the verticillate and commonly larger plants of the Pacific Slope of both North America and central Chile.

The published names applied to members of the *Microcarpi* are as follows:

L. microcarpus Sims, Bot. Mag. **50**: *pl. 2413*. 1823.
L. densiflorus Benth. Trans. Hort. Soc. II. **1**: 409. 1835.
L. Menziesii Agardh, Syn. Gen. Lup. 2. 1835.
L. palustris Kell. Proc. Cal. Acad. Sci. **5**: 16. 1873.
L. Menziesii aurea Kell. *ibid.* **5**: 16. 1873.
L. lacteus Kell. *ibid.* **5**: 37. 1873.
L. luteolus Kell. *ibid.* **5**: 38. 1873.
L. Bridgesii Gray; Watson, Proc. Am. Acad. **8**: 538. 1873.
L. malacophyllus Greene, Pittonia **1**: 215. 1888.
L. ruber Heller, Muhlenbergia **2**: 75. 1905.
L. arenicola Heller, *ibid.* **2**: 75. 1905.
L. horizontalis Heller, *ibid.* **2**: 74. 1905.
L. glareosus Elmer, Bot. Gaz. **39**: 53. 1905.
L. subvexus C. P. Smith, Bull. Torrey Club **44**: 405. 1917.

[The Bulletin for December (**44**: 535–579. *pl. 25, 26*) was issued December 27, 1917.]

L. Bridgesii Gray is evidently the same as *L. luteolus* Kell. and is so acknowledged by Watson (Bib. Index 238). *L. arenicola* has been referred by Heller (Muhlenbergia **6**: 70) to *L. lacteus* Kell., which, as noted by Heller, was referred by Watson first to *L. densiflorus* and later to *L. microcarpus*. *L. malacophyllus* Greene might easily be considered as a connecting link between the *Pusilli* and the *Microcarpi*. Since so many variations occur, it is really surprising that no more names have been published. Several specimens have been marked "var." by the collector or student; but evidently no one has cared to attempt a critical study of the group. Except for the material easily determined as *L. luteolus* Kell., most specimens have been labeled either *L. microcarpus* or *L. densiflorus*, or left unnamed.

During four years of field observations in middle western California, my efforts to determine the variations I collected led to unsatisfactory results, and a survey of the material found in the herbaria visited in 1908 brought me to the determination to some day seek a classification that might possibly eliminate some of the evident confusion as to proper identifications. With this object in mind, I recently undertook to look into the status of the forms already described, and then to work out the relationships and characters of the seemingly undescribed forms known to me.

MATERIAL EXAMINED

The National, Stanford University, and University of California herbaria kindly placed many sheets in my hands for study. Two weeks were spent in Cambridge, New York, and Philadelphia, where the material in the herbaria in those cities was given due attention. Thus some 225 sheets have been considered in forming the opinions put forth in this paper.

GEOGRAPHICAL DISTRIBUTION

This group is peculiar to the west coast of America, the range generally ascribed to the initial species, *L. microcarpus* Sims, being the range of the entire group. In South America, the plants seem to be confined to central Chile, having an altitudinal distribution from the coast far up into the Andes. In North America the longitudinal range is from Vancouver Island to Lower California;

Vancouver and the adjacent islands have one isolated form, the Yakima Valley in Washington another. This latter, one local form of central Oregon, and one of western Nevada are the only ones peculiar to the country east of the Cascade-Sierra ranges. The more widely distributed form northward is apparently common both to the waterways in Oregon east of the Cascades and also to southwestern Oregon and the northern counties of California. Central California is evidently the center of distribution of the group, and there many specialized and localized forms occur, from the coast well up into the Sierras.

DIAGNOSTIC CHARACTERS

Most of the characters ascribed by Sims and Bentham to their species are common to all members of the group, and cannot be used to distinguish between the two species. Agardh's treatment of the species was mainly based upon the specimens seen by him in Lindley's herbarium. A small-flowered plant collected by Douglas in California, as well as all the Chilean material there, he referred to Sims's species. A more robust and longer-haired plant he accepted as Bentham's *L. densiflorus*, and this he acknowledged as having the aspect and nearly all the characters of *L. microcarpus*,

> sed robustior et villo longiore praecepue in partibus floribus obsitus. Ceterum petioli longiores, verticilli densiores floresque albescentes videntur. Unica autem differentia, quae ad speciem distinguendam valere videatur, e bracteis sumenda est.

The yellow-flowered, short-pubescent form with long racemes of distinct verticels was set apart as his *L. Menziesii*. Three certain forms collected by myself in California were very readily determined as these three species of Agardh; but when I considered other forms found by me, the original plates of *L. microcarpus* and *L. densiflorus*, and also the conflicting determinations and opinions of various botanists, it seemed logical to conclude that the group needed special attention.

Upon taking up the study, I soon found that reliable diagnostic characters are not as readily selected as I expected them to be. Many which at first recognition appeared to be all-sufficient for clear-cut distinctions finally suffered complete or partial abandonment after being carefully weighed. As a rule, the general aspect will appeal to the eye first and the general structure of the vegetative parts of the plant merits reasonably close attention. Evidently the environment, and especially competition with plants of other genera, has much to do with whether the plant is low or tall. Presumably the amount of available plant food may determine whether the plant is acaulescent and unbranched, or more or less caulescent and branched. The axial terminal bud, unless injured by some external cause, may be depended upon to produce a fruitful peduncle. Branching is, of course, merely the result of the development of axillary buds, and it is common, in large well-branched plants, to find matured or ripened seeds in the pods of this axial peduncle when the racemes of at least some of the branches are still in bloom. A low unbranched acaulescent plant is a record of its own environment, and a dry barren hillside or desert area the habitat in which it is able to both exist and persist. On the other hand, a tall plant, branched more or less above the base perhaps, almost always comes from an environment also favorable to plants of other genera; and abundance of nourishment, assisted by the stimulation of competition, is fundamentally responsible for the extensive vegetative growth developed. The "fistulous" character, especially, is certainly the evidence of a rapid growth during a warm moist season. I see no "specific" characters in the stem structures of these plants, excepting, to some extent, in *L. luteolus* Kell.; but I have admitted into my treatment of varieties more than one definite reference to such stem characters, especially when coupled with other characters or supported by geographical distribution. The length of the petioles and the size of the leaflets and stipules vary with the stem portions and seem to me to be of no value for specific distinctions. Even the pubescence failed to give satisfaction in my effort to draw specific lines.

Most reliable of all, I have concluded, is the position of the flowers in anthesis and soon after anthesis. This may not always be strictly constant in all the flowers of a particular raceme, nor in all the racemes of a certain plant; but I am convinced that, with occasional allowance here for some little variation, this character will prove to be as positive a one as can be found in the *Microcarpi*, and certainly is more usable than the very indefinite distinctions as yet proposed by those who have treated any of the group. The verticels are regularly crowded in *L. luteolus* and *L. horizontalis*, usually well separated in *L. microcarpus* and *L. subvexus;* but in *L. densiflorus* is found a full range of variations from densely crowded to quite remote. The floral bracts vary much in length, usually becoming reflex-withering as the flower-buds open; but in one variety of *L. subvexus* they are rather conspicuous for their tardiness in reflexing. Their length seems to be too inconstant to be of much diagnostic value.

With few exceptions, I have not been able to accept size and color of petals for specific distinctions, though such are abundantly used in the varietal characterizations. At the free edges above, the keel petals are usually ciliate, often densely so, and a tendency to be ciliate at the free edges below is more or less pronounced in a few of the forms herein designated as varieties; but in *L. luteolus* this ciliation below is as dense and prominent as that above, usually extends backward onto the claws, and seems to be worthy of special notice. Variation in size, shape, apex and base of banner; ciliation, length, and width, but not detailed form, of wings; size, shape, and curvature of keel—are all worthy of consideration in the delineation of varieties. The pubescence of the calyx usually agrees rather closely with that of the peduncles, petioles, etc. The lower lip, I am persuaded, yields good varietal characters as to length, dentation, and inflation; but the upper lip, at least in many cases, varies too much within the flowers of a given raceme to be trusted for any distinctions. The presence or absence of bracteoles is usually a decided uncertainty; but their presence may be diagnostic in *L. horizontalis* and in Elmer's *L. glareosus*.

The size, relative thickness, surface, color, and marking of the seeds—when more of same have been collected and properly identified—will probably be found of value in the varietal, if not in the specific, classification; but in *L. luteolus* again, I find a seed character seemingly distinctive and peculiar to that species. The mature pods show much variation in size, but otherwise give little evidence of deserving much consideration.

PATHOLOGICAL MATERIAL

Abnormal specimens are occasional, and care should be exercised to avoid them in the designation of varieties. Field work may sometimes be necessary in order to establish that a certain variation is really the result of a diseased condition. Usually, however, an abnormal development is indicated by pronounced elongation or multiplication of some of the floral parts. One very interesting case is that represented by sheet 366288 in the U. S. National Herbarium (*K. Whited 536*, Ellensburg, Washington). In both specimens the flowers dissected have three wing-petals each, and in one all the wing- and keel-petals are very abnormal in shape (FIG. 1). In the case of sheet 620193 (*V. Bailey 91*, Toppenish, Washington) the flowers are of the same narrow form and seemingly fruitful.

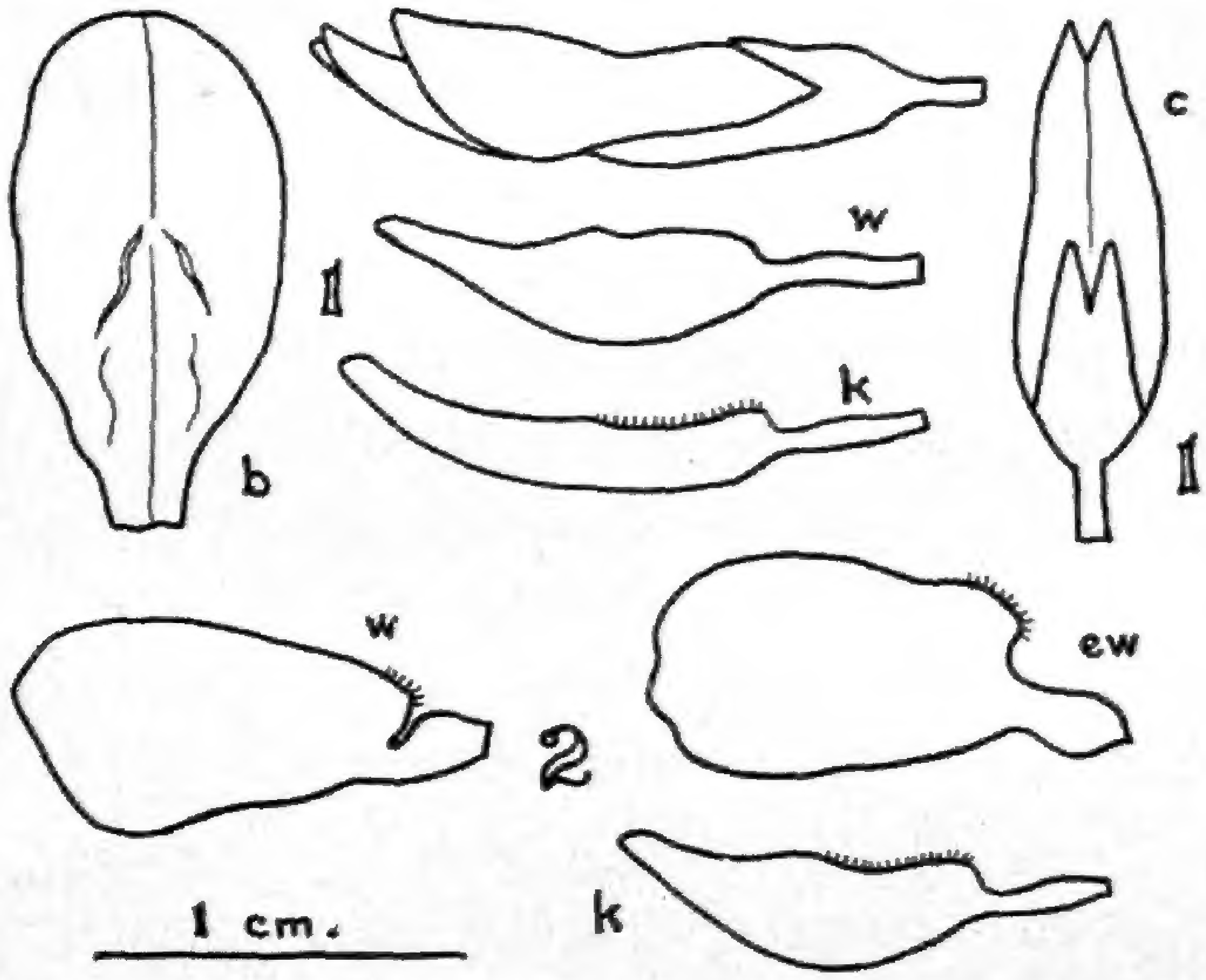

FIG. 1. LUPINUS SUBVEXUS FLUVIATILIS C. P. Smith. *K. Whited 536* (US 366288). 1. From specimen on right, *b*, banner; *w*, wing (three like this); *k*, keel; *c*, calyx as seen from above; side view of entire blossom above. 2. From specimen on left: *w*, wing (two like this); *ew*, extra wing petal; *k*, keel; no banner present.

SPECIAL ABBREVIATIONS

The location of each specimen cited is indicated by an abbreviation. The abbreviations used are as follows:

DS, Dudley Herbarium of Stanford University;
UC, herbarium of the University of California;
ColU, herbarium of Columbia University;
T, Torrey Herbarium (at New York Botanical Garden);
NY, herbarium of the New York Botanical Garden;
G, Gray Herbarium of Harvard University;
US, United States National Herbarium;
PA, Philadelphia Academy of Arts and Sciences;
CPS, private herbarium of the writer.

ILLUSTRATIONS AND MEASUREMENTS

The figures are mere outline representations of the dissected floral parts, mounted in water under cover-glass slips. The calyx is represented as seen from above, the upper lip having been pressed down to show its proportional relations to the lower lip. By this method, the interstitial bracteoles, if present, are not apt to be overlooked. One wing-petal is often added merely to show the extent or absence of the ciliation. The banner is flattened out sufficiently to get the measurements and show the shape of the apex and claw. The measurements, with necessary exception in a very few cases, were made from these dissected floral parts after same had been softened in boiling water and mounted for drawing.

Key to the species of the Microcarpi

Bracts subulate throughout, mostly stiff and not reflex-withering, about 5–6 mm. long, little more than twice the length of the pedicels; flowers 9–11 mm. long. 1. *L. malacophyllus.*

Bracts linear-lanceolate with a dilated thin base, mostly reflex-withering as the flower-buds open, at least the lower much longer than the pedicels; flowers 11–19 mm. long.

- Flowers ascending to suberect in anthesis.
    - Banner 4–6 mm. wide; wings naked below and often above; calyx ebracteolate. 2. *L. microcarpus.*
    - Banner 7–11 mm. wide; wings and keel ciliate near the claw both below and above; calyx bracteolate. 3. *L. horizontalis.*
- Flowers spreading in anthesis.
    - Flowers soon becoming suberect after anthesis, not secund. 4. *L. subvexus.*
    - Flowers spreading or distinctly secund after anthesis.
        - Plants 30–90 cm. tall, strictly fibrous, often widely branched above; banner ovate; keel densely ciliate at base both below and above; verticels crowded; seeds uniformly blackish brown, regularly tuberculate. 5. *L. luteolus.*
        - Plants 4–50 cm. tall, stems short and fibrous or elongated and fistulous; banner elliptic to oval, rarely ovate; keel usually naked near base below; but sometimes sparsely ciliate; verticels crowded or remote; seeds smooth or irregularly roughened. 6. *L. densiflorus.* *

1. LUPINUS MALACOPHYLLUS Greene, Pittonia 1: 215. 1888.

I quote from the original description as follows:

> Annual, erect, a span high, with a few ascending branches from the base; soft throughout, with a long white villous pubescence . . . . racemes verticillate, at

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* *L. densiflorus* and its varieties will be discussed in the third paper of this series.

least below, . . . calyx-lips very unequal; the upper short, scarious, slightly notched; lower . . . distinctly 3-toothed: corolla ½ inch long, light blue and dark purple; keel moderately falcate, naked . . . seeds orbicular, white.

Dry hills, near Verdi, Nevada, 2 May, 1888; collected by Mr. C. F. Sonne . . . related to the homely small-flowered *L. pusillus* and *L. brevicaulis*, but with . . . showy verticillate racemes of large flowers, ..."

This species might well be viewed as a connecting link between the *Pusilli* and the *Microcarpi*. Its possession of verticillate flowers is my only excuse for referring to it in this paper. Forms of *L. subvexus transmontanus*, of northern California and Oregon, are the only specimens of the *Microcarpi* that have already been, and may yet be expected to be, confused with *L. malacophyllus*. Seeds in my collection, collected by Heller, from about Reno, are from pale flesh-color to dark reddish.

NEVADA. Without definite locality, *C. L. Anderson* (UC 170306). Ormsby County: Carson City, 1865, *C. L. Anderson* (UC). Washoe County: along track below Verdi, 16 May, 1897, *C. F. Sonne* (UC); same locality, June, 1889 (UC); Reno, 13 May, 1901, *T. W. Cowgill* (UC); seed only, road between Laughten Springs and Reno, 26 July, 1911, *K. Brandegee* (UC).

2a. LUPINUS MICROCARPUS Sims, Bot. Mag. **50**: *pl. 2413*. 1823. [FIGS. 2, 3.]

The original description is as follows:

Lupinus microcarpus; foliis digitatis, calycibus verticillatis in appendiculatis: labio superiore emarginato inferiore bifido ter breviore, leguminibus rhombeis hirsutis dispermis.

Descr. Stem branched. Leaves digitate: leaflets 9–10, lanceolate, hairy on the under surface, smooth on the upper; petioles twice the length of the leaflets, pubescent. Stipules subulate. Peduncle terminal. Flowers blue, in a verticillate spike:whorls six-flowered. Bracts small, hairy. Calyx inappendiculate (unless the bracts, which are distinct from the calyxes, are to be called the appendices) bilabiate; upper lip much the shortest, emarginate; lower lip bifid. Vexillum oblong. Alae equalling the vexillum. Carina monopetalous, sharp-pointed. Anthers 10, five oblong, and five orbicular. Style the length of the stamens. Stigma capitate. Legume small, rhomb-shaped, mucronate by the persistent style, hairy; seeds two, variegated with black lines and dots.

This species of Lupin is a native of Chili. It has not, we believe, been heretofore described; and differs from all the known species by its small two-seeded pods. We regret however that we did not receive these in time enough to be added to the engraving.

Raised from seeds by John Walker, Esq., of Arnos Grove. It flowered in April, and appears to be annual.

Authors generally, following Agardh, seem to have assumed that any and all Chilean specimens are necessarily *L. microcarpus* Sims. One of my early hypotheses was that the Chilean plant ought to be specifically distinct from all the North American forms referred to this species of Sims. As I now see it, however, neither of these assumptions is altogether in agreement with the facts. A new viewpoint is evidently necessary and the conclusions finally accepted by me are: (1) that the strongest specific character possessed by *L. microcarpus* has never been properly recognized; (2) that most of the North American forms regularly, or occasionally, referred here belong rather to two other species; and (3) that both of these "two other species" are likewise represented in Chile. This viewpoint, as I see it, permits a much more satisfactory classification of the forms under consideration.

FIG. 2. LUPINUS MICROCARPUS Sims. Copied from original plate.

The original description serves little more than to indicate the group, of which this species was the first named and described. The illustration (from which FIG. 2 was copied) shows quite plainly, however, that the flowers must have been ascending to suberect in anthesis, a character that, as stated above, my studies have led me to accept as of real diagnostic value. This character, I am persuaded, will be found to persist under cultivation, at least for a few generations. I find, moreover, amongst the very limited array of Chilean material available for my study, specimens which show this character and which certainly, it seems to me, represent much better the form used for the original illustration than the other Chilean specimens referred elsewhere by myself, or the North American specimens referred here by others. It is very probable that the species, as here limited, is a composite of more than one recognizable form; but I await the opportunity to study new and additional material before attempting to do more with the South American varieties.

CHILE. Vicinity of Santiago, springy hillsides, 4500 ft., near Rio Colorado, 21 Jan., 1902, *G. T. Hastings 468*; without definite locality, *C. Gay*, ex Herb. Mus. Paris (G); Coquimbo, July–Aug., 1856, *W. H. Harvey* (G).

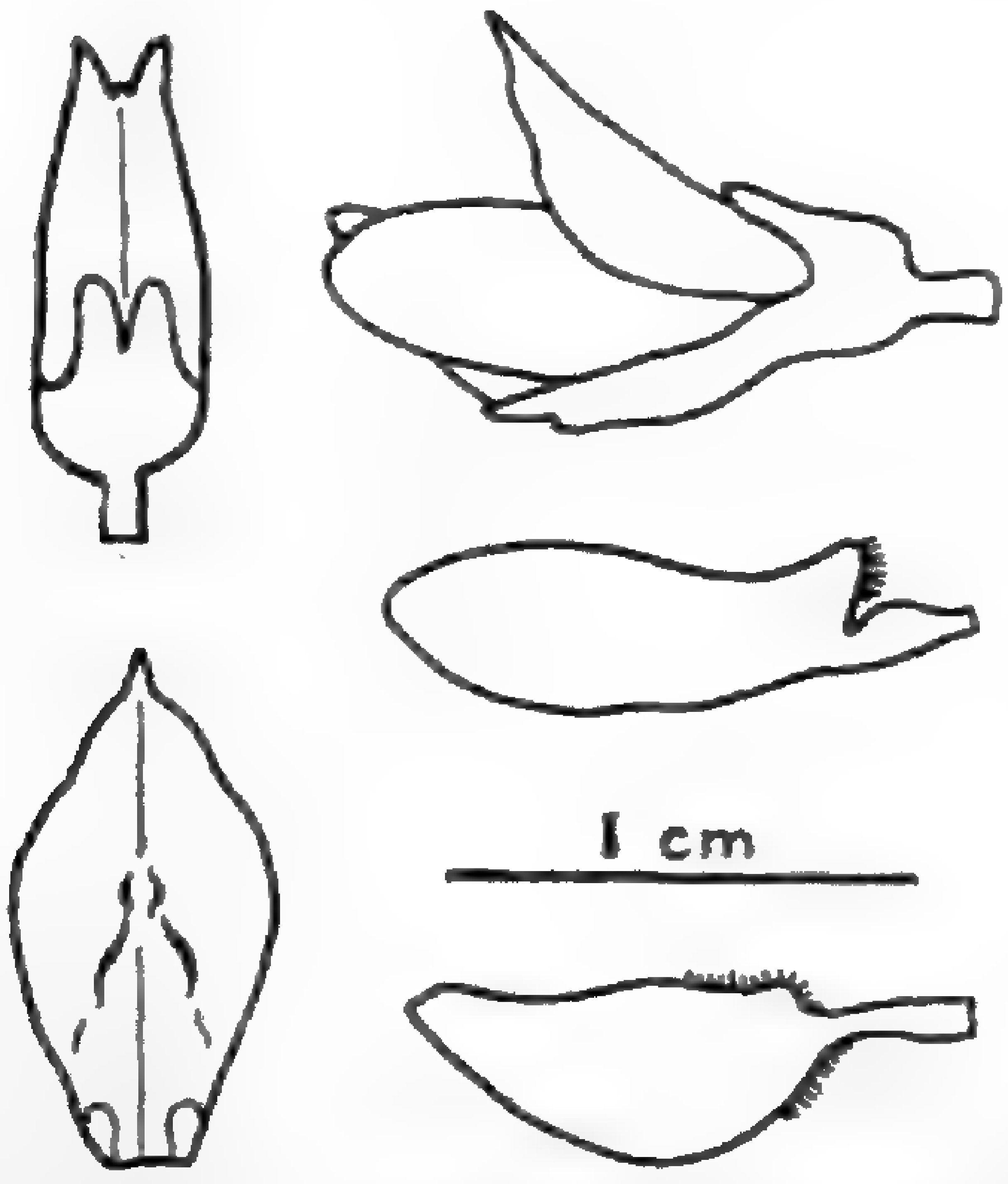

FIG. 3. LUPINUS MICROCARPUS Sims. *G. T. Hastings 468* (UC 65806).

FIG. 3 represents the floral characters of Hastings' No. 468, as recorded above. The specimen may be briefly described as follows: about 15 cm. tall, branches and foliage congested; villous, branched near the base and rebranched above; leaflets about 10–15 mm. long, petioles 50–70 mm. long; flowers ascending to suberect in anthesis; verticels 2–3; legumes 13–15 mm. long, seeds about 5 x 4 mm., straw-colored, unmarked, perhaps immature.

The species is represented in North America by the following variety:

2*b*. **Lupinus microcarpus ruber** (Heller) comb. nov. [FIG. 4.]

Lupinus ruber Heller, Muhlenbergia **2**: 73. 1905.

From Heller I quote:

> Branched from the base, the branches diffuse . . . leaflets blue-green . . . smooth above . . . : flowers erect in from 2 to 4 whorls, . . . dull red, 1 cm. long, about 4 mm. across: . . . lower calyx lobe 8 mm. long, barely 3 mm. wide at the base, the apex cleft for 2 mm., with a short cusp in the sinus; upper lip practically obsolete, represented by two short lanceolate teeth of 1 mm.: banner almost plane, ovate-lanceolate, 4 mm. wide at base, slightly keeled; wings narrow, 2 mm. wide, the lower edges not meeting until near the apex; keel not strongly curved, barely 2 mm. wide at the middle, bearded only near the slightly narrowed base. . .
>
> The type is no 7827, collected May 5, 1905, at Tehachapi, Kern County, California, along the railroad a short distance west of the town. It is a species remarkable for its small narrow red flowers. Some of the specimens show only a short central flowering branch much shorter than the leaves, while others have in addition lateral branches about equalling the leaves. It is a relative of *L. brevicaulis*, but that has "deep blue" flowers, the parts all but the keel differing in shape, and that is glabrous, while in ours it is bearded near the base.

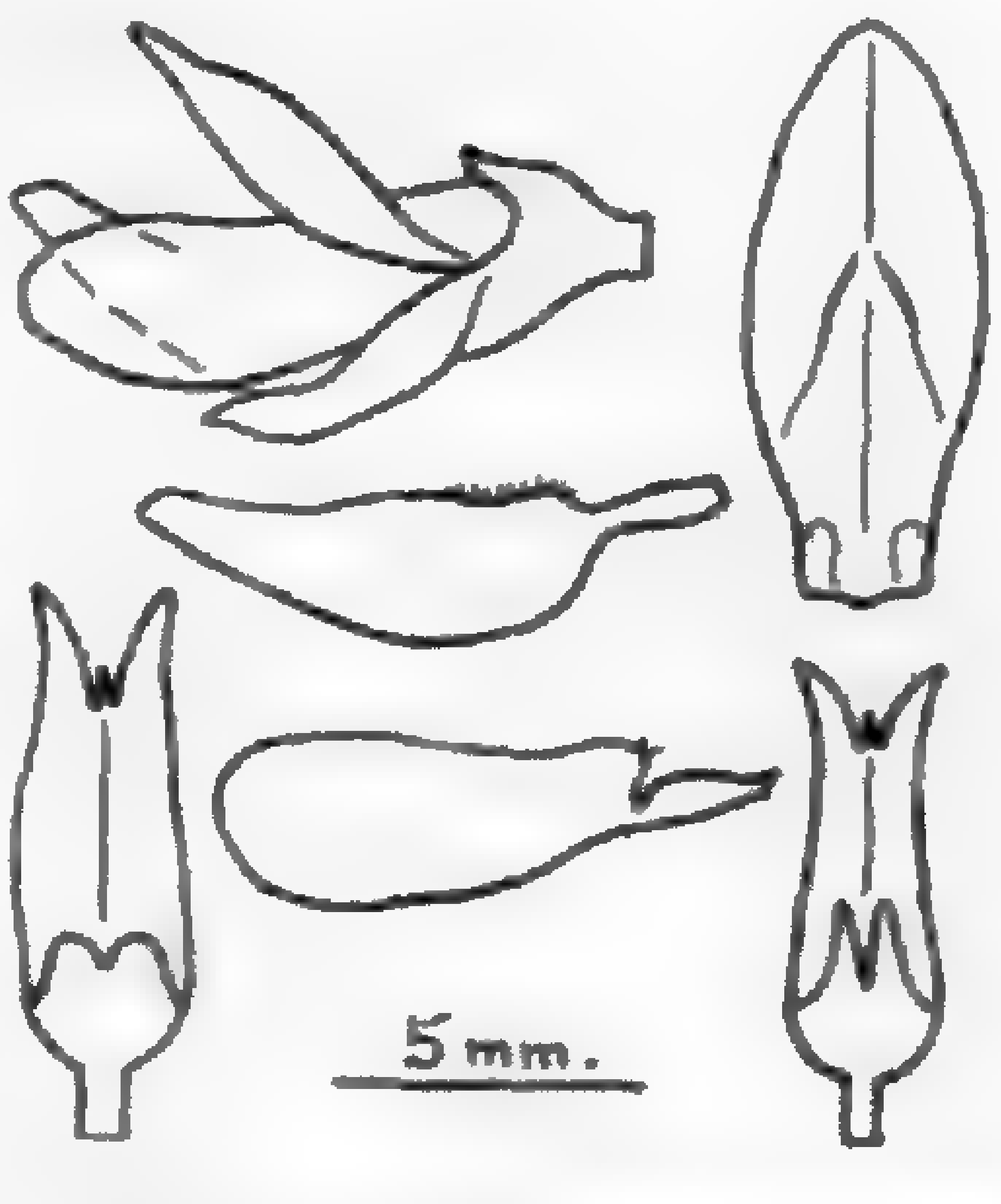

FIG. 4. LUPINUS MICROCARPUS RUBER (Heller) C. P. Smith. *K. Brandegee* (UC 149863).

The calyx is mostly 7–9 mm. long, the teeth of the lower lip are about 1.5 mm. long, commonly slender and curved-diverging, and the interstitial "cusp" is conspicuous. The flowers vary from dark red to merely pinkish. The seeds are yellowish gray to flesh-color, about 3.5 mm. x 3 mm., flattish, coarsely rugose, unmarked or nearly so. *L. brevicaulis*, with which Heller compares the plant, is a member of the *Pusilli.*

CALIFORNIA. Kern County: Tehachapi, 5 May, 1905 *A. A. Heller 7827* (US, PA, NY, G); Tehachapi, June, 1911, *K. Brandegee* (UC). San Diego County: Jacumba Hot Springs, near Monument No. 233, 26 May, 1894, *L. Schoemfledt*, U. S. & Mex. Int. Bound. Comm. No. 3307 (US); same locality, 29 May, 1894, *E. A. Mearns*, U. S. & Mex. Int. Bound. Comm. No. 3336 (US); Banner, 25 Mar., 1901, *T. S. Brandegee* (UC); Jacumba, 2500 ft., 9 July, 1916, *E. A. McGregor 88* (CPS). San Bernardino County: Mesas, Argus Mountains, Apr.–Sept., 1897, *C. A. Purpus 5437* (US, G, UC). ?San Luis Obispo County: La Panza, 26 May, 1888, *Mrs. Mathews* (UC).

3*a*. LUPINUS HORIZONTALIS Heller, Muhlenbergia **2**: 74. 1905. [FIG. 5.]

I quote from the original description, as follows:

> Branches several, all floriferous . . . the lowest ones horizontal, the ones above them more ascending, the middle ones erect . . . lower lip of calyx green, pubescent with somewhat tangled hairs, ovate-lanceolate, 6 mm. long, over 3 mm. wide at base, barely acutish, the apex minutely 2-toothed; upper lip ovate, membranous, barely 2 mm. long, cleft nearly to the base, the lobes lanceolate with rather wide sinus, villous and ciliate: flowers pale violet-blue, whorled and crowded . . . erect, 1 cm, long, 7 mm. across; banner plane or only slightly turned back, with a prominent midvein; wings . . . 2 mm. wide . . . keel not much curved, ciliate on the lower third . . . seeds nearly 3 mm. across marked with small dark spots.

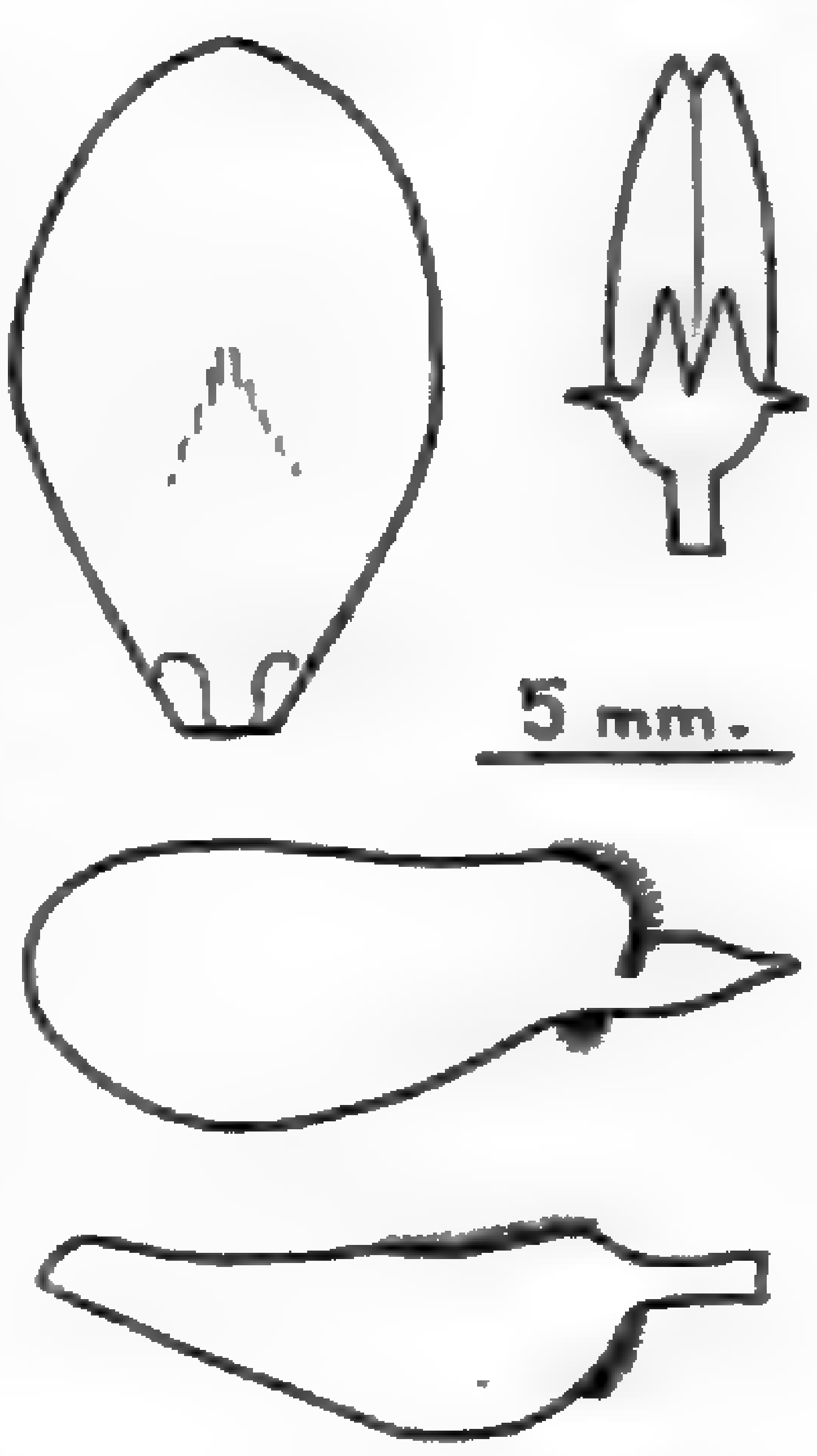

FIG. 5. LUPINUS HORIZONTALIS Heller. *A. A. Heller 7725* (G).

I accept this as a well-marked species. It is probably peculiar to the region of the type locality, though represented southeastward by a distinct variety.

CALIFORNIA. Kern County: Sunset, 20 Apr., 1905, *A. A. Heller 7725* (US, PA, G, NY).

3*b*. **Lupinus horizontalis platypetalus** var. nov. [FIG. 6.]

A *L. horizontali* differt partibus omnibus florum majoribus latioribusque; vexillo 15 x 11 mm., alis 15 x 7 mm., carina 12 x 4 mm.; calyce 9 mm. longo; ramis exterioribus specie non prostratis; seminibus prope 3.5 x 3 mm. crassis.

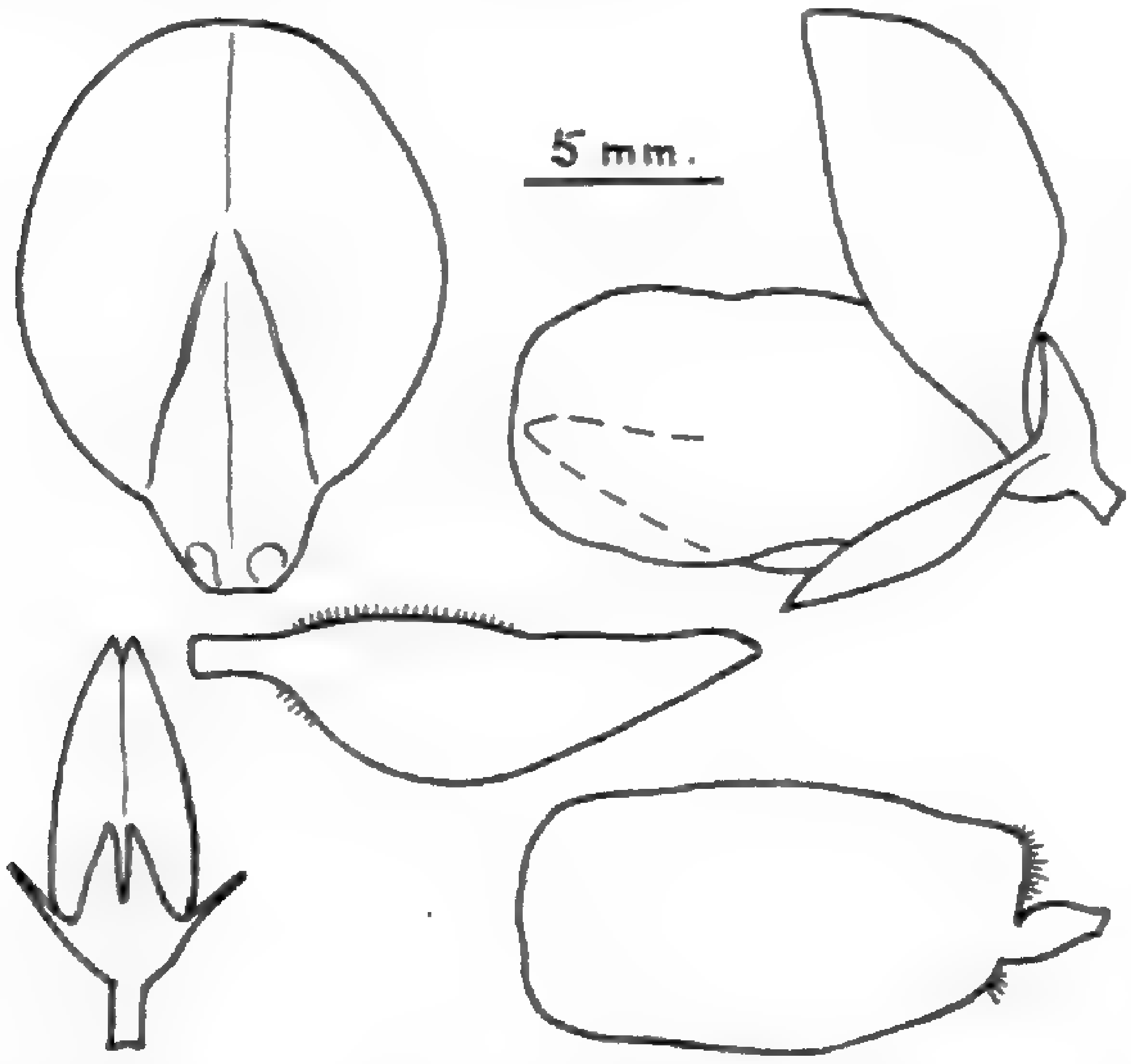

FIG. 6. LUPINUS HORIZONTALIS PLATYPETALUS C. P. Smith. *Hall & Chandler 6860* (UC 127296).

All the floral parts are much larger and broader than in the typical form of the species, and the outer branches are apparently not prostrate. The seeds are of a buff ground, marbled with purplish brown.

CALIFORNIA. San Bernardino County: eastern base of Fremont's Peak, Mojave Desert, 6 May, 1906, *Hall & Chandler 6860* (TYPE, UC 127296); Mojave Desert, May, 1882, *S. B. & W. F. Parish 1271* (G). Kern County: near Randsburg, May, 1913, *K. Brandegee* (UC).

Platypetalus is Greek for "broad petal."

4*a*. LUPINUS SUBVEXUS C. P. Smith, Bull. Torrey Club 44: 405. 1917. [FIG. 7.]

The following is a part of the original description:

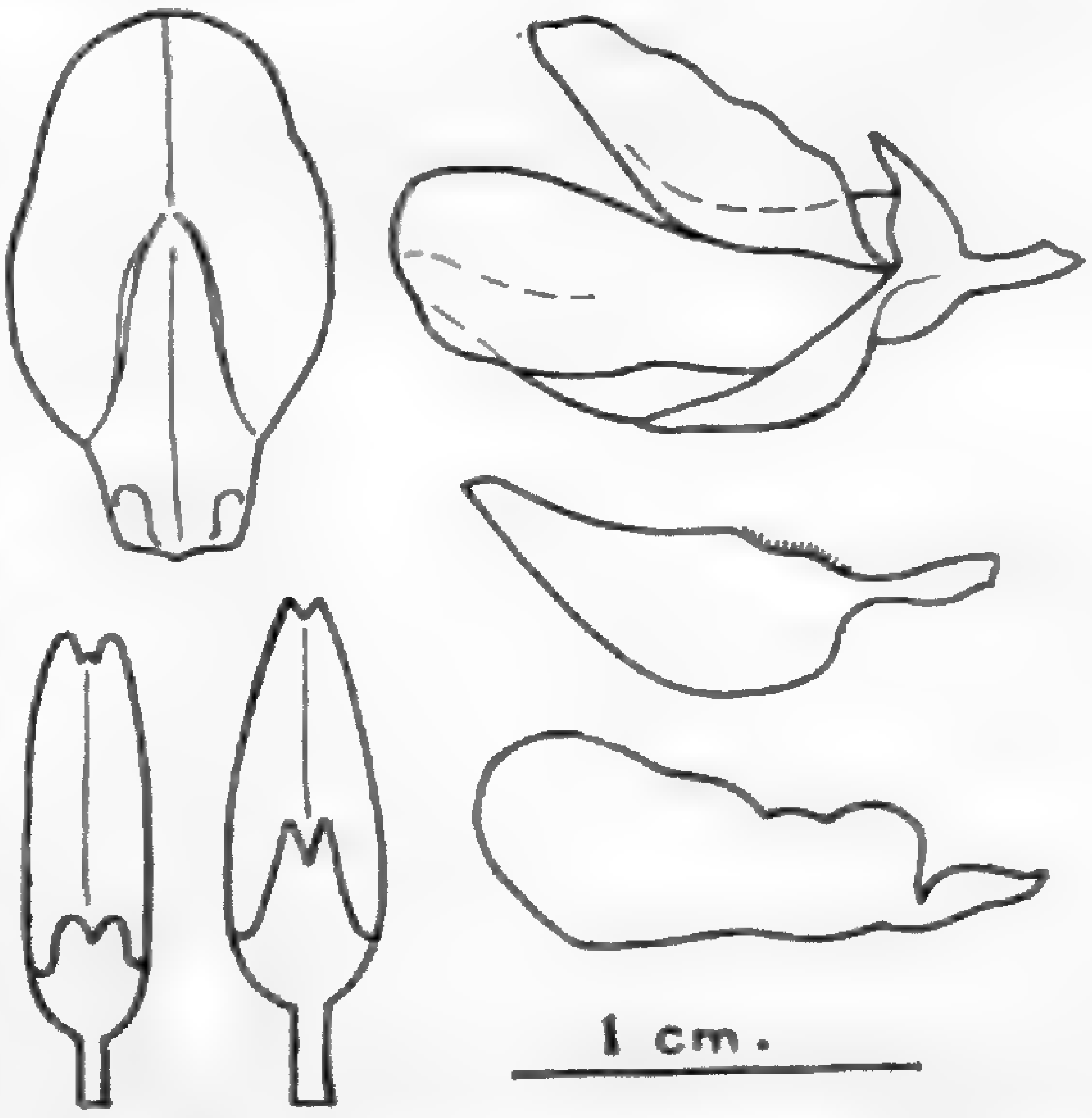

FIG. 7. LIPINUS SUBVEXUS C. P. Smith. *Heller & Brown 5415* (DS 9586).

> Simple or branched, loosely villous, the hairs 2–4 mm. long; whorls 3–7, well- separated; flowers spreading in anthesis, evidently ascending to suberect later; calyx ebracteolate, quite villous below; pods not secund. The typical plant has the lower lip of the calyx evidently inflated (subsaccate) near the base, large flowers with much of the banner and wings dark purple, and the banner rounded apically. Most of the varieties have the lower calyx-lip scarcely or not at all inflated and smaller flowers with the banner gradually narrowed to an acute apex.

CALIFORNIA. Yolo County: Madison, *Heller & Brown 5415* (DS, US, PA, NY, G). Contra Costa County: Antioch, 3 May, 1894, *A. Eastwood* (G, UC); Antioch, 8 Apr., 1895, *A. Eastwood* (US); Clayton, 17 Apr., 1889, *Chesnut & Drew* (UC). Alameda County: Oakland Hills, 1866, *H. N. Bolander 100* (G); Alameda, *T. S. Brandegee* (DS 9589); Livermore Pass, May, 1898, *J. B. Davy* (UC); Cedar Mountain, May, 1903, *A. D. E. Elmer 4371* (US, NY). San Francisco County: San Francisco, Apr., 1893, *I. Tidestrom* (UC).

Most, if not all, of these specimens are labeled *L. microcarpus* Sims, though the type sheet bears a correction, by A. A. H., changing the determination to *L. densiflorus* Benth.

Subvexus, "sloping upward," refers to the position assumed by the flowers upon withering.

Key to the varieties of Lupinus subvexus

- Calyx 9–11 mm. long.
  - Banner truncate, rounded, or obscurely angled at apex, usually 7–8 mm. wide.
    - Bracts normally reflex-withering as the flower-buds open.
      - Flowers 14–17 mm. long; calyx 10–11 mm. long; leaves not blackening in drying. 4*a*. typical *subvexus*.
      - Flowers about 14 mm. long; calyx 9 mm. long; leaves blackening in drying. 4*b*. var. *nigrescens*.
    - Bracts tardily or not at all reflex-withering. 4*c*. var. *fluviatilis*.
  - Banner evidently angled at apex, 5–7 mm. wide.
    - Wings usually non-ciliate; keel naked below.
      - Verticels approximate; plants 8–18 cm. tall, bushy. 4*d*. var. *transmontanus*.
      - Verticels remote; plants 20–40 cm. tall, with stems and branches elongated and fistulous below. 4*e*. var. *Leibergii*.
    - Wings strongly ciliate near base above; keel ciliate below. 4*f*. var. *insularis*.
- Calyx 7–8 mm. long; banner 5–6 mm. wide, angled at apex.
  - Leaflets 20–40 mm. long, 7–10 mm. wide, green; banner 9–11 mm. long.
    - Verticels distinct; keel straight. 4*g*. var. *phoeniceus*.
    - Verticels crowded; keel evidently arcuate. 4*i*. var. *Wilkesii*.
  - Leaflets 10–20 mm. long, 4–6 mm. wide, conspicuously white woolly-villous; banner more slender, 12–14 mm. long. 4*h*. var. *albilanatus*.

4*b*. **Lupinus subvexus nigrescens** var. nov. [FIG. 8.]

A *L. subvexo* typico differt foliolis nigrescentibus cum siccantes; pilis brevioribus inconspicuuis; floribus paulo minoribus; labio inferiore calycis vix inflato; alis superne ad basin ciliatis.

Differs from the typical form in that the leaflets turn black in drying, hair-covering less conspicuous, flowers smaller, lower lip of the calyx but slightly subsaccate, and the wings ciliate above near the base.

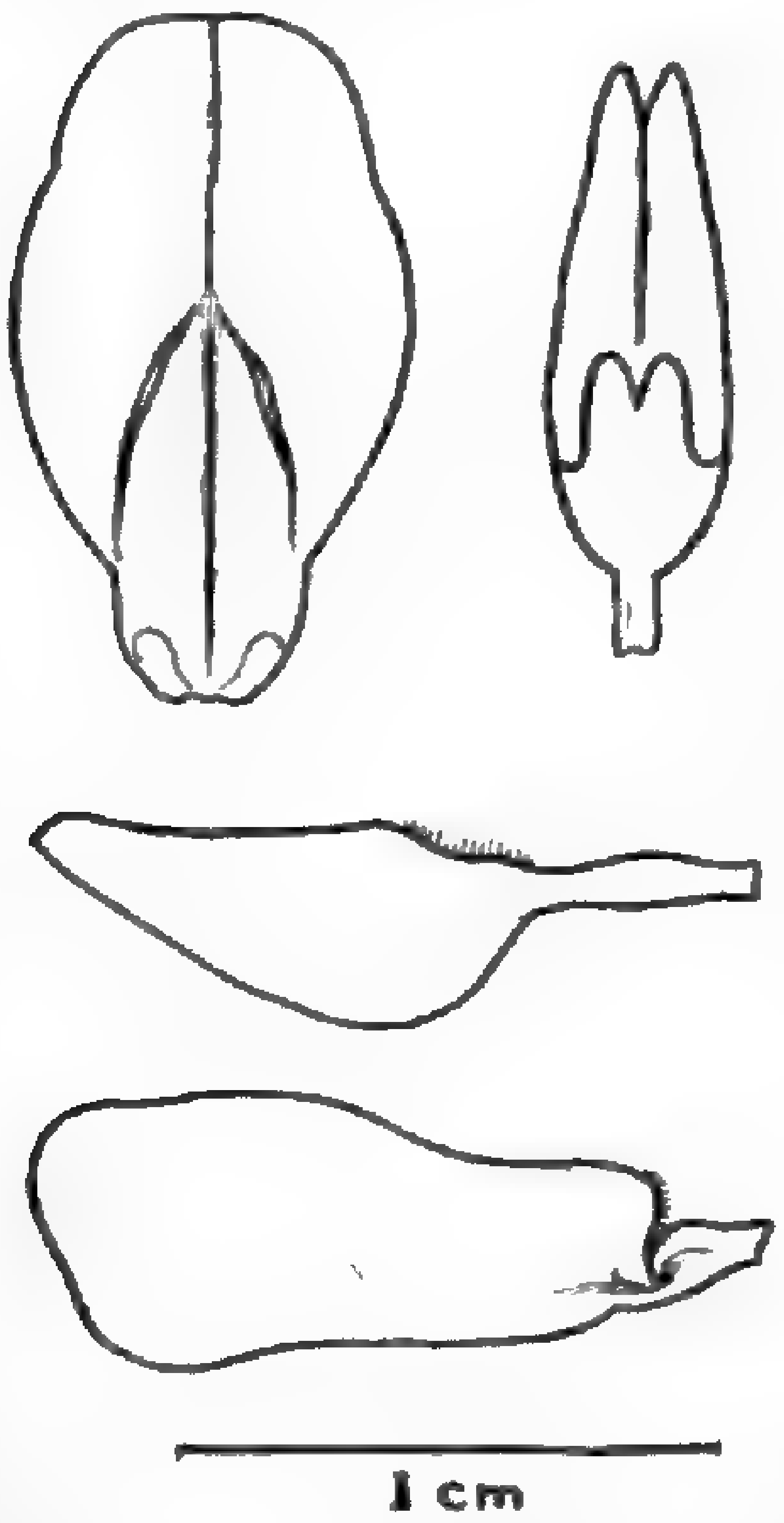

FIG. 8. LUPINUS SUBVEXUS NIGRESCENS C. P. Smith. *A. D. E. Elmer 4006* (US466205).

CALIFORNIA. Ventura County: Griffins, Mt. Pinos, July, 1902, *A. D. E. Elmer 4006* (TYPE, US 466205; type-duplicates, DS, NY). Kern County: hills, near the summit of Tejon Pass, on desert slope, 27 May, 1914, *S. B. Parish 9256* (UC).

This variety merits special study in the field, with collection of considerably more material. It is very different from Elmer's *L. glareosus*, taken at the same locality, but shares with that variety the peculiar character of the leaflets turning black in drying. The specimens are labeled *L. microcarpus*.

4*c*. **Lupinus subvexus fluviatilis** var. nov. [Fig. 9.]

Eramosus vel ramosus ad basin ramis suberectis vel pandentibus, 10–25 cm. altus, conspicue villosus; foliis paulo congestis cum planta humilis eramosaque est, plus patentibus cum planta ramosa est; pilis 1–1.5 mm. longis; petiolis 4–10 cm. longis, villosis, pilis saepe paulo plus 2 mm. longis; foliolis 5–10, 15–25 mm. longis, saepe obovatis vel spatulatis nonnumquam oblanceolatis, apice rotundatis vel angulatis, ciliato-villosis ad medio-costis marginibusque: pedunculis foliis plerumque brevibus; verticillis 3–5, plus minusve appositis; floris ad anthesin pandentibus, postea ascendentibus vel suberectis, 14–16 mm. longis; pedicellis paulo plus 1 mm. longis, plurimum gracilibus; bracteis verticilli humillimi calyce prope aequantibus longitudine, tarde vel nequaquam

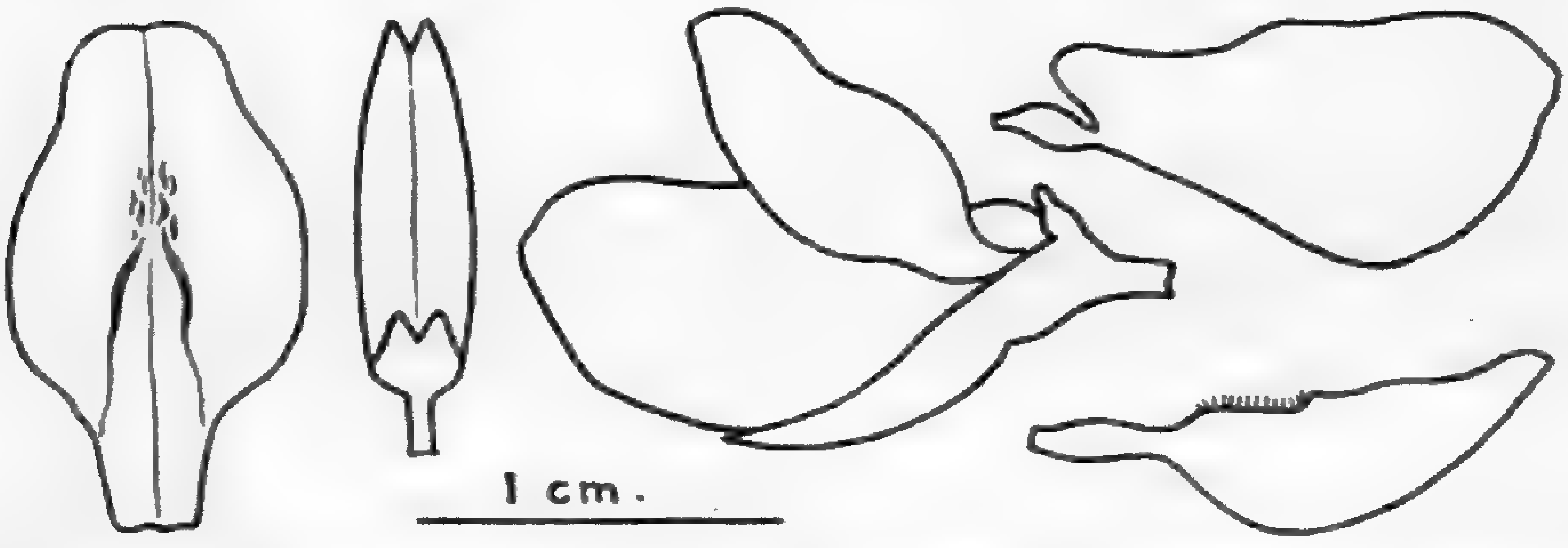

FIG. 9. LUPINUS SUBVEXUS FLUVIATILIS C. P. Smith. Fritillaria Club (US 205559).

reflectentibus et marescentibus, laxe villosis vel sublaevibus: calyce ebracteolato 9–10 mm. longo, subter dense villoso pilis prope 2 mm. longis, labio superiore diverso 2-dentato, prope 2 mm. longo, inferiore subrecto vel ad basin paulo inflato 3 mm. lato 2-dentato, sinu plerumque sine vestigio; corolla pallido-rosea vel-purpurea; vexillo 12–14 mm. longo, 7–8 mm. lato, apice paulo contracto, rotundato vel truncato, plus contracto ungue 2–4 mm. lato; alis 11–14 mm. longis, 5–7 mm. latis, ad basin non ciliatis; carina 9–11 mm. longa, subrecta: leguminibus usitatibus prope 14 x 8 mm.; seminibus pallidis maculatis, 4.5 x 4 mm.

WASHINGTON. Without definite locality, 1889, *G. R. Vasey 259* (TYPE, US 296664; type-duplicates, G, NY). Yakima County: Yakima region, 1882, *T. S. Brandegee 42* (UC); North Yakima, Oct., 1885, *T. S. Brandegee* (UC); Fritillaria Club, North Yakima, 1890, (US); Toppenish, 17 July, 1897, *V. Bailey 91* (US); Yakima, 3 June, 1898, *A. B. Leckenby* (US); North Yakima, 29 May, 1899, *J. B. Flett* (US); Wenas, 1 June, 1902, *Griffith & Cotton 85* (US, NY). Kittitas County: Ellensburg, 25 June, 1897, *K. Whited 536* (US); Ellensburg, June, 1897, *A. D. E. Elmer 371* (US, NY).

Seemingly peculiar to the valley of the Yakima River in central Washington. The flowers are relatively large with broad petals. Perhaps the strongest individual character is that the floral bracts are tardily or not at all reflex-withering as the flower-buds open. The seeds are flesh-color, mottled with a pale reddish brown, the hilum of the darker color. FIG. 1 illustrates abnormal specimens of this variety.

Fluviatilis is Latin for "of a river," and refers to the habitat.

4*d*. **Lupinus subvexus transmontanus** var. nov. [FIG. 10.]

A var. *fluviatili* differt foliolis oblanceolatis plerumque acutis; calyce 9–11 mm. longo, sinu labii inferioris plerumque dentis vestigio instructo; vexillo apice angulato, 11–12 mm. longo, prope 6 mm. lato ad basin paullatim contracto.

Similar to var. *fluviatilis*, but the leaflets are usually acute at the apex, the floral bracts usually reflex and wither as the flower-buds open, the lower lip of the calyx has the vestigial median tooth, and the banner is evidently acute at the apex.

OREGON. Wasco County: Antelope, May, 1885, *T. Howell* (TYPE, US 20844; type-duplicate, PA). County not given: Currant Creek, 11 May, 1885, *T. Howell 361* (G); John Day River, Crown Rock, 19 June, 1896, *V. Bailey 65* (US). Malheur County:

Malheur River, June, 1883, *Cusick 1113* (G). Jackson County: Antelope Creek, near Eagle, 4 June, 1898, *E. I. Applegate 2388* (US).

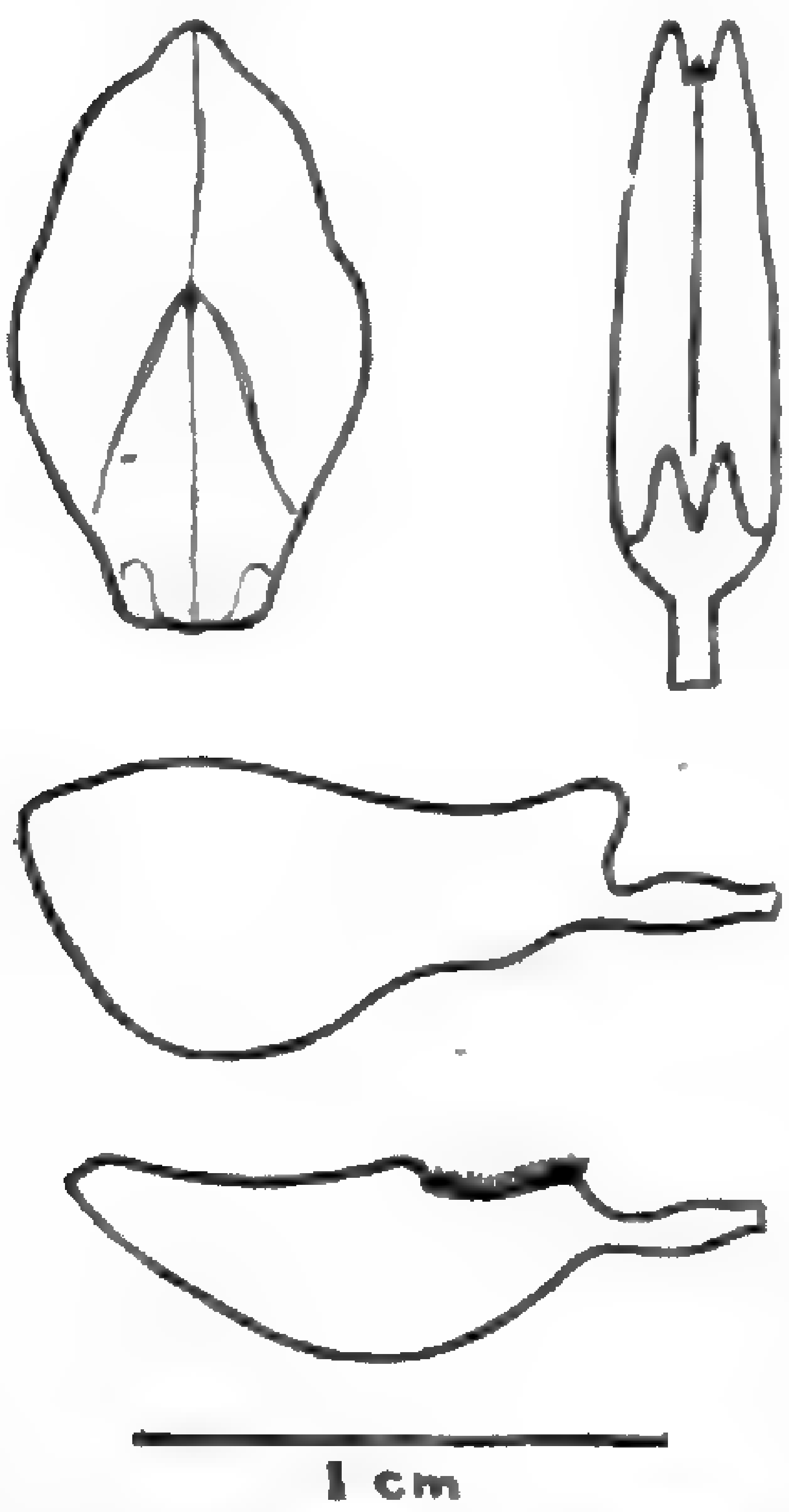

FIG. 10. LUPINUS SUBVEXUS TRANSMONTANUS C. P. Smith. *T. Howell* (US 20844).

CALIFORNIA. Modoc County: meadow bank along stream, 28 July, 1893, *Milo S. Baker* (UC); shore of Goose Lake, Aug., 1895, *Mrs. R. M. Austin* (US); sagebrush at Tule Lake, 31 May, 1897, *E. I. Applegate 879* (US); Goose Lake, July, 1898, *Mrs. R. M. Austin & Bruce 154* (UC). Lassen County: Craigs, 1893, *M. S. Baker* (UC); Madeline Plains, June, 1898, *Mrs. R. M. Austin & Bruce 2145* (DS, NY, UC). Siskiyou County: Klamathon, 2 July, 1903, *E. B. Copeland*, Baker Distribution 3537 (US, NY, G); Klamath Hills, 13 May, 1909, *G. D. Butler 704* (UC); Klamath Hills, 21 May, 1910, *G. D. Butler 1373* (US, UC).

Transmontanus is Latin for "across the mountains" and refers to the fact that the form is found on both sides of the Cascade ranges. It has been determined as *L. densiflorus*, *L. microcarpus*, and *L. malacophyllus*.

4*e*. **Lupinus subvexus Leibergii** var. nov. [FIG. 11.]

A var. *transmontano* differt altitudine 25–40 cm.; caule fistuloso ramoso aliquantum super basin; pedunculis ramisque elongatis: verticillis 4–5, distantibus; floribus suberectis mox post anthesin prope 13 mm. longis: bracteis mox marescentibus; calyce 2-dentato, 10 mm. longo, prope 3 mm. lato; vexillo 11 mm. longo, 5 mm. lato, apice acuto vel prope acuminato, ungue 4 mm. lato basi; alis 11 mm. longis; carina 8 mm. longa, recta.

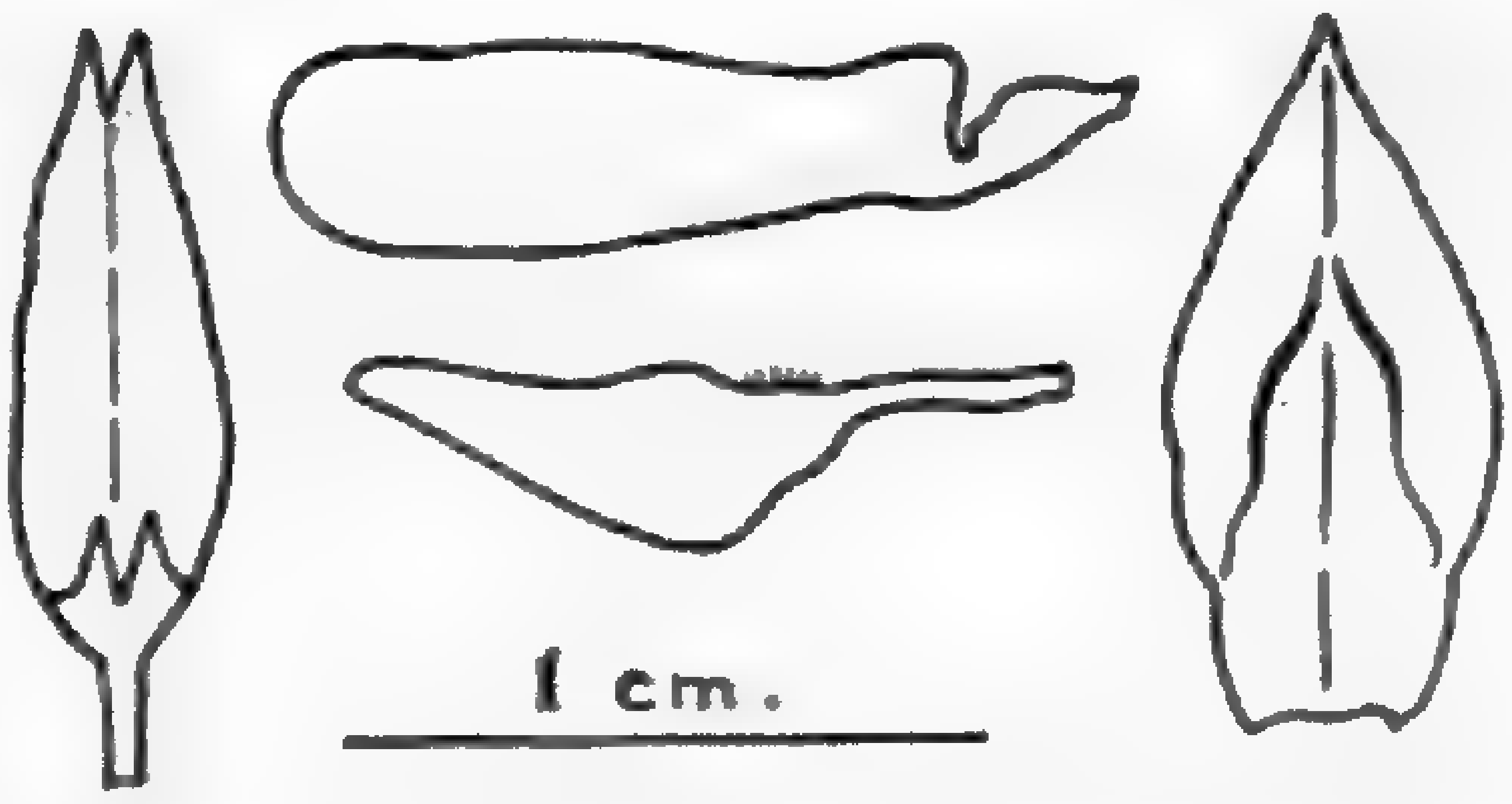

FIG. 11. LUPINUS SUBVEXUS LEIBERGII C. P. Smith. *J. B. Leiberg 317* (US 291134).

Unlike the other northern races of *L. subvexus*, this variety is branched from well above the base and has the lower parts distinctly fistulous. The verticils are remote, the banner is almost acuminate at the apex and its claw is poorly defined, and the flowers are evidently far from being showy. It is probably very local and rare and should be carefully studied in the field.

OREGON. Crook County: near Prineville, 955 m. alt., 1894, *J. B. Leiberg 317* (TYPE, US 291134; type-duplicates, G, US 291133).

4*f*. **Lupinus subvexus insularis** var. nov. [FIG. 12.]

Ad basin ramosus; foliis aliquantum congestis, foliolis gracilibus 2–3 cm. longis; racemis pluribus, floribus ad anthesin pandentibus ascendentibus postea, bracteis reflectentibus, bracteis petiolis pedicellisque laxe villosis; calyce dense villoso; carina curva.

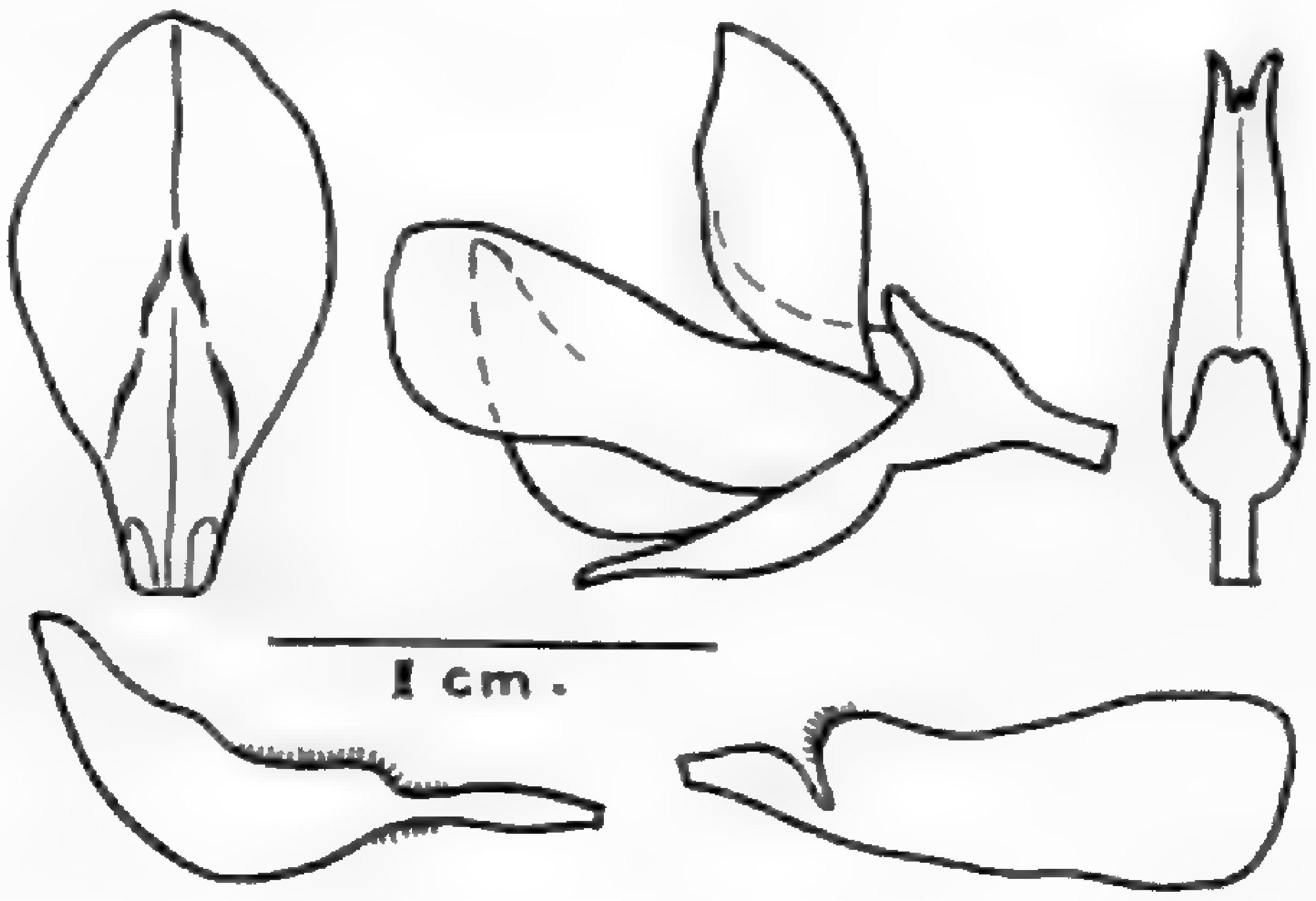

FIG. 12. LUPINUS SUBVEXUS INSULARIS C. P. Smith. *T. S. Brandegee* (UC 82003).

Much branched near the base, foliage congested, leaflets slender and 2–3 cm. long; racemes several with the flowers spreading in anthesis but ascending soon afterwards, bracts reflexing as the flower-buds open, the bracts, petioles and pedicels loosely villous; calyx densely villous; keel distinctly curved.

CALIFORNIA. Santa Cruz Island: Apr., 1888, *T. S. Brandegee* (TYPE, UC 82003).

Mounted on the sheet with the above specimen are some small plants (UC 82002) collected by Brandegee at San Telmo, Lower California, 28 Apr., 1893. These may represent the variety *insularis*, but should prove to be different. They are so small and in such condition I prefer to attempt no definite classification of them at this time.

4*g*. **Lupinus subvexus phoeniceus** var. nov. [FIG. 13.]

Eramosus vel ad basin laxe ramosus, ramis ramulosis laxe breve-villosis: verticillis 2–5 vel plus, appositis vel distantibus; floribus ad anthesin pandentibus, postea ascendentibus vel suberectis, 12 mm. longis; calyce ebracteolato, 7 mm. longo, subter paulo laxe villoso, pilis 1–1.5 mm. longis, paulo retrorsis, labio superiore minus 2 mm. longo, inferiore lanceolato-oblongo, vix 3 mm. lato, 2-dentato dentibus 1 mm. longis parallelis plerumque dentis vestigio instructo; corolla phoenicea vel pallidiora; vexillo 10–11 mm. longo, 6 mm. lato, apice angulato; alis 9 mm. longis ad basin superne paulo ciliatis; carina 8 mm. longa, plerumque recta: leguminibus 13 x 7 mm.; seminibus planis angulatis, 5 mm. longis, 4 mm. latis, atro-cineraceis, minute nigromaculatis circum cicatricula pallidioribus, superficie minute inaequaliterque rugoso simile quartzo.

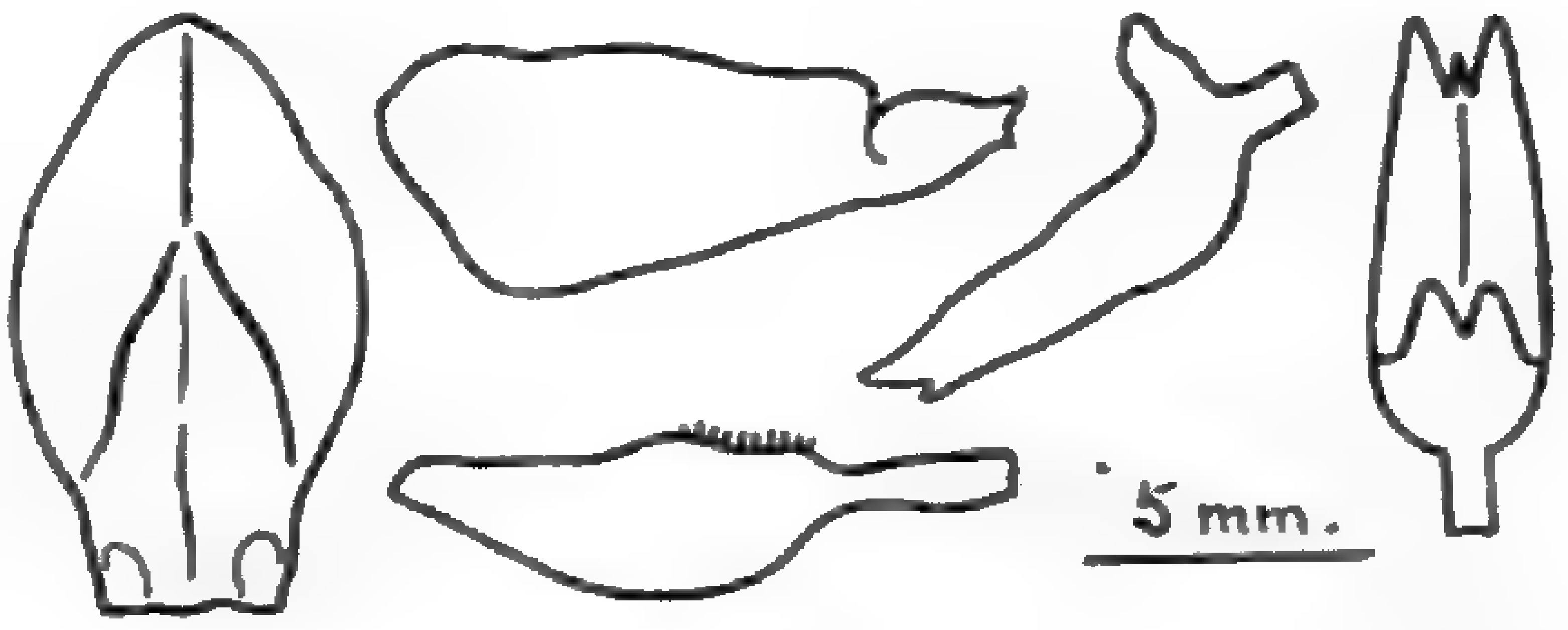

FIG. 13. LUPINUS SUBVEXUS PHOENICEUS C. P. Smith. *A. A. Heller 8632* (US 612641).

Simple or loosely branched from near the base, loosely short villous; whorls usually two to five, crowded or distinct; flowers spreading in anthesis, soon becoming suberect, about 12 mm. long; calyx retrorse-villous below with hairs 1–1.5 mm. long, the lower lip with a vestigial median tooth; petals reddish purple or paler, the banner about 10 x 6 mm., angled at the apex; seeds 5 x 4 mm., somewhat flattened and angled, dark-gray, minutely dotted with black, paler about the hilum, the entire surface minutely roughened, resembling quartz.

CALIFORNIA. Santa Clara County: Mt. Hamilton road, 2300 ft. alt., "on a roadside bank near oak trees," 31 May, 1907, *A. A. Heller 8652* (TYPE, US 612641; type-duplicates, PA, NY, G); seed only, type locality proper, 17 June, 1908, *C. P. Smith* (CPS); tilled soil below Smith Creek bridge, 17 June, 1908, *C. P. Smith 1479;* Calaveras Valley, May, 1914, *K. Brandegee* (UC 178195, except as to raceme in upper left hand corner).

This seemingly well-marked variety may be peculiar to the Mt. Hamilton Range. The plants are low and mainly simple in poor soil, but in richer and looser soil may be 2–3 dm. tall with a spread of 3–4 dm. The Smith Creek specimens were in seed as to the primary branches, while secondary branches, in the axils of the primary branches, were in flower.

Probably related to this, but certainly not typical, are the following: Atascadero, San Luis Obispo County, 30 Apr., 1861, *W. H. Brewer 493* (US); Ojai and vicinity, Ventura County, 24 May, 1866, *Peckham* (US). Additional material from these localities would be welcome and worthy of careful study.

The type collection has been recorded as *L. microcarpus* by Heller (Muhlenbergia **2**: 294. 1907).

Phoeniceus is Latin for "purple-red."

4*h*. **Lupinus subvexus albilanatus** var. nov. [FIG. 14.]

A var. *phoeniceo* differt foliis gracillimis acutis plurimum solum 10–20 mm. longis; foliis petiolis pedunculisque conspicue brevilanato-villosis; vexillo 12–14 mm. longo, graciliore; seminibus plurimum minoribus pallidioribus, immaculatis vel maculatis.

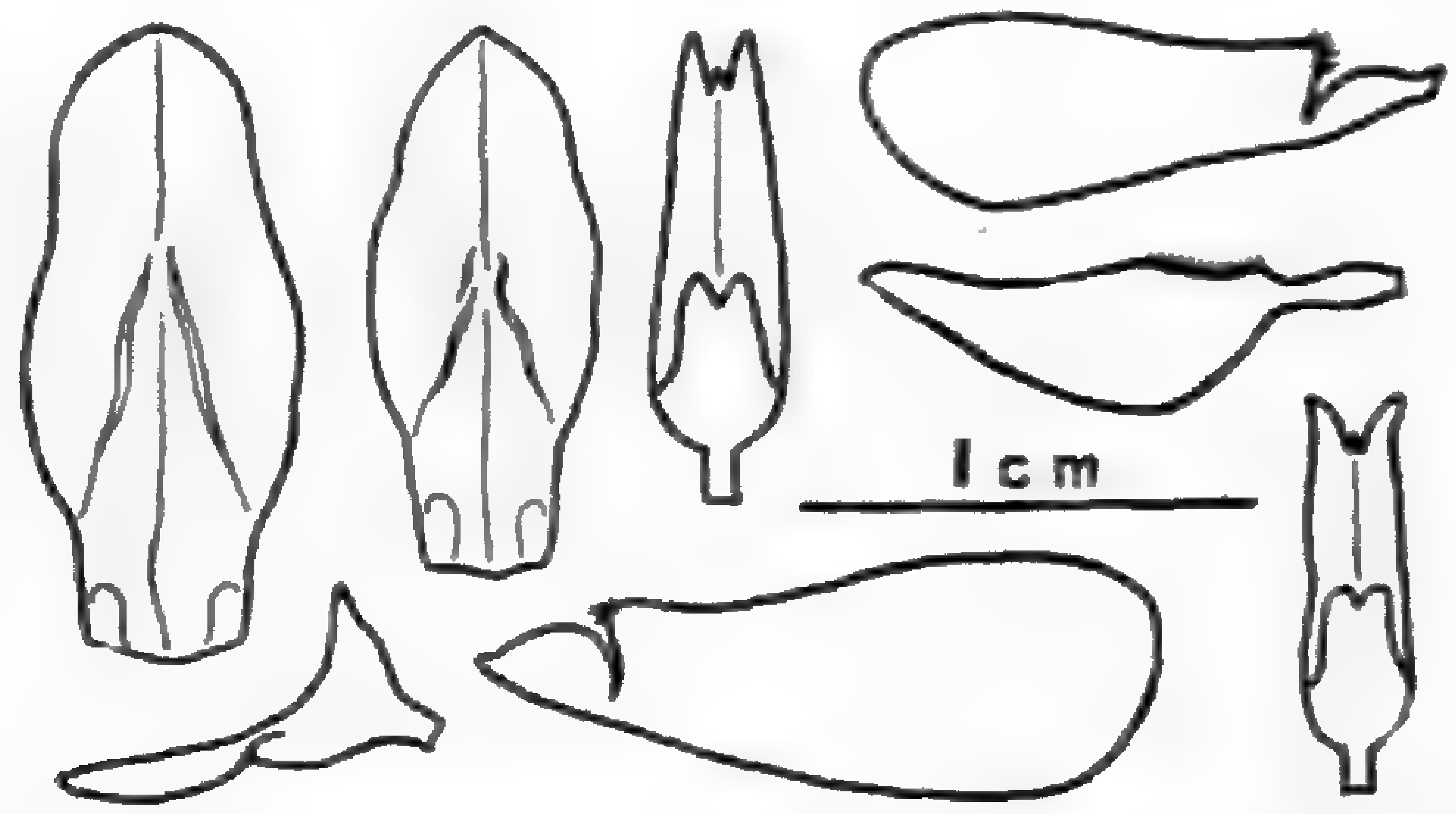

FIG. 14. LUPINUS SUBVEXUS ALBILANATUS C. P. Smith. *K. Brandegee* (UC 149886).

CALIFORNIA. San Luis Obispo County: Paso Robles, July, 1911, *K. Brandegee* (TYPE, UC 149886; type-duplicates, UC 149884, 149885, and 149947). Monterey County: near Plaskett's ranch, on road to Jolon, about seven miles from Kings City, *K. Brandegee* (UC); Manfield's ranch, Santa Lucia Mountains, ten miles from Kings City, 1–12 May, 1897, *A. Eastwood* (G).

This variety is conspicuous for its whitish cast and the narrowness of its banner. The seeds are variable in size and color, as shown by Mrs. Brandegee's collections. Those with sheet 149884 are about 5 x 4 mm., some milky- or bluish-white unmarked with the hilum area flesh-color, while others are drab with an occasional dark speck and a conspicuous bluish-white or pale area about the scar. Those with sheet 149885 are 4 x 3 mm. with a drab ground much speckled with black, the hilum area little or conspicuously paler and unspotted. Those with sheet 125917

(Monterey County) are 4 x 3 mm., heavily marbled with dark-brown, the hilum area unmarked and pale. The variety is evidently confined to the upper Salinas Valley.

Albilanatus is Latin for "white-woolly," which is descriptive of the general pubescence in this plant.

4*i*. **Lupinus subvexus Wilkesii** var. nov. [Fig. 15.]

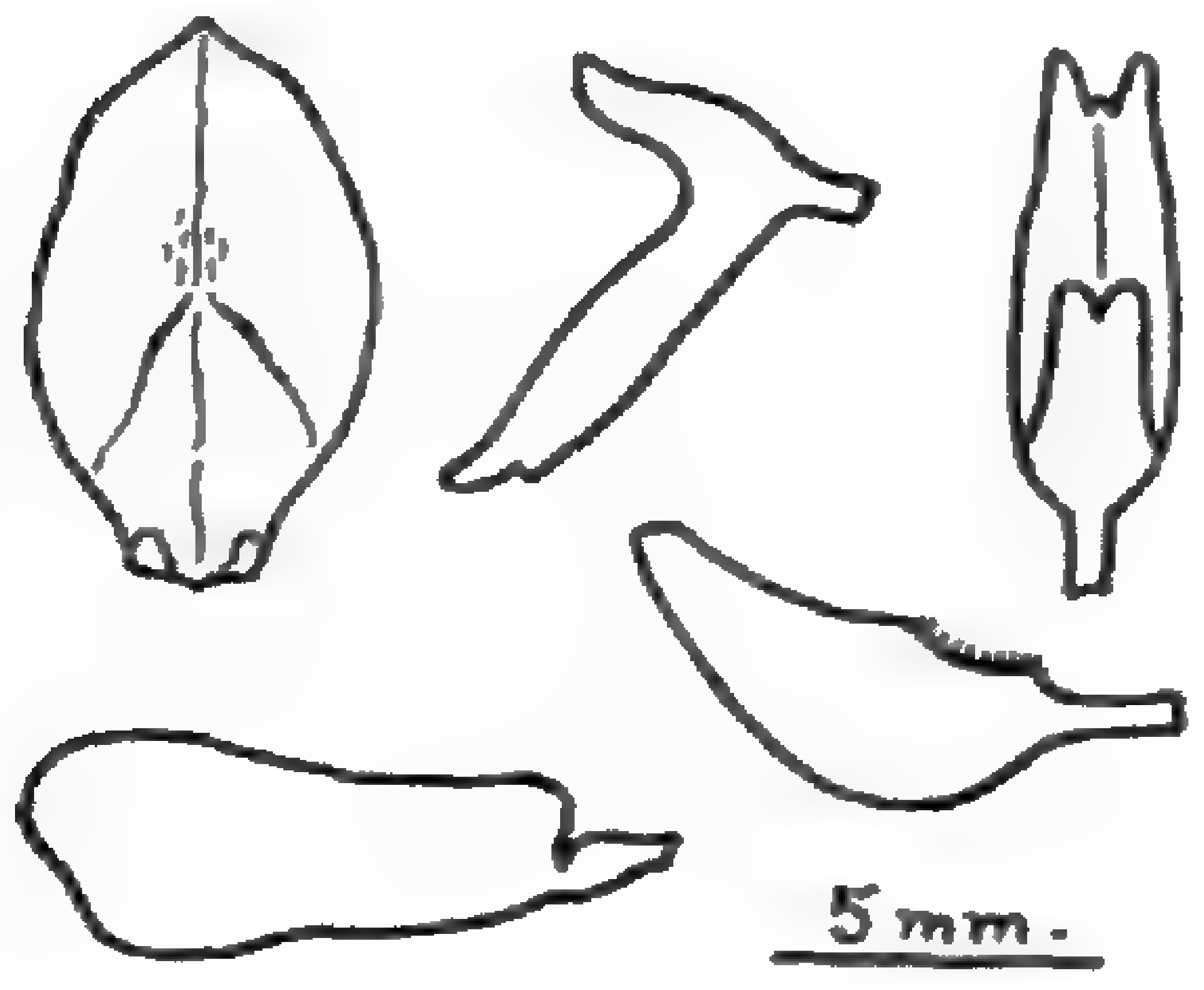

Fig. 15. Lupinus subvexus Wilkesii C. P. Smith. *Capt. Wilkes* (US 20841).

A var. *phoeniceo* differt verticillis confertis et carina curva: caulo plus minusve erecto, 20–30 cm. alto, gracili aliquantum super basin ramoso, laxe villoso pilis 1 mm. longis; petiolis gracillimis 5–8 cm. longis; foliolis 7–9, oblanceolato-spatulatis prope 15 mm. longis; pedunculis folia aequantibus, laxe villosis; verticillis prope 8, inferioribus distantibus, superioribus confertis; floribus 9–10 mm. longis ad anthesin pandentibus mox postea suberectis; pedicellis gracillimis; bracteis prope 5 mm. longis mox reflectentibus; calyce 7–8 mm. longo, labio inferiore 2-dentato, sinu dentis vestigio instructo: legumina et semina non vidi.

CHILE. Valparaiso, *Capt. Wilkes*, U. S. Explor. Exped. (TYPE, US 20841).

The specimen is labelled "*L. microcarpus*, var.," but is so different from all other Chilean material seen by me that I think it best to set it apart as a variety of *L. subvexus*. The flowers become suberect soon after anthesis and have several characters in common with var. *phoeniceus*, but this differs in the greater number of whorls, more crowded above, in the very slender pedicels, and in the curved keel.

5. LUPINUS LUTEOLUS Kell. Proc. Cal. Acad. Sci. **5**: 38. 1873. [Fig. 16.]

Lupinus Bridgesii Gray; Watson, Proc. Am. Acad. **8**: 538. 1873.

From Kellogg's description I quote:

> Stem 1–2 feet high, suffruticose, glabrous below, bark light creamy hue, satiny fibrous; numerously branched toward the top, forming a very symmetrical rather wheel-shaped cone. . . . Leaflets . . . silky above and below. . . . Flowers light yellow . . . in a dense crowded spike 6 to 12 inches in length . . . calyx tube scarious, very short and widely gaping, 2-bracteolate . . . upper lip ovate-lanceolate, acute, entire; lower lip herbaceous, 3-toothed, slightly deflexed and subsaccate at the junction of the scarious portion . . . wings broad and somewhat inflated, glabrous, with scarcely

> a few hairs on the margin at the base; keel acute, villous on the margins above at the lower third. . . .
>
> Found on the Coast range of mountains, near Senal, Mendocino County, Cal. 1872.

From Watson I quote:

> Stem 1–2 feet high . . . leaflets . . . pubescent both sides or somewhat smooth above . . . petals pale yellow. . . .
>
> Sacramento Valley. Collected by Bridges (55), Bolander (6512), and Dr. Kellogg.

Jepson (Fl. West. Mid. Cal. 2d ed. 216. 1911) emphasizes the "herbaceous" character of the upper calyx-lip.

As shown by my drawings, I have made studies of dissected flowers from specimens taken at five different stations, representing the geographical range of the species. I also studied with a lens several others of the specimens listed below. Only one specimen evidently supports the claim for an herbaceous upper lip, and just three sheets plainly show bracteoles present. The banner is usually ovate, acute, with the claw distinct and stiffened. The wings are sometimes strongly ciliate at the base below, as well as above, and the keel seems to be generally as densely ciliate below as above, the ciliation extending well out onto the slender claw. The upper lip of the calyx is sometimes emarginate and

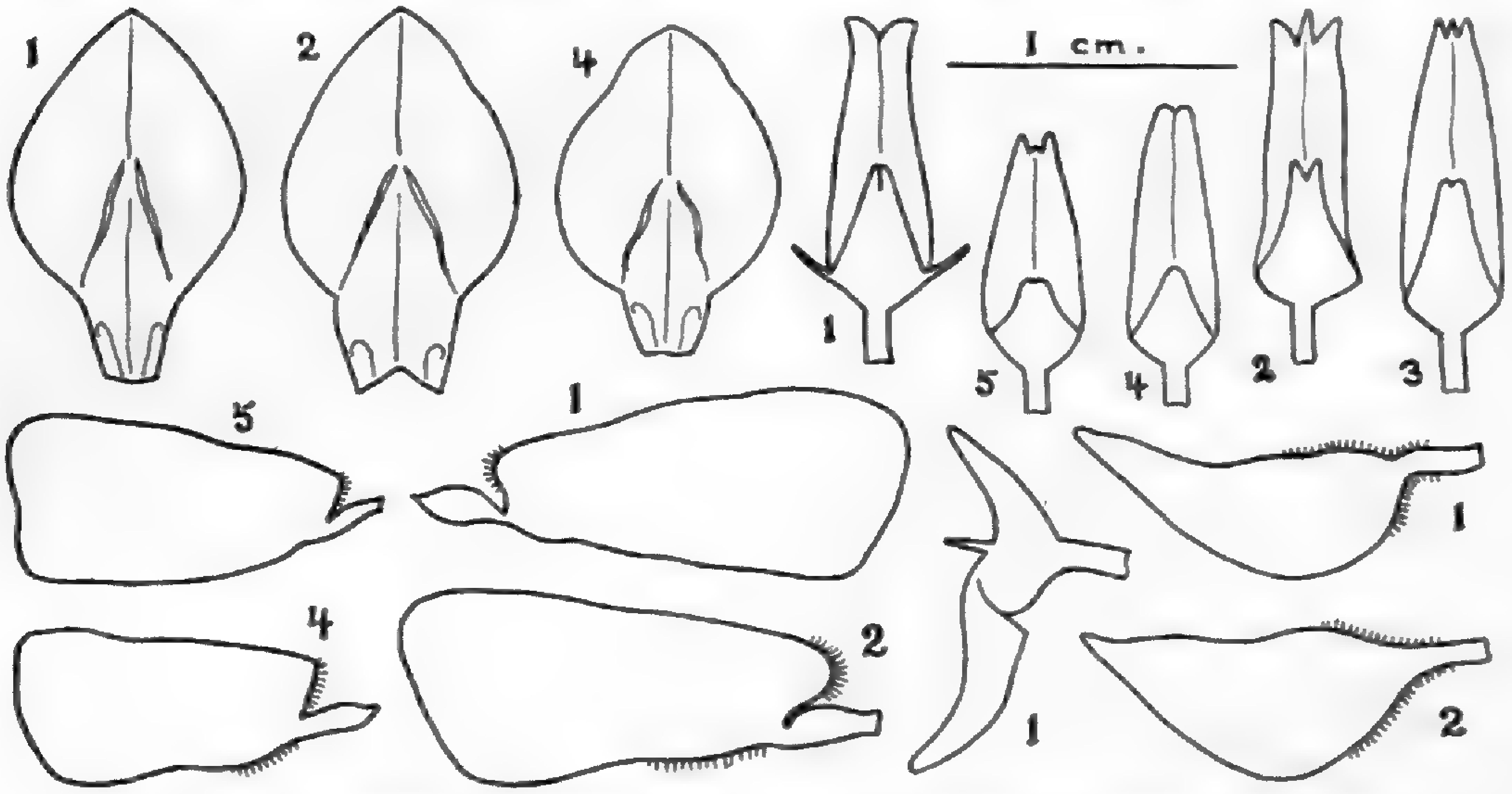

FIG. 16. LUPINUS LUTEOLUS Kell. 1. *A. Eastwood*, Mendocino County (US 468711); 2. *H. N. Bolander 6512* (US 321126); 3. *F. P. Nutting*, Contra Costa County (UC 15918); 4. *J. P. Tracy 3496*, Humboldt County (US 542773); 5. *M. W. Gorman 411*, Oregon (US 280475).

the lower lip is sometimes two-toothed. The seeds are about 4 x 3.5 mm., uniformly dark brown, regularly and roughly tuberculate as to the specimens seen.

CALIFORNIA. County not given: *Bridges 55* (T); 1866, *H. N. Bolander 6512* (US); head of Penn Creek, 5100 ft., Aug., 1875, *J. T. Rothrock 224* (US); near Cheswick, 30 July, 1899, *J. B. Leiberg 4318* (US). Contra Costa County: Fish Ranch, 29 June, 1893, *F. P. Nutting* (UC); Walnut Creek, 28 July, 1897, *Mrs. T. J. Maynard* (UC). Lake County: Lakeport, 16 Aug., 1882, *C. G. Pringle* (US); Allen's Spring, 6 July, 1882, *D. Cleveland* (UC); between Potter Valley and Hullville, 21 July, 1902, *A. A. Heller 5938* (US, CPS); Scott Valley, 21 Aug., 1905, *J. P. Tracy 2372* (UC); Kelseyville, 2 July, 1911, *K. Brandegee* (UC); Kelseyville, July–Aug., 1892, *W. L. Jepson* (UC); between Houghs and Bartlett Springs, 11 Aug., 1910, *K. Brandegee* (UC); Sanhedrin, June, 1894, *Purpus 1132* (UC); Mt. Sanhedrin, 18 July, 1913, *H. M. Hall 9514* (UC). Mendocino County: Covelo, 20 July–3 Aug., 1897, *V. K. Chesnut 543* (US); Cloverdale, Russian River, 9 July, 1902, *A. A. Heller 5830* (US); Calito, 5 Aug., 1902, *A. Eastwood* (US). Humboldt County: valley of Trinity River, near mouth of Willow Creek, 10 July, 1911, *J. P. Tracy 3496* (US); valley of Van Duzen River, opposite Buck Mountain, 27 June–30 July, 1908, *J. P. Tracy 2696* (US, UC); Kneeland Prairie, 26 July, 1912, *J. P. Tracy 3871* (UC); Eel River, July, 1894, *Purpus 1206* (UC). Shasta County: near Middle Creek station, 3 June, 1905, *A. A. Heller 7951* (US). Siskiyou County: Klamathon, 2 July, 1903, *E. B. Copeland*, Baker Distribution 3535 (US); Yreka, 8 June, 1905, *A. A. Heller 7990* (US); Hornbrook, July, 1887, *K. Brandegee* (UC); dry land near Yreka, June, 1908, 1909, 1910, *Butler 375, 910, 1447* (UC).

OREGON. Jackson County: Rogue River Valley, 14 July, 1887, *T. Howell* (UC); Ash Creek, near Ashland, July, 1893, *Mrs. R. M. Austin* (UC); Ash Creek, Rogue River Valley, July, 1893, *Mrs. Austin* (UC); Medford, 25 Aug., 1897, *Mrs. Austin 1651* (US); Spouting Springs, thirteen miles south of Ashland, 13 Aug., 1896, *M. W. Gorman 411* (US). County not given: Dead Indian road, western slope Cascades, 12 Aug., 1902, *W. C. Cusick 2945* (US).

COLLEGE PARK,
MARYLAND

The plant population of northern lower Michigan and its environment

ROLAND M. HARPER

(WITH THREE TEXT FIGURES)

Introduction.—The northern third of the Lower Peninsula of Michigan, an area of about 11,000 square miles, seems to differ from all other parts of the United States sufficiently to be treated as a distinct geographical region. Its most striking characteristic is probably the prevailing sandiness of the soils. (In this particular, as well as in the abundance of lakes, swamps and bogs, it reminds one strongly of Florida.) It differs further from the Upper Peninsula, the nearest land to the northward, in being warmer and therefore in having less of the boreal conifer element in its forests, and from the territory adjoining it on the south in being colder and in having a somewhat different seasonal distribution of rainfall (as will be pointed out farther on) and more swamps.

The southern boundary is very indefinite, but may be located arbitrarily for statistical purposes at the parallel of latitude 44° 15′, which crosses the state from near the mouth of the Manistee River to the mouth of Saginaw Bay, and passes through or near Manistee, Cadillac, and Tawas City. Only about one sixth of the area is under cultivation, so that there is no lack of vegetation to study. But as the lumbermen spoiled the looks of the country before there were many botanists in Michigan, and nearly all the plants happen to belong to widely distributed species, comparatively few botanical explorers have investigated this region. Aside from incidental references in Cowles's well-known monograph on the dunes of Lake Michigan (1899), Beal's Michigan Flora (1904), and a few local plant lists, the following seem to be about the only easily accessible papers on this region that a phytogeographer would need to consult. Some of them contain references to earlier literature of some importance. The arrangement is chronological.

V. M. Spalding. "The Plains" of Michigan. Am. Nat. **17**: 249–259. 1883.

C. S. Sargent. (Forests of) Michigan. Tenth Census U. S. **9**: 550–554. 1884.

R. C. Kedzie. The jack pine plains. Mich. Exp. Sta. Bull. 37. 8 pp. 1888.

S. M. Coulter. An ecological comparison of some typical swamp areas. Rep. Mo. Bot. Gard. **15**: 38–71. *pl. 1–24.* 1904. (See pp. 41–49 for Michigan.)

B. E. Livingston. The relation of soils to natural vegetation in Roscommon and Crawford Counties, Michigan. Bot. Gaz. **39**: 22–41, with map. Jan. 1905. Also in Rep. Mich. Geol. Surv. **1903**: 9–30. *pl. 3.*

H. H. Rusby. Observations in economic botany at Oscoda, Michigan. Jour. N. Y. Bot. Gard. **7**: 211–213. Sept. 1906.

W. J. Geib. Soil survey of Wexford County, Michigan. Field Operations U. S. Bur. Soils **1908**: 1051–1066. 1911. (Advance copies, separately paged, distributed in October, 1909.)

E. S. Whitaker. A vacation in northern Michigan. Forest & Stream **77**: 806–807. Dec. 2, 1911.

Hu Maxwell. Wood-using industries of Michigan. (State publication, no series or number.) 101 pp., 2 folded tables. Lansing, 1912. (The notes on this region are mostly on pp. 7–10. See criticism in Proc. Soc. Am. Foresters **11**: 350. 1916.)

Frank Leverett. Surface geology and agricultural conditions of the southern peninsula of Michigan. (With a chapter on climate by C. F. Schneider.) Mich. Geol. & Biol. Surv. Publ. 9 (Geol. Series 7). 144 pp., 15 plates (including 3 folded maps), 16 figs. 1912.

F. C. Gates. The vegetation of the region in the vicinity of Douglas Lake, Cheboygan County, Michigan, 1911. Rep. Mich. Acad. Sci. **14**: 46–106, with 24 half-tones on 17 plates. 1913.

H. A. Gleason & F. T. McFarland. The introduced vegetation in the vicinity of Douglas Lake, Michigan. Bull. Torrey Club **41**: 511–521. Oct. 1914.

F. C. Gates. The relation between evaporation and plant succession in a given area. Am. Jour. Bot. **4**: 161–178. *f. 1–9* (including 5 half-tones). March, 1917. (Area treated is in Cheboygan County, Michigan.)

H. A. Gleason. Some effects of excessive heat in northern Michigan. Torreya **17**; 176–178. Oct. 1917.

The plant population statistics given below are based on notes taken by the writer while occupying the post of research assistant in botany at the Biological Station of the University of Michigan in the summer of 1912. Most of the observations were made while walking out in all directions from the station (which is on Douglas Lake), as far as Cheboygan and Topinabee on the east and Pellston on the west. Copious notes were also taken from trains on the Michigan Central R. R. from Cheboygan to Mackinaw City, on the Grand Rapids & Indiana Ry. from Cadillac and Mackinaw City to Pellston, and on the Pere Marquette R. R. from Petoskey southward to the limits of the region and beyond.

Geology and soils.—The whole of lower Michigan is underlaid by nearly horizontal Paleozoic strata, largely limestones and shales of Devonian and Carboniferous age, but in the region under consideration these are exposed only in limited areas near the Great Lakes, and have little influence on soil or topography. The interior is covered by glacial drift, averaging several hundred feet thick and composed of sand, clay, pebbles and small boulders in various proportions. The pebbles and boulders are quite diverse lithologically, but most of them are more or less calcareous. Few of the boulders are more than a foot or two in diameter, or large enough to support any characteristic vegetation.

There is only one government soil survey for this region as yet, and that is for one of the counties at its southern edge. But Leverett's bulletin, above cited, divides the soils of the Lower Peninsula into about half a dozen classes, and gives the approximate acreage of each in every township and county. From the returns from the twenty-one northernmost counties the following percentages have been computed; and the corresponding figures for the remaining forty-seven counties are given in an adjacent column for purposes of comparison.

Soil classes	Northern counties	Central and southern counties
Sandy till	26.9	21.0
Sand	25.9	24.7
Clayey till	18.6	38.2
Swamps and lakes	17.9	8.8
Gravelly loam	9.7	6.7
Gravel	1.0	0.5

The clayey till includes both moraines and glacial-lake deposits, which could have been separated if it had seemed worth while. (The latter type in Michigan is chiefly confined to the vicinity of Saginaw Bay and Lake Erie, and is very sparingly represented in the region under consideration). Some of the larger interior lakes are excluded from the estimate for swamps and lakes.

The sand on many of the uplands is so deep and loose as to make walking and hauling on unimproved roads somewhat difficult in dry weather, just as in many parts of Florida. No satisfactory chemical analyses of the soils seem to be available, but they are doubtless below the average in fertility.

Topography and hydrography.—The topography is that common to many glaciated regions, undulating to hilly, with numerous depressions containing lakes, ponds, swamps, bogs, marshes, etc. The largest lakes cover about thirty-five square miles. The highest elevations are only about nine hundred feet above the Great Lakes, and are near the southern edge of the region, so that there are probably no differences in vegetation that can be ascribed to altitude alone. Several series of supposed ancient beaches, formed in glacial times when the Great Lakes were considerably higher than at present, have been traced by Leverett and others, but as in the case of the supposed marine Pleistocene terraces of Maryland and other Atlantic states,* these episodes of geological history seem to bear no obvious relation to the present vegetation, except as they may have locally influenced soil or topography. (In other words, the vegetation of an area that has been above the water say a hundred thousand years does not differ noticeably from that of one only ten thousand years old, if the soil is the same. And if the soil is not the same, that is a matter for the geologist to explain, not for the botanist.)

Being on a peninsula not exceeding a hundred and fifty miles in width, this region has no large rivers. The drainage area of the largest, the Cheboygan, covers about sixteen hundred square miles. On account of the absence of rock ledges there are no waterfalls, but in descending a few hundred feet from their sources to their mouths the rivers necessarily traverse some gravelly rapids, which are being utilized more and more for water-power. The presence of many lakes and swamps and the coincidence of the hottest season with the season of greatest precipitation makes the flow of all the streams pretty steady, and on account of the prevailing sandy soil and the scarcity of cultivated fields they carry very little sediment. (In these respects also this region resembles Florida more than it does most of the intervening states.)

Climate.—The average temperature is 41°–45° F., the January mean 18°–23°, and the July mean 66°–69°. The proximity of two of the Great Lakes presumably makes the difference between summer and winter climate a little less than it would be otherwise. The average growing season or period free from killing frosts is 125 to 145 days, the average annual snowfall about seventy inches, and the absolute minimum temperature about —40° F.

This is one of the driest parts of the eastern United States, having only about thirty inches of rain and melted snow annually.

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* See Geog. Review 4: 224–225. Sept. 1917.

An interesting feature of the precipitation is that late summer is the wettest season, by a small margin. In this particular our region resembles the pine-barren portions of the coastal plain, and differs notably from southern Michigan and the whole Mississippi valley, where spring and early summer are the rainy seasons. Coming as it does just when the evaporating power of the sun tends to be greatest, the late summer rain helps keep the ground-water level constant and favors the formation of peat. It may be a mere coincidence that two such sandy and peaty and "piney" and thinly settled regions as northern Michigan and peninsular Florida should both have a late summer rainy season, but it is more than likely that the rainfall has influenced the soil somewhat, or even *vice versa* through the vegetation, for there is no apparent physiographic reason why the seasonal distribution of rain should be any different in Michigan from what it is in Ohio and Indiana, for example.

Vegetation.—The aspects of the vegetation or the composition of the plant associations have been described at considerable length in some of the papers cited, particularly those by Livingston and Gates (and Gates's are illustrated), so that it is not necessary to say much more on the subject here, except for pointing out some fundamental principles often overlooked, and giving quantitative data, which have not been supplied before except for very small areas or for only a few species.

The dry uplands have vegetation of three principal types, correlated with soil differences. On the more clayey soils the original forests evidently were mainly of hardwoods and hemlock, making a dense shade and considerable humus. On the most sterile sands forests of jack pine prevail,* while in intermediate habitats, covering most of the upland area, white and red pines seem to have been the dominant trees before the lumbermen appeared on the scene.

The streams have more or less meadow and river-bank vegetation along them, but few species seem to be confined to such situations in the region under consideration. Flat areas adjacent

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* See Spalding's paper on "The Plains" previously referred to, and Beal's Michigan Flora, pp. 16–18. The jack pine, ***Pinus Banksiana,*** resembles the Florida spruce pine, *P. clausa,* very much in general appearance, habitat, and relations to fire. (See Ann. Rep. Fla. Geol. Surv. **7**: 142–144, 155. 1915.)

to streams and lakes, with a slow circulation of water through the muck or peat, are generally densely wooded with spindle-shaped, short-leaved conifers of the type characteristic of snowy climates.*

FIG. 1. Peat bog in a small sandy depression close to south shore of Douglas Lake, but apparently quite independent of the lake. Water deep and cool and not subject to much fluctuation. The floating leaves are *Nymphaea variegata*. Bog vegetation of the common slow-growing "high moor" or muskeg type, or the *Chamaedaphne* association of Gates (1913, p. 57); mostly evergreen. The trees are *Picea mariana* and *Larix*, and the shrubs mostly *Chamaedaphne*, *Nemopanthes*, *Andromeda*, and *Kalmia polifolia*. Herbs are relatively inconspicuous, but there is an abundance of sphagnum. (This is one of the few known localities in Michigan for *Razoumofskya pusilla*, which is parasitic on the spruces.)

The basin-like depressions, which may or may not have visible outlets, have quite a variety of vegetation, depending on their size, depth, etc. The larger ones contain lakes, with little vegetation in their deeper parts, many characteristic aquatics in sheltered shallow bays, and still other species, mainly of rush-like aspect, on wave-washed sandy beaches. Around the lakes are also numerous lagoons cut off by barrier beaches, and these commonly contain marsh vegetation, composed largely of grasses, sedges and rushes. The isolated depressions which are too small for wave action are usually occupied, at least around their edges,

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* See Pop. Sci. Monthly **85**: 340–341. 1914.

by either marsh or bog vegetation (corresponding to Warming's "low moor" and "high moor" respectively.*)

The most significant difference between marsh and bog vegetation (and one apparently overlooked by Warming in contrasting his low and high moors) is in the rate of growth; and just why rank grasses should occupy one pond and the slow-growing sphagnum, evergreen shrubs, and stunted conifers another has never been fully explained. The depth of the water undoubtedly has a great deal to do with it, for a shallow pond is quickly warmed by the sun, and one in Michigan, where the sun shines nearly sixteen hours a day in midsummer, may be nearly as warm during the growing season as one in Florida, where there is not more than fourteen hours of sun in a day. Furthermore, a deep pond, besides being colder, may be too deep in the middle for aquatic plants rooted in the soil (such as the Nymphaeaceae) to reach the surface, so that it

FIG. 2. Looking north across a shallow marsh or sedgy pond, with stagnant water quite warm in summer, a sort of "low moor", 20–25 acres in extent, about 2 miles southeast of Douglas Lake. Vegetation mostly *Carex filiformis*, with a few island-like patches of *Chamaedaphne* and *Andromeda*. Partly burned conifer swamp in background. (A little to the left of this view, near a moderately rich hillside, was some ranker and therefore faster-growing vegetation, including *Calamagrostis canadensis*, *Typa latifolia*, *Sparganium*, and *Iris versicolor*.)

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* See his Oecology of Plants (1909), pp. 196–199, 200–205.

can be filled only by means of a floating mat of vegetation growing out from the edges.* And plants not connected with the soil, whether epiphytic or floating, cannot grow very fast on account of the dearth of mineral plant food. The peculiarities of bog vegetation have been commonly attributed to the acidity of the water, but the acids in bog water are not a fundamental part of the environment, but are derived from the vegetation, so that offering such an explanation is only reasoning in a circle.†

The size of the basin in which the pond or bog is located also influences the vegetation through the amount of seasonal fluctuation of water (as was observed in Florida a few years ago‡). For considerable fluctuation of water in or above the ground hastens the decay of dead vegetation and the liberation of the food in it, and peat is formed best in places where the water-level is nearly constant.§

The occurrence of typical slow-growing (sometimes erroneously called xerophytic) bog vegetation in flat, slowly drained areas as well as in deep stagnant basins is probably to be explained largely by the fact that seeping water, having just emerged from the ground, is considerably cooler in summer than shallow standing water.|| The dense growth of conifers in such places still further protects the water from the heat of the sun, after they are once established. Another important factor is that in a perpetually saturated soil the lack of aëration restricts the availability of the mineral plant food in the soil, particularly the potassium compounds. Of course it may be said that the soil of a marsh is also perpetually saturated, which is true enough; but in a marsh, whether stagnant or estuarine, the water has been exposed to evaporation much longer than that in a seepage or spring-fed swamp, and thus the soluble salts in it are more concentrated.

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* Probably the best description of this process is that by C. A. Davis in Rep. Mich. Geol. Surv. **1906**: 125–172. 1907.

† For a summary of bog theories, in which however the question of mineral nutrients is hardly considered at all, see G. B. Rigg, Plant World **19**: 310–325. "Oct." [Nov.], 1916.

‡ See Torreya **11**: 225–234. 1911; Ann. Rep. Fla. Geol. Surv. **6**: 202, 203. *figs. 46–48*. 1914.

§ See Ann. Rep. Fla. Geol. Surv. **3**: 211. 1911.

|| The temperature of springs, other than thermal springs, is usually very close to the average annual temperature of the locality where they occur.

Furthermore, most marsh plants have hollow or spongy stems or petioles, or aerenchyma, or pneumatophores, all of which doubtless serve to conduct air to the roots.

It might be observed here, parenthetically, that many plants which in the region under consideration are chiefly confined to bogs grow equally well on uplands in colder climates.* This is probably because the low temperature and short growing season farther north so limit the availability of the nutrients in the soil that none but slow-growing plants can thrive.

An elaborate system of hypotheses of succession has been postulated by Gates and others who have worked in this or somewhat similar regions, and some have even gone so far as to try to connect all the plant associations in a limited area by successional relations. But some of the imagined successions can never take place without profound topographic changes, which may or may not come to pass, and with which the botanist is not particularly concerned. There are, however, two genuine types of succession (biotic succession as defined by Cowles,† and distinguished from his regional and topographic successions) which can be studied to advantage in this region. The first is that connected with the filling of lakes, etc., with vegetation and the gradual accumulation of peat and humus. In a coniferous swamp the falling leaves, twigs, trunks, etc., gradually pile up high enough above the ground-water level to be subject to ordinary decay, and thus form humus or duff instead of true peat. In such humus grow many plants which are equally characteristic of the upland hardwood forests, and this has led some to believe that the swamps, barring human interference and unforeseen complications, will ultimately be replaced by beech-maple-hemlock forests. But there are quite a number of plants in this region which seem to demand both humus and access to mineral soil or alkaline peat, such as *Acer saccharum*, *Tsuga*, *Fagus*, *Tilia*, *Ulmus*, *Quercus alba*, *Viburnum acerifolium*, *Vagnera racemosa*, *Carex arctata*, *C. laxiflora*, *Washingtonia*, *Actaea alba*, *Circaea*, *Adiantum pedatum*, *Geranium Robertianum*, *Caulophyllum*, and several others less common here, and we have no

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* See Livingston, Bot. Gaz. **39**: 40. 1905; Harper, Pop. Sci. Monthly **85**: 340. 1914.

† Bot. Gaz. **51**: 161–183. 1911.

evidence that these will ever grow on top of deep sour peat. Furthermore, the swamps are colder at night than the adjoining slopes, and lack some of the characteristic soil fauna of clayey uplands, and these fundamental differences can hardly be obliterated by succession.

It has been assumed also that the pine forests on the sandy uplands would likewise be succeeded by hardwood forests, if fire and lumbering did not prevent the accumulation of humus. Although the sand is undoubtedly poorer than the clay, one might suppose that in the course of centuries the pines could bring up enough mineral matter from a depth of several feet, and deposit it on the surface in decaying leaves, to make a rich soil that would support trees that make a complete new crop of leaves every year, and that such a forest when once established would be self-perpetuating, as it would return to the soil every fall what it took up in the spring and summer. But the difficulty is that in sandy soils leaching probably goes on fast enough to prevent the accumulation of any considerable amount of plant food on the surface of the ground. (On clayey slopes there is less leaching, and erosion is constantly exposing fresh layers of soil, and thus maintaining its fertility indefinitely.) It seems that in many if not most cases the proportion of deciduous trees in a forest does not increase with succession, but depends on fundamental soil characters.*

Another type of succession is a periodic one resulting from fire. In a state of nature the hardwood forests were rarely visited by fire, and one might say figuratively that the plants in such habitats made no provision for such an occurrence. The pine forests have been so nearly destroyed that it is difficult to determine what the normal frequency of fire in them may have been. As *Pinus resinosa* is not very sensitive, it may have been subject to ground-fires every few years, like some of the southeastern pines;† while in the white-pine forests fire may have been almost as rare as in the hardwoods. Be that as it may, the "pernicious activities" of the lumbermen a few decades ago removed the greater part of these two valuable pines,‡ and the ground formerly occupied by

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* See H. W. Wiley, Science II. **17**: 794–795. May 15, 1903; Harper, Bull. Torrey Club **41**: 209–220. 1914; B. Moore, Bot. Gaz. **61**: 59–66. Jan. 1916.

† See Pop. Sci. Monthly **85**: 343. 1914.

‡ The effects of lumbering in this part of Michigan have been described by several

them has now a low scrubby growth of birch and aspen, which is burned too often for the white pine to reëstablish itself, though the red pine is making some headway.

On steep bluffs and small islands, and in ravines, where fire is necessarily rare, we find some plants that are sensitive to fire but do not require as rich a soil as that of the hardwood forests, such as the few woody vines of the region. (Most of the existing white pines are found in such places, too.) The low sandy "ice ramparts" around the larger lakes are protected from fire on one side by the water and at the same time are too sterile to support vegetation dense enough to carry fire readily, so that certain fire-sensitive (or *pyrophobic*, if one may coin a new term) plants, such as *Amelanchier* sp., *Prunus pumila*,* *Rosa* sp., *Rhus Toxicodendron*, *Arctostaphylos Uva-ursi*, *Equisetum hyemale*, *Elymus* sp., and *Potentilla Anserina*, are characteristic of such places.

The normal frequency of fire in the jack-pine and spruce types of forest seems to be about once in the average lifetime of a tree. *Pinus Banksiana* is one of several pines whose cones remain closed and attached to the tree for many years, but open soon after a fire and discharge their seeds, thus re-stocking the forest. In the spruce bogs, as in the white-pine forests, one of the first effects of a fire sweeping through the crowns of the trees is to liberate the potash and other mineral substances stored up in several years' growth of leaves and twigs, which falls to the ground and acts as a high-grade fertilizer. Several quick-growing and short-lived trees and shrubs, such as *Betula*, *Populus tremuloides*, *P. grandidentata*, *Prunus pennsylvanica*, and a few characteristic herbs, known collectively as fire-weeds, soon invade the burned areas by means of seeds carried by wind or birds, and flourish until the surplus potash, etc., is exhausted. In the swamps one of the conifers itself, namely the deciduous one, *Larix*, acts as a sort of fireweed, being especially common in the first few decades after a fire; and its career is commonly terminated by saw-flies instead of fire. As it renews its whole crop of leaves every year it needs a larger food supply than the spruces, and it also extends farther into the

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of the writers cited in the bibliography, particularly Dr. Rusby. Dr. H. A. Gleason told me in 1912 that he did not know of a single acre of virgin white-pine forest in lower Michigan.

* See Rhodora **18**: 202. Sept. 1916.

richer regions of southern Michigan, Ohio, etc., than they do. While the fireweeds are flourishing, seeds of the original conifers are being brought in in the regular manner, and by the time the birches and aspens have run their course the conifers that have been growing up in their shade may be ready to dominate the situation again.*

FIG. 3. Scene in large tamarack swamp with a few feet of peat, about four miles north of Douglas Lake, bordering a sluggish stream flowing into Carp Lake. Trees in background all or nearly all *Larix laricina*. (See Gates, 1913, pp. 64-66.) Open space in foreground evidently severely burned several years before. Woody plants in it mostly *Larix* seedlings, *Salix pedicellaris*, *Betula pumila*, *Rhamnus alnifolia*, *Chamaedaphne*, *Alnus*, *Lonicera canadensis* and *Ledum*. Evergreens in the minority; little or no sphagnum. (This view was taken a mile or more from the stream, and near the south edge of the swamp, where it is bordered by clayey hills mostly cultivated. Toward the stream the percentage of evergreens increases considerably.)

Since the best pines have disappeared the lumbermen have attacked the hardwood forests also, and much hemlock has been destroyed for tan-bark. The slash left from these operations is subject to fire too, but the fireweeds on hardwood land are not quite the same as on pine land. *Sambucus pubens* and *Rubus* spp.

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* So many papers have been written about the effects of fire in boreal coniferous forests that it would not be worth while to attempt to cite them here, but references to several of them can be found in Bull. Torrey Club **35**: 349. 1908, and in Pop. Sci. Monthly **85**: 341. 1914.

are quite characteristic, and the vacciniums are rare or absent. A hardwood area after logging, and even after the slash is burned, is very disagreeable to traverse, on account of the numerous logs and tops cumbering the ground, many of the logs being held up by stiff branches at such a height that it is just as hard to climb over them as to crawl under them, and only the smaller branches are consumed by fire, the larger ones making veritable *chevaux-de-frise* that last for many years. (Ten or twelve degrees farther south fallen trees decay much more rapidly, and do not materially impede the explorer after two or three years.*)

Farmers have damaged the vegetation still further by totally eradicating much of it to make room for crops. This influence has been chiefly concentrated on the hardwood land, on account of its richer soil, but only about 17 per cent. of the area was classed as "improved land" in 1910. The extension of farms ought to have one indirect beneficial effect on the pine land, however, by multiplying the barriers to fire and thus diminishing its frequency at any one point.†

Plant census.—The following plant list is based on the writer's observations in northern lower Michigan between June 28 and August 24, 1912. Although only nine of the twenty-one counties were visited in that time, the results are probably representative enough, except for the dunes and cliffs along the Great Lakes, which were not examined. The relative abundance of the species has been determined in the manner explained in several previous papers which are easily accessible.‡ Although some may question the accuracy of my rapid reconnoissance methods, there is probably no one at the present time in a position to assert that the results

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* In this connection see W. H. Long, Investigations of the rotting of slash in Arkansas. U. S. Dept. Agr. Bull. 496. Feb. 1917.

Curiously enough, however, twenty degrees farther south the tropical hardwood forests of extreme southern Florida are subject to fire at long intervals, followed by a few characteristic fireweeds (*Trema*, *Carica*, etc.), and are just as disagreeable to traverse for some time afterward as these Michigan forests, on account of the hardness and durability of the wood of many of the trees.

† For an interesting account of the effects of farming on fire frequency in the Ozarks, see Marbut, Field Operations U. S. Bur. Soils **1911**: 1740. 1914. (Or page 20 of the separates.)

‡ Ann. Rep. Fla. Geol. Surv. **6**: 177–180. 1914; Bull. Torrey Club **41**: 557–559. 1914; **44**: 47–50. 1917; Torreya **17**: 1–2, 5–6. 1917.

are incorrect. Future explorations will doubtless necessitate changing the sequence of many of the species remote from the head of the list; but as it is, the present sequence corresponds very well with what one might obtain by counting the number of times each species is mentioned in previous descriptions of the vegetation of the same region.

The species are first divided into large trees, small trees, vines and large shrubs, small shrubs, and herbs. Large trees are large enough to be sawn into lumber, small trees large enough for posts, large shrubs for canes or bean-poles, and so on down. Woody vines are combined with large shrubs, because otherwise in the absence of numbers there would be nothing to indicate how relatively scarce they are, but their names are italicized to distinguish them. Some small evergreen plants which have perennial stems above the ground, such as *Equisetum* spp., *Lycopodium*, *Chimaphila*, *Gaultheria*, *Epigaea*, *Chiogenes*, *Oxycoccus*, *Mitchella*, and *Linnaea* (the "chamaephyte" class of Raunkiaer, in part), are classed with the herbs on account of their small size and lack of true woody tissue.

Evergreens are indicated by heavier type, as usual, and the names of weeds enclosed in parentheses, whether they are treated as exotics in the manuals or not.* The three commonest modes of dissemination are indicated by somewhat arbitrary but suggestive symbols, as follows: wind-borne seeds, Y; fleshy fruits, O; barbed fruits, X. It would have been interesting to indicate annuals, biennials, perennials, etc.† (or better still perhaps the Raunkiaerian growth-forms‡), as well as the blooming periods and color of flowers, but there are too many cases in which these data are not yet known accurately enough. The usual habitats of the different species are given in a few words.

In each major group the species are arranged as nearly as possible in order of present abundance. Very likely a similar census taken fifty years ago would have placed *Pinus Strobus* at the head of the list, and arranged some of the other trees differently, and excluded some of the weeds entirely. On account of

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* See Bull. Torrey Club **35**: 347–360. 1908; **37**: 117–120. 1910.

† As in Ann. N. Y. Acad. Sci. **17**: 36–37. 1906, for example.

‡ For an easily accessible reference to Raunkiaer's system, and an illustration of its use, see Taylor, Am. Jour. Bot. **2**: 32. 1915.

the incompleteness of the data, and the great changes that have been made by lumbermen and others, percentage numbers are not attempted. But the numbers when finally determined probably will not depart much from a geometrical progression.* (The commonest herb, however, seems to be about four times as abundant as the next one.) The rarer species, and all cellular cryptogams, are omitted, because they make up such an insignificant part of the total vegetation.

TREES

Y	Larix laricina	Swamps and bogs
	Thuja occidentalis	" " "
Y	**Pinus Strobus**	Sandy uplands, etc.
Y	Acer saccharum	Rich uplands
Y	**Tsuga canadensis**	" "
	Fagus grandifolia	" "
Y	**Picea mariana**	Swamps and bogs
Y	**Abies balsamea**	" " "
Y	Acer rubrum	Various habitats
Y	Tilia americana	Rich uplands
Y	Fraxinus nigra	Swamps
Y	**Pinus resinosa**	Sandy uplands
Y	Ulmus americana	Richer soils
	Quercus borealis maxima†	Sandy uplands
Y	**Picea canadensis**	Swamps and bogs
Y	Betula lutea	Rich woods
Y	**Pinus Banksiana**	Poorest soils
	Quercus alba	Uplands
Y	Fraxinus americana	Richer soils

SMALL TREES

Y	Betula papyrifera	Various habitats
Y	Populus tremuloides	Burned areas mostly
Y	Populus grandidentata	" " "
O	Prunus pennsylvanica	" " "
Y	Populus balsamifera	Lake shores, etc.
	Ostrya virginiana	Rich uplands
Y	Salix fluviatilis?	Lake shores, etc.

LARGE SHRUBS AND VINES

	Alnus incana	Swamps, etc.
Y	Salix lucida	Wet places
Y	Salix spp‡	Swamps, etc.
Y	Acer pennsylvanicum	Rich woods

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* See Torreya **13**: 244. Oct. 1913.

† Long known as *Q. rubra*. See Torreya **17**: 135. Aug. 1917.

‡ This includes several unidentified species. If they had been separated they would of course stand lower in the list.

O	Sambucus pubens	Burned or cleared hardwood land
O	Rhus sp.*	Burned uplands
O	Rhus glabra	“ “
Y	Acer spicatum	Rich woods
O	Cornus stolonifera	Low grounds
O	Nemopanthes mucronata	Swamps
O	Ilex verticillata	Swamps
O	Amelanchier sp.	Various habitats
O	*Vitis vulpina*	Lake shores and bluffs
	Celastrus scandens	Bluffs and islands
O	Viburnum cassinoides	Swamps
Y	Salix discolor?	Low grounds

SMALLER SHRUBS

	Diervilla Lonicera	Sandy uplands
O	Rubus strigosus	Burned or cleared hardwood land
	Chamaedaphne calyculata	Open bogs
	Comptonia peregrina	Sandy uplands
O	Rubus allegheniensis?	Burns, clearings, etc.
O	Rhus Toxicodendron	Ice-ramparts, etc.
	Ledum groenlandicum	Bogs and swamps
Y	Salix rostrata?	Swamps
O	Vaccinium pennsylvanicum	Sandy uplands
O	**Taxus canadensis**	Rich woods and swamps
O	Rhamnus alnifolia	Bogs and swamps
	Myrica Gale	“ “ “
O	Vaccinium canadense	Sandy uplands
Y	Betula pumila	Bogs and swamps
O	Lonicera canadensis	“ “ “
O	**Arctostaphylos Uva-ursi**	Barren sands
O	Rosa sp.	Lake shores, etc.
	Spiraea latifolia	Swamps and meadows
O	Viburnum acerifolium	Rich woods and bluffs
	Decodon verticillatus	Swamps and marshes
	Andromeda glaucophylla	Open bogs
O	Aronia nigra	Bogs, etc.

(and about 15 others)

HERBS

Y	Pteris aquilina	Sandy uplands, etc.
Y	Typha latifolia	Marshes, etc.
Y	Chamaenerion angustifolium	Burns and clearings
	(Poa pratensis)	Roadsides, etc.
	Calamagrostis canadensis	Marshes
O	Aralia nudicaulis	Rich woods, shady bogs, etc.
O	Unifolium canadense	“ “ “ “ “
Y	(Solidago canadensis)	Fields and roadsides

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* The sumacs of this region present a bewildering variety of forms, ranging from the perfectly smooth *R. glabra* to some almost pubescent enough to be called *R. typhina*; but no typical *R. typhina* was observed.

Y	(Asclepias syriaca)	Fields and roadsides
	(Achillea Millefolium)	" " "
	Scirpus validus	Lakes, etc.
	Carex filiformis	Bogs and marshes
Y	Dryopteris Thelypteris	" " "
O	**Gaultheria procumbens**	Sour soils, dry or moist
O	Cornus canadensis	Rich woods and bogs.
	Dulichium arundinaceum	Marshes, etc.
	(Verbascum Thapsus)	Pastures, roadsides, etc.
Y	Eupatorium purpureum	Swamps and meadows
O	Clintonia borealis	Rich woods and shady bogs
	Nymphaea variegata*	Quiet water
	Scirpus americanus	Lake shores, etc.
O	Rubus triflorus	Bogs and swamps
O	Vagnera racemosa	Rich woods
	Iris versicolor	Marshes
Y	Osmunda regalis	Swamps and marshes
Y	Scirpus cyperinus pelius	Marshes and meadows
	Comarum palustre	Marshes, etc.
Y	Eupatorium perfoliatum	Meadows, etc.
	Triadenum virginicum	Bogs and marshes
	Trientalis americana	Rich woods and shady bogs
Y	Asclepias incarnata	Marshes, etc.
O	Vagnera trifolia	Rich woods and shady bogs
O	**Chiogenes hispidula**	" " " " "
Y	Onoclea sensibilis	Marshes, etc.
	Lysimachia terrestris	" "
	(Pastinaca sativa)	Roadsides
O	**Mitchella repens**	Rich woods mostly
	Potentilla Anserina	Lake shores
	Carex arctata	Rich woods and bluffs
	Coptis trifolia	Rich woods and shady bogs
	Spartina Michauxiana	Lake shores, etc.
	Lathyrus palustris	" " "
Y	(Leptilon canadense)	Burns and waste places
	(Equisetum arvense)	Along railroads, etc.
O	**Linnaea americana**	Rich woods and shady bogs
Y	**Lycopodium annotinum**	" " " " "
	Lilium philadelphicum	Swamps and meadows
	Thalictrum dasycarpum	" " "
	(Chrysanthemum Leucanthemum)	Roadsides, etc.
	Danthonia spicata	Sandy uplands
	Equisetum palustre	Swamps and bogs
	Equisetum hyemale	Lake shores, etc.
X	(Cynoglossum officinale)	Roadsides
X	Washingtonia Claytoni	Rich woods
O	Actaea alba	" "

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* For a discussion of the nomenclature of this plant, see Fernald & St. John, Rhodora **16**: 137–141. Aug. 1914.

	Mitella nuda	Rich woods and bogs
	Epigaea repens	Sour soils
	Campanula uliginosa	Marshes
	Equisetum fluviatile	"
O	Aralia racemosa	Rich woods
	(Convolvulus spithamaeus)	Sandy uplands
Y	Apocynum androsaemifolium	" "
	(Phleum pratense)	Roadsides, etc.
	Menyanthes trifoliata	Bogs and marshes
	Eleocharis palustris	Shallow water
O	Trillium grandiflorum	Rich woods
	Cladium mariscoides	Lake shores
Y	Eriophorum viridicarinatum	Bogs, etc.
O	**Oxycoccus macrocarpus**	Bogs
Y	(Apocynum cannabinum)	Ice ramparts, etc.
	Oryzopsis asperifolia	Sandy bluffs, etc.
X	Circaea alpina	Rich woods
X	(Arctium minus)	Waste places
Y	Euthamia sp.	Lake shores, etc.
	Equisetum laevigatum	" " "
	Botrychium virginianum	Rich woods
	Panicum depauperatum	Sandy uplands
	Equisetum scirpoides	Bogs
Y	Aster macrophyllus	Rich woods, etc.
	Scirpus atrovirens	Meadows, etc.
	(Ambrosia artemisiifolia)	Waste places
	Lobelia cardinalis	Along brooks
	Caltha palustris	" "
X	Galium triflorum	Rich woods
	Geranium Robertianum	" "
	(Trifolium pratense)	Roadsides, etc.
	(Trifolium repens)	" "
O	Polygonatum biflorum	Rich woods
	Naumburgia thyrsiflora	Marshes
	Comandra umbellata	Sandy uplands
Y	**Dryopteris spinulosa**	Rich woods
	Elymus sp.	Lake shores
	Phalaris arundinacea	" "
	Cypripedium hirsutum	Shady bogs

Summary.—The species above listed probably constitute something like nine tenths of the vegetation and one tenth of the flora of the region under consideration. About 275 additional species, nearly all herbs, were observed, but not often enough to be worth mentioning.

Not one of the large trees has fleshy or barbed fruits, while few of the smaller shrubs are wind-distributed. There are no barbed fruits on any of the woody plants, but a few of the small trees and many of the shrubs, vines and herbs have fleshy fruits.* Herbs with barbed fruits are in this region chiefly confined to rich woods and roadsides, probably partly because of the exemption of such places from fire,† though it is not at present apparent why that should affect them more than it does the fleshy fruits. (Barbed fruits seem to be more characteristic of warmer climates and more calcareous soils, too.) Plants with erect capsules on stiff stems which stand up through the winter (called "tonoboles" by Clements‡) are much rarer here than a few degrees farther south, possibly because the snow interferes with their dissemination.

About half the large trees are evergreen, but none of the small trees, vines and large shrubs are, strange to say. It would seem from this that no evergreens except conifers (and one of those is deciduous) can stand the Michigan winters without the protection of snow.§ Vines are scarce, only two being listed, and those are not found much farther north.

The Ericaceae and allied families are largely represented among the small shrubs and evergreen herbs, as in many other places with similar climate. Other families pretty well represented in proportion to the total number of species in them, or the total flora of this region, or both, are Equisetaceae, Cyperaceae. Orchidaceae, Salicaceae, Rosaceae, and Caprifoliaceae, while the opposite might be said of the Fagaceae, Cruciferae (native), Caryophyllaceae (native), Leguminosae, Polygalaceae, Violaceae, Hypericaceae, Umbelliferae, Labiatae, Scrophulariaceae, and Lentibulariaceae, The sedges seem to be more numerous and also more abundant than the grasses.

Nearly all the species listed are widely distributed, extending from Nova Scotia to Minnesota at least, and most of them are represented in northern Europe by identical or closely related forms. Those peculiarly American plants which are confined to

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* See Torreya **14**: 16. 1914.

† See Torreya **17**: 138–139. 1917. (In the text on page 138 *Allium* and *Deringa* were included inadvertently, and should be striken out.) Two additional references that should have been given there are: S. M. Coulter, Rep. Mo. Bot. Gard. **15**: 44. 1904; Harper, Torreya **10**: 60–61. 1910.

‡ Bot. Surv. Neb. **7**: 47. 1904.

§ In this connection see Gates, Torreya **12**: 257–262. 1912; Harper, Rep. Mich. Acad. Sci. **15**: 194. 1914.

the glaciated region and coastal plain or nearly so* are scarcely represented here, presumably because the climate is a little too cold.

A list of the commoner plants of the eastern part of the Upper Peninsula, based wholly on car-window notes, was published by the writer a few years ago.† In that a slightly different method of computation, which did not do justice to the conifers, was used, and the different sizes of trees and shrubs were not separated. But it is probably safe to say that *Abies*, *Picea canadensis*, *Betula pumila*, and *Andromeda glaucophylla* (to mention woody plants only) are more abundant in the Upper Peninsula than here; while the reverse is true of *Acer saccharum*, *Tsuga*, *Fagus*, *Tilia*, *Ulmus*, *Acer pennsylvanicum*, *Sambucus*, *Rhus glabra* (etc.), *Diervilla*, *Rubus strigosus*, *Comptonia*, *Rubus allegheniensis* (?), *Rhus Toxicodendron*, *Taxus canadensis*, and a few others, most of which are not evergreen.

Comparing this region with that adjoining it on the south we get a greater contrast, due to better soil and climate both. The commonest trees in the central third of lower Michigan (not counting the lake plains around Saginaw Bay, which are still more fertile), as determined from a few hours of car-window observations, seem to be as follows:

Quercus velutina (?), *Pinus Banksiana*,‡ *P. Strobus*, *Ulmus americana*, *Larix laricina*, *Quercus borealis maxima* (?), *Acer saccharum*, *Fagus*, *Thuja*, *Tsuga*, *Abies*, *Tilia*, *Pinus resinosa*, *Quercus alba*, and *Picea mariana*.

Still farther south the change in composition of vegetation continues in the same direction, and in extreme southern Michigan nearly all the trees are deciduous.

COLLEGE POINT,
NEW YORK

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* See Rhodora **7**: 69–80. 1905; **8**: 27–30. 1906.

† Rep. Mich. Acad. Sci. **15**: 193–198. 1914.

‡ If I had left northern Michigan by way of the Michigan Central R. R. instead of the Pere Marquette, *Pinus Banksiana* would doubtless have stood higher in the first list and lower in the one on this page; for along the former railroad it is said to be abundant in Crawford and Roscommon Counties, while along the latter I saw it mostly in Lake and Newaygo Counties, south of the limits assigned in this paper. (See second map between pages 550 and 551 of the 9th volume of the Tenth Census.)

INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1917

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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On the constancy of cell shape in leaves of varying shape

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(WITH ONE TEXT FIGURE)

Introduction

Since the publication of Sanio's observations on the size of the wood cells of *Pinus sylvestris*, the subject has aroused considerable interest, as is shown by the work of Amelung, Sachs, Strasburger, Gates, Keeble, Neilson Jones, Jakushkine and Wawilow, and Sierp. Among the zoologists who have investigated the same problem are Gaule, Donaldson, Hardesty, Levi, Morgan, Driesch, Rabl, Chambers, Popof, Berezewski, Jennings, and Conklin.

Sanio (1872) shows that in the Scotch pine, the wood cells attain a definite (final) size, which is constant for the following annual rings. He finds, however, that the size of the wood cells does vary according to the height at which they are situated in the stem. The size of the wood cells increases as the stem is ascended, until a maximum is reached, then decreases toward the apex. The branches always have smaller wood cells than the main stem at the level at which the branch arose; but branches which arise from that portion of the main stem which had the largest wood cells, have also larger wood cells than the branches situated higher or lower on the stem.

Amelung (1893) studied cell size in its relation to the size of the organ. He raised the question whether differences in the size of homologous organs within a species are accompanied by corres-

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ponding variations in cell size, or whether the cell size of each species is a constant and distinct character. That is, do environmental conditions, which modify the size of plant organs, affect the size of their cells? Are giants and dwarfs due to greater or lesser development in size of the individual cells, or to more or less numerous cell divisions?

Amelung estimated the size of the various cells of plants having homologous organs differing in size. He made ten longitudinal sections, or, in other plants, ten cross sections of each of the organs to be compared. These he mounted in water or in glycerine. In each section he counted the number of cells of a given tissue that were intersected by a line on the stage micrometer, a line usually 1 mm., sometimes 5 mm., in length. He thus obtained ten cell counts on each organ. From these he determined the average number of cells to 1 mm. and the average length or average breadth of the cells of a given tissue both of the giant and of the dwarf organs. He compared the palisade and epidermal cells of large leaves with similar tissue cells of small leaves, the wood cells of poorly developed and of well-developed shoots, and the parenchyma of large and small fruits. The organs compared were taken from the same plant, or from different plants of the same species, or from closely related species. He found that the cell size of a given tissue of an organ is constant for the species, regardless of the average size of the individual or of the organ. Thus, the epidermal cells of a small leaf of *Ficus macrocarpus* were as large as those of a leaf twice as long and broad; the wood cells of a twig of *Vitis vinifera*, 6 mm. in thickness, measured as much in cross section as those of another shoot, only half as thick; a leaf of *Victoria regia*, measuring 900 × 900 mm., and one of *Nymphea alba*, 190 × 190 mm., had cells that were identical in size.

Amelung concludes that not the cell size, but the cell number, determines the size of an organ.

Sachs, with whom Amelung worked, confirms the statement that the cell size of a given species is constant, and is not influenced by body size.

Strasburger (1893), in a series of studies on the relation of nuclear and cell size in the embryonic cells of the growing points of stems and roots of many species of plants, reached the same conclusion, regarding the size of these cells in large and small individuals of the same species, although varieties of the same species may differ greatly as to their cell size.

Conklin (1912) has made an elaborate and extended study of cell size compared with body size in the genus *Crepidula*. He found great variability in the body size of these gasteropods. In *Crepidula plana*, there are dwarf and normal females. These latter are larger than the normal-sized males. The average size of individuals of the same sex differs greatly for the different species. Yet, in spite of all these differences in body size, the tissue cells of corresponding organs or parts of organs were in general of the same size in all the adult animals examined.

The muscle fibres and ganglion cells formed an exception to this rule. In *Crepidula plana*, the size of these cells was greater in the largest animals. This, he notes, agrees with the observations of Gaule, Donaldson, Hardesty, and Levi, who measured these cells in frogs and various mammals. In connection with the size differences found in these cells, Conklin cites the observation made by Levi, that these cells cease to divide early in life, whereas such cells as the epithelial and the gland cells, where Levi found no correlation with body size, continue to divide throughout life.

The size of the sex cells, also, varied in the different species. In general, the smaller species produced larger eggs. These resulted in larger embryos, having larger cells. Conklin says the fact that the species with smaller eggs produce, in the end, larger adults, and that the final cell size is almost the same for all the crepidulas, is due to a longer duration and more rapid rate of cell growth and division in the larger species.

A very notable case bearing on the question of the constancy of cell size in a species, is that of *Oenothera gigas*, a so-called mutant of *Oenothera Lamarckiana*, with double the number of chromosomes found in the parent species. Gates (1909) found that the cells of *Oenothera gigas*, which have twenty-eight or twenty-nine chromosomes, were conspicuously larger than the cells of *Oenothera Lamarckiana*, whose chromosome number is only fourteen.

Boveri (1905), on the basis of extended studies on sea-urchin larvae, formulated the law that the cell size in sea-urchin larvae is directly proportional to the number of chromosomes. According to this law, one would expect to find here a direct relation between the amount of chromatin, the nuclear size, and the size of the cell. Gates (1909) does not find that this holds equally for all the tissues. While the chromosome number of *Oenothera gigas* is double that of *Oenothera Lamarckiana*, the cells of the former are not uniformly twice as large as those of corresponding tissues of *Oenothera Lamarckiana*.

Gates estimated the size of rectangular cells, as those of the epidermis, by multiplying the three dimensions. The length and breadth of the cells he estimated from measurements made on camera-lucida drawings, magnified about 1,380 diameters, the third dimension being considered as identical with the length of the cell. By length of the cell he means the measurement along the long axis of the organ, though this is not necessarily the longest dimension of the cell; the width being the measurement at right angles to the surface of the organ, that is in the direction of the thickness of the organ in which it occurs. The epidermal cells of the petals of *O. gigas* were 1.9 times as large in volume as those of *O. Lamarckiana*, which is closely in accordance with Boveri's law. However, other tissue cells depart widely from the expected ratio of 2 : 1. The stigmatic cells, the cells of the anther epidermis, and the inner wall of the anther, were more than three times as large in *O. gigas* as in *O. Lamarckiana*, while the pollen mother cells of the former, both during synapsis and in the reduction divisions, were only 1.5 times as large.

Moreover, the increase in size of the *O. gigas* cells was not equally great in all dimensions. The epidermal cells of the anther increased 72.8 per cent. in length, and only 28.4 per cent. in width; the stigma cells increased 51.9 per cent. in length, and 32.2 per cent. in width. The anthers of *O. gigas* are approximately twice as long as those of *O. Lamarckiana*. Gates believes that both have approximately the same number of cells, "and that the greater length of the *O. gigas* anthers is accounted for by the greater length of the individual cells." Gates concludes that there is evidently some regulating factor determining that the increase in length of the epidermal cells shall be greater than the increase in their width, in the anther epidermis, but less in the petal epidermis.

Similarly, Keeble (1912), in a comparative study of the cells of the stem and leaf tissues of White Queen Star, a horticultural variety of *Primula sinensis*, and those of its mutant, Giant White Queen Star, showed that the latter is a giant because its cells are larger and not because they are more numerous than those of the parental type. Indeed, in the cortex of Giant White Queen Star, Keeble found fewer cell layers than in the normal type. The measurements he gives for the cortical cells of the flower peduncles, taken for the layer immediately external to the endodermis, are:

Radial measurements	$g : n :: 100 : 48$
Tangential measurements	$g : n :: 100 : 81$
Longitudinal measurements	$g : n :: 100 : 57$

The cells are larger in all three dimensions, radial, tangential and longitudinal, and the gigantism is common to all tissues. He does not state how many cells were measured nor does he describe his methods. The chromosome number in both varieties is the same. The nuclei of the giant form are larger, as Keeble shows in his drawings of pollen grains, but he does not give any measurements of them. It is therefore impossible to tell, in the case of White Queen Star and its giant mutant, Giant White Queen Star, whether or not the amount of chromatin material is the factor determining the relative cell size in these plants.

In *Avena sativa*, Jakushkine and Wawilow (1913) found that different varieties may have different-sized cells, but they were unable to discover any relation between the size of either the stomata or the epidermal cells, and that of the leaf surface, when varieties with different-sized organs were compared. For instance, a small-celled variety had the largest leaves. Like Sanio these authors found that the cell size of the leaves varied according to their position on the stem, the cells of the highest leaf being smaller than those of the third leaf from the top of the stem. They found that in any given variety, the cell size of any tissue at a definite part of an organ was a constant character, and further that each of the seventeen pure lines obtained through selection from a mixed population of German and west Russian oats, fell into one of two groups, namely:

1. A large-celled group, the average length of the stomata of the highest leaf being 0.063 mm., that of the third leaf down being 0.0735 mm.

2. A small-celled group, the first leaf from the summit having stomata whose average length is 0.054 mm., those of the third leaf being 0.067 mm. long.

In his paper on species hybrids of *Digitalis*, Neilson Jones (1912) does not give any measurements of the cell size of *D. grandiflora* and *D. purpurea;* but his general observations are most interesting. He finds that *D. grandiflora*, which has smaller leaves than *D. purpurea*, has larger leaf cells. Hybrids of these two species are intermediate in both external and cytological characters, but in both respects there is a tendency to favor the seed parent. Thus, in the hybrid resulting from the cross *p.* ♀ × *g.* ♂ the leaves are somewhat larger and the cells smaller, than they are in the progeny of the reciprocal cross. Evidently the size of the leaves and cells of the hybrids cannot be due to heterozygosity, since in that case we would expect the reciprocal crosses to have the same effect on the leaf and cell size of the resulting hybrids.

One of the most careful studies of the relation between body size and cell size is that of Sierp (1913). He made measurements of the cells of various tissues of dwarf and normal plants, the dwarfness being in some cases a fluctuating characteristic, in other cases hereditary. Under the first group come dwarfs of *Panicum sanguineum*, *Draba verna*, *Aethusa Cynapium* and *Urtica dioica*. This type of dwarfs always had cells more or less reduced in size. Some of the differences in cell size were very slight. True, that is, hereditary dwarfs, he found were of three kinds:

1. Those having smaller cells than the normal plants, as certain dwarf varieties of *Solanum tuberosum*, *Pisum sativum*, *Clarkia pulchella*, and *Zea Mays*.

2. Dwarfs with cells slightly smaller than, or almost the same as, those of the normal type, as those of *Lathyrus odoratus*, *Mirabilis Jalapa*, *Phaseolus vulgaris*, and *Lens esculenta* (Rote Kleine Winter).

3. Dwarfs with larger cells than found in the normal plants, as *Nigella damascena nana*.

Sierp found great variability in the cell size of each tissue, though the average value was quite constant. He lays great stress on the importance of measuring exactly corresponding places, when comparing cell size of any tissue of the stem or leaf, since it varies according to the height of the stem. Moreover, in each leaf, the cells at the apex, at the base, and midway between these two regions differ in size.

Sierp used the Schwendener-Ambronn method for finding the average cell size. This method gives the average area of the cell from a surface view, or of its cut surface in longitudinal or cross section. A camera-lucida drawing is made of a group of the cells of the epidermis, or of the cells of any other tissue, of each of the organs compared. These drawings are made on a piece of Bristol board of as uniform thickness as possible, the area and weight of this piece of Bristol board being carefully noted. The drawing of the group of cells is then cut out and weighed also. The product of the weight, times the area of the original piece of Bristol board, divided by the weight of the camera-lucida drawing, gives the area of the group of cells drawn. This area, divided by the number of cells in the group, gives the average area of the cell. The area of the organs compared is ascertained in a similar way.

Possibility of error lies in the uneven thickness of the Bristol board, in its absorption of moisture from the atmosphere, and in the lack of precision in cutting inside or outside of, not through, the outline of the group of cells. However, as many tissue cells, especially those of the epidermis, are very irregular, this method of determining cell size would seem preferable to that of basing one's comparisons on the average length or average width of the cell or on the product of these two dimensions, as if the cells were indeed rectangular.

The work of Sanio, Amelung, Jakushkine and Wawilow, and Conklin seems to warrant the conclusion that while the cells of an organ may differ greatly in size for various and obscure reasons, the average cell size of an organ is constant for the species or variety. The work of Gates, Keeble, Neilson Jones and Sierp shows that hereditary differences in body size of varieties or species may be due to corresponding or reverse differences in cell size, in cell number, or to both these factors.

THE PROBLEM OF CELL FORM

The further questions suggest themselves: Is there any correlation between the shape of the plant organ and the shape of its constituent cells? Are the long narrow stem leaves of many plants due to the length and narrowness of their cells as compared with those found in the more rounded basal leaves, or to a greater number of cell divisions in the long axis of the leaf? Are the cells of the lobes of incised leaves wider than those of the constricted portions of the leaves, or are the constrictions the result of a slower rate or shorter duration of cell division?

Gates (1909) seems to think such a direct relation between cell shape and leaf shape is probable. "Increase [in cell size]," he says, "has been greater in one dimension than in another, resulting in a change in the relative dimensions of the cells. This in all probability accounts for the altered shape of some of the organs, as leaves and capsules." He holds that the greater cell size, together with the difference in cell shape of *O. gigas*, is sufficient to have produced external differences between the two plants, without the introduction of any new factors. Except for stating that the anthers of *O. gigas*, which are about twice as long as those of *O. Lamarckiana*, have cells which are not only larger but relatively longer than those of the parent plant, Gates does not give any comparative measurements on corresponding dimensions of organs and their cells, to prove the relation of cell shape and body shape.

According to both Familler (1900) and Goebel (1908) there is a direct relation between the light intensity and the form of leaf produced in *Campanula rotundifolia*. Plants placed where they were well shaded, instead of developing typical linear stem leaves, produced only round leaves on the stem, similar to the basal leaves which appear earlier in spring.

In my cultures of *Lobelia Erinus*, plants grown in the greenhouse during the dull winter months flowered less profusely than during the summer. These winter plants had only spatulate leaves along the whole length of the floral shoot and none of the small linear leaves which are usually found on the upper part of the stem.

Familler's explanation for such phenomena is that the light, food supply, and other optima are higher for the production of the flowers and the long leaves than for the production of the round leaves. Thus, it is not until the warm weather of early summer, when the illumination is stronger and the plant already possesses a well developed root system and numerous basal leaves, that the narrow stem leaves and flowers appear. Even then, a diminution of the light intensity, or any great disturbance in the development of the plant can occasion the production of the juvenile form of leaf. Thus, if the *Campanula* plant is propagated by cuttings from shoots bearing only long narrow leaves, the young leaves sent out by these plants are round, like the basal leaves of the parent plant. These propagated plants cannot produce long leaves until they have better developed root systems, and the plants have become well established in their new food relations.

I have studied the shape, i. e., the relation of length to breadth of leaves and their constituent cells, in the following three types of plants.

1. Species with broad basal leaves, narrow stem leaves near the inflorescence, and transitional leaves on the lower part of the stem: *Campanula rotundifolia, Lobelia Erinus.*

2. Broad-leaved and narrow-leaved species belonging to the same genus: *Plantago major* and *P. lanceolata, Linum angustifolium* and *L. usitatissimum.*

3. Varieties of the same species having entire leaves, as compared with others having lobed leaves: *Cichorium Intybus.*

METHODS

The Schwendener-Ambronn method used by Sierp, which gives the average area of the cells, was not suited for my investigations on the relation of the length to the breadth of the cells of variously shaped leaves. The method used in finding the average length and the average breadth of the cell resembles that of Amelung, except that an ocular micrometer instead of a stage micrometer was used. The number of cells to a unit of the scale in the ocular micrometer were counted, and the average dimensions in millimeters were estimated from these numbers. Whenever the line of measurement passed through the two opposite sides of a cell, as it appeared in the section regardless of how small a fragment of the entire cell was thus cut, its measurement was recorded as the measurement of the length or of the breadth of the cell in that particular portion of the leaf. If, as sometimes happened in the irregular cells of the epidermis, the same line passed twice through any cell, the two fragments were recorded together as the measurement of the cell in that region. Frequently the end of the line of measurement did not reach the opposite wall of a cell. In such a case I estimated as accurately as possible what fractional part of the length or of the breadth of that cell fell upon the line of measurement, and this fraction was recorded. Thus, if the line passed through nine cells and reached only one fifth of the way across the tenth cell, the cell count was recorded as nine and one fifth cells. This method cannot of course be regarded as giving absolute length and breadth of the epidermal cells especially, but is probably the best available. It seems on the whole preferable to record the fractional parts of cells lying on the scale unit. The alternative would be to make all the measurements on single cells, and in this method the problem of selection and the errors in determining the cell axes would probably involve still greater inaccuracies.

The maximum length and width of each leaf examined was recorded, and an outline tracing was made. In most cases one hundred counts were made on each type of leaf as the basis for comparison, with the exception of *Linum*, in which case I made nineteen counts on the palisade cells and forty-five counts on the epidermis, and of the palisade cells of *Plantago*, on which thirty counts were made.

Except in the comparison of leaf shapes in lobes and constrictions, the cell counts were made in the middle region of the leaf, and about 2 mm. away from the midrib. As the comparison was between leaves differing from each other in length and breadth, only these two dimensions of their cells were measured. I have not concerned myself with the third dimension, as the difference in thickness of the leaves is too small for easy study.

All the measurements were made from the surface of the leaf. The epidermal cells of the under surface of the leaf were measured from below. The palisade cells were measured from above. Thus in any one portion of a given tissue I could make measurements of the length and of the width of the cells at the same time. The length of the cell I considered to be that dimension of the cell which was parallel to the midrib of the leaf and the long axis of the entire leaf, the width of the cell as taken was the dimension corresponding to the width of the leaf.

I found that, if the sections of the lower epidermis to be measured were prepared by stripping this tissue away from the leaf, it was difficult to determine which axis of the cell had been parallel to the midrib. The possibility of error in this respect was greatest in cells having irregular outlines. I therefore prepared these sections by removing the upper epidermis and the green tissues from that portion of the leaf which was to be examined, leaving the lower epidermis intact. The entire leaf, or the exposed epidermis with a portion of the midrib, was then mounted in water and placed under the microscope. Before measuring the palisade cells, both the upper and the lower epidermis of the region to be examined were stripped off, care being taken to remove none of the green tissue. When the leaf was placed flat on a slide the remaining tissues were sufficiently transparent to enable me to make measurements of the two dimensions of the upper ends of the palisade cells. All the measurements were made on the living cells, thus avoiding the possibility of shrinkage or distortion due to fixation.

I found an ocular micrometer preferable to a stage micrometer, as, by moving the slide or by rotating the micrometer, I could more easily bring the specimen to be examined in the proper position in relation to the scale, without handling the specimen itself.

Throughout the investigations I used a Leitz ocular micrometer. The scale consists of a large square, divided into four smaller squares, one of which is again divided into twenty-five equal squares. The value of these divisions of course depends upon the magnification, and it was ascertained with the aid of a stage micrometer for each eye-piece and objective used. For example, when a one-inch ocular and two-thirds objective were used with a Bausch and Lomb microscope, each side of any one of the smallest squares was equal to 0.116 millimeter. All cell counts on all the plants examined are stated in terms of cell diameters per millimeter.

The section to be measured was placed on the stage of the microscope in such a position that the midrib of the leaf was parallel to one side of the ocular micrometer scale.

In measuring the palisade cells, a favorable area of this tissue, uncrushed and free from veins, was chosen, equal to one of the smallest squares of the ocular micrometer. The number of cells cut by each side of the square was counted. The length of this line was then divided by the cell number to obtain the average cell diameter. In this way, with one placing of the micrometer, I could make four measurements, two giving the length and two giving the width of the palisade cells of the region.

To measure the epidermal cells, a suitable area, free from veins, was selected. To avoid errors due to the presence of stomata, care was taken in each case to so place the micrometer that the stomata came between but not on the lines of measurement. In plants having numerous stomata, this was often a difficult matter. In this case I used twice as large a micrometer unit, the sides of two squares, corresponding roughly to the larger size of the cells.

CAMPANULA ROTUNDIFOLIA

Campanula rotundifolia is well known as a plant whose radical and cauline leaves differ widely in shape. It produces numerous radical leaves, which are often wanting at the time of flowering. These are petioled, almost orbicular in shape, with cordate base. In May or June the plant sends up several shoots which bear flowers at their summits throughout the summer. The upper stem leaves are sessile and linear, but the lower stem leaves are intermediate in shape, being ovate and acute. These three types of leaves are designated in the tables as basal, transitional, and linear.

Measurements were made of the length and the width of the cells of the lower epidermis of typical leaves of the three forms described. TABLE I gives the results of these measurements. The average number of cells in each leaf that were cut by a line 1 mm. in length, is given for each of six leaves of each shape. The final averages are from the original data and differ fractionally from the average of the averages in the following table.

A comparison of the average number of cells to 1 mm. found in the long and the broad axis of each basal leaf shows that there is some variation in the size of the cells, for example, in leaf *C* the average number being 22.02 cells to 1 mm. in the long axis and 20.91 cells in the transverse axis, while in leaf *D* the cell counts were 26.95 cells in the long axis and 29.56 cells in the transverse axis of the leaf. These figures also serve as an example of the variability found in the relative dimensions of the cells, the cells in leaf *C* being somewhat broader than long, while in leaf *D* this relation of length to breadth of the cells is reversed. This variability in cell size and cell shape is found in all three forms of leaves examined. However, in most leaves as in the final averages, the numbers indicate that the cells are nearly isodiametric or somewhat longer than they are broad. The table also gives the average measurements of the cells in fractional parts of a millimeter.

TABLE I

CAMPANULA ROTUNDIFOLIA

Comparative length and width of the three types of leaves and the corresponding dimensions of the cells of the lower epidermis of each type of leaf. Numerals in parentheses show number of counts. Line of measurement = 1 mm.

	Basal leaves		Transitional leaves		Linear leaves	
	Length	Width	Length	Width	Length	Width
Leaf *A*	11.	14.5	23.	5.5	56.	3.
Average cell size (15)	0.037	0.036	0.04	0.029	0.033	0.03
Average number of cells (15)	26.99	27.74	24.81	33.45	29.78	32.97
Leaf *B*	15.	17.	49.	8.5	32.	3.
Average cell size (15)	0.046	0.047	0.038	0.038	0.036	0.035
Average number of cells (15)	21.54	21.38	26.02	25.92	27.75	28.
Leaf *C*	17.	18.	55.	8.	39.	4.5
Average cell size (15)	0.045	0.047	0.035	0.036	0.033	0.034
Average number of cells (15)	22.02	20.91	28.52	27.55	29.98	28.92
Leaf *D*	13.	11.	20.	8.	49.	3.
Average cell size (15)	0.037	0.033	0.043	0.037	0.03	0.027
Average number of cells (15)	26.95	29.56	25.95	26.56	32.28	35.77
Leaf *E*	10.	12.5	27.	6.	50.	3.
Average cell size (15)	0.042	0.037	0.035	0.036	0.032	0.033
Average number of cells (15)	23.55	26.97	28.3	27.32	30.6	29.86
Leaf *F*	19.	19.	21.	6.	57.	3.5
Average cell size (25)	0.037	0.039	0.037	0.03	0.04	0.032
Average number of cells (25)	26.74	25.62	26.61	32.36	24.7	30.31
Average measurement of leaves	14.16	15.33	32.5	7.	47.16	3.33
Average measurement of cells (100)	0.04	0.039	0.038	0.034	0.034	0.032
Average number of cells (100)	24.85	25.34	26.26	29.21	28.74	30.91
Ratio dimensions of leaf	.92 : 1		4.64 : 1		14.15 : 1	
Ratio dimensions of cell	1.02 : 1		1.11 : 1		1.07 : 1	

A glance at the ratio of the length to the width of the cells of the lower epidermis of the three forms of leaves shows that the percentage of difference between these two dimensions does not approach that found between the leaf dimensions. The basal leaves are on the average slightly shorter than broad, and their epidermal cells are slightly longer than broad, almost isodiametric.

The transitional leaf is more than four times as long as broad, yet its cells are of almost the same shape as those of the basal leaf, being slightly longer than wide. In the linear leaves, which are about 14.15 times as long as they are broad, the cells are only .07 longer than wide. That is, the difference between the length and the width is 287 times greater in the leaf than in the cell. Moreover this difference in cell dimensions is least in the basal leaves and greatest in the transitional leaves. There seems to be no relation here between the shape of the cell and that of the leaf.

The slight difference between the ratios of length to breadth of cells obtained in the different leaves is almost equaled by the variability of the individual cells in any one leaf. In some leaves the cell proportions, as compared with the leaf proportions, may be found reversed in certain areas. Thus fifteen measurements of cells in a basal leaf *E*, which was 10 mm. long by 12.5 mm. broad, showed that the cells averaged 0.042 mm. long and 0.037 mm. wide (a ratio of 1.13 : 1) while similar measurements of cells of a linear leaf, 50 mm. by 3 mm., showed that they had an average length of 0.032 mm. and an average width of 0.033 mm. (a ratio of .97 : 1). The forms of the three types of leaves found in *Campanula rotundifolia* are not therefore directly correlated with the shape of their cells.

The cells of the stem leaves show a smaller average size than those of the basal leaves, the cells of the linear leaves being most reduced. In TABLE II are given the relative length and relative width of the cells of the three types of leaves. The difference in the dimensions of the three types of cells is very slight, and might seem at first to fall within the limits of individual cell variability. I therefore plotted frequency curves (FIG. 1) showing the number of times that I found a given number of cells to a line of 0.232 mm., in the long and in the broad axis of the basal and the linear leaves. A greater number of cells to a given line indicates smaller cell size.

TABLE II

CAMPANULA ROTUNDIFOLIA

Relative size of the lower epidermal cells of the three types of leaves.

	Length of cells	Width of cells
Transitional leaf : basal leaf	.94 : 1	.86 : 1
Linear leaf : basal leaf	.86 : 1	.82 : 1

All cases where there were four and a fractional part of a cell to 0.232 mm. were recorded as four cells—all cases of more than five cells and less than six cells were recorded as five cells, etc. These curves show that both in the long axis and in the transverse axis of the leaf, there are most frequently five cells to 0.232 mm. in the basal leaf, while in the linear leaf there are six. The curves prove conclusively that the decrease in both dimensions of the lower epidermal cells of the linear leaves is regularly present in the material studied.

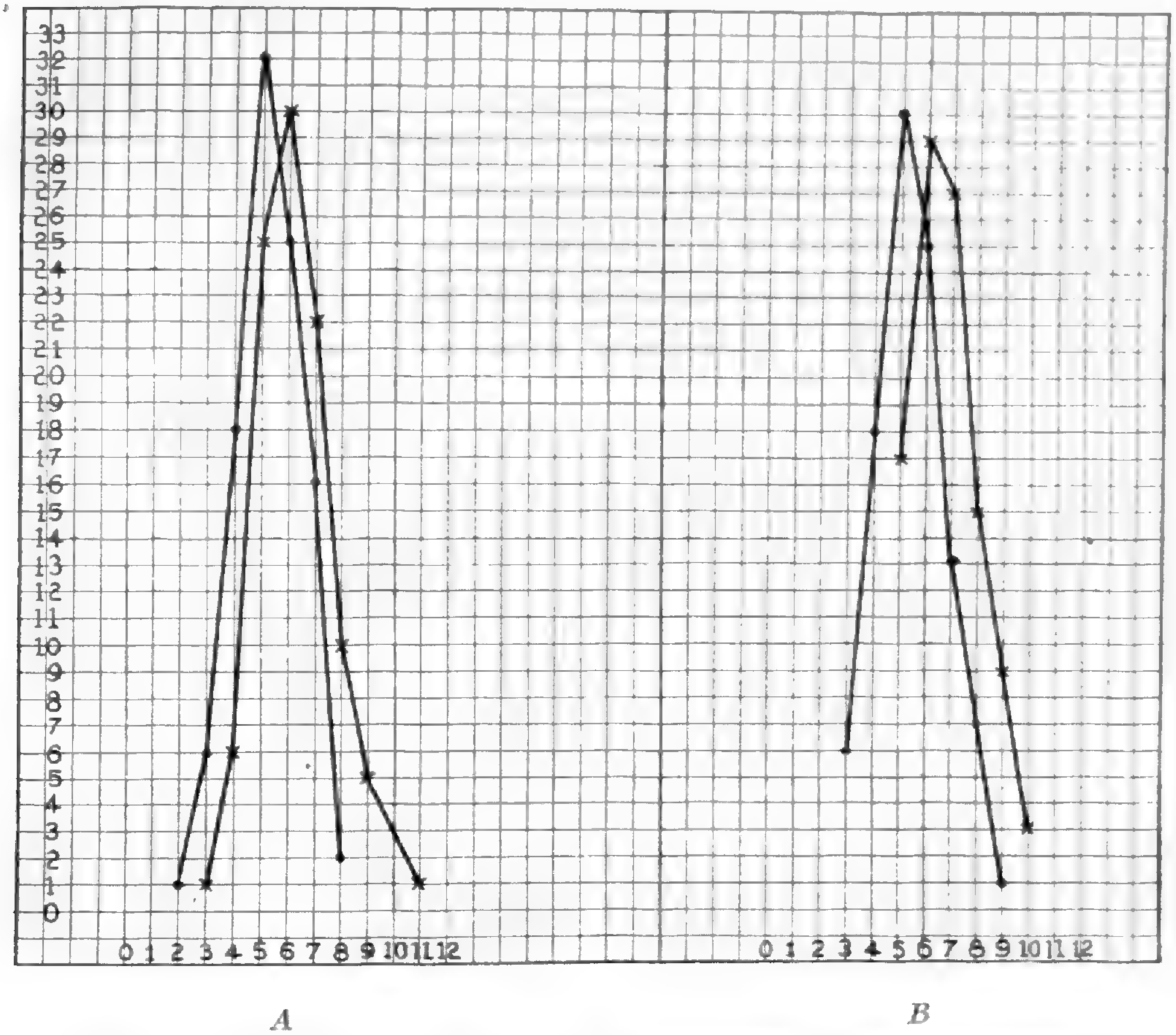

FIG. 1. Curves denoting frequency of dimensions of lower epidermal cells of *Campanula rotundifolia*. *A*, Transverse axis. *B*, Longitudinal axis. Abscissas denote the number of cells to 0.232 millimeter. Ordinates record the number of instances in which a given number of cells per 0.232 mm. occurred. Unbroken lines used for cells of basal leaf; lines broken by x's, for linear stem leaf.

This observation agrees with that made by Sierp, who found that in *Mirabilis Jalapa*, *Nigella damascena*, and *Pisum sativum* (Laxton's Alpha) the higher the leaf was situated on the stem, the smaller its cell size, as well as that of the node from which the leaf sprang.

Neither in the case of *Campanula* nor the other plants studied did I find the size of the individual cells to be as constant as Amelung's measurements would indicate. Because of the wide range of variation in cell size, the average cell size could be determined only through numerous counts. Usually one hundred counts were made on each form of leaf, so that the average cell size given is the average size of from six hundred to seven hundred cells.

LOBELIA ERINUS

This plant, like *Campanula rotundifolia*, has three distinct forms of leaves. The orbicular radical leaves are developed before the flower shoots appear, and are rarely found at the time of flowering. The slender, somewhat recumbent shoots bear at first only spatulate or obovate leaves, but later, as the stem elongates, it has small linear leaves near its summit. The flowers grow from the axils of these linear leaves. Each type of leaf produced is not only smaller than the one which preceded it but it is also proportionately narrower.

A comparative study was made of the shape of the cells of the lower epidermis of the three forms of leaves, in relation to the shape of the whole leaf. Only those linear leaves were examined in whose axils the flowers had already faded, as I thought these leaves were probably fully grown. Measurements were made on six such leaves after two intervals of two weeks each, to see if they had ceased to grow by the time the flowers had bloomed. There was some further growth, but scarcely enough to seriously affect the proportions of the leaf, or noticeably alter its shape (TABLE III).

TABLE III

LOBELIA ERINUS

Record of further growth of linear leaves, after flowers in their axils had faded. Line of measurement = 1 mm.

Plant	*A*	*B*	*C*	*D*	*E*	*F*
	Length × width	Length × width	Length × width	Length × width	Length × width	Length × width
First measurements...	10 × 1.5	10 × 1	12 × 2	14 × 2	19 × 8	19 × 4
End second week.....	10 × 1.87	11 × 1.5	12 × 2.5	15 × 2.5	—	20 × 4
End fourth week.....	11.5 × 1.87	11 × 1.5	Died	16 × 2.5	21 × 9	20.5 × 4

The results of the cell measurements made are given in TABLE IV, which shows both the number of cells per millimeter and the dimensions of the cell. The ratio of the length to the width of these cells by no means agrees with that of the corresponding dimensions of the leaves. While the difference between the length and the width of the linear leaves is almost four times greater than that of the basal leaves, the cells of the linear leaves are relatively only .11

TABLE IV

LOBELIA ERINUS

Comparative length and width of the three types of leaves and the corresponding dimensions of the lower epidermal cells of each type of leaf. Numerals in parentheses show the number of counts. Line of measurement = 1 mm.

	Basal leaves		Transitional leaves		Linear leaves	
	Length	Width	Length	Width	Length	Width
Leaf *A*	29.	27.	19.	9.	10.5	2.5
Average cell size (15)	0.066	0.053	0.044	0.048	0.032	0.033
Average number of cells (15)	14.99	18.73	22.8	20.79	30.9	30.11
Leaf *B*	27.	25.	21.	8.	13.	2.
Average cell size (15)	0.06	0.058	0.052	0.043	0.057	0.04
Average number of cells (15)	16.53	16.95	19.02	23.2	17.45	24.46
Leaf *C*	34.	31.	15.	9.	14.	3.5
Average cell size (15)	0.063	0.057	0.04	0.042	0.045	0.041
Average number of cells (15)	15.76	17.45	24.63	23.27	22.02	24.16
Leaf *D*	33.	30.	18.	8.	12.	2.5
Average cell size (5)	0.094	0.068	0.054	0.046	0.042	0.045
Average number of cells (5)	10.6	15.48	18.18	21.33	23.49	22.17
Leaf *E*	33.	29.	16.	5.5	14.	3.
Average cell size (9)	0.067	0.074	0.036	0.035	0.047	0.033
Average number of cells (9)	14.83	13.37	27.42	28.07	21.27	29.98
Leaf *F*	30.	25.	20.	7.	20.	3.5
Average cell size (9)	0.085	0.062	0.046	0.045	0.051	0.046
Average number of cells (9)	11.68	15.91	21.37	21.8	19.29	21.47
Leaf *G*	50.	31.	22.	10.	15.	3.5
Average cell size (12)	0.06	0.079	0.042	0.038	0.04	0.033
Average number of cells (12)	16.49	12.56	23.45	25.77	25.54	29.64
Leaf *H*	37.	32.	15.	8.	16.	3.
Average cell size (11)	0.056	0.06	0.036	0.039	0.041	0.031
Average number of cells (11)	17.84	16.57	27.03	25.57	23.92	31.55
Leaf *I*	41.	31.	24.	7.	19.	3.5
Average cell size (9)	0.064	0.062	0.043	0.04	0.054	0.043
Average number of cells (9)	15.48	15.96	23.16	24.85	18.44	23.08
Average measurements of leaves	34.88	29.	18.88	7.94	14.25	3.
Average measurements of cells (100)	0.065	0.062	0.043	0.042	0.044	0.037
Average number of cells (100)	15.15	15.96	22.84	23.54	22.47	26.31
Ratio dimensions of leaf	1.2 : 1		2.37 : 1		4.75 : 1	
Ratio dimensions of cell	1.05 : 1		1.03 : 1		1.17 : 1	

longer than those of the round leaves. That is, the difference in these two leaf shapes is almost forty times as great as the difference in the shapes of the cells. Furthermore, the transitional leaves have proportionately wider cells than the basal leaves.

There is a considerable range of variability in the shape of the cells of any one type of leaf. For example, in a basal leaf, *D*, 33 mm. long by 30 mm. wide, the average length of the cells of the lower epidermis was 0.094 mm., the average width 0.068 mm., while in another leaf, *G*, 50 mm. by 31 mm., the average cell measurements were 0.06 mm. for the length and 0.079 mm. for the width. The great range of variability of the cell shape of each type of leaf may account for the slight difference between the ratios of the cell dimensions of the round, the narrow and the transitional leaves.

The decrease in cell size, that is, in both length and width, found in the linear leaves as compared with the basal leaves, is even more marked than in *Campanula rotundifolia*. The ratios between the corresponding dimensions of the cells of the three forms of leaves are given in TABLE V. It will be seen that the cells of the transitional and linear leaves, both of which grow on the stem and are produced at almost the same stage of development of the plants, have cells which are almost identical in size, although differing considerably from those of the earlier, radical leaves.

TABLE V

LOBELIA ERINUS

Relative size of the cells of the lower epidermis of the three types of leaves.

	Length of cells	Width of cells
Transitional leaf : Basal leaf	.66 : 1	.67 : 1
Narrow leaf : Basal leaf	.67 : 1	.60 : 1

PLANTAGO MAJOR AND PLANTAGO LANCEOLATA

The leaves of the two species of plantain, *Plantago major* and *P. lanceolata*, differ greatly in shape. The largest and best developed leaves of each species that could be obtained, were chosen for comparison. *P. lanceolata*, when crowded, produces leaves which are somewhat dwarfed, particularly in their breadth, being relatively only two-thirds to three-fourths as wide as is usual. Such leaves also were examined.

Measurements were made of the cells of the lower epidermis of such leaves of *P. lanceolata*, as well as those of the normal *P. lanceolata* and *P. major* leaves. Also the palisade cells of the two species of plantain leaves were compared. The results of these measurements are given in cell size and in cell number per millimeter in TABLE VI.

TABLE VI

PLANTAGO

Measurements of the length and the width of the leaves of two species of plantain, and of the corresponding dimensions of the cells of their lower epidermis and their palisade tissue in transverse section, expressed in millimeters and in number of cells to one millimeter. B = average size of cells in mm. C = average number of cells to 1 mm. Numerals in parentheses show the number of counts.

	Leaf		Cells of lower epidermis	
	Length	Width	Length	Width
P. major	176.09	110.06	*B*(100), 0.031 *C*(100), 30.09	0.044 22.63
Ratio	1.6 :	1	.75 :	1
P. lanceolata	310.3	32.63	*B*(100), 0.035 *C*(100), 27.97	0.041 23.97
Ratio	9.2 :	1	.85 :	1
P. lanceolata (narrow)	153.5	10.5	*B*(100), 0.032 *C*(100), 30.71	0.038 25.81
Ratio	14.6 :	1	.83 :	1

	Leaf		Palisade cells	
	Length	Width	Length	Width
P. major	48.	27.	*B*(30), 0.022 *C*(30), 44.1	0.021 46.28
Ratio	1.71 :	1	1.04 :	1
P. lanceolata	70.	23.	*B*(30), 0.021 *C*(30), 46.92	0.021 46.79
Ratio	3.04 :	1	1 :	1

In both species the palisade cells are quite round in transverse section. The cells of the lower epidermis of *P. major* are slightly shorter than those of *P. lanceolata*, but the disproportion does not approach that between the length and width of the leaves of the two species. The *P. lanceolata* cells are only 7 per cent. longer and 6 per cent. shorter than those of *P. major*.

I have plotted frequency curves for each species showing the number of times that a given ratio of the length to the width of the epidermal cells occurred. It would be difficult to determine, from curves as irregular as these, the mean ratio of length to width in either species.

This does not mean that the shape of the lower epidermal cells is the same in both cases. While the difference does not lie in the length and width of the cells, their outlines are quite different, the cells of *P. major* being quite wavy in outline, while in both types of leaves of *P. lanceolata* the cells are only slightly wavy in outline. The cells of the normally developed and the narrow leaves of *Plantago lanceolata* are practically the same in shape and size.

LINUM ANGUSTIFOLIUM AND LINUM USITATISSIMUM

The leaves of *Linum usitatissimum* are lanceolate, those of *L. angustifolium* are oblong or oblong-elliptical. The leaves of both species are sessile, acute and entire. Those of *L. usitatissimum* are about as broad, but at least twice as long as the leaves of *L. angustifolium.* The cells of the lower epidermis and the palisade cells were measured in each species. The measurements show a striking similarity in the cell shape of these two species of *Linum.* The cells of *Linum usitatissimum* are only .04 longer than those of *L. angustifolium*, and show no relation therefore to the greater difference in their leaf dimensions.

CICHORIUM INTYBUS

The first leaves of the common type of *Cichorium Intybus* are entire but these are soon succeeded by other radical leaves which are distinctly lobed. The degree of lobing varies greatly in different plants, but the leaves of any one plant are quite similar in shape. For this reason all the leaves of *Cichorium Intybus* whose cell shape was measured were selected from one plant, which had deeply constricted leaves. The Witloof type of *Cichorium Intybus* is a cultivated variety of chicory, which has large and relatively entire leaves. All the leaves of this type studied were taken from the same plant. These, as well as the leaves of the common type of *Cichorium Intybus* with which they were compared, were basal leaves. In both, the cells of the lower epidermis near the midrib and near the margin of the broadest part of the leaf, and midway between these two regions were measured and their two dimensions compared with the length and breadth of the leaves to which they belonged (TABLE VII).

TABLE VII

CICHORIUM INTYBUS, COMMON TYPE

Maximum length and width of each leaf, the width of each leaf across the lobes, and the constricted portions, and the length and width of the cells of the lower epidermis in these two regions of the leaf. A = width of leaf from midrib to margin. B = average size of cells in mm. C = average number of cells to 1 millimeter. Numerals in parentheses show the number of counts.

Leaf Size			Constricted portion		Lobe below this constricted portion					
					Near Midrib		Midway out from midrib		Apex of lobe	
Length	Width		Length	Width	Length	Width	Length	Width	Length	Width
250	95	*A*		2.		28.				
		B (15)	0.36	0.29	0.03	0.028	0.33	0.03		
		C (15)	27.57	34.1	32.67	34.6	30.11	32.48		
220	61	*A*		6.		28.				
		B (15)	0.033	0.027	0.028	0.029	0.03	0.029		
		C (15)	29.48	36.8	35.65	34.28	32.99	33.8		
135	53	*A*		6.		15.				
		B (15)	0.025	0.029	0.026	0.027	0.034	0.023		
		C (15)	38.55	34.12	37.81	35.95	29.22	42.28		
186	65	*A*		5.5		34.				
		B (15)	0.037	0.027	0.03	0.03	0.032	0.027		
		C (15)	26.43	35.85	33.21	32.94	31.03	35.95		
229	71	*A*		4.		29.				
		B (15)	0.033	0.028	0.033	0.028	0.029	0.027	0.028	0.026
		C (15)	29.42	34.99	29.35	35.47	33.5	36.1	33.56	37.45
153	57	*A*		4.		32.				
		B (15)	0.033	0.029	0.029	0.028	0.034	0.028	0.027	0.029
		C (15)	30.	34.11	34.02	34.68	29.36	34.6	36.52	33.69
151	55	*A*		4.		21.				
		B (10)	0.034	0.025	0.03	0.032	0.026	0.026		
		C (10)	29.24	39.46	32.92	30.41	37.21	37.07		
Av. 189	Av. 65	Av. *A*		4.5		26.				
		Av. *B* (100)	0.033	0.028	0.029	0.029	0.031	0.027		
		Av. *C* (100)	30.14	35.92	33.7	34.23	31.62	35.99		
Ratio dimensions of cell......				1.17 : 1		1.01 : 1		1.13 : 1		

The lower epidermal cells of the broadest lobes of each leaf were compared with those of the constriction immediately adjacent to it. The ratio of the average length to the average width of the cells is .04 greater in the constricted portion than in the middle region of the lobe, and .16 greater than in the lobe near the midrib. This rather slight difference is apparently due to the fact that the cells in the constricted portions of the leaf are longer, rather than narrower, than the cells of the lobes, whereas in the leaf as a whole the difference is plainly one of greater breadth of the leaf in the lobed portion than in the constricted portion, the length

TABLE VIII

CICHORIUM INTYBUS, WITLOOF TYPE

Maximum length and width of the leaves of a cultivated chicory and corresponding dimensions of the cells of the lower epidermis in different regions of the leaf. A = width of leaf from midrib to margin. B = average size of cells in mm. C = average number of cells in 1 millimeter. Numerals in parentheses show the number of counts.

Leaf size			Basal portion		Broadest part of blade					
					Near midrib		Midway out from midrib		Marginal	
Length	Width		Length	Width	Length	Width	Length	Width	Length	Width
		A		6.		45.				
350	92	*B* (15)	0.062	0.029	0.032	0.032	0.038	0.026	0.027	0.024
		C (15)	16.01	33.98	30.35	30.87	26.15	37.18	35.82	40.5
		A		13.		52.				
386	105	*B* (15)	0.059	0.027	0.03	0.039	0.032	0.034		
		C (15)	20.04	36.59	32.43	25.5	30.98	29.34		
		A		13.		51.				
352	102	*B* (15)	0.055	0.03	0.033	0.033	0.034	0.033		
		C (15)	17.89	32.43	29.52	29.93	29.13	30.05		
		A		6.		48.				
412	104	*B* (15)	0.053	0.029	0.036	0.04	0.037	0.036	0.037	0.037
		C (15)	18.85	33.71	27.75	24.67	26.63	27.66	26.94	27.01
		A		8.5		50.				
472	94	*B* (15)	0.066	0.026	0.032	0.037	0.031	0.032		
		C (15)	14.95	37.17	30.65	26.42	31.29	30.69		
		A		8.		49.				
425	107	*B* (15)	0.062	0.03	0.041	0.034	0.033	0.033	0.029	0.026
		C (15)	15.92	32.42	24.06	28.58	30.04	29.43	33.5	37.68
		A		9.		51.				
350	104	*B* (10)	0.041	0.035	0.03	0.03	0.035	0.036	0.032	0.031
		C (10)	24.01	28.28	24.02	32.95	28.49	27.26	31.07	31.84
		Av. *A*		9.07		49.42				
Av. 404	Av. 99	Av. *C* (100)	0.055	0.029	0.034	0.035	0.034	0.032		
		Av. *B* (100)	17.95	33.76	28.62	28.19	28.98	30.38		

Ratio dimensions of cell..........1.88 : 1 .98 : 1 1.04 : 1

of the two regions being the same, or even less in the constricted portion. The cell shape in the wild chicory leaf is practically the same both in the lobes and the constrictions of the leaf.

The cells near the base of the Witloof chicory leaf are apparently modified in their shape by their relation with the numerous veins.

The lobing of the wild chicory leaf is not due to greater width of the cells in the lobes as compared with the constricted areas, but rather to the greater number of cells in the long axis of the lobe, which is almost at right angles to the midrib. This greater cell number is apparently due to a more rapid rate of division in the lobe cells as compared with those in the constricted regions (TABLE VIII).

The cells of the leaves of the Witloof variety are larger than those of the wild chicory leaves, but the shape of the cells is almost the same in both varieties. The ratio of the length to the width of the Witloof cells is 1.01 : 1, that of the wild chicory cells being 1.11 : 1.

SUMMARY AND CONCLUSIONS

Cell size

The cells of the plants above described show a considerable variability in size in the same tissue but that the average cell size for any one tissue of a species or variety, however, is a fairly constant and hereditary character, has been previously shown by Sanio, Amelung, Sachs, Strasburger and Conklin.

The cell size of closely related species, as *Linum usitatissimum* and *Linum angustifolium*, may be the same, which agrees with the conclusions of Amelung and Conklin, or again, in closely related varieties of the same species, as the common and Witloof types of *Cichorium Intybus*, the cell size may differ considerably, as was also proved to be true in certain plants investigated by Gates, Keeble, Neilson Jones, Jakushkine and Wawilow, and Sierp.

As Sanio, Jakushkine and Wawilow, and Sierp have already shown, the cell size in an organ depends in some degree on the stage of development of the plant at the time the organ was produced. Thus the transitional leaves of *Campanula rotundifolia* and *Lobelia Erinus* which are developed after the basal leaves, have smaller cells, while the linear leaves, which appear latest, have the smallest cells. In both these plants, the average cell size of each type of leaf is a constant characteristic. Differences in the size of any given organ of a species are due to differences in the number of its cells, and not to variations in cell size. The extreme limits of the number of cells of which each type of leaf may be made up, are obviously determined by heredity, and the hereditary size of the organ is due to factors of periodicity in growth, which determine the rate and duration of cell division.

Cell shape

Livingston (1901) describes the cells of *Stigeoclonium* as having two characteristic shapes: a spherical form when growing in loose masses on the trunks of trees, in highly concentrated media, or when partially desiccated; and a cylindrical form, when growing in filaments in extremely dilute media. Instances like the above might lead one to believe that cell shape is largely a matter of environmental conditions, such as mutual pressure, turgor as influenced by environment, etc. However, there are unicellular algae, for example the desmids and diatoms, having a characteristic cell shape which cannot be due to pressure nor any simple turgor relations.

My studies show that the cells of the lower epidermis of the leaves of any species of plant, in the regions between the veins, have a characteristic length and breadth. The cell shape may, in other regions, be modified to a considerable extent by various factors, as by the presence of stomata, veins, etc. The relative length and breadth of the cells of any tissue may be the same in different species or varieties, as in *Linum usitatissimum* and *Linum angustifolium*, or it may be somewhat different, as in *Plantago major* and *Plantago lanceolata*.

Differences in the shapes of the leaves of the same plant, or of related species, are not correlated with corresponding differences in the shape of their cells. The linear leaves of *Campanula rotundifolia* and *Lobelia Erinus* are not composed of longer, narrower cells than those found in the round leaves, but have a larger number of cells in the long axis of the leaf. The cells of *Cichorium Intybus* are of the same size and shape in the lobed and in the constricted portions of the leaf.

The shape of the leaf obviously cannot be the result of the differences in cell shape but must rather be due to factors for periodically limiting the number and direction of the cell divisions in each type of leaf. The form of incised leaves like those of *Cichorium Intybus* must be due to a factor or factors for differential periodicity, which determines that the rate or duration or both, of cell division, shall be greater in one part of the leaf than in another, thus producing the lobes and constrictions.

In concluding, I wish to express my gratitude to Dr. R. A. Harper, under whose direction these investigations were undertaken, for the many helpful suggestions he gave me throughout the course of this work. I also thank Dr. A. B. Stout, from whom I obtained my chicory material, for his kind interest and help.

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Two remarkable Discomycetes

EDWARD T. HARPER

(WITH PLATES 1–3)

1. UNDERWOODIA COLUMNARIS Peck

I have collected this rare plant in several localities in Michigan and Illinois. The first collection was on Neebish Island, Michigan, in August, 1897. A cluster of small plants about two inches high were found growing beside a path in balsam woods. The next year some larger plants were found growing among dead leaves in a ravine on Mackinac Island. In September three different collections were made on Neebish Island, and the photographs on PLATE 1 were taken. In May, 1908, the two plants shown on PLATE 2 were found on a hillside in open woods at Bureau, Illinois. A single plant was found at Neebish during the past summer.

The species was described and illustrated by Dr. Peck in the 43d Report of the New York State Museum, p. 78, *pl. 4* (1890), from plants found near Kirksville, New York, and sent to Dr. Peck by Professor Underwood. A note in Underwood's Moulds, Mildews and Mushrooms, p. 65 (1899), says that six plants were found in the same locality in three different years. Peck's description is accurate as far as it goes, but his account of the base and method of branching of the plant is incomplete. The plant is so unique in structure and so remarkable in habit and size that I have thought it worth while to discuss its structure and relationships on the basis of my specimens.

Peck's illustration shows the part above the ground only, and he describes it as stemless and everywhere acigerous. This led Schroeter to place the genus among the Rhizinaceae. The plant does, however, have a short stem and is more or less bulbous at the base. The lower margin of the hymenium is uneven, running down in points on the stem while naked strips extend upward for short distances into the hymenium as in some species of *Geoglossum*. There is a definite though inconspicuous margin to the hymenium and in dried plants the hymenium becomes reddish brown where the asci are numerous, while the stem remains whitish. The base of the plant is rounded like the base of species of *Morchella*. No thick mycelial root or sclerotium of any kind was found.

Sometimes the clubs are simple as shown on PLATE 2 and in Peck's illustration but they usually divide into fingers. The plant on PLATE 1 was divided near the middle. The halves have split and sprung apart as shown in *B*. The left branch shown at *A* is forked near the apex. The right branch was nearly destroyed by insects but appeared to have been more deeply divided. Other plants in the collections were divided a little below the middle. PLATE 2 shows two plants, one of which has been sectioned, closely caespitose and apparently connected at the base. In the cluster of small plants first discovered there were at least three connected at the base.

The whole interior of the plant—bulbous base, stem and ascoma—is perforated by irregular longitudinal cavities, as shown in the section on PLATE 2, *A*. The walls of the cavities are of nearly uniform thickness. The interior of the walls is composed of a mesh of septate hyphae 6–8μ in diameter. The cavities are lined with a palisade layer of regular, septate hyphae about 6μ in diameter. The layer is about 50μ thick and there are three or four septa in each hypha. The appearance of a cross section of one of the walls is like that shown in Hesse's Hypogaeen Deutschlands, *pl. 18, f. 12* (1894), except that the interior is composed entirely of septate hyphae.

The outside walls are covered with the hymenium on the outside and the palisade layer on the inside. The surface of the hymenium is wrinkled and corrugated, PLATE 2, *C*, but there appears to be no definite relation in position between the wrinkles of the hymenium and the internal cavities. The interior of the walls is composed of hyphae, and there appears to be no definite subhymenial layer. A palisade layer like that on the walls of the interior cavities covers the stem and base of the plant.

The asci, PLATE 2, *B*, are club-shaped, 10–12 × 160–200μ. They open by a lid as far as I can make out but I have not been able to find empty asci, which Boudier says must be examined to determine the nature of the opening. The character of the plant and the spores is that of Boudier's division Opercules. The paraphyses are septate, a little longer than the asci, slightly thickening upward and somewhat curved at the apex, 4–6μ in diameter.

The colors of the plant are whitish or cream colored outside and pure white within.

I have rewritten Peck's description to include the form of the base and method of branching, as follows:

Ascocarps single or caespitose, simple or more or less deeply and somewhat dichotomously divided, divisions columnar, straight or slightly curved, sulcate-costate and uneven; ascigerous layer definite but not separated from the short stem. Base even or slightly bulbous, interior perforated by irregular longitudinal cavities, separated by thin walls, whitish or brownish outside, pure white within, cavities lined with a regular palisade layer of septate hyphae; asci club-shaped, 10–12 × 160–200μ; paraphyses slightly longer than the asci, rarely branched, septate, 4–6μ in diameter; spores tuberculate, hyaline or slightly colored, elliptical, 10–13 × 18–24μ.

Varying greatly in size, 5–35 cm. high, 2–5 cm. thick.

Growing on the ground among grass or dead leaves in mixed woods.

Underwoodia columnaris is not closely related to any known discomycete. It forms a monotypic genus, as the term is usually understood. It appears to be the only representative of its group.

The group arrangement is especially applicable to the large discomycetes, for the groups are few and well marked; and, while the forms within them are closely related, the kinship of the groups themselves appears remote. Apart from *Underwoodia* there are only seven groups in the family Helvellaceae in our region: the *Morchella esculenta*, *Morchella hybrida* and *Verpa digitaliformis* groups in the *Morchella-Verpa* series and the *Gyromitra esculenta*, *Gyromitra infula*, *Helvella crispa* and *Helvella elastica* groups in the *Gyromitra-Helvella* series. In the Geoglossaceae there may be about thirteen groups, nine of which are in the large *Geoglossum* series and one each in *Spathularia*, *Cudonia*, *Leotia* and *Vibrissea*. The groups are also few and well defined among the larger Pezizaceae. The order Helvellales is based on little more natural relationship than that its members are the large conspicuously stemmed discomycetes.

Forms within the groups offer a most fruitful field for ecological and comparative study. Most of the groups of large discomycetes, such as the *Verpa, Cudonia, Leotia,* and *Geoglossum glutinosum* groups, appear in a variety of forms. In some groups the forms are very abundant and variable. Boudier has named and given beautiful illustrations of twenty-three forms in the *Morchella esculenta* group, offering a fine opportunity for students to compare other *Morchella esculenta* floras with that of France. Durand lists seven forms in the *Geoglossum glabrum* group. *Underwoodia* is so rare that its variation is little known, though it may have had a bloom period at some time in the past.

But while the kinship and variation of *Underwoodia* are unknown it possesses a striking combination of characters found singly in other groups. Most of these characters are more highly developed than in other groups where they occur and this gives to *Underwoodia* a unique position and a special interest. I can only briefly compare the most striking characters and do it without implying any close kinship between *Underwoodia* and the groups in which similar characters are found.

The cancellated stem of *Underwoodia* is more highly developed than in any other discomycete. It contrasts strongly with the hollow stems of species of *Morchella* and the solid stems of the Geoglossaceae. The character is found in the *Acetabula vulgaris* and the *Helvella crispa* groups, but the stems in these groups are deeply sulcate as well as cancellate, the cavities are much less regular and the walls of the cavities as far as I have examined them are not covered with a regular palisade layer. The stems of species of *Morchella* often have a few cavities near the base. They are very markedly developed in the specimen of *Gyromitra gigas* illustrated by Boudier (Icon. Mycol. *pl. 221.* 1904). Such cavities are not lined with a palisade layer of hyphae.

Many discomycetes have lacunae and cavities in the stem. An interesting case for comparison with *Underwoodia* was identified for me by Durand as *Lachnea* (or *Macropodia*) *semitosta.* The stem bears a close resemblance to that of *Underwoodia.* There are a few sulcations on the outside, but the walls of the cavities are not lined with such a regular palisade layer. *Macropodia semitosta* is remarkable in the development of the cancellated stem. Note the illustration of *Peziza semitosta* in Cooke's Mycographia, *f. 109* (1879). The palisade layer lining the cavities in the body of the fungus is most highly developed in species of Hypogaei, but in them it is connected with the hymenium. Bucholtz derives the Helvellaceae from *Lachnea* through the Hypogaei.

The cancellated stem is combined in *Underwoodia* with a club-shaped ascoma, not cup-shaped or saddle-shaped as in the *Acetabula* and *Helvella* groups. Such club-shaped ascomata are found in the groups of the *Geoglossum* series. In size, however, in substance, in the spores, and probably in the opening of the asci *Underwoodia* is widely removed from any of the groups in that series. The hymenium is also more sulcate than in species of *Geoglossum* and resembles in this respect the hymenium of *Verpa*. Compare Boudier's illustrations on *pl. 219* and *220*. We may also compare the ascoma of *Gyromitra gigas* referred to above. *Gyromitra gigas*, as illustrated by Boudier in *pl. 221*, is nearer in general shape and appearance to *Underwoodia* than any other discomycete with which I am familiar.

The spores of *Underwoodia* have a tuberculate wall and in this respect are more highly developed than is usual among the Helvellaceae, the other species of which have smooth, hyaline spores.

The question whether *Underwoodia* is a gymnocarp or an angiocarp cannot be settled without the young stages. In the ascoma of the species of *Helvella* the young hymenium is overgrown by surrounding tissue as in very many cup fungi and the same is true of the elements of the compound hymenium of *Morchella*. The hymenium of *Underwoodia* does not appear to have been so overgrown at any time, but whether it was covered at any stage with a weft of fibers, as is the case with many of the Geoglossaceae is not known. Nor is it known whether the hymenium originated on or below the surface of the primitive ascocarp. Questions as to the protection of the young hymenium in the discomycetes are not yet settled.

The high development of the different characters in *Underwoodia* gives it a most important position. It is one of the largest and certainly the most highly developed of all the discomycetes.

2. PUSTULARIA GIGANTEA Rehm

In July, 1899, I found some large cup fungi on the ground among dead leaves on Mackinac Island, Michigan. Later I sent them to Dr. H. Rehm, who described them as a new species under the name *Pustularia gigantea.* The description was published in Annales Mycologici (3: 517. 1915). I have since found the plant several times in coniferous woods on Neebish Island. In September, 1907, it was abundant in a piece of cedar and balsam woods, and I secured the photograph of the opened plant, PLATE 3, A, and preserved a number of unopened plants in alcohol, from which the photograph of the section, B, was made. The specimens sent to Dr. Rehm were dried and somewhat torn, so that they did not show the peculiar folding in of the edges of the apothecium and the way in which the mature plants burst open, which are two of the most striking characters of the species.

The unopened apothecia are irregularly ellipsoid with a deep groove across the top. The apothecia often occur in clusters in which the orientation of the members is irregular. The surface of the apothecia is nearly smooth, whitish in color, and much soiled by the earth or mould in which the plants are buried.

The apothecia have a definite interior structure which is shown in PLATE 3, B. This figure represents a vertical section cut from the center of an unopened apothecium. There is no stem and the flat under surface lies directly on the soil, with which it is connected by strands of white mycelium. Quite frequently the connection with the substratum is lost, as is the case with the Hypogaei.

The cup is roughly and partially divided into two chambers by the infolding of the edges of the apothecium. The chambers can be recognized in all the plants examined, though they are at times more or less distorted. The infolded edges extend to the bottom of the cup. In a section like this made through the center of the apothecium the infolded walls are divided at the base. In sections near the ends of the apothecium they are united. The walls have been infolded till the usual apical opening or mouth of the cup in other Pezizaceae lies on the bottom of the cup. Neither the lips nor the walls are grown together, though they are pressed closely against each other. In the section before us the walls have sprung apart. The lips are like those of other cup fungi with the hypothecium extending a little beyond and embracing the hymenium. The bottom of the cup is thickened and raised into a sort of cushion covered like the rest of the interior by the hymenium. Such a cushion is evident on the bottom of all the cups examined. Around the cushion is a narrow zone which is destitute of hymenium. It has apparently resulted from a rupture of the hymenium during growth. In the larger chamber is an irregular outgrowth covered by the hymenium such as may occur in almost any position on the hymenium of these plants.

An end section of another specimen shows an apothecium in which the basal cushion is very large. The chambers are irregular and there are several minor cavities. The general structure is however the same as in the plant figured on PLATE 3. The basal cushion in this second specimen is hollow and it was deeply indented on the under side in a zone around the central portion, which was attached to the soil as a sort of stem.

When the apothecia are mature and the growth tension becomes great; instead of opening at the mouth as in most species of *Peziza*, the walls of the chambers burst irregularly as shown in PLATE 3, *A*. The appearance of such opened plants is striking. The walls of the internal cavities are pure bluish white and the thick reflexed segments give the plant the appearance of a large white flower. When the weather is unfavorable to rapid growth the apothecia do not open as far as my observation goes but dry up or decay without exposing the hymenium. Sometimes irregular openings are found in the walls of old plants.

In regular plants the walls of the apothecia are of nearly equal thickness throughout. They are covered on the inside by the hymenium. The hypothecium is made up of irregular septate hyphae of different diameters with many large irregular cells and cavities, especially in the center. The hyphae are much more dense directly beneath the hymenium where they form an indefinite subhymenial layer. On the outside there is a compact cortical layer of hyphae which run somewhat parallel to the surface. In the center of the walls the tissue is looser and the cells larger. Often the tissue breaks down and leaves hollow spaces in the walls, as can be seen in the sections.

The asci are long and narrow and closely packed together with relatively few paraphyses. They measure 10–12 × 200–300μ. They are linear for most of their length, rounded-truncate at the apex and narrowed near the base. The base is enlarged and irregular. The paraphyses are about 2μ in diameter, slightly enlarged at the upper end, rarely branched and with few septa. The spores are oblong with rounded ends, smooth, usually with two oil drops when mature, 5–8 × 10–14μ.

Rehm placed the plant in the genus *Pustularia* and compared it with *Pustularia vesiculosa*, noting that it differed from that species in the larger size and smaller spores. According to Rehm's key *Pustularia* contains species of fleshy Pezizaceae, which have smooth and entire cups, asci turning blue with iodine, elliptical spores and sessile apothecia. It includes species like *Peziza vesiculosa*, *P. Stevensoniana*, and *P. coronaria*. Boudier disregards the surface of the apothecia and places species like *Peziza coronaria* and *Sepultaria sepulta* in a genus *Sarcosphaera*, on the ground that they are semi-subterranean with the apothecia closed at first and bursting irregularly at maturity. *Pustularia gigantea* is semi-subterranean in its habit and bursts irregularly at maturity and might be placed in this genus, but it has a definite mouth the walls of which have simply become infolded during growth.

The natural arrangement of the species of Pezizaceae has not yet been discovered. All that was said about the groups of the Helvellaceae above applies equally to the groups of the large cup fungi. As Dodge has emphasized, a knowledge of the early stages is a necessary prerequisite of a natural classification.

It is not certain to which group *Pustularia gigantea* belongs. It is not close to *Pustularia vesiculosa*, as Rehm suggests, for in addition to the difference in the size of the spores the subterranean habit and character of the mouth are very different from that species. Our collections of *Pustularia vesiculosa* have mouths of the ordinary form and grow in the mulching about trees and on manure heaps. They agree with Lloyd's photograph in Hard's Mushroom, *f. 432* (1908). *Pustularia gigantea* appears to be closer to *Peziza coronaria*, for that species is subterranean. Boudier's illustration, *pl. 302*, resembles our expanded plant. Cooke's illustration in Mycographia, *f. 238*, agrees in size and method of opening, and the same is true of Kalchbrenner's illustration of *Peziza coro-*

naria var. *macrocalyx* (Icon. Select. *pl. 40, f. 2*). The spores also are nearer in size to those of *Peziza coronaria* than to those of *P. vesiculosa*. Saccardo's Sylloge (**8**: 81. 1889) gives the spores of *P. coronaria* 8–9 × 15–18μ. The spores of *Pustularia gigantea* are often 8 × 14μ, though Rehm gives 5–6 × 10–12μ. The descriptions of *Peziza coronaria* do not, however, give the internal structure of the unopened apothecia. It is supposed that the young plants have no evident mouths. The species of *Sepultaria* also are said to be closed at first and to open irregularly. Yet what is known of the structure of the cup fungi suggests that in all these forms the hymenium has been overgrown by surrounding tissue, and the location of the mouth should be determinable even in young unopened apothecia. *Pustularia gigantea* is very enlightening on this point and the unopened apothecia of species like *Peziza coronaria* should be carefully examined to see if there is not evidence of the location of the mouth. It is uncertain whether *Pustularia gigantea* should be associated with *Peziza coronaria* or placed in a group by itself. Further observation may bring to light other more closely related forms.

The most striking feature of *Pustularia gigantea* is the degree in which the walls of the apothecia are infolded. It is very common among the discomycetes for the hymenium to be covered by the surrounding tissue during the formative period. In small species of *Peziza* the ascoma usually remains circular, but in large plants the walls of the cup are flattened and folded together from the sides. This is also true of species of *Helvella* which have a cup-shaped or saddle-shaped ascoma. The saddle-shaped ascoma in the *Helvella elastica* group is folded and flattened in the same way when young and later opens at the ends instead of in the middle giving it the characteristic saddle-shaped form.

Bucholtz has shown that in many of the Tuberaceae the hymenium is formed on the outside of the ascocarp and then overgrown by surrounding tissue until it is entirely enclosed in cavities of the fruit body. *Pustularia gigantea* has many characters in common with the Tuberaceae. The closed chambers, subterranean habit and loose connection with the soil are all suggestive of the Tuberaceae. We need only mention the Hysteriaceae to show how common the inrolling of the disk and consequent covering of the hymenium is among the discomycetes and their allies. The striking feature of *Pustularia gigantea* is the extent to which the walls are infolded The mouth is completely inverted and lies on the bottom of the cup. In this the plant appears to be unique.

Explanation of plates 1-3

PLATE I. UNDERWOODIA COLUMNARIS Peck

A, upper half of the left branch of a large plant; *B*, lower half of the plant.

PLATE 2. UNDERWOODIA COLUMNARIS Peck

A, longitudinal and cross sections; *B*, ascus and paraphyses; *C*, one of a pair of plants grown together at the base.

PLATE 3. PUSTULARIA GIGANTEA Rehm

A, expanded plant. *B*, vertical section through an unopened apothecium; *C*, asci and paraphyses.

INDEX TO AMERICAN BOTANICAL LITERATURE

1916-1917

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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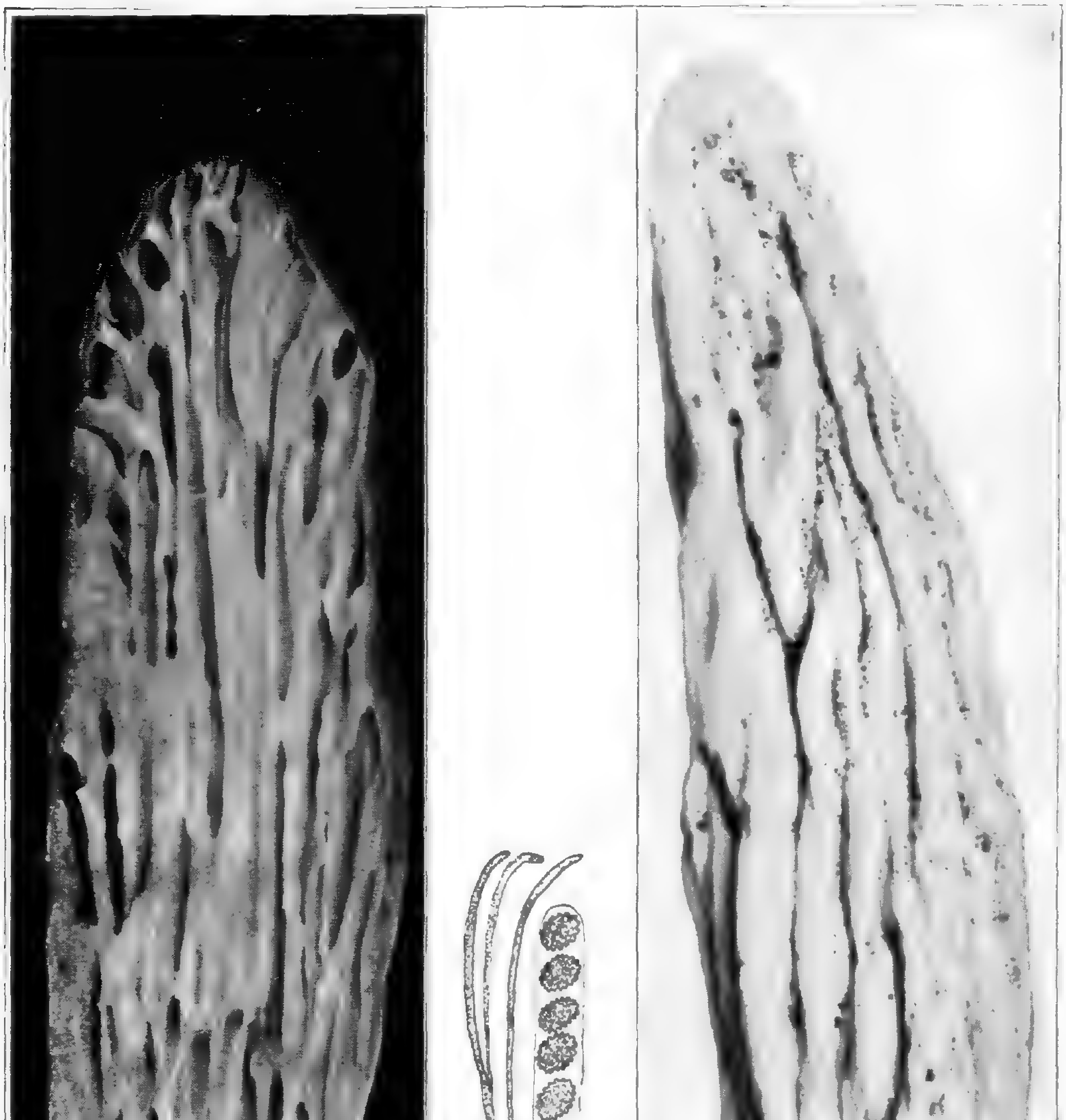

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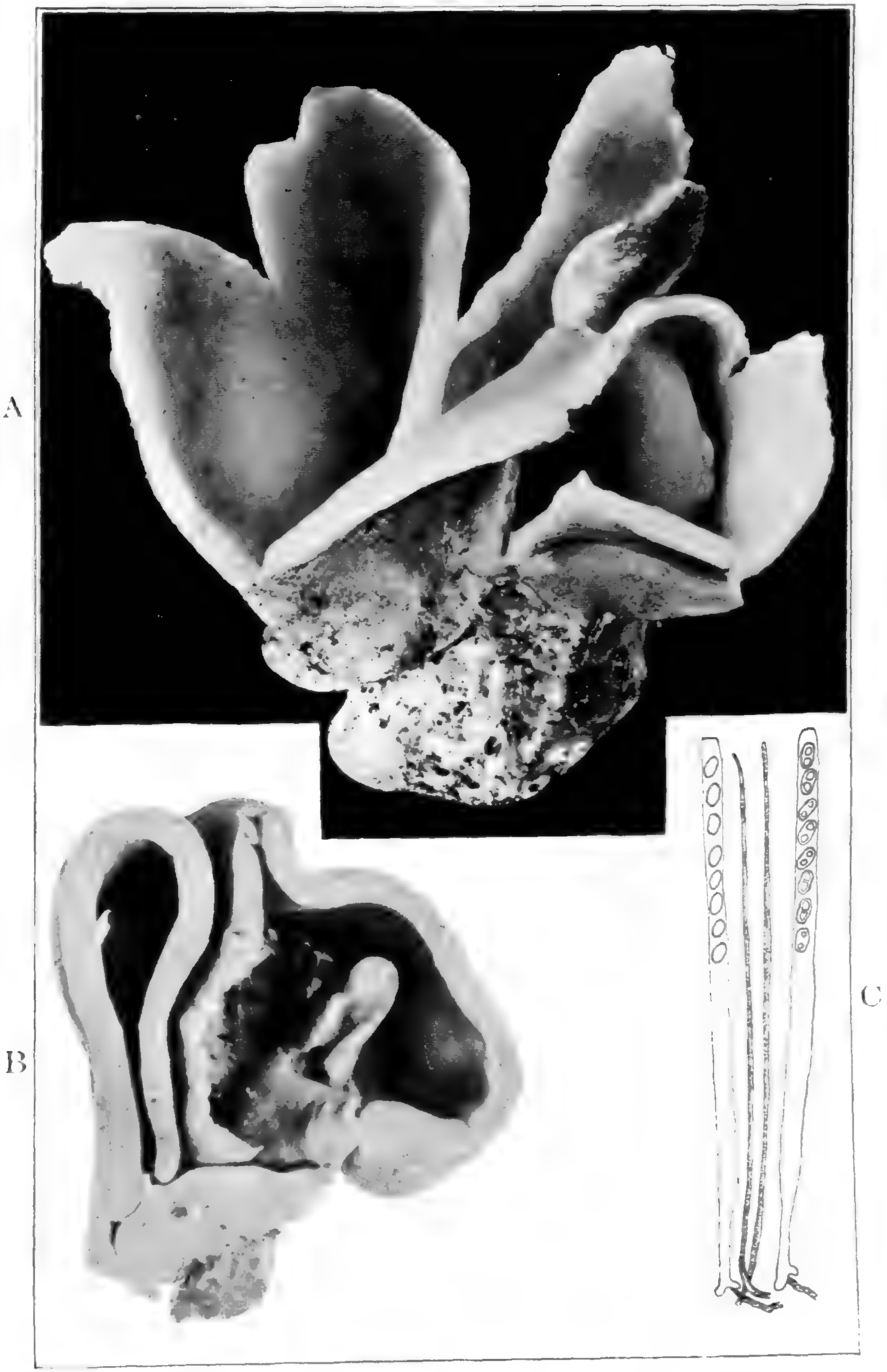

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Studies of some new cases of apogamy in ferns

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(WITH PLATES 4 AND 5)

INTRODUCTION

During the past six years, the writer has made an attempt to determine to what extent under normal cultural conditions apogamy occurs in the homosporous leptosporangiate ferns and especially in the genera *Pellaea*, *Pteris*, and *Aspidium*. Since the nuclear history in only a few apogamous ferns has been investigated, it was believed that further studies in the cytology of such ferns would be desirable. Hence an investigation of this nature was undertaken in the species in which apogamy was discovered, and this part of the work has been considered more interesting and important than the discovery of new cases of apogamy. In some of the ferns studied the nuclear history is wholly or partly known, but the discussion of this subject is reserved for another paper. At this time new cases of apogamy will be reported and briefly considered.

METHODS AND MATERIALS

On account of the great difficulty experienced in securing spores for cultural work, the investigation, so far as the discovery of new cases of apogamy is concerned, cannot be regarded as wholly successful. Some of the spores were collected in the field. A large number of plants were grown in the university greenhouse, and

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spores were collected from these. Spores from a still larger number of species were obtained through the kindness of the following persons: Dr. A. B. Stout, New York Botanical Garden; Dr. R. C. Benedict, Brooklyn Botanic Garden; Dr. G. T. Moore, Missouri Botanical Garden; Dr. E. B. Copeland, Los Banos, Philippine Islands; Mr. F. C. Greene, Rollo, Missouri; and Rev. George Moxley, Los Angeles, California. To these gentlemen the writer wishes to express his sincerest thanks, for in no small measure they contributed to the investigation.

The spores were generally sown on the surface of a nutrient solution or on sphagnum. The latter was placed in a Stender dish and saturated with a nutrient solution. Before sowing the spores, the medium was thoroughly sterilized. Other media, such as nutrient agar, peat clay and loam, were also used, but none of these proved as satisfactory for the cultural work as the sphagnum. The Stender dishes were placed under bell-jars in a Wardian case in the university greenhouse. The jars were tilted on edge, so that the prothallia were provided with a sufficient supply of oxygen and carbon dioxid. The temperature of the Wardian case varied from 65° F. in winter to about 110° F. in summer. The prothallia were protected from too intense illumination by shading. The light was very favorable for the growth of fern prothallia since, when they were not crowded in the cultures, they became heart-shaped. The moisture supply was always sufficient for fertilization to occur in the non-apogamous species grown at the same time under precisely the same cultural conditions.

In a large number of species in which fertilization is known to occur, including *Pteris aquilina* L., *P. serrulata* L., *Osmunda regalis* L., *O. Claytoniana* L., *O. cinnamomea* L., and *Adiantum pedatum* L., sex organs were produced under the conditions just described, and embryos were formed only as a result of the union of the gametes.

The prothallia of *Nephrodium molle* Desv. and *Asplenium nidus* L., in which Yamanouchi (1908) and Nagai (1914) respectively induced apogamy, were grown under the same conditions, but while embryos were produced in large numbers, none were formed apogamously.

The spores of some of the apogamous species were sown on soil in the university greenhouse, but the prothallia never showed any peculiarities in their development, and embryos were never produced by fertilization. Hence it appears that cultural conditions were not a factor in inducing apogamy in any case.

In the majority of cases, the prothallia were grown until embryos were formed, either as a result of fertilization or apogamously. Parthenogenesis was not excluded in the non-apogamous species. To determine this point a cytological investigation would have been necessary.

The conclusions are in no case based on a single culture but on a large number of cultures. Cultures in which only a few prothallia were obtained were always discarded. Great care was exercised in handling the spores before sowing in order to avoid, so far as possible, mixing those of different species.

Two sets of cultures were made of each of the ferns tested for apogamy. In one set only a small number of spores were sown to avoid crowding the prothallia. The prothallia under these conditions grew to a good size and became heart-shaped. It was believed that these cultures were favorable for the development of archegonia. The other cultures were made by sowing a large number of spores. The majority of the prothallia in these cultures were irregular in form and usually produced numerous antheridia. If embryos were produced, they appeared in both types of cultures. From the two sets of cultures it was possible to determine whether sex organs developed.

While the prothallia of the different species were growing, they were carefully examined from time to time with a microscope. Since in a number of species investigated tracheids appeared among the prothallial cells, it was not difficult to determine the apogamous forms. In all the apogamous species a region composed of small cells made its appearance posterior to the apical notch. In every instance when such an area of small cells appeared on the surface of the prothallium, the embryo proved to be of apogamous origin. When archegonia were produced in any of the apogamous species, they were absent on many of the prothallia. These, however, always produced embryos apogamously. In some species longitudinal sections of the prothallia were made in order to determine with more certainty the origin of the embryo.

APOGAMY IN PELLAEA AND NOTHOLAENA

The first case of apogamy in the genus *Pellaea* was discovered by Goebel (1905) in *P. nivea* (Poir.) Prantl. Later Woronin (1907, 1908) found apogamy in *P. flavens* (Sw.) C. Chr., and *P. tenera* (Gill.) Prantl., and also in *Notholaena Eckloniana* Kunze and *N. sinuata* (Lag.) Kaulf., belonging to a genus closely related to *Pellaea*. Berggren (1888), however, had already described apogamy in *N. distans* R. Br. The writer has described apogamy in *Pellaea atropurpurea* (L.) Link (Steil, 1910) and *P. adiantoides* J. Sm. (Steil, 1915*b*). New cases have since been found in *P. atropurpurea* var. *cristata* Trelease and *P. viridis* (Forksk.) Prantl.

APOGAMY IN PTERIS

Farlow (1874) discovered apogamy in *P. cretica* L. var. *albolineata* Hort. This was the first reported case in plants. Up to the present time, no other case of apogamy has been reported in any other species of *Pteris*, although Stephens and Sykes (1910) assumed that apogamy occurred in *Pteris Droogmantiana* L. Linden, on account of the presence of binucleate cells in the prothallia.

Wigand (1849) appeared to be convinced that the fern embryo did not owe its origin to fertilization. He undoubtedly described apogamous embryos, and from his descriptions and figures it is probable that he studied the development of such embryos in some species of *Pteris*. Although Wigand gives a good description of an apogamous embryo, the true nature of apogamy was first recognized by Farlow.

Tracheids were observed in the prothallium of *P. sulcata* Meyen by Leszczyc Suminski (1848). Later Mercklin (1850) confirmed the observation. Neither, however, knew the significance of the presence of such sporophytic tissue elements in the cells of the gametophyte. DeBary (1878) grew the prothallia of *P. quadriaurita* Retz. var. *argyraea* Moore but failed to find the fern apogamous.

Several years ago, without a knowledge of the observations of these investigators, the writer discovered apogamy in *P. sulcata*. Spores were obtained from the New York Botanical Garden, and from Dr. E. B. Copeland, Los Banos, Philippine Islands. A plant obtained from Mr. Anderson, fern specialist, Short Hills, New Jersey, was grown in the university greenhouse, and spores were also collected from this plant. Archegonia were never found on any of the prothallia. However, apogamous embryos in large numbers were produced. Since numerous cultures of *P. sulcata* were made and from spores obtained from different plants, there can be no doubt that apogamy is of constant occurrence in the fern.

P. argyraea Moore has also been found by the writer to be apogamous. In many respects the prothallia and apogamous embryos are similar to those of *P. sulcata*.* In *P. Parkeri* Hort. The writer has also discovered apogamy. The prothallia become large as compared with those of the former but develop in a similar manner.

During the course of the investigation a large number of *P. cretica* varieties have been tested for apogamy, and so far none have been found which form embryos as a result of fertilization. The following is a list of these apogamous horticultural varieties: *albo-lineata Alexander*, *maxima*, *magnifica*, *Mayii*, *major*, *Wimsettii*, *Wimsettii compacta*, *Wimsettii multiceps*, *Wimsettii grandis*, and *Ouvrardi*. For the identification of some of the above varieties the writer is indebted to Mr. James C. Clark, of Philadelphia. *P. cretica* var. *albo-lineata Alexander* Hort. resembles the *P. cretica albo-lineata* in which Farlow discovered apogamy only in its second set of leaves, which are linear but with a broader band of white along the main veins of the pinnae. The first leaves are nearly all crested, while the linear leaves show sometimes a slight tendency to become crested. From the investigations which have already been made, it may be predicted that all *Pteris cretica* forms are apogamous. Apogamy has not so far been found in any of the varieties of *P. serrulata* L. f.

APOGAMY IN ASPIDIUM

Apogamy was found by De Bary (1878) in *Aspidium falcatum* (L. f.) Sw. and in a crested cultivated variety of *A. Filix-mas* (L.)

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* According to Christensen (Ind. Fil. 593, 608. 1906) *P. sulcata*, *P. quadriaurita* and *P. argyraea* are all synonyms of *P. biaurita* L. According to Underwood and Benedict (Bailey's Stand. Cycl. Hort. 2852. 1916) *P. quadriaurita* is distinct from *P. biaurita*, *P. argyraea* being given as a var. *argyraea* Hort. under *P. quadriaurita*.

Sw. ("*A. Filix-mas cristatum*"). In the former Miss Allen (1911) described nuclear and cell fusions in the sporangia, previous to the formation of the spores. Kny (1895) discovered apogamy in an uncrested form of *A. Filix-mas* ("*A. Filix-mas genuinum*"). Lang (1898) found apogamy in the aberrant varieties of *A. Filix-mas*, known as "*Nephrodium pseudo-mas* var. *polydactylum* Wills" and *N. pseudo-mas* var. *polydactylum* Dadds." In these same varieties (discussed under the name "*Lastrea pseudo-mas* var. *polydactyla*"), Farmer, Moore and Digby (1903) and Farmer and Digby (1907) described remarkable nuclear fusions in the prothallium before the formation of the apogamous embryos. In a preliminary note on apospory Miss Digby (1905) had already reported apogamy in "*Lastrea pseudo-mas* var. *cristata apospora* Druery."

Heilbron (1901) found apogamy in *Aspidium aculeatum* (L.) Sw. var. *cruciato-polydactylum* Jones and *A. angulare* Willd. forma *grandidens* Moore. Five years later (Steil, 1915 *a* and *b*) apogamy was reported in *A. hirtipes* Bl. (*Nephrodium hirtipes* Hook.), *A. Tsus-Simense* Hook. and *A. chrysolobum* Kaulf. (*Lastrea chrysoloba* Presl). Apogamy has also been discovered as a result of the investigations herein described in *A. varium* (L.) Sw., *A. auriculatum* (L.) Sw., *A. caryotideum* Wallich, *Cyrtomium Fortunei* J. Sm. and *C. Rochfordianum* Hort.*

THE DEVELOPMENT OF THE PROTHALLIA AND SEX ORGANS

In all the species so far studied, the prothallia become typically heart-shaped. Between the prothallia of apogamous and nonapogamous species no difference was noted excepting that in the latter tracheids sometimes appear. The prothallia of all the species of *Aspidium* in which apogamy has been discovered bear glandular hairs on both surfaces and on the margins (PLATE 4, FIGS. 1, 2, and 5; PLATE 5, FIGS. 20 and 21), while in both *Pellaea* (PLATE 5, FIGS. 13, 14, and 15) and *Pteris* (PLATE 4, FIGS. 3, 4, and 6) such hairs are always absent. The prothallia in *Aspidium* grow to a much larger size than in *Pellaea* and in most species

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* Benedict (Bailey's Stand. Cycl. Hort. 2852. 1916) gives *C. Rochfordianum* as a synonym of *C. falcatum* J. Sm. (= *A. falcatum* Sw.); Christensen (Ind. Fil. 460. 1916) includes both *A. caryotideum* and *Cyrtomium Fortunei* among the synonyms of the same species.

of *Pteris.* Those of *Aspidium chrysolobum, A. varium,* and *A. auriculatum* become especially large.

Antheridia are produced on the prothallia of all of the apogamous species. The antherozoids responded to the chemotactic influence of the archegonia of non-apogamous species in all cases in which tests were made. The mature antherozoid appears perfectly normal and is probably capable of functioning. In a former note (Steil, 1910) it was reported that antheridia had not been observed on the prothallia of *Pellaea atropurpurea,* but in many of my cultures made since this time they have been formed in large numbers.

Archegonia have been found on the prothallia of *Aspidium chrysolobum,* but in a large number of the prothallia they are never produced (PLATE 4, FIG. 5). The embryo always appears at the anterior portion of the cushion and can be readily observed to begin its development as a vegetative outgrowth from the prothallial cells. Over 50 per cent. of the prothallia of *Pellaea viridis* bear archegonia. Whether embryos are produced as a result of fertilization in either case has not been determined. In a few instances two embryos were observed to develop from a single prothallium of *P. viridis.* One of these was apogamously produced, but the other appeared to owe its origin to an egg. Archegonia were never found in the prothallia of *P. adiantoides,* and for this reason especial care was exercised in making the cultures of *P. viridis.* Spores were obtained from the New York and the Missouri Botanical Gardens and from two plants grown in the university greenhouse, but the embryos in all of the cultures made from the spores thus obtained were produced apogamously. In some of the *Pteris cretica* varieties archegonia were observed very rarely, but an embryo was never found to be developed from an egg.

THE DEVELOPMENT OF THE APOGAMOUS EMBRYO

The apogamous embryo usually appears as a compact region of small cells on the ventral side of the prothallium and posterior to the apical notch (PLATE 4, FIGS. 2–5, and PLATE 5, FIGS. 13 and 20). When the embryo begins its development, the prothallium has not yet attained its maximum growth. In some species, such as *Aspidium chrysolobum* (PLATE 4, FIGS. 1 and 2), *A. hir-*

tipes and *A. auriculatum*, the prothallia increase considerably in size as the young embryo is developing. In most instances the cushion has not been formed when the embryo makes its appearance. The embryo proceeds in development with the growth of the cushion. On account of the early appearance of the embryo. it was easy to determine when apogamy occurred in any species,

While the embryo usually occurs back of the apical region its position varies in the different species and even in the same species. In some cases the embryo is developed directly in the apical notch (PLATE 5, FIGS. 14 and 15). A cylindrical or conical process produced as an outgrowth of the apical region may bear on some portion of it the apogamous embryo. Sometimes the embryo may be produced at a considerable distance posterior to the notch (PLATE 5, FIGS. 13 and 20). In still other instances the embryo is formed on the lobes of the prothallium (PLATE 5, FIG. 19). From the foregoing, it is seen that the apogamous embryo can be produced on portions of the prothallia where archegonia have never been observed to be formed in any non-apogamous species.

Tracheids are visible among the prothallial cells of some of the apogamous species long before the prothallium has reached its maximum growth (PLATE 4, FIG. 3, and PLATE 5, FIG. 20).

It is usually in the portion of the prothallium where the tracheids appear that the apogamous embryo begins its development. The tracheids are readily observed in many cases, since the prothallium frequently becomes pale in the region of the notch and where these elements are produced. The cells in this portion of the prothallium contain fewer chloroplasts than the neighboring prothallial cells (PLATE 5, FIG. 20). In the species of *Pteris* the tracheids are most frequently observed (PLATE 4, FIGS. 3, 4, and 6). In many instances the light area extends forward as a cylindrical or conical process, already mentioned (PLATE 4, FIG. 6).

The embryo is usually surrounded by hairs, each composed of a single row of cells (PLATE 5, FIG. 13). In some species, as in *Aspidium chrysolobum* and *A. Tsus-Simense*, scales are also produced.

In only a few species has the development of the apogamous embryo been studied in sections. It seems that the apical cell of the leaf always appears first, then that of the root, and finally that of the stem. A foot has never been observed to develop in any of the species in which the embryos were studied from prepared slides. Usually the leaf is much in advance of the root (PLATE 4, FIG. 9). A leaf, however, may be just making its appearance after the root has grown considerably in length (PLATE 4, FIG. 8). Both root and leaf, in the large majority of cases, are produced on the ventral side of the prothallium (PLATE 4, FIG. 7). PLATE 4, FIG. 12, represents a prothallium with an apogamous embryo the leaves and roots of which are ventral. Either root or leaf or both may appear on the dorsal surface (PLATE 4, FIGS. 10 and 11, and PLATE 5, FIG. 16). In the cultures of *Aspidium chrysolobum* and *A. hirtipes* embryos of this nature have been observed. Such anomalies may be produced by light conditions as Leitgeb (1885) has shown.

As a result of studies thus far made, it has not been determined whether the apogamous embryo owes its origin to a single superficial cell or to inner and outer cells of the prothallium.

Frequently, in some of the cultures, more than one embryo was observed to develop from a single prothallium. This was especially the case when the prothallia showed a tendency to become lobed (PLATE 4, FIGS. 3 and 4). PLATE 4, FIG. 3, represents a prothallium of *Pteris cretica albo-lineata Alexander* with a young embryo posterior to the apical region, and tracheids in each of the two secondary regions of growth. Another prothallium of the same variety is shown in PLATE 4, FIG. 4. In this instance tracheids are present in the apical region, and two embryos have been produced on other portions of the prothallium. One of these is produced in the apical region of one of the main lobes, and the other is a vegetative growth on the inner margin of a lobe itself. Each of these embryos has produced a small leaf, *l*, and a root, *r*. The embryos in such cases, as is readily seen, are wholly independent of one another. In some instances it was observed that some of the tracheids extended from the apical notch of the prothallium to one or both of the inner margins of the lobes where the embryo was produced (PLATE 5, FIG. 19). It may be stated in this connection that embryos are not always produced when tracheids are formed, but in most cases these tissue-elements indicate the beginning of an apogamous embryo.

In one of the cultures of *Pteris sulcata*, conical and nearly spherical projections were observed in the lobes of the prothallia. Some of these prothallia were transferred to another culture, and the growth of the projections was followed in both cultures. The projections produced either secondary prothallia or apogamous embryos. The former were often cylindrical at the point of origin, but in other respects they resembled the ordinary prothallia of *Pteris sulcata*. As many as six embryos were observed on the lobes of a single prothallium. In most instances these were normal, producing both roots and leaves.

By cultural conditions secondary prothallia have been produced from the primary prothallia of many of the apogamous species. These prothallia also form embryos apogamously. DeBary (1878) reported that such prothallia of *Pteris cretica albo-lineata* seldom produced embryos. However, in my cultures of the same species, the secondary prothallia usually produced embryos of apogamous origin. Secondary prothallia of *Pellaea atropurpurea*, *Aspidium hirtipes*, *Pteris sulcata*, *Pteris argyraea*, and *Pteris cretica albo-lineata Alexander* frequently produce apogamous embryos.

THE INFLUENCE OF WEAK ILLUMINATION ON THE DEVELOPMENT OF THE PROTHALLIA AND OF THE APOGAMOUS EMBRYOS

When the prothallia of the apogamous species were placed under the influence of weak light, the same results were obtained as with the non-apogamous ferns. Filaments were formed from the margin and both surfaces of the prothallia (PLATE 5, FIG. 21), and these under the normal conditions of illumination in the wardian case became independent prothallia, which in nearly all instances formed also apogamous embryos. When the prothallia were maintained in weak light, they remained simple or branched filaments, producing neither sex-organs nor embryos (PLATE 5, FIG. 18). Under somewhat more favorable conditions of illumination, ribbon-like plates were produced, which frequently bore numerous antheridia and occasionally apogamous embryos. When the illumination was slightly less than that in the greenhouse, the prothallia became lobed (PLATE 5, FIGS. 14 and 15). In the new apical regions which were formed embryos also made their appearance (PLATE 5, FIG. 17).

The conical or cylindrical processes already described grew considerably in length when the cultures were placed in weak light. In such instances an apical cell could be readily distinguished. The embryo in these cultures was frequently formed on the process, and usually it was produced as a direct outgrowth of the apical notch. The "light" area, or pale portion of the prothallium where the embryo begins its development, remains more conspicuous under these conditions. The colorless plastids, present in large numbers in the cells of the pale region, become chloroplasts under favorable conditions of light, and hence the nearly colorless region is not so clearly differentiated in the latter case.

ATTEMPT TO INDUCE APOGAMY IN OSMUNDA REGALIS

In the latter part of July, 1912, a large number of prothallia of *Osmunda regalis* were found by the writer in a swamp in the vicinity of Madison. Most of the prothallia at this time were small but had produced numerous antheridia. Some of the prothallia were removed with a depth of about three inches of soil and placed under bell jars in the university greenhouse. Several cultures were kept in a Wardian case where the illumination was very favorable for the normal development of the prothallia. Other prothallia were placed under bell jars and in different parts of the greenhouse where strong light was obtained for the greater part of the year. The latter were watered only from below and great care was exercised to prevent condensation of moisture on the prothallia. In this manner fertilization was prevented for nearly a year and a half. During this period, however, the prothallia grew to a large size, and numerous antheridia and archegonia were produced. Many of the prothallia reached a length of three centimeters. On such prothallia most of the archegonia were formed in acropetal succession, but frequently a number were produced among the older archegonia. In one instance the archegonia on one side of the "midrib" of a prothallium, measuring two centimeters in length, were counted and approximately five hundred were found to be present. Therefore this prothallium had produced about one thousand archegonia.

When the prothallia were freely watered, embryos were produced in large numbers as a result of fertilization. Hence it is certain that the cultural conditions which were maintained rendered fertilization impossible. The prothallia grown under favorable conditions were smaller, but produced numerous sex organs and embryos only as a result of fertilization.

Since the prothallia for the cultural work were found growing under plants of *Osmunda regalis*, and since no other osmundas were growing in the immediate vicinity, it could hardly be assumed that the prothallia could be referred to any other species. Nevertheless, spores of *O. regalis* were collected and sown in the Wardian case, and in every respect the prothallia grown corresponded to those brought from the field.

The experimental work with *Osmunda regalis* was of especial interest, since Leitgeb (1885) reported in this species the occasional occurrence of apogamy. No one, however, has confirmed the observation. Although Lang (1898), Yamanouchi (1908), Pace (1913), and Nagai (1914) believed that apogamy might be brought about by cultural conditions, Miss Black (1909) and Mottier (1915) were unable to produce a single apogamous embryo by cultural conditions.

SUMMARY

1. The prothallia of a number of species of ferns in which apogamy was discovered were grown under cultural conditions favorable for the development of sex-organs and embryos in non-apogamous species.

2. The prothallia of all the apogamous ferns become heart-shaped before the formation of the embryo. Antheridia are produced on the prothallia of all apogamous forms, but archegonia are formed on the prothallia of only a few forms.

3. The embryo usually appears as a compact region of cells posterior to the apical notch and on the ventral side of the prothallium. In a number of species tracheids are visible among the prothallial cells in the pale portion of the gametophyte.

4. First to make its appearance is the apical cell of the leaf, then that of the root, and later that of the stem. A foot has not, so far, been observed to develop in connection with the apogamous embryos.

5. Either root or leaf or both of these organs may develop on the dorsal side of the prothallium. As a rule, however, they are produced on the ventral side.

6. While the embryo is produced as a rule posterior to the apical notch, it may be formed on a cylindrical or conical "process" and in some instances on the lobes of the prothallium.

7. Several apogamous embryos may be formed on a single prothallium.

8. As in non-apogamous species, secondary prothallia are readily produced, and these form embryos like those of the ordinary prothallia.

9. The "light" area present on the prothallium of some of the apogamous species is rendered more conspicuous in cultures maintained in weak light. The conical or cylindrical "process" increases considerably in length when the prothallia are grown under these conditions. As a result of weak illumination, the embryo is frequently produced as a direct outgrowth of the apical region of the prothallium.

10. By growing the prothallia of *Osmunda regalis* in strong light and preventing fertilization for a year and a half, no embryos were produced apogamously.

11. An investigation extending over a period of six years has resulted in the discovery of apogamy in a large number of ferns. The conclusion that apogamy is of frequent occurrence in the genera *Pellaea*, *Pteris*, and *Aspidium*, is justified on the basis of the many cases so far found in these genera.

I wish to thank Professor C. E. Allen for suggestions and criticisms received during the progress of the foregoing investigation.

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Description of plates 4 and 5

The photomicrographs of the prothallia on PLATE 4, and FIGS. 13, 14, 15, and 18 on PLATE 5, represent a magnification of about twenty diameters. FIGS. 19, 20, and 21 on PLATE 5 show a much higher magnification. The apogamously produced sporophytes were magnified about two and one half times. All the figures were reduced one seventh in reproduction.

PLATE 4

FIG. 1. A ventral view of a prothallium of *Aspidium chrysolobum* just before the beginning of the apogamous embryo.

FIG. 2. A similar view of a prothallium of the same species. The apogamous embryo is represented as a black region posterior to a pale region in the apical portion of the prothallium.

FIG. 3. A ventral view of a prothallium of *Pteris cretica albo-lineata Alexander.* In the apical region a young embryo is developing. In the apical regions established in the lobes tracheids are present.

FIG. 4. A ventral view of a prothallium of *Pteris cretica albo-lineata Alexander.* An embryo with root and leaf has been produced in the new apical region of one of the lobes. On the inner margin of the other lobe a young embryo has also appeared. In the main apical region tracheids are visible.

FIG. 5. A dorsal view of a prothallium of *Aspidium chrysolobum.* The prothallium produced no archegonia. The apogamous embryo appears as a dark region posterior to the apical notch.

FIG. 6. A prothallium of *Pteris cretica albo-lineata.* A tongue-like portion has developed as an outgrowth of the apical region. In the larger secondary prothallium the "pale" region has already appeared.

FIG. 7. A ventral view of a prothallium of *Aspidium hirtipes* with an embryo whose root and leaf are produced on the ventral surface.

FIG. 8. An embryo of *A. hirtipes* with a well-developed root.

FIG. 9. An embryo of *A. hirtipes* with only the leaf well developed.

FIG. 10. An embryo of *A. chrysolobum*, one root of which is on the dorsal surface, and the other on the ventral.

FIG. 11. An embryo of *A. chrysolobum* whose root is on the dorsal surface and leaf on the ventral surface.

FIG. 12. A young sporophyte of *A. hirtipes* with three primary leaves and a single ventral primary root.

PLATE 5

FIG. 13. A ventral view of a prothallium of *Pellaea adiantoides*. The young embryo is surrounded by hairs.

FIG. 14. A prothallium of *Pellaea adiantoides* grown in slightly weaker illumination than that maintained in the Wardian case. The prothallium has become distinctly lobed, and the embryo is developed in the apical region.

FIG. 15. A similar prothallium of the same species. The lobes are still more conspicuous and the embryo has grown to a larger size.

FIG. 16. An embryo of *Aspidium chrysolobum*, one leaf of which is on the dorsal surface and the other on the ventral surface of the prothallium. The long root is also on the ventral surface.

FIG. 17. A portion of a lobed prothallium of *A. hirtipes* bearing two embryos, each of which has a well-developed leaf and root.

FIG. 18. Filaments of a single row of cells of prothallia of *A. hirtipes* grown in weak illumination.

FIG. 19. A prothallium of *Pteris sulcata*, showing the beginning of an embryo in the apical notch. Tracheids pass upward to the young embryo, which has been produced on the inner margin of a lobe.

FIG. 20. An embryo of *A. hirtipes* beginning its development in the apical region. The "pale" region and tracheids are clearly differentiated.

FIG. 21. Secondary prothallia of *A. hirtipes* produced from the margins and surfaces of a prothallium placed in weak light.

Correlation of morphological variations in the seedling of Phaseolus vulgaris

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INTRODUCTORY REMARKS

During the past several years one of us has had under way extensive experiments on the differential death-rate of bean seedlings. Individuals differing in structure also differ in their capacity for survival under field conditions,* and in such physiological characteristics as capacity for the development of the tissues of the primordial† and of the subsequent leaves.‡

Some tens of thousands of seedlings of known morphological characteristics have been exposed to risk, as the life insurance statisticians express it, in an attempt to determine the selective value of the various morphological variations. These seedlings were, for technical reasons, necessarily planted in the field at a time when the cotyledonary node and the primordial node only could be studied. It is evident that the capacity of the plant for survival may be in some degree dependent upon characters developed later in ontogenesis, but correlated with characters of the first or second node of the seedling.

However this may be, it is certainly true that a full knowledge of the morphology and physiology of the variant bean seedling demands a thoroughgoing investigation of the correlation between the structure of the first two leaf whorls and that of later whorls. We have, therefore, been forced to consider the problem of the morphological character of the leaf whorls produced at the third

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* Harris, J. Arthur. A simple demonstration of the action of natural selection. Science II. **36**: 713–715. 1912.

† Harris, J. Arthur. Studies on the correlation of morphological and physiological characters: the development of the primordial leaves in teratological bean seedlings. Genetics **1**: 185–196. 1916.

‡ Harris, J. Arthur. Further studies on the interrelationship of morphological and physiological characters in seedlings of *Phaseolus*. Mem. Brooklyn Bot. Gard. **1**. *In press.*

node in the case of plants showing various structural abnormalities at the first two nodes.

Phaseolus is well suited for such investigations. The normal seedling has two cotyledons, inserted at the same level, and two opposite primordial leaves. A large number of structural variations, four types of which will be considered in this paper, may occur. The chief disadvantage lies in the rarity of many of the variations in the lines with which we have dealt. The securing of adequate series is excessively laborious. The present paper is based upon a careful study of the variations in the first three nodes of 16,348 plants, which were selected from about 450,000 seedlings examined for the characters of the first and second node.

When in the following paragraphs we refer to normal and abnormal plants or seedlings, it must be understood that this applies to the characteristics of the individual as determined on the basis of the first two nodes, the cotyledonary and the primordial only. In its later development the "abnormal" plant may remain "abnormal" or become "normal," and the "normal" plant may either continue to be "normal" or become "abnormal."

The nature and method of classification of the abnormalities dealt with will be discussed in the presentation of the data below.

MATERIALS AND METHODS

The materials upon which this study is based are a series of lines of White Navy beans grown at the Station for Experimental Evolution during the past several years. The seeds were harvested from field cultures in 1915 and germinated in sand in the autumn of 1916.

Seedlings which were abnormal in the characters of the first or second node, i. e., in the number or insertion of the cotyledons or of the primordial leaves, were sorted out for potting in soil and subsequent study of the third node, that normally giving rise to the first compound leaf.

For each abnormal individual, a normal control seedling from the same parent plant was taken at random to serve as a basis of comparison. Both were potted in soil and grown to a stage when the characteristics of the third node could be accurately determined.

For the onerous preliminary examination of nearly a half a million seedlings we are greatly indebted to Miss Edna K. Lockwood, Miss Margaret Gavin and especially to Miss Lillie Gavin.

PRESENTATION AND ANALYSIS OF DATA

The slightest abnormality which we have been able to discover occurring in considerable numbers of bean seedlings is the vertical separation of the two normally opposite cotyledons. So imperceptible is the line of transition between normal and abnormal that personal equation must play some part in classification. The cotyledons may be much more widely separated. The variation is a purely graduated one, with no sharp lines of demarcation between the different degrees of separation. Generally we have recognized three grades, but because of the rarity of plants with more widely separated cotyledons we have in this paper grouped our data into two classes only. The first comprises plants with cotyledons 2–3 mm. apart. The second includes all those in which they are more distant.

The number as well as the position of the cotyledons may vary. Plants with three instead of two cotyledons fall into two groups; those with the normal pair of primordial leaves and those with a whorl of three leaves. The latter are by far the more abundant.

Abnormality developed subsequently to the selection of the seedlings in the preliminary sorting may affect either the internode between the second and the third nodes, that is, between the primordial leaf whorl and the point of insertion of the first compound leaf or leaf whorl, or it may be confined to the number or structure (or number and structure) of the leaves inserted at the third node.

In the original selection of individuals abnormal in the characters of the first or second node, only those with sensibly normal axes (hypocotyl and epicotyl) were chosen for the purposes of the present study.

Two types of abnormality in the axis beyond the second (the primordial) node have been considered.

The first is a sensible broadening of the axis, identical with or similar to fasciation. This is a graduated character. The line of demarcation between normal and abnormal is not clearly marked.

and personal equation may influence in some degree the classification of the seedlings.

The second is a division of the axis into two coördinate branches each with a terminal bud.

The frequencies of the two types of axial variation are too small to justify detailed discussion. The entries in TABLE I show that in every instance in which any individuals at all are available the seedlings which are abnormal in either the cotyledonary or the primordial node show a higher percentage of abnormality in the structure of the internode beyond the second node than do the normal controls.

TABLE I

FREQUENCIES OF ABNORMALITY OF SECOND INTERNODE IN NORMAL AND ABNORMAL SEEDLINGS

Class of abnormality	Actual frequencies			Percentage frequencies		
	Normal internode	Broadened internode	Divided internode	Normal internode	Broadened internode	Divided internode
Two cotyledons slightly separated; two primordial leaves	4,017	5	8	99.6774	.1240	.1985
Normal control	4,029	0	1	99.9751	......	.0248
Difference	−12	+ 5	+ 7	−.2977	+ .1240	+.1737
Two cotyledons widely separated; two primordial leaves	878	2	1	99.6594	.2270	.1135
Normal control	881	0	0	100.0000	......	......
Difference	−3	+ 2	+ 1	− .3406	+ .2270	+.1135
Three cotyledons; two primordial leaves	813	12	0	98.5454	1.4546	......
Normal control	825	0	0	100.0000	......	......
Difference	−12	+12	0	−1.4546	+1.4546	......
Three cotyledons; three primordial leaves	2,410	14	14	98.8515	.5742	.5742
Normal control	2,436	2	0	99.9179	.0820	......
Difference	−26	+12	+14	−1.0664	+ .4922	+.5742

We now turn to a consideration of variation in the leaves inserted at the third node. The leaves of plants with abnormality of the axis should not be combined with those having normal axes. They are not sufficiently numerous for separate consideration.

Confining our attention to seedlings which have a normal axis for at least the length of the second internode of the epicotyl, we have the frequencies shown in TABLES II–V.* The character of the control plants is also given.

TABLE II

SEEDLINGS WITH TWO COTYLEDONS SLIGHTLY SEPARATED AND TWO PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	3,791	3,853	94.37	95.63	−1.26
2	225	176	5.60	4.37	+1.23
3	1	0	.02	.00	+ .02
Totals......	4,017	4,029	99.99	100.00	

TABLE III

SEEDLINGS WITH TWO COTYLEDONS WIDELY SEPARATED AND TWO PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	811	840	92.37	95.35	−2.98
2	67	41	7.63	4.65	+2.98
Totals......	878	881	100.00	100.00	

TABLE IV

SEEDLINGS WITH THREE COTYLEDONS AND TWO PRIMORDIAL LEAVES

Numbes of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	591	792	72.69	96.00	−23.31
2	221	33	27.18	4.00	+23.18
3	1	0	.12	.00	+ .12
Totals......	813	825	99.99	100.00	

TABLE V

SEEDLINGS WITH THREE COTYLEDONS AND THREE PRIMORDIAL LEAVES

Number of leaves per node	Actual frequencies		Percentage frequencies		Difference
	Abnormal	Control	Abnormal	Control	
1	1,632	2,200	67.72	90.31	−22.59
2	771	236	31.99	9.69	+22.30
3	7	0	.29	.00	+ .29
Totals......	2,410	2,436	100.00	100.00	......

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* In these tables the numbers of control plants are not exactly identical with the numbers of abnormal plants, since some of those selected as normal in the seedling stage showed abnormality of the axis in subsequent development and are omitted here, where we are discussing abnormalities of foliar characters only.

In each of the types of abnormality dealt with the abnormal series show a higher proportion of the individuals with two or three leaves at the third node than do their normal controls.

Furthermore, seedlings showing different types of abnormality at the first nodes also differ among themselves in the extent of abnormality at the third node. Thus plants which are normal except for slight separation of the cotyledons have two or three leaves at the second node instead of the single leaf normally found in 5.63 per cent. of the individuals. Plants with the cotyledons more widely separated have 7.63 per cent. of their number with two or three instead of a single leaf.

When one turns to the groups of plants which have three instead of two cotyledons, a conspicuous difference is at once apparent. Plants which have three cotyledons and a normal pair of primordial leaves produce two or three instead of a single leaf at the third node in 27.31 per cent. of the cases. Seedlings with three cotyledons and a whorl of three primordial leaves instead of the normal pair at the third node have 32.29 per cent. of the individuals with two or three leaves at the third node.

Heretofore the number of leaves inserted at the third node has furnished the only measure of variation at this region of the axis. We now propose to consider variation in the organization of the leaves themselves. It will not be possible to do this in the detail in which we hope to treat the problem ultimately. The range of variation in the division of the bean leaf is rather great, and the laws governing it are doubtless very complicated. Some progress has already been made on the problem, but for the present we shall limit our discussion to the number of leaflets, leaving the problem of their arrangement for treatment when even larger series of data are at our disposal.

The actual frequencies of number of leaflets per leaf produced at the third node are shown in TABLE VI.

The most conspicuous feature of this table is the bimodal nature of the distribution. The modes are on three and six, as is to be expected from the fact that the distribution of the whole number of leaflets depends upon plants with from one to three leaves at the third node.

Because of the wide range of variation in leaflet number it is not feasible to reduce these frequencies for the individual classes to a percentage basis for comparisons. This has, however, been done for larger groups secured by combining all the seedlings

TABLE VI

NUMBER OF LEAFLETS PRODUCED AT THE THIRD NODE BY SEEDLINGS OF VARIOUS TYPES

Number of leaflets	Two cotyledons slightly separated and two primordial leaves		Two cotyledons widely separated and two primordial leaves		Three cotyledons and two primordial leaves		Three cotyledons and three primordial leaves	
	Abnormal	Control	Abnormal	Control	Abnormal	Control	Abnormal	Control
1	5	2	1	...	1	...	....	....
2	16	6	4	...	3	2	2	5
3	3,741	3,825	801	835	572	782	1,602	2,185
4	27	21	5	4	14	5	28	8
5	10	2	1	2	6	3	9	2
6	215	173	65	40	203	33	751	236
7	1	....	1	...	12	...	12	....
8	....	....	...	...	1	...	....	....
9	1	....	...	...	1	...	3	....
10	1	....	...	...	...	...	2	....
11	....	....	...	...	...	...	1	....
Totals	4,017	4,029	878	881	813	825	2,410	2,436

showing merely separation of the cotyledons and all those showing three cotyledons instead of the normal two. The results are shown in the accompanying TABLE VII, which is self explanatory.

TABLE VII

COMPARISON OF THE NUMBER OF LEAFLETS IN DICOTYLEDONOUS AND TRICOTYLEDONOUS SEEDLINGS WITH THAT IN THEIR NORMAL CONTROLS

Number of leaflets	Seedlings with cotyledons separated		Seedlings with three cotyledons	
	Abnormal	Control	Abnormal	Control
1	.12	.04	.03	....
2	.41	.12	.16	.21
3	92.79	94.91	67.45	90.98
4	.65	.51	1.30	.40
5	.22	.08	.47	.15
6	5.72	3.52	29.60	8.25
7	.04	.81	.74	....
8	....	....	.03	....
9	.02	....	.12	....
10	.02	....	.06	....
11	....	....	.03	....

A comparison may be made without the combination of different grades of abnormality by grouping the number of leaflets around the modal classes 3, 6 and 9. The results in TABLE VIII show essentially the same relationships as those given in TABLES VI–VII. First, the higher leaflet numbers are more extensively represented in the abnormal plants of each of the four types than they are in the controls. Second, the tricotyledonous plants show a far greater increase in the number of leaflets inserted at the third node than do those abnormal only in the position at which the two cotyledons are inserted.

TABLE VIII

PERCENTAGE FREQUENCIES OF NUMBERS OF LEAFLETS IN SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Number of leaflets		
	1–4	5–7	8–11
Two cotyledons slightly separated and two primordial leaves	94.32	5.62	.05
Control	95.66	4.34	....
Difference	− 1.34	+ 1.28	+.05
Two cotyledons widely separated and two primordial leaves	92.37	7.63	....
Control	95.23	4.77	....
Difference	− 2.86	+ 2.86	....
Three cotyledons and two primordial leaves	72.57	27.18	.24
Control	95.64	4.36	....
Difference	−23.07	+22.82	+.24
Three cotyledons and three primordial leaves	67.72	32.03	.25
Control	90.23	9.77	....
Difference	−22.51	+22.26	+.25

In substantiation of these conclusions the reader will note that in the class with slightly separated cotyledons 5.68 per cent. of the plants have from five to ten leaflets as compared with 4.34 per cent. with five and six leaflets in the control series. In seedlings with more widely separated cotyledons but no other abnormality there are 7.63 per cent. of the plants with five to seven leaflets as compared with 4.77 per cent. of the normal controls with five or six leaflets. Seedlings with three cotyledons but the normal number of primordial leaves have 27.43 per cent. of the individuals with from five to nine leaflets as compared with 4.36 per cent. with five or six leaflets in the normal controls.

Plants with a trimerous cotyledonary and primordial whorl have 32.28 per cent. of the seedlings with from five to eleven leaflets as compared with 9.77 per cent. with five and six leaflets in the normal controls.

Taking the average number of leaflets per plant as a basis of comparison between the abnormal plants and their controls we find the results in TABLE IX.

TABLE IX

MEAN NUMBER OF LEAFLETS IN SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Mean number of leaflets in abnormals	Mean number of leaflets in controls	Difference
Two cotyledons slightly separated; two primordial leaves	3.170	3.133	+0.037
Two cotyledons widely separated; two primordial leaves	3.228	3.191	+0.037
Three cotyledons; two primordial leaves	3.847	3.131	+0.716
Three cotyledons; three primordial leaves	3.990	3.294	+0.606

Note (*a*) that for each type of normality the average number of leaflets is greater in the abnormal individuals than in the normal, and (*b*) that the difference between the abnormal class and its control is far greater in the case of the plants with three cotyledons than in those in which the abnormality in the cotyledonary whorl consists merely in the separation of the two cotyledons.

Thus the results for number of leaflets substantiates the conclusion based upon number of leaves.

Evidently, however, the number of leaflets is to a great extent determined by the number of leaves. The problem now arises: Are there differences in the average number of leaflets per leaf in the abnormal and normal individuals?

Means and their differences have been determined, but are so slight that conclusions must be deferred until further series of data are available.

Just one other method of dealing with the problem of the correlation in structural variation may now be considered.

Number of leaflets is, in the materials dealt with, practically an integral variate. In examining a large series of plants those with partial division of a leaflet, representing transition stages between a leaf with n and one with $n + 1$ leaflets are sometimes found. Such cases are, however, relatively rare. The lobing of the leaflet has therefore been disregarded in the foregoing treatment. A leaf with three leaflets, one of which has a lobe, has been recorded as 3 in the tables, not as an intermediate between three and four. This has simplified the tabling of the data, and the calculation of the simple constants necessary to the interpretation the data, without any material loss in accuracy.

One may, however, inquire whether there are differences in the degree of lobing of the leaflets produced at the third node in plants which are normal and in plants which are abnormal in the characters of the first and second node. Because of the very low percentages of lobing in the leaflet no stress whatever is to be laid upon the exact values found, even in samples containing several hundreds or thousands of plants, because of the great difficulties of determining the probable error of a small percentage.

The results are given in TABLE X.

TABLE X

PERCENTAGE OF LOBING IN THE LEAVES OF SEEDLINGS OF VARIOUS TYPES

Class of abnormality	Abnormal plants	Control plants	Difference
Two cotyledons slightly separated; two primordial leaves	0.349	0.273	+0.076
Two cotyledons widely separated; two primordial leaves	0.456	0.112	+0.344
Three cotyledons; two primordial leaves	1.599	0.242	+1.357
Three cotyledons; three primordial leaves	0.954	0.328	+0.626

Here the percentage frequency of plants with one or two lobes on the leaflets* are given for each type of abnormality dealt with and compared with that found in the control series.

Two relationships seem clearly indicated by the constants in this table.

First, the tendency to the production of lobes is greater in the leaflets produced by abnormal plants of all four types than in their normal controls.

Second, the tendency to the production of lobes is greater in the leaflets of plants with a trimerous cotyledonary whorl, and either a dimerous or trimerous primordial whorl, than it is in plants in which the sole abnormality consists in the separation of the two cotyledons in their insertion on the axis of the plant.

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* In the case of two lobes both may occur on the same leaflet or they may be on different leaflets.

RECAPITULATION

This paper presents the results of a first attempt to determine some of the correlations in the structural variations of the seedling of *Phaseolus vulgaris*.

The materials are drawn from a series of lines of Navy beans grown for the past several years at the Station for Experimental Evolution. The seeds used were harvested from plants of selected ancestry. Neither of these factors will, we believe, invalidate the conclusions drawn in this paper. These conclusions will not necessarily apply to certain entirely abnormal races.

Fasciation-like broadening of the axis and longitudinal division of the axis distal to the insertion of the primordial leaves are both more frequent in seedlings showing separation of the cotyledons and in tricotyledonous seedlings than in those which are normal.

Seedlings which are normal except for the separation of the cotyledons and those which have three cotyledons and a normal pair of primordial leaves or three cotyledons and a whorl of three primordial leaves produce a larger number of leaves, a larger number of leaflets and a higher percentage of leaves with lobes at the third node than do those which are normal in their cotyledonary and primordial leaf characters.

Seedlings which are tricotyledonous, with either a normal pair or a whorl of three primordial leaves, show higher percentages of variation in the axis, or the leaves produced by the axis, distal to the primordial leaves than do those which are normal except for the separation of the two cotyledons.

These studies will be continued.

STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, NEW YORK

INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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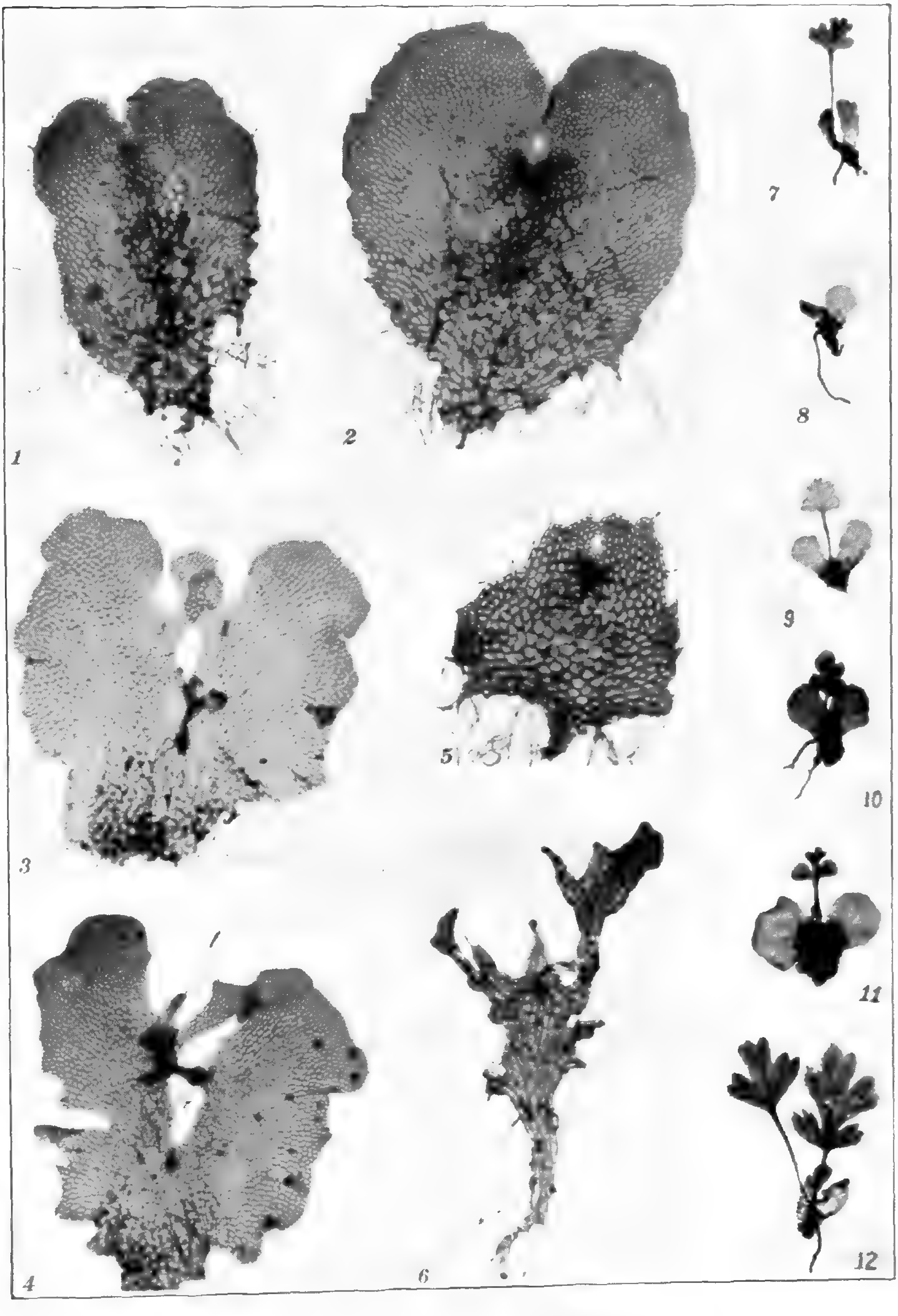
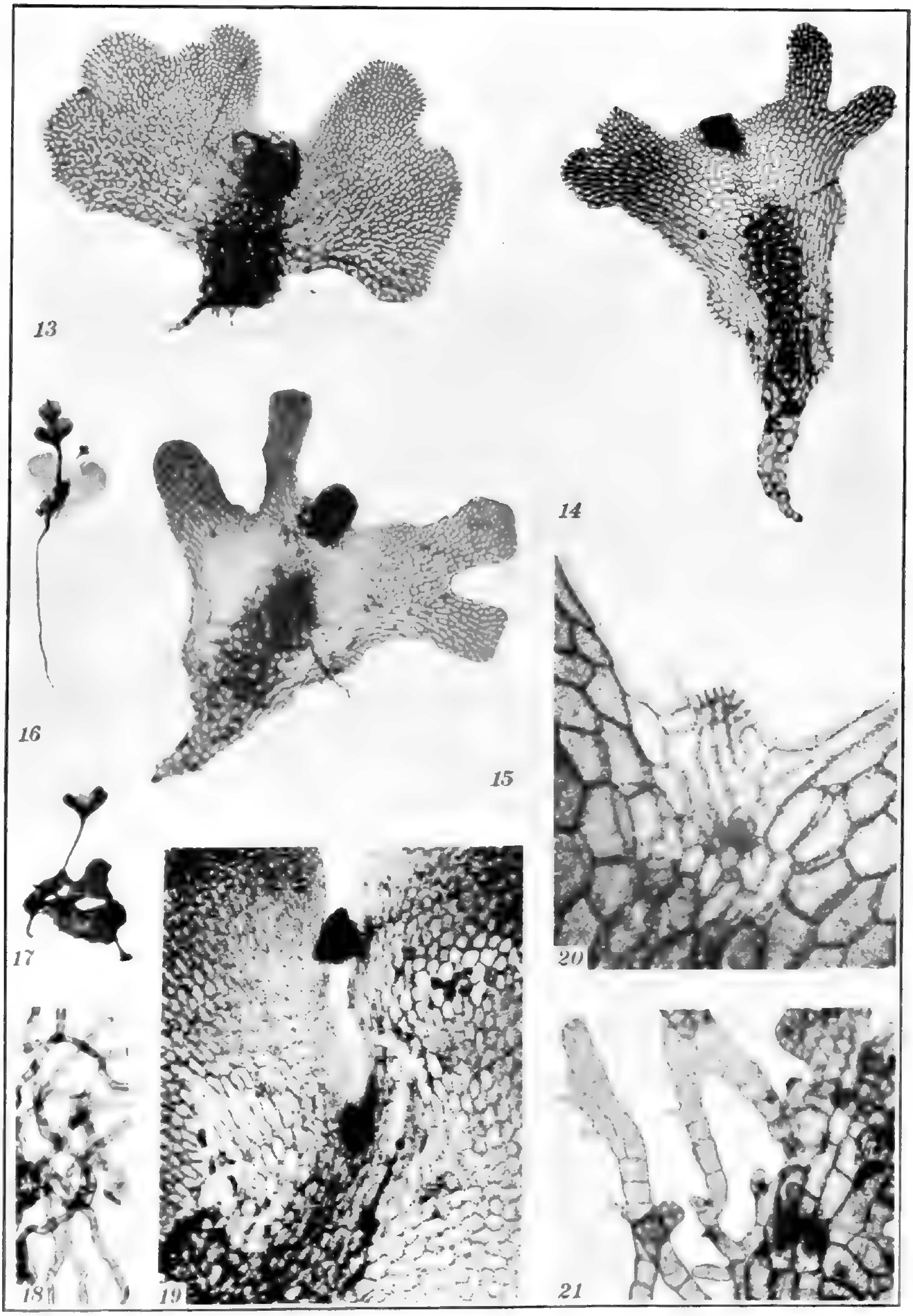


STEIL: APOGAMY IN FERNS



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Vol. 45 No. 4

BULLETIN

OF THE

TORREY BOTANICAL CLUB

APRIL, 1918

New species of Hawaiian plants

Joseph F. Rock

(with plate 6)

1. **Cyanea Giffardii** sp. nov.

A tree 5–10 m. tall with a single trunk 15 cm. in diameter near the base, gradually tapering towards the apex, bark smooth, grayish green, with scattered leaf-scars, woody zone thin near the apex of the trunk, the medullary cavity septate by chartaceous diaphragms; leaves obovate-oblong, about 50 cm. long and 12–15 cm. wide, broadest portion in the upper third, margins strongly undulate and minutely denticulate, appearing sinuate, due to strong undulation, subentire with exception of the base, which is unevenly lobed, acuminate at the apex, mucronate, gradually tapering at the base into a stout petiole 3.5–6.5 cm. long, thin, subchartaceous, dark green and shining above, pale and dull underneath, midrib stout and prominent as are the lateral veins, the latter arcuate and united with other arcuate veins near the margin, the whole surface of the leaf covered with a pellucid reticulate net work, glabrous above, pubescent underneath, especially on the midrib and veins; peduncles axillary, drooping, stout, terete, glabrous, 10–16 cm. long or slightly longer, about 1 cm. thick, distantly bracteate the entire length, the upper bracts linear, 15–30 mm. long, 3–5 mm. wide, rounded and mucronate at the apex, bracts less distant towards the apex and also smaller; flowers on pedicels 2–3 mm. long with three small, acute bractlets at the base and dorsal side of the flower; calyx glabrous, dark purplish black, tube obconical, usually seven-ribbed, with two

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tubercles at the base, 18 mm. long, 15 mm. wide; calycine lobes broadly triangular, acute, 5 mm. each way, with broad sinuses intervening; corolla strongly arcuate, 7–8 cm. long, glossy, glabrous, dark purplish outside, slit at the back three fourths its length only when fully mature, the five lobes of the corolla entirely connate; staminal column protruding, perfectly glabrous, pale, anthers glaucous, glabrous, the two lower only penicillate; style black, the stigmatic hairs encircling the stigma, the latter yellowish tinged with purple; flowers usually ten on a peduncle, crowded at the apex; fruits globose, nearly 25 mm. each way, dark purplish black, locules small, each containing from six to twelve rather large whitish seeds; milky juice of the plant yellowish. [PLATE 6.]

HAWAII: in the forest on the windward slope of Mauna Loa, near Glenwood at 22 miles, along the Homestead Road at an elevation of 2,200 feet, August 27, 1917, *W. M. Giffard 12802*, (flower buds) in the herbarium of the College of Hawaii; along the Volcano Road at 23 miles, in wet forest, September 1, 1917, *Rock & Holm 12802b*, (flowering and fruiting specimens), TYPE, in the herbarium of the College of Hawaii.

This very remarkable plant, which is closely related to *Cyanea superba* (Cham.) Gray, differs from it in the pubescent, deeply undulate leaves, which are lobed at the base instead of being entire; in the glabrous, much shorter peduncle, and in the glabrous deep purplish black flowers and fruits. *Cyanea superba* occurs on the island of Oahu in the gulches of Makaleha and Mt. Kaala, while *Cyanea Giffardii* occurs on the southernmost island of the group. It is also much statelier than *Cyanea superba*, as it reaches a height of thirty feet, with a single crown of leaves at the apex. It grows in company with *Antidesma platyphyllum* Mann, *Labordia*, *Cyrtandra*, *Straussia hawaiiensis* Gray, *Strongylodon lucidum* Seem., *Clermontia parviflora* Gaud., *Cibotium Menziesii* Hook. and *C. Chamissoi* Kaulf., the last two being the common tree ferns of the region.

When the species was first discovered by Mr. W. M. Giffard, in whose honor it is named, only two plants were observed, one with large flower buds and the other without flowers, the latter plant divided into three branches at the apex, on account of an injury. The mature type specimens, with flowers and fruit, were collected on the road to Glenwood and the Volcano, at an elevation of 2,400 feet. The largest plant seen was thirty feet in height. The plants are difficult to see in the forest as the trunk, which is usually covered partly with moss, does not branch and the crown of leaves is hidden amongst the foliage of other trees.

Cyanea Giffardii may be Hillebrand's β var. of his *Cyanea arborea* from the woods of Hilo, Hawaii. The writer is well acquainted with *Cyanea arborea* and can only state that the new species is exceedingly different from the latter, and that it comes much closer to *Cyanea superba. Cyanea arborea* has a much larger and denser crown of leaves, which are sessile, and linear-oblong; the peduncles are much longer and the flowers are very thin, narrow and slender, suberect and whitish to gray.

2. **Cyanea rollandioides** sp. nov.

Plant 1–1.5 m. high, stem simple, fleshy towards the apex, woody towards the base, stem muricate to spinose in the upper portion; leaves obovate-oblong, acute, fleshy when fresh, papery when dry, dark green above, paler underneath, but with dark purple midrib and veins and a prominent dark purple reticulate network, puberulous or glabrous on both surfaces, but more or less covered with spines on both sides, those of the upper surface yellow, those of the lower surface deep purple, margins eroso-dentate to irregularly notched, and somewhat uneven-sided at the base, 30–50 cm. long, 8–15 cm. wide in the widest portion, which is in the upper third, on fleshy stout spinose or muricate petioles, 8–15 cm. long; racemes glabrous, peduncle 3–6 cm. long, naked three fourths its lower length, but distantly covered with scars of fallen flowers, bearing in its upper fourth about fifteen flowers; bracts subulate, 3 mm. long, supporting each pedicel, the latter filiform, 10–25 mm. long, bibracteolate, the bracteoles alternate, one at about the middle of the pedicel the other near the apex, 0.25 mm. long; calyx tube turbinate to obovate-oblong, 7–10 mm. high, the linear calycine lobes as long as the tube; corolla deep purplish red or purple to pale yellowish white with dark purplish streaks, moderately arcuate, broadest at the middle, 5–8 mm., about 4.5 cm. long, thin and glabrous, dorsal slit very shallow, extending only one fourth of the length of the tube or a little beyond the two upper linear subulate lobes, the three lower lobes a little shorter; staminal column glabrous, as are the pale greenish anthers, the lower ones only penicillate; fruit unknown.

HAWAII: Forest of Puna in dense woods along the Kalapana Road, not far from Pahoa, September 3, 1917, *Rock & Newell*

12831 (flowering specimens), TYPE, in the herbarium of the College of Hawaii.

This rather variable species is remarkably like a *Rollandia*. The plant varies considerably in the spinosity of the leaves, petioles and stems; some of the specimens almost approach *Cyanea noli-me-tangere* Rock in spinosity, while others are only muricate. The color of flowers is also variable, ranging from pale yellowish white with deep purplish streaks to entire dark purple. It is difficult to state to what known species the plant is closest related; in habit it approaches *Rollandia lanceolata* Gaud., but actually seems to come close to *Cyanea noli-me-tangere;* from the latter it differs in the long-petioled leaves, which are much larger, and in the longer naked peduncles which are not spinose. The plant as a whole is much larger in every way, the flowers are purple as are the veins and midrib of the leaves; the whole inflorescence is glabrous. *C. noli-me-tangere* is very loosely foliate, while *C. rollandioides* is simple-stemmed and has at its apex a dense crown of leaves, this feature bringing it under the section *Palmaeformes*.

The plants grow in the wet forests of Puna on Hawaii, a little-explored district and one of the most primitive regions on the island of Hawaii. A stalwart Hawaiian gave the writer the native name *Aku-aku* for the species in question, of which he said that the leaves were cooked with meat and eaten like cabbage. The name *Aku* alone is applied to *Cyanea tritomantha* Gray, to which our plant has no resemblance. The species was collected in company with Brother Matthias Newell, of Hilo, an ardent naturalist.

3. **Rollandia angustifolia** (Hillbrd.) sp. nov.

Rollandia longiflora β var. *angustifolia* Hillbrd. Fl. Hawaiian Isl. 246. 1888.

Stem smooth, 1–1.5 m. high, leaves linear-lanceolate, 18–35 cm. long, 2.5–3.75 cm. wide, thick, fleshy, dark green, glossy above, pale whitish underneath, with dark purplish midrib and veins, acuminate, mucronate at the apex, gradually narrowing at the base into a fleshy petiole 2–4.5 cm. long, glabrous on both sides; racemes slender, 3–4 cm. long, four- to five-flowered; pedicels thin, about 14 mm. long, bracteate at the base, bi-bracteolate about the middle; calyx turbinate, 1 cm. long, the apex truncate-dentate, or oftener lobed, the calycine lobes acute, of irregular length, usually

3 mm. long, with a median nerve; corolla deep purplish red, 7–8.5 cm. long, 1 cm. wide, the lobes 1.5 cm., the dorsal slit extending one fifth the length of the tube; staminal column glabrous adherent up to about the middle of the corolla, the anthers glabrous, the lower only bearded; fruits globose, crowned by the tubular limb of the calyx, which disappears at the maturity of the fruit.

OAHU: Mt. Konahuanui trail, Palolo Valley, Mt. Olympus, and Manoa Valley, Kalihi Valley, January, 1870, *W. F. Hillebrand*, without number, in Berlin Herbarium; June 14, 1908, *H. L. Lyon 8816* in the herbarium of the College of Hawaii; September, 1912 and 1914, *J. F. Rock 10250a, 10250b,* in the herbarium of the College of Hawaii.

The plant in question is certainly worthy of specific rank. Young plants which the writer observed were of the same habit as mature ones, both having linear-lanceolate leaves, while the true *Rollandia longiflora* Wawra has sinuate leaves when young and also when in a mature state. *R. angustifolia* differs mainly in the linear, entire, minutely denticulate leaves, which give the plant an entirely different appearance from that of *R. longiflora.*

4. **Lobelia oahuensis** sp. nov.

Plant rather stout, stem short and thick, solid and not hollow; rosette of leaves very dense and about 1 m. in diameter; leaves densely packed around the apex of the stem, linear-oblong, acuminate at both ends, merging at the base into a winged fleshy petiole about 2.5 cm. in length, 50 cm. long, 4.5–5 cm. wide, thick, coriaceous, dark green, glabrous above and covered with a strongly impressed, very close, reticular net work, young leaves densely hirsute underneath, especially along the very prominent projecting midrib and veins, of a dirty grey or fawn color on the older leaves, the margins revolute, denticulate with thick callous teeth; flowers not seen, a single dead terminal flower stalk was seen on one of the plants, which was about 1 m. long.

OAHU: at the very top of the main crest of the island, overlooking the cliffs of Waimanalo at an elevation approaching 3,000 feet, September 14, 1917, *J. F. Rock 12836*, TYPE, in the herbarium of the College of Hawaii. Several plants were seen growing together, the lower ones of which could not be reached owing to the vertical cliffs on which they grew, immediately below the knife-edge crest of the backbone of the island of Oahu. The plant forms a large rosette with the leaves densely packed at the apex in an almost horizontal position, that is, at right angles to the stem. It grows in company with *Trematolobelia macrostachys* (Hook. & Arn.), Zahlbr., *Dubautia laxa* Hook. & Arn., *Metrosideros rugosa* Gray, and other species. Notwithstanding that the flowers of this new species are unknown, the plant is so distinct from all of our other lobelias that it can well be described at present.

The plant is evidently related to *Lobelia hypoleuca* Hillbrd., from which it differs in the solid stem, thick, coriaceous, closely reticulate leaves, not silvery underneath but hirsute, being covered with fawn-colored or dirty gray hair. In *Lobelia hypoleuca*, which is a branching species, the leaves are few and more or less scattered, thin and chartaceous; it does not ascend to such high elevations, but remains more at the lower levels, from 1,000 to 1,500 feet, in very sheltered situations, especially deep ravines.

5. **Straussia glomerata** sp. nov.

A medium-sized tree, 10 m. or more in height, trunk straight, crown round and of rather small dimension; stipules cup-shaped, not triangular, sheathing and of even height, 3 mm. high, soon deciduous; leaves obovate, coriaceous, glossy and smooth above, dull and pubescent beneath, especially along the midrib and veins, pubescent glands present in the axils of veins and midrib, 5–10 cm. long, 4.5–6.5 cm. wide, on petioles 15 mm. long, rounded at the apex, cuneate at the base; panicle erect, not drooping save when in full fruit, 2–4 cm. long, distinctly angular, hirsute with dirty yellowish hair, whorls two or three, of very short rays 2–6 mm. long; flowers sessile; calyx minute, 0.5–0.75 mm. long, densely hirsute, truncate; corolla greenish white, minute, tube 0.5 mm. long, lobes 1.5 mm. long, glabrous, stamens minute, filaments 0.25 mm. long; the convex disk densely hirsute; fruits numerous, densely agglomerate, forming a densely packed globose head, hiding all whorls and rays, fruits yellow, pubescent to hirsute, obovate, 9 mm. long, 6–6.5 mm. wide, crowned by a rounded, dome-shaped, projecting disk.

HAWAII: North Kona, in the forest of Waihou and on the lava flows of Puuwaawaa, at an elevation of 3,700 feet, August 24, 1917, *J. F. Rock 12829* (flowering and fruiting specimens), TYPE, in the herbarium of the College of Hawaii.

This interesting species is very distinct from the other species in the genus, and is remarkable for the minute flowers, hirsute panicles and fruits which are densely glomerate, forming a densely packed, globose head, nearly as long as broad. It is related to *Straussia hawaiiensis* which differs however in the loose and open-whorled drooping, glabrous panicle.

COLLEGE OF HAWAII,
HONOLULU, TERRITORY OF HAWAII

Explanation of plate 6

Cyanea Giffardii Rock. Photograph of the type specimen, showing the crown of a flowering tree, twenty-four feet in height.

New species of Uredineae—X *

Joseph Charles Arthur

The preceding number in this series† was issued in November, 1915. Since that time some collections of Uredinales have come to hand, or have been awaiting study, which appear to be undescribed. The discovery of additional spore forms for previously named species admits of their transfer to more suitable genera, thus necessitating new combinations. Both new names and new combinations are required in order to make the material more available in future studies. All the species are North American. Although the localities range from Wyoming and Vermont to Panama and the West Indies, yet the majority are in Mexico and Central America, where the rust flora is abundant, but much less known than northward.

Uromyces Atriplicis (Shear) comb. nov.

Aecidium Atriplicis Shear, Bull. Torrey Club **29**: 453. 1902.

The aecia of this rust have been known for a number of years. They are abundant in Colorado on *Atriplex confertifolia* (Torr.) S. Wats., and were distributed in Griffiths, West Amer. Fungi *321* (type), Ellis & Ev., Fungi Columb. *1294*, and Barth., North Amer. Ured. *401*. On August 29, 1911, telia were gathered by Mr. E. Bethel at Delta, Colorado, from the same plants that had yielded a large crop of aecia earlier in the season. This collection shows the same plentiful sprinkling of telia over the under side of the leaves as marks the presence of the aecia, a few sori in both cases usually appearing on the upper side of the leaves. The collection from Delta also includes aecia, both on the same leaves

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* Reprints may be obtained by application to the Botanical Department, Purdue University Agricultural Experiment Station, Lafayette, Ind., under whose auspices the work was carried on.

† New Species of Uredineae I–IX: Bull. Torrey Club (I) **28**: 661–666. 1901. (II) **29**: 227–231. 1902; (III) **32**: 1–8. 1904; (IV) **33**: 27–32. 1906; (V) **33**: 513–522. 1906; (VI) **34**: 583–592. 1907; (VII) **37**: 569–580. 1910 (VIII) **38**: 369–378; 1911; (IX) **42**: 585–593. 1915

with the telia, and intermixed with them, and also separately. The telia were also found at Pueblo, Colorado, by Mr. Bethel, and on September 13, 1911, Dr. F. D. Kern and the writer, following Mr. Bethel's directions, visited the spot, but were only rewarded with aecia. On August 13, 1912, Dr. Kern repeated the visit and found plenty of telia. Both the position of the telia on the leaves, and their succession to the aecia on the same plants, indicate their genetic relationship. The telia may be described as follows:

III. Telia chiefly hypophyllous, scattered, round or irregular, 0.2–0.4 mm. across, early naked, pulverulent, cinnamon-brown, ruptured epidermis noticeable; teliospores broadly ellipsoid or ovoid, 18–23 by 23–30 μ, rounded at both ends, or somewhat narrowed below; wall cinnamon-brown, 1.5–2 μ thick, 4–5 μ above, including a low semi-hyaline umbo, smooth; pedicel colorless, fragile.

The type collection, made by Shear & Bessey at Montrose, Colorado, July, 1897, showing only aecia, was distributed as on *Atriplex Nuttallii*, an error for *A. confertifolia.*

Uromyces fuscatus sp. nov.

I. Aecia amphigenous, in dense groups 3–5 mm. across; peridia short-cylindric, the margin erect, coarsely and deeply lacerate; peridial cells rhomboidal, 13–19 by 28–37 μ, considerably overlapping, the outer wall 7–9 μ thick, finely striate transversely, the inner wall 2.5–3.5 μ thick, moderately verrucose; aeciospores globoid, 16–22 μ in diameter; wall colorless, 1–1.5 μ thick, finely and closely verrucose, often appearing smooth when wet.

II. Uredinia amphigenous, scattered, round, 0.3–0.8 mm. across, elevated, early naked, puberulent, dark cinnamon-brown, ruptured epidermis conspicuous; urediniospores globoid or broadly ellipsoid, 18–24 by 22–29 μ; wall cinnamon-brown, 2–3 μ thick, closely and finely verrucose, the pores 3 or 4, approximately equatorial.

III. Telia amphigenous, scattered, round or irregular, 0.5–2 mm. across, often confluent, early naked, prominent, dark chestnut-brown, ruptured epidermis evident; teliospores broadly ellipsoid or globoid, 18–23 by 23–28 μ, rounded at both ends; wall chestnut-brown, 2–2.5 μ thick, slightly thicker above, 3–5 μ, moderately verrucose in longitudinal lines; pedicel colorless, as long as spore, but fragile and usually broken off short.

On *Polygonum alpinum* All., House Creek, Idaho, June 29, 1912, *Nelson & Macbride 1794* (type); near Gogorza, Summit County, Utah, June 29, 1915, *A. O. Garrett 2286.* Among autoecious species this appears to be most like *Uromyces Acetosae* Schröt., a European species on *Rumex*, but the urediniospores are verrucose and not echinulate and have a different number of pores, while the teliospores are contrasted in the coarseness and arrangement of the markings. There appears to be no correlated form among the many species of *Puccinia* on either *Polygonum* or *Rumex*. The rust covers the leaves heavily with the conspicuous sori, inducing a more or less mottled, reddish appearance of the tissues. The specimen from Utah was labelled *Pentstemon procerus*, but both host and rust appear identical with the one from Idaho.

Uromyces Krameriae Long, sp. nov.

III. Telia amphigenous and caulicolous, soon opening by a longitudinal slit, chestnut-brown, loosely and prominently pulvinate, oblong, 0.1–2 mm. long, ruptured epidermis conspicuous; teliospores broadly ellipsoid or globoid, 21–23 by 23–29 μ; wall cinnamon-brown, 2.5–3 μ thick, thicker above, 6–9 μ, including a broad paler umbo, smooth; pedicel hyaline, once to twice or more the length of the spore.

On *Krameria glandulosa* Rose & Painter, Denton, Texas, October 21, 1901, *W. H. Long 1071.* The host has usually passed under the name of *K. parvifolia*, a species of Lower California. This rust was received a long time since with the name as given above. I do not find that the species has yet had the name established, and so take this opportunity to place it in use. It is one of the numerous finds made by Mr. W. H. Long, while living in northern Texas, and affords one more evidence of Mr. Long's extended and efficient study of the rusts. No urediniospores were detected, but the appearance of the rust is not that of a short-cycle form; it is more likely to possess cupulate aecia. Only the one collection is known.

Puccinia wyomensis sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia chiefly hypophyllous, scattered, oblong to linear, 0.6–2 mm. in length, 0.2–0.4 mm. wide, tardily naked, finally opening by a longitudinal slit, pulverulent, golden-brown, ruptured epidermis conspicuous; urediniospores broadly ellipsoid or obovoid, 18–21 by 26–29 µ; wall pale yellow or quite colorless, 1–1.5 µ thick, closely and rather inconspicuously echinulate, the pores 6–8, scattered.

III. Telia amphigenous, scattered, oblong to linear, 0.2–3 mm. in length, compact, dark gray, long covered by the epidermis, surrounded by a thin dark-brown stroma; teliospores oblong or clavate, 15–21 by 50–60 µ, truncate or somewhat rounded above, narrowed below, slightly or not constricted at septum; wall cinnamon-brown, darker above, thin, 1–1.5 µ, not or slightly thickened above, 2–5 µ, smooth; pedicel very short, tinted.

On *Scirpus americanus* Pers., Arcola, Wyoming, August 23, 1916, *E. Bartholomew 6089.* A subepidermal form of *Scirpus* rust abundantly distinct from all others.

Puccinia Rosenii sp. nov.

O and I. Pycnia and aecia unknown.

II. Uredinia hypophyllous, scattered or in series, oval or linear, 0.5–2 mm. long, rather tardily naked, ruptured epidermis conspicuous; urediniospores 30–35 µ long, when seen with pores in optical section oblong, 10–20 µ wide, when seen with pores central globoid or broadly ellipsoid, 28–35 µ wide; wall cinnamon-brown, 1.5–2.5 µ thick, moderately echinulate, the pores 2, superequatorial.

III. Telia few, disposed like the uredinia, tardily naked, chocolate-brown; teliospores clavate, or elongated oblong, 16–23 by 43–67 µ, rounded or truncate above, usually narrowed below, slightly constricted at septum; wall chestnut-brown above, somewhat lighter below, 1–2 µ thick, 5–10 µ above, smooth; pedicel colorless, nearly as long as spore.

On *Schoenus nigricans* L. (?), Daytona, Florida, December 27, 1915, *R. A. Harper 5.* This rust, found in scanty amount on a somewhat uncertain host without inflorescence, is apparently nearest like *P. Eriophori* Thüm. This species is named for H. R. Rosen, who has made the careful study of this material on which the diagnosis and conclusions are founded.

Puccinia Heliconiae (Diet.) comb. nov.

Uredo Heliconiae Diet. Hedwigia **36**: 35. 1897.

The uredinial stage of this rust was described from a collection made at Rio de Janeiro, Brazil, in December, 1891, on an undetermined species of *Heliconia* (*Bihai*). In North America it was collected in Martinique, West Indies, on *Bihai borinquena* Griggs, August, 1913, and again by Whetzel and Olive in Porto Rico, West Indies, on the same host, April, 1916, both collections showing only uredinia. In a collection on *Bihai latispatha* (Benth.) Griggs, made by E. Bethel, at Montelinio, Canal Zone, Panama, March 4, 1913, an abundance of telia accompany the uredinia. The characters of the telia are as follows:

III. Telia hypophyllous, scattered, soon naked, round, 0.3–0.5 mm. across, cinnamon-brown, ruptured epidermis evident; teliospores elongated clavate, 15–19 by 60–72 µ, rounded above, not or slightly constricted at septum; wall pale cinnamon-brown, thin, 1 µ, much thickened above, 9–13 µ, smooth, pedicel short, colorless.

The urediniospores of this species appear to be quite variable. Those of the West Indian collections are thin and dark, as compared with most of those of the Panama collection, in which, however, all gradations occur. The sori of the present material are much parasitized, and both uredinia and telia are consequently unnaturally conspicuous.

Puccinia Viornae sp. nov.

O. Pycnia epiphyllous, crowded upon swollen areas 2.5–5 mm. in diameter, dark brown, noticeable, subepidermal, globoid, 98–110 µ in diameter, with ostiolar filaments.

I. Aecia hypophyllous, crowded upon swollen areas opposite the pycnia, cupulate, short, 0.2–0.5 mm. in diameter; peridium recurved, the peridial cells rectangular, abutted, 19–23 by 22–24 µ, the outer wall 7–9 µ thick, the inner wall 3–5 µ thick, finely verrucose; aeciospores irregularly globoid or ellipsoid, 13–16 by 14–18 µ; wall colorless, thin, 1.5 µ, finely and closely verrucose.

II. Urediniospores in the telia, ellipsoid or elliptic-obovoid, 16–19 by 24–32 µ; wall pale golden-brown, thin, 1–1.5 µ, thicker above, 3–5 µ, closely echinulate, the pores indistinct, 2 or possibly more, equatorial; paraphyses in the telia, intermixed with the spores, or surrounding groups of spores, cylindric, clavate or clavate-capitate, 7–23 by 47–64 µ, the wall nearly colorless to golden-brown, darker above, thin, 1–1.5 µ, somewhat thickened above, 2–7 µ.

III. Telia caulicolous, scattered, oblong or linear, 1–3.5 mm. long, somewhat tardily naked, inclined to be pulverulent, chestnut-brown, ruptured epidermis conspicuous; paraphyses sparingly intermixed, doubtless of uredinial origin, often wanting; teliospores apparently in groups, ellipsoid or oblong, 16–21 by 28–35 µ, rounded at both ends, deeply constricted at the septum; wall dark chestnut-brown, uniformly 1.5–2 µ thick, moderately and closely verrucose with conical warts, at times almost echinulate; pedicel short, colorless, fragile.

On *Viorna* sp., Abilene, Texas, May 17, 1900, *T. A. Williams*. The specimen, which was communicated by the National Museum, Washington, D. C., has been in hand for a considerable time, hoping that additional material would come to light. The appearance of the rust is much like that of species belonging to the genus *Tranzschelia*, but the uredinial stage is yet imperfectly known; moreover, the pycnia are unequivocally subepidermal. It finds its nearest representative seemingly in *Tranzschelia cohaesa* (Long) Arth. (*Puccinia cohaesa* Long), a species from Texas on *Anemone*. But not only are the pycnia subepidermal, both pycnia and aecia are grouped instead of systematically scattered. It might be assumed that the aecia here described, which occur upon the leaves and are entirely dissociated from the caulicular telia, do not belong to this species, but are heteroecious and the aecia of *Puccinia Agropyri* E. & E., which occur upon species of *Viorna* further north, and are common in Texas on *Clematis Drummondii*. However, the aeciospores measure much smaller than those of any collection known for that species. An interesting feature is the grouping of the teliospores, which can be fairly well seen in sections of sori, which have not yet opened. It is a character exactly in accord with the telial characters selected for the genus *Tranzschelia*. The paraphyses are also essentially like those of that genus, both in form and position in the sorus, and the urediniospores as well. The characters of the latter can not, however, be fully made out until the uredinial sorus is studied. Altogether it would seem that in this new and highly distinctive ranunculaceous species of rust we have another candidate for the genus *Tranzschelia*, and one which will necessitate some modification in the generic characters.

Puccinia missouriensis sp. nov.

O. Pycnia epiphyllous, few in small groups, honey-yellow, inconspicuous, subepidermal, flask-shaped, 60–75 µ in transverse diameter, with ostiolar filaments.

I. Aecia hypophyllous, usually few in somewhat indefinite groups opposite the pycnia, cylindric, 0.3–0.5 mm. long, 0.1–0.2 mm. in diameter; peridium erect, erose; peridial cells rhombic or rectangular, abutted or somewhat overlapping, 15–23 by 18–27 μ, the outer wall thick, 10–15 μ, transversely striate, smooth, the inner wall much thinner, 2–3 μ, coarsely verrucose; aeciospores globoid or ellipsoid, 13–16 by 16–20 μ; wall colorless, thin, 1–1.5 μ, finely and closely verrucose.

III. Telia hypophyllous, scattered among the groups of aecia, round, early naked, pulvinate, chestnut-brown, ruptured epidermis inconspicuous; teliospores oblong, 10–14 by 40–48 μ, obtuse or rounded at both ends, slightly constricted at septum; wall dark cinnamon-brown, 1.5–2 μ thick, much thicker above, 5–9 μ, smooth; pedicel short, more or less tinted.

On *Ranunculus recurvatus* Poir., Creve Coeur Lake, Missouri, May, 1887, *L. H. Pammel.* The collection came to the writer's attention ten years ago, when consulting the cryptogamic herbarium of the New York Botanical Garden. It was there labelled *Aecidium ranunculacearum*, and was for a long time considered one of the common heteroecious aecia belonging to grass rusts. When critically examined, however, it was found that the abundant aecia differed somewhat from those belonging to grasses, and were accompanied by telia, which had before been overlooked. It is remarkable that no other similar collection has turned up in the thirty years since it was gathered.

Puccinia obesispora sp. nov.

II. Uredinia chiefly hypophyllous, confluent on discolored spots, often in rings about a central area that becomes dry and dead, or scattered, early naked, cinnamon-brown, ruptured epidermis prominent; urediniospores broadly ellipsoid or globoid, 19–26 by 24–30 μ; wall variable in thickness, 1.5–3 μ, dark cinnamon-brown, sparsely and strongly echinulate, the pores 2, equatorial.

III. Telia chiefly hypophyllous, scattered, usually following the uredinia, irregular in outline, 0.1–0.5 mm. across, early naked, dark chocolate-brown; teliospores ellipsoid or oblong, large, 26–35 by 55–70 μ, rounded at both ends, or obtuse or even acute above, slightly or not constricted at septum; wall chocolate-brown, thick, 3–4 μ, much thicker above, 6–12 μ, coarsely and rather sparsely verrucose; pedicel tinted near the spore, and twice length of spore, or less.

On *Achyranthes obovata* (Mart. & Gal.) Standley, Oaxaca, Mexico, October 24, 1899, *E. W. D. Holway 3732*. The species is remarkable for its large, coarsely verrucose teliospores, which greatly resemble those of the euphorbiaceous species, *P. Euphorbiae* P. Henn. In that species the uredinia are sometimes accompanied by pycnia. In the present species the annular groups of uredinia appear like a primary stage, but no pycnia could be found by sectioning or otherwise.

Puccinia incondita sp. nov.

III. Telia hypophyllous and caulicolous, densely pressed or confluent into more or less rounded pulvinate masses, 1–3 mm. across, dark cinnamon-brown, early naked, ruptured epidermis inconspicuous; teliospores irregularly ellipsoid or oblong, 16–20 by 23–29 μ, rounded at both ends or somewhat narrowed below, slightly or not constricted at septum; wall cinnamon-brown, 1.5–2.5 μ thick, not or somewhat thicker above up to 6 μ, smooth; pedicel colorless, sometimes longer than spore, usually breaking near the spore.

On *Solanum triquetrum* Cav., Austin, Texas, January 5, 1916, *B. C. Tharp*. A short-cycle rust which appears to be different from any species on *Solanum* heretofore described.

Puccinia adducta sp. nov.

O. Pycnia epiphyllous, in small orbicular groups, dark brown, noticeable, subepidermal, globoid, 80–105 μ broad.

II. Uredinia hypophyllous, at first grouped opposite the pycnia on larger yellowish spots 2–5 mm. across, afterward scattered, small, round, rather tardily naked, cinnamon-brown, surrounding epidermis noticeable; urediniospores broadly obovoid, 19–23 by 27–35 μ; wall pale cinnamon-brown, 1–2 μ thick, moderately and strongly echinulate, the pores indistinct, possibly 3 and equatorial.

III. Telia hypophyllous, following the uredinia in the same sori; teliospores ellipsoid or oblong, 19–26 by 35–40 μ, obtuse or rounded at both ends, slightly or not constricted at septum, wall cinnamon-brown, 1–2 μ thick, usually with a slight papilla-like thickening at apex, smooth; pedicel short, rather thick, often deciduous.

On *Solanum racemosum* Jacq., Antigua, West Indies, February 4–16, 1913, *Rose, Fitch & Russell 3473*. A seemingly distinctive species.

Puccinia Notopterae sp. nov.

O. Pycnia amphigenous, crowded on brownish areas 2–3 mm. across, dark brown, conspicuous, subepidermal, globoid, 85–140 μ in diameter, with ostiolar filaments.

III. Telia epiphyllous, becoming amphigenous, circinating about the pycnia at first, then becoming confluent and causing hypertrophy, early naked, very pulverulent, chestnut-brown, ruptured epidermis noticeable; teliospores ellipsoid, 19–24 by 26–34 μ, rounded at both ends, slightly constricted at septum; wall dark cinnamon-brown, evenly 1.5 μ thick; coarsely and rather sparingly verrucose; pedicel colorless, short, fragile.

On *Notoptera hirsuta* (Sw.) Urban, Mandeville, Jamaica, February 23, 1915, *E. W. D. Holway 226*. A distinctive, short-cycle rust, on a host genus not before represented among those bearing rusts.

Aecidium anthericicola sp. nov.

O. Pycnia amphigenous, in small orbicular groups, small, honey-yellow, inconspicuous, subepidermal.

I. Aecia hypophyllous, in annular groups 2–7 mm. across about the pycnia, at first bullate then erect, the margin erose; peridial cells quadrate, 16–20 by 20–26 μ, abutted, the outer wall slightly or no thicker than the inner wall, 3–6 μ; aeciospores globoid, 16–20 by 19–23 μ; wall colorless, thin, 1.5 μ, very finely verrucose, appearing smooth when wet.

On *Anthericum nanum* Baker, Dedregal near Tlalpam, Valley of Mexico, Mexico, June 30, 1905, *Rose, Painter & Rose 8246*. The species is similar to the aecia of *Uromyces Hordei* on *Nothoscordium*, but both the peridial cells and aeciospores are smaller than in that form.

Aecidium plenum sp. nov.

O. Pycnia amphigenous, crowded in groups 0.2–0.3 mm. across, cinnamon-brown, small, inconspicuous, subepidermal.

I. Aecia hypophyllous, crowded in circular groups about the pycnia, 1–2 mm. across, without conspicuous spots, cupulate or short cylindric; peridium erect, or somewhat recurved, irregularly and deeply lacerate; peridial cells angularly oblong in face view, about 20 by 30 μ, narrowly oblong in radial section, somewhat overlapping, about 8–10 by 30 μ, the outer wall 5–9 μ thick, smooth, the inner wall 3–6 μ, coarsely verrucose; aeciospores globoid or ellipsoid, 16–21 by 18–24 μ; wall colorless, thin, 1 μ, finely and closely verrucose.

On *Argemone intermedia* Sweet, Burkburnett, Texas, May 29, 1917, *B. O. Dodge.* The collection shows a remarkably heavy infection, the leaves being wholly covered with groups of aecia on the lower side, with scarcely an aecium showing above. The groups rarely become confluent and indistinguishable, although often somewhat intermingling. The general appearance of the rust is that of a heteroecious form, and is not unlike that on *Agoseris*, *Lactuca* and *Crepis*, belonging to the *Carex* species, *Puccinia patruelis.* No aecia have heretofore been reported on any papaveraceous host, and no safe prediction can be made regarding its relationship.

Aecidium Thenardiae sp. nov.

I. Aecia hypophyllous, in circular groups 8–10 mm. across, often circinating, on somewhat larger, yellowish spots, short cylindric; peridium white, the margin erect, erose, or torn; peridial cells in face view oblong, 16–22 by 24–30 µ, somewhat overlapping, moderately verrucose; aeciospores quadrately globoid, 14–16 µ in diameter; wall colorless, thin, 1–1.5 µ in diameter, somewhat thicker above, 2–5 µ, finely and closely verrucose.

On *Thenardia Galeottiana* Baill., near Oaxaca, Mexico, August 20, 1894, *C. G. Pringle*, communicated by E. W. D. Holway. The form is undoubtedly heteroecious.

Aecidium Cyrillae sp. nov.

I. Aecia hypophyllous, in groups of 2–8, rarely more, on reddish-brown spots, 2–4 mm. across, short-cylindric, white; peridium erect, erose; peridial cells quadrangular in radial section, with a strongly overlapping projection, the outer wall 5 µ thick, smooth, the inner wall 7–9 µ thick, verrucose; aeciospores irregularly ellipsoid or globoid, 19–23 by 23–26 µ; wall colorless, thin, 1–1.5 µ, greatly thickened above, 7–9 µ, closely and finely verrucose.

On *Cyrilla racemiflora* L., Ocean Springs, Mississippi, June 15, 1896, *Underwood & Earle.* A sparse amount of the rust was found on the same host in the phanerogamic herbarium of the New York Botanical Garden, collected at New Orleans, Louisiana, 1832, *Drummond 202.* A well-marked species, which is probably heteroecious.

Aecidium Tithymali sp. nov.

O. Pycnia hypophyllous, scattered sparsely over the surface of the leaf, preceding and accompanying the aecia, punctiform, honey-yellow or brownish, noticeable, subepidermal, globoid or flask-shaped, 110–150 µ broad; ostiolar filaments 60–100 µ long.

I. Aecia hypophyllous, evenly and loosely scattered, at first bullate and opening by a pore or irregular break of the epidermis; peridia erect or recurved, torn, fragile; peridial cells rhomboidal, 10–15 by 23–27 µ, somewhat overlapping, the outer wall 5–7 µ thick, striate, the inner wall 2–3 µ thick, verrucose; aeciospores globoid or broadly ellipsoid, 18–22 by 19–24 µ; wall nearly or quite colorless, thin, 1–1.5 µ, finely verrucose.

On *Tithymalus commutata* (Engelm.) Kl. & Garcke (*Euphorbia commutata* Engelm.), Decorah, Iowa, June, 1883, *E. W. D. Holway;* same, June 20, 1885, *E. W. D. Holway* (Barth. N. Am. Ured. *703*); Beloit, Wisconsin, May 30, 1910, *J. J. Davis;* Lafayette, Indiana, June 7, 1901, *H. B. Dorner* (type); same, May 13, 1910, *Kern & Billings;* Plummer Island, Maryland, May 30, 1903, *P. L. Ricker 1055;* Crawfordsville, Indiana, May 17, 1913, *F. D. Kern.*

On *Tithymalus leiococcus* (Engelm.) Small (*Euphorbia texana* Boiss.), San Antonio, Texas, March 16, 1900, *Wm. Trelease;* same, February 16, 1914, *Arthur & Fromme 5300.*

On *Tithymalus missouriensis* (Norton) Small (*Euphorbia dictyosperma* Auct.), Lincoln, Nebraska, April 28, 1902, *Geo. G. Hedgcock.*

On *Tithymalus robusta* (Engelm.) Small (*Euphorbia robusta* Small), Colorado, July, 1888, *C. H. Demetrio* (Ellis & Ev. N. Am. Fungi *2215*); Flagstaff, Arizona, June, 1891, *D. T. MacDougal;* Larimer County, Colorado, July 2, 1894, *C. F. Baker 261;* Colorado Springs, Colorado, August 2, 1900, *E. T. Harper 368;* Wasatch County, Utah, August 3, 1905, *A. O. Garrett* (Fungi Utah. *96*); La Veta, Colorado, 2,100 m. alt., June 21, 1907, *F. E. & E. S. Clements* (Crypt. Form. Colo., *594*); Boulder, Colorado, May 13, 1910, *E. Bethel;* same, August 23, 1911, *Bethel, Arthur & Kern 509;* Denver, Colorado, May 24 and June 2, 1915, *E. Bethel;* Ft. Collins, Colorado, May 23, 1916, *J. C. Arthur;* Golden, Colorado, May 27, 1916, *J. C. Arthur;* Rimrock Station, Montana, August 2, 1917, *E. Bartholomew 6213.*

This is a common and conspicuous species in the Rocky Mountains, and extends sparingly eastward across the plains and over the Allegheny Mountains. For a long time it has been considered heteroecious and probably the early stage of the common *Uromyces* on *Astragalus*. Both its distribution and morphological characters favored this view, and many attempts at cultures were undertaken to substantiate the assumed connection but without success. Observations in the field have yielded no strong evidence that the aecia were followed by telia on *Astragalus*, but rather that they were not. At various times it has been suggested that the telial form on the same hosts as the aecia, *Uromyces Tranzschelii*, an apparently short-cycle species having pycnia associated with the telia, might be derived at times from the aecia, and all be one autoecious species. If this were true, we should have the anomalous condition of a short-cycle and a long-cycle form associated at times so intimately that only culture demonstration could separate them. In the meantime while actual experimental knowledge is awaited, it seems best to designate the aecia by a name that will distinguish them from other aecia on similar hosts. Some of the collections above cited are said to be on *Euphorbia montana*, which may be true, although the preponderance of probability points to *E. robusta*, a far more common species in the region covered, and under this name they have been listed.

Aecidium Mozinnae sp. nov.

O. Pycnia chiefly epiphyllous, few in orbicular groups, honey-yellow, inconspicuous, subepidermal, globoid, 90–125 μ across; ostiolar filaments present, abundant.

I. Aecia hypophyllous, encircling the pycnial area, on yellowish spots 2–5 mm. across; peridium cylindric, the margin erect and erose; peridial cells quadrate or rectangular, 19–24 by 29–34 μ, abutted or slightly overlapping, the outer wall 10–12 μ thick, transversely striate, smooth, the inner wall 3–5 μ thick, strongly verrucose; aeciospores angularly ellipsoid or globoid, 19–23 by 24–29 μ; wall nearly or quite colorless, 2–2.5 μ thick, closely and noticeably verrucose.

On *Mozinna spathulata* (Müll.-Arg.) Ortega (*Jatropha spathulata* Müll.-Arg.), State of Guanajuato, Mexico, July 11, 1899, *J. N. Rose & Walter Hough 8999.*

The species appears to be well defined, and is quite likely heteroecious.

Aecidium conspicuum sp. nov.

O. Pycnia amphigenous, numerous, crowded in round groups, 0.3–1 mm. across, small, honey-yellow, subepidermal, flask-shaped, 100–125 μ in transverse diameter.

I. Aecia amphigenous, in large, dense groups 3–8 mm. across, on slightly larger discolored spots; peridium erect or somewhat recurved, finely lacerate; peridial cells angularly oval in face view, 26 by 32–38 μ, oblong in radial section, 16 by 32–38 μ, strongly overlapping, the inner wall 10–12 μ thick, verrucose, the inner wall about 1 μ, smooth; aeciospores globoid, 19–23 μ in diameter; wall colorless, thin, 1 μ, finely verrucose.

On *Dugaldea Hoopesii* (A. Gray) Greene (*Helenium Hoopesii* A. Gray), La Plata River, Colorado, 9,500 ft. alt., July 16, 1898, *Baker, Earle & Tracy 1075;* mountains near Pagosa Peak, Colorado, 9,000 ft. alt., August 10, 1899, *C. F. Baker 113;* Cloudcroft, New Mexico, July 19, 1899, *E. O. Wooton;* Winsor Creek, Pecos National Forest, New Mexico, July 28, 1908, *Paul C. Standley 4581;* Rio Pueblo, New Mexico, August 11, 1910, *E. O. Wooton;* Little Colorado River, White Mts., Arizona, July 20, 1910, *L. N. Goodding;* Trout Lake, Colorado, 10,000 ft. alt., August 2, 1912, *Arthur & Kern 5108;* Snowball Creek near Pagosa Springs, Colorado, 7,200 ft. alt., August 6, 1912, *Arthur & Kern 5521* (type); Ute Park, Colfax County, New Mexico, August 25, 1916, *Paul C. Standley 13756.*

This rust is quite common in the Rocky Mountains from 7,000 to 10,000 feet altitude. The plants grow from two to three feet tall, and the long lanceolate leaves are often conspicuously yellowed by the abundant aecia, which show strongly against the cinereous surface of the host. It is undoubtedly a heteroecious species. In 1912 Dr. F. D. Kern and the writer searched the two localities where the rust was found by them for a possible alternate form, but in vain. Similar efforts have been made by Mr. E. Bethel, but with no better success.

Aecidium Pereziae sp. nov.

O. Pycnia chiefly epiphyllous, closely grouped, honey-yellow becoming brown, punctiform, noticeable, subepidermal.

I. Aecia hypophyllous, numerous, opposite the pycnia, in well-defined groups 0.3–0.6 mm. across, on roseate or yellowish spots 10–15 mm. across, cupulate; peridium usually erect, the margin erose or lacerate; peridial cells easily separating, rhomboid, little or no longer than broad, 19–26 by 26–37 μ, the outer wall 8–10 μ thick, faintly striate, the inner wall 3–6 μ thick, moderately verrucose; aeciospores globoid, 13–18 by 16–19 μ; wall nearly or quite colorless, thin, 1–1.5 μ, very minutely verrucose, appearing smooth when wet.

On *Perezia* sp., Barranca, Mexico, July 25, 1893, *C. G. Pringle*, communicated by W. G. Farlow. A distinctive species, and doubtless heteroecious.

Aecidium steviicola sp. nov.

O. Pycnia amphigenous, numerous, in loose groups, punctate, honey-yellow becoming brown, noticeable, subepidermal.

I. Aecia hypophyllous, in loose groups surrounding the pycnia on yellowish spots 10–15 mm. across, cupulate, the margin somewhat reverted, erose or lacerate; aeciospores globoid, large, 24–32 by 30–40 μ; wall colorless, rather thin, about 1.5 μ, considerably thickened above, 6–9 μ, minutely and closely verrucose.

On *Stevia* sp., Popo Park, Federal District of Mexico, August 4–8, 1910, *A. S. Hitchcock*.

This is doubtless a heteroecious form. It much resembles *A. roseum* Diet. & Holw., which occurs in Mexico on species of *Stevia*, but more abundantly on *Eupatorium*, and which is believed to be the aecial stage of a grass rust, probably *Aegopogon*, but the spores are nearly half as much longer than in that form, although in other respects there is close similarity.

Aecidium Keerliae sp. nov.

O. Pycnia amphigenous, in close groups 1–2 mm. across, honey-yellow becoming brown, punctiform, noticeable, subepidermal.

I. Aecia hypophyllous, in groups 3–8 mm. across, on somewhat larger, yellowish spots, cupulate, low; peridium slightly recurved, erose or lacerate; aeciospores globoid or ellipsoid, small, 12–18 by 15–20 μ; wall nearly or quite colorless, thin, 1 μ, much thicker above, 3–6 μ, finely and closely verrucose.

On *Keerlia mexicana* A. Gray, Guadalajara, Mexico, July 14, 1893, *C. G. Pringle*, communicated by W. G. Farlow. A species of the general characteristics of *A. roseum* and *A. steviicola*, both of which are also on carduaceous hosts, but with very much smaller spores. It is likely to prove to be heteroecious.

Uredo egenula sp. nov.

II. Uredinia epiphyllous, scattered, oblong or linear, 0.1–1.2 mm. long, early naked, pulverulent, cinnamon-brown, ruptured epidermis evident; urediniospores globoid to broadly ellipsoid, 21–25 by 26–34 μ; wall cinnamon-brown, 1.5–2.5 μ thick, moderately echinulate, the pores 2, equatorial, prominent.

On *Sporobolus argutus* (Nees) Kunth, alkali soil below Gregory Park, Healthshire Hills, Halfmoon Bay, Jamaica, West Indies. The specimen was removed from a phanerogamic collection in the National Herbarium, made October 31, 1912, by *A. S. Hitchcock 9760*, and communicated by Mrs. Agnes Chase. The form is one that seems to fit no recorded species on *Sporobolus*. It is named and described in order to call attention to the need of search for the telial stage, and of observations that may eventually lead to finding the aecia.

Uredo panamensis sp. nov.

II. Uredinia hypophyllous, crowded in circinating groups 2–3 mm. across on slightly discolored spots of nearly the same size, round or oblong, 0.3–0.5 mm. in diameter, the central one usually much larger, subepidermal, early naked, applanate, cinnamon-brown, ruptured epidermis evident; urediniospores globoid or broadly ellipsoid, 20–27 by 24–31 μ; wall cinnamon-brown, rather thick, 2–3 μ, very closely echinulate, often appearing verrucose, the pores distinct, 3, approximately equatorial.

On *Phytolacca decandra* L., Panama, December 7, 1915, *E. W. D. Holway 234*. The sorus is without special inclosing structures, and resembles the form common for the genera *Puccinia* and *Uromyces*. The species is quite unlike *Puccinia Rivinae* (B. & C.) Speg., the only other rust known on this family of hosts.

Uredo unilateralis sp. nov.

II. Uredinia hypophyllous, in groups 2–4 mm. across, more or less circinate, or scattered, round, 0.2–0.8 mm. in diameter, soon naked, cinnamon-brown, somewhat pulverulent, ruptured epidermis evident; urediniospores broadly obovate, or spatulate-obovate, flattened or concave on one side, 20–26 by 26–32 µ; wall cinnamon-brown, uniformly thick, 1.5–2 µ, sparsely and noticeably echinulate except on concave side which is smooth, with one pore on concave side, subequatorial, sometimes near hilum.

On *Geranium mexicanum* H.B.K., Amecameca, Mexico, October 6, 1900, *E. W. D. Holway.* A unique form on account of the spore having a smooth, concave side, bearing the single pore.

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A striking variation in Silene noctiflora

E. P. HUMBERT

(WITH TWO TEXT FIGURES)

From some *Silene noctiflora* seeds planted in the greenhouse December 1, 1917, one very interesting plant has developed. The normal *Silene noctiflora* seedling has two seed-leaves and succeeding leaves are in whorls of two, or opposite, each pair being placed over the intervals between the preceding pair. The pairs cross at right angles or decussate. This is illustrated in FIG. 1, a reproduction of a normal seedling. The plant which is the occasion of this sketch produced three seed-leaves and the succeeding leaves were arranged in whorls of three, each leaf of the

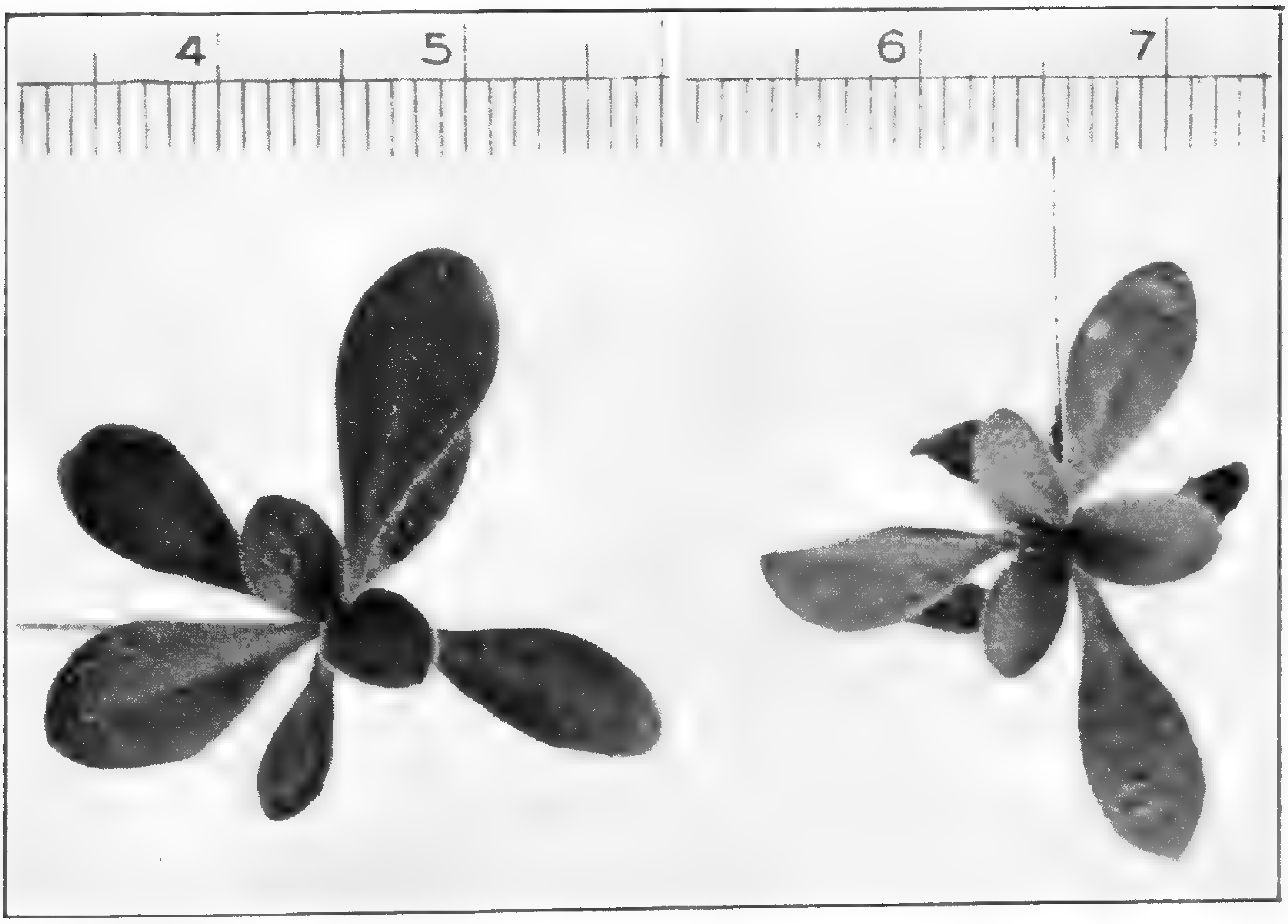

FIG. 1. FIG. 2.

FIG. 1. Normal *Silene noctiflora* seedling with two seed-leaves and two leaves in each succeeding whorl, × 2.

FIG. 2. *Silene noctiflora* seedling with three seed-leaves and three leaves in each of the two succeeding whorls, × 2.

new whorl being placed above an interval between leaves of the preceding whorl. FIG. 2 is reproduced from a photograph of this plant.

It is no uncommon thing to find *Silene noctiflora* seedlings with divided seed-leaves. All gradations have been noted from the extreme where both seed-leaves are completely divided, giving the appearance of four seed-leaves, to a partial division of one seed-leaf. When one seed-leaf is divided the seedling has the appearance of a plant with three seed-leaves. In all such monstrosities, however, the leaves which follow the seed-leaves are opposite and the plant is thereafter quite normal. The plant here pictured in FIG. 2 is the first one observed to show a completely altered phyllotaxy.

Silene noctiflora seeds were secured from the Department of Plant Breeding, Cornell University, in the fall of 1916, and an attempt was made to grow seedlings in the garden in 1917. Only one (very much stunted) plant produced seed, due to unfavorable environment. The seed from this plant produced the seedlings pictured.

AGRICULTURAL EXPERIMENT STATION,
COLLEGE STATION, TEXAS

INDEX TO AMERICAN BOTANICAL LITERATURE

1911-1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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Includes *Tilletia Wilcoxiana* from America.

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Vol. 45 No. 5

BULLETIN

OF THE

TORREY BOTANICAL CLUB

MAY, 1918

Studies in the genus Lupinus—III. Lupinus densiflorus

CHARLES PIPER SMITH

(WITH TEXT FIGURES 17–42)

Having, in my last paper, disposed of all the other species of the *Microcarpi*, I will confine this paper to my discussion and classification of *L. densiflorus* and its numerous varieties.

6. LUPINUS DENSIFLORUS Benth. Trans. Hort. Soc. II. **1**: 410. 1835. [FIG. 17.]

The original description reads:

> L. annuus, caulibus adscendentibus basi foliosus foliisque subsericeo-pilosis, foliolis oblongo-spathulatis, verticillis numerosis approximatis 6–10 floris, pedicellis ebracteatis, calycis labiis subintegris superiore membranaceo inferiore piloso duplo longiore, leguminibus villosis dispermis.
>
> The flowers, which grow in distinct whorls, are white, delicately stained with pink, they are also a little speckled at the base of the vexillum. The leaves are closely clustered together, are covered with fine soft hairs, and each has about nine narrow divisions. The stem does not grow above six or seven inches high.
>
> This species has hitherto produced its seeds, which are of an olive green, smooth, and minutely dotted with black, in very small quantity. It is probable that it requires shade.

In the same year Lindley, in the Botanical Register (**20**: *pl. 1689*), published a very interesting plate of *L. densiflorus* (see FIG. 17), and, in addition to quoting Bentham's description, gave a description of his own. From this I quote:

> Annuus; caulo erecto . . . villoso, in spontanea pedunculo communi multo breviore . . . foliolis in spontanea pedunculo longioribus, culta brevioribus. . . . Verticilli villosissimi, 6–10 flori . . . approximati inferioribus magis distantibus. . . . Calyx villosus, in cultu tantum pubescens; bracteolis setaceis labii superioris longi-

---

[The BULLETIN for April (**45**: 133–166, *pl. 6*) was issued May 1, 1918.]

tudine; lab. sup. bipartito . . . intermedio minimo, superiore breviore. (Obs. partes in icone incuria pictoris false delineantur.) Vexillum lacteum, acutiusculum, basi viridi-punctatum; alae et carina acuminatae, roseae. . . . Semina olivacea, laevia, nigro maculata.

Lindley thus records his observation as to the differences between the specimens collected by Douglas in California and those grown in England from seed also collected by Douglas. While the plate may not be altogether satisfactory, it at least shows that the flowers were spreading in anthesis, and substantiates my conception of the species *sensu lato*.

About the same time Agardh saw the specimens in Lindley's herbarium and decided that there were at least two species. In his monographic "Synopsis Generis Lupini," also bearing the date of 1835, he described his *L. Menziesii* and made his own disposition of Bentham's species, without making mention of the specimens grown from seed. His two descriptions, in part, follow:

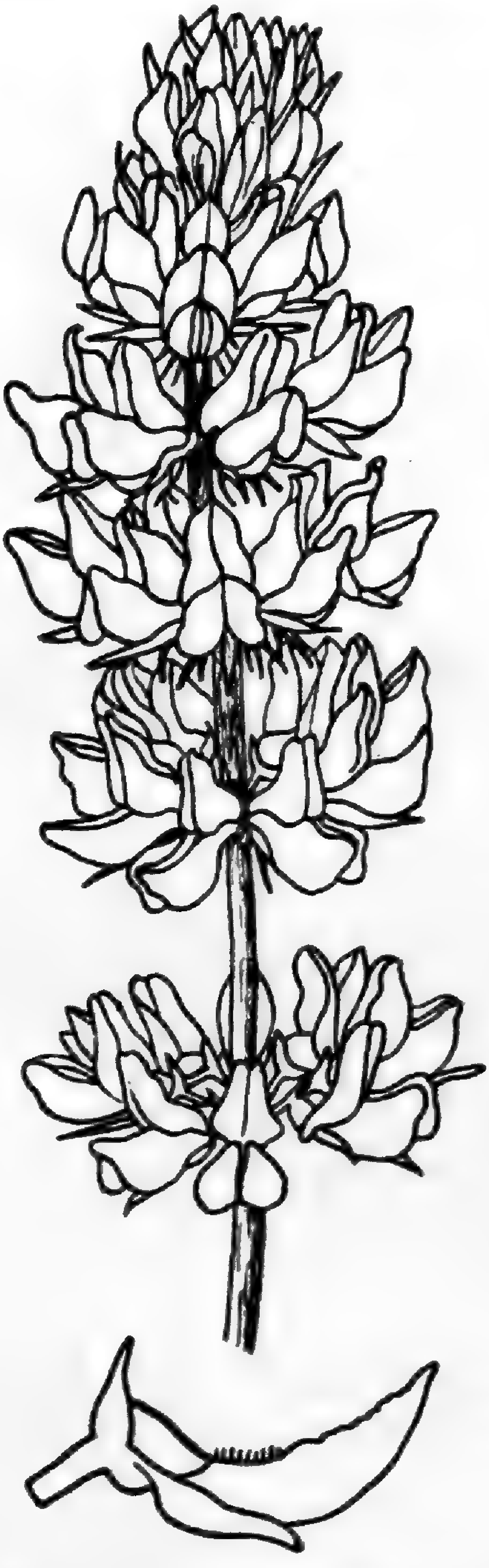

FIG. 17. LUPINUS DENSIFLORUS Benth. Copied from the original plate.

2. L. Menziesii nob. floribus in spica longissima verticillatis pedicellatis, pedicellis bracteas setaceas persistens subaequentibus, calycis ebracteolati labiis integris, superiore scarioso, inferiore herbaceo duplo longiore.

Hab. A Douglas e California reportatum. Vidi in Hb. Lindleyi.

Pedunculus terminalis longissimus (ultra pedalis) . . . subglaber, inferne pilis sparsis. . . . Foliola supra glabre, subtus pilosa. . . . Verticilli longe distantes, 5–6 flori. . . . Calyx ebracteolatus, pubescens, labio inferiore viridi, maximo, subinflato, superius scariosum, acuminatum plus duplo superante. Corollae luteae . . . carina valde curvata, apice ochracea. . . .

Singularis species primo aspectu corollis luteis verticillatis L. luteum referens; notis allatis tamen abunde diversa. Calyce singulari ad sequ. accedens, inter utramque collocanda videtur.

4. L. densiflorus Benth. floribus in spica densa verticillatis . . . bracteis persistentibus reflexis, corollam aequantibus, calycis ebracteolati labio sup. emarginato, inf. duplo longiore villosissimo tridentato.

L. densiflorus Benth. Hort. Trans. n. ser. v. I p. 409. Edwards Bot. Register. t. 1689.

Hab. E. California reportavit Douglas. Vidi in Hb. Lindl.

Habitus et fere characteres omnes praecedentis, sed robustior et villo longiore praecepue in partibus floralibus obsitus. . . . In speciminibus, quae coram habeo, differentia stipularum insignis; . . . Habitus etiam aliquantulum diversus, ita ut 2: as species hic latere, facile crediderum.

Agardh's treatment, perhaps because published in a monograph, was followed by Torrey and Gray in their Flora of North America; but Bentham (Pl. Hartweg. 303. 1848), some fifteen years after publishing his species, recorded a Monterey specimen thus:

1692 (53). *Lupinus densiflorus*, Ag.—Torr. & Gr. Fl. N. Amer. 1, p. 371, excl. syn. Benth.—In pascuis juxta Monterey.—Planta Douglasiana quam sub nomine L. densiflori olim descripsi est *L. Menziesii* Ag.—Torr. et Gr. Fl. N. Amer. 1, p. 371, quam etiam legit cl. Coulter inter San Miguel et Santa Barbara.

A few years later, Dr. Torrey (Pac. R. R. Report, 1853–4, Botany **4**: 81. 1856) gave us the following views:

LUPINUS DENSIFLORUS, Benth. . . . Mr. Bentham (in Pl. Hartweg p. 303) points out that Agardh has founded his L. Menziesii upon the Douglasian plant, which he had described as L. densiflorus. All confusion about the synonymy may be avoided, however, for the two species, L. densiflorus and L. Menziesii, Ag., cannot be kept distinct. Both have white flowers (Agardh wrongly attributes yellow corollas to his L. Menziesii, but his guess from the appearance in dried specimens is not correct in this, nor in some other instances); and the longer bracts and very villous calyxes of Agardh's L. densiflorus are evidently not available for a specific distinction. Dr. Bigelow's specimens, however, correspond in this respect with L. Menziesii.

In Watson's review (Proc. Amer. Acad. **8**: 538. 1873) the species is treated thus:

L. DENSIFLORUS, Benth. Much resembling the last [*L. microcarpus*], but more sparingly villous with shorter hairs; bracts much shorter than the calyx, which is smooth or short-pubescent, the upper lip often entire; petals yellow, or ochroleucous, white or pink.—From the Sacramento Valley southward. It includes *L. Menziesii*, Agh.; and *L. succulentus*, Koch, is probably but a garden form.

None of the writers quoted above may be credited with having done much field work in California, and it may be well to note here a mere gleaning from the writings of a Californian, Dr. Kellogg of San Francisco, a man of extended field observations with a keen appreciation for plant differences. In his comments upon the plant named by him as *L. lacteus* (Proc. Cal. Acad. Sci. **5**: 38. 1873), he says:

> Admitting *L. densiflorus* to be the same as *L. Menziesii*, with variations, it would then bring us to a " dense subsessile spike " . . . with which to contend. . . . If these and many more varieties prove ultimately to run into one, it is not our fault; as the literature now stands, we are obliged, in self-defence, to set it apart, when called upon for determinations.

Agardh's descriptions are certainly more comprehensive than Bentham's, but the evidence is clear that the specimens selected by him for his description of *L. densiflorus* were not typical of the species as known to Bentham. The latter's statement, however, that *L. Menziesii* of Torrey & Gray is the same as his *L. densiflorus* may be worthy of some careful weighing. I agree with both Torrey and Watson that these two names do not represent two separate species; but Torrey's statement in respect to the "yellow corollas" in *L. Menziesii* is evidently erroneous, as attested by many herbarium specimens and by my own and others' field observations. I also appreciate Kellogg's observation that "these and many more varieties" exist, and feel, as he felt, the need of a classification for their naming.

Very little can be gleaned from the published records of Douglas's sojourn in California. In his letter dated "Nov. 23rd 1831," written from "Monterey, Upper California" and published by Dr. Hooker (Comp. Bot. Mag. **2**: 149. 1836), he states that he arrived at Monterey on December 22, 1830. About the end of April, after various short excursions out of Monterey, he "undertook a journey southward, and reached Santa Barbara, 34° 25′, in the middle of May . . . and returned late in June, by the same route. . . . Shortly afterwards [he] started for San Francisco, and proceeded to the North of that port." His "last observation was at 30° 45′"; therefore in what is now Sonoma County, or possibly, but not probably, in Solano or Yolo County.

Study of the collectors' data with the numerous specimens examined by me while preparing this paper permits of some speculations that may be worthy of attention. One might thus conclude that Douglas's specimens were secured before leaving

Monterey for the north. Mature seed, however, might have been taken by him almost anywhere from Santa Barbara to Sonoma County. The "type" of Agardh's *L. Menziesii* probably came from San Luis Obispo County, while the "type" of *L. densiflorus* Agardh almost certainly came from the vicinity of Monterey. *L. densiflorus* Benth., however, was based upon specimens grown from seed collected by Douglas. The seed characters given by both Bentham and Lindley ought to be useful; but, unfortunately, the seeds of most of the varieties herein recognized are unknown, and none of those seen help much in the study from this angle. Therefore, what may be accepted as reliable diagnostic seed characters are yet to be worked out.

To sum up:—It seems to be an easy matter to establish the identity of *L. densiflorus* Benth., when such is recognized as a composite of numerous variable forms; but it is certainly a much more difficult matter to determine which of the several forms is properly to be designated as the typical plant. None of the varieties herein considered are known to combine a low stem six or seven inches high with pink-veined white petals and seeds smooth, olive-green, and minutely dotted with black. For the present, however, to serve as the typical form of the species, I am accepting a Sonoma County plant whose inflorescence, flower-color, and pubescence agree fairly well with Bentham's description and the plate in the Botanical Register, and whose period of blossoming at Santa Rosa, June 2, as found by Heller, would have permitted the collecting of seed by Douglas at the time of his visit to that region.

The following key will probably be useful in determining most of the material in the larger herbaria in terms of the varieties recognized in this paper. Undoubtedly additional varieties are yet to be added to the list.

Key to the varieties of Lupinus densiflorus

Calyx not bushy-villous below, the hairs 0.3–1.5 mm. long, bracteoles frequently present.

  Pubescence of stems and peduncles usually less than 1 mm. long, rather dense and subappressed or sparse and closely appressed; lower calyx-lip usually distinctly subsaccate and bent near base. DENSIFLORI.

    Leaflets thin or thickish, not blackening in drying.

- Simple or branched well above the base, foliage mostly open.
  - Calyx 7–8 mm. long; petals not yellow.
    - Banner 8 mm. wide; lower calyx-lip acute, the two teeth slender and parallel. 6*a*. typical *densiflorus*.
    - Banner 6 mm. wide; lower calyx-lip with broad sinus and a vestigial tooth. 6*b*. var. *stenopetalus*.
  - Calyx 9–12 mm. long; petals often yellow.
    - Flowers 16–19 mm. long; calyx 11–12 mm. long; banner 15–17 mm. long; petals usually not yellow, often rose-tinted. 6*c*. var. *perfistulosus*.
    - Flowers 13–15 mm. long; calyx 9 (rarely 10) mm. long; banner 14 mm. long; petals evidently yellow, often reddish- or purplish-tinged at the edges. 6*d*. var. *Menziesii*.
- Much branched at or near the base, the foliage congested.
  - Calyx bracteolate; lower lip obtuse, the teeth broad and diverging; petals drying a dark rose-purple. 6*e*. var. *latilabrus*.
  - Calyx ebracteolate, lower lip acutish, the teeth small and parallel; petals drying a rich blue. 6*f*. var. *Tracyi*.
- Leaflets almost succulent, blackening in drying; calyx bracteolate, lower lip acute and entire or minutely two- to three-toothed. 6*g*. var. *glareosus*.

Pubescence of stems and peduncles 1–1.5 mm. long, spreading or retrorsely spreading.

- Lower calyx-lip nearly straight, inconspicuously or not at all subsaccate and bent near base. LACTEI.
  - Acaulescent or nearly so, commonly simple with the central peduncle elongated.
    - Keel nearly straight; banner rather abruptly contracted into a well-defined claw. 6*h*. var. *lacteus*.
    - Keel evidently curved; banner gradually contracted into a poorly defined claw. 6*l*. var. *vastiticola*.
  - Stems and branches elongated, the branches usually all floriferous.
    - Flowers 14–16 mm. long; banner 15–16 mm. long; calyx hairs conspicuously retrorse-spreading, about 1 mm. long. 6*i*. var. *sublanatus*.
    - Flowers 12–14 mm. long; banner 11–14 mm. long.
      - Calyx 7 mm. long; banner rather abruptly contracted into a well-defined claw; keel nearly straight. 6*j*. var. *McGregori*.
      - Calyx 8 mm. long; banner gradually contracted into a poorly defined claw; keel evidently curved. 6*k*. var. *altus*.
- Lower calyx-lip usually distinctly subsaccate and bent near base; flowers 13–19 mm. long, banner 13–16 mm. long, calyx 8–10 mm. long. VERSABILES.

  - Branches ascending to suberect; whorls five to several.
    - Calyx commonly bracteolate, the hairs mostly 0.3–0.5 mm. long.
      - Calyx 10 mm. long, lower lip acutish, the teeth not broader than long. 6*m*. var. *versabilis*.
      - Calyx 8–9 mm. long, lower lip obtuse, the teeth broader than long. 6*n*. var. *latidens*.
    - Calyx rarely bracteolate, the hairs mostly 1.5 mm. long. 6*o*. var. *Dudleyi*.
  - Branches short and widely spreading; whorls two to five; flowers and fruits conspicuously secund. 6*p*. var. *persecundus*.
- Calyx bushy-villous below, the hairs 1.5–4 mm. long, ebracteolate. PALUSTRES.
  - Lower calyx-lip usually distinctly bent and inflated near base.
    - Flowers 13–14 mm. long; calyx 8 mm. long.
      - Lower lip two-toothed; keel slender; plants 30–60 cm. tall. 6*t*. var. *curvicarinus*.
      - Lower lip three-toothed; keel stout; plants low. 6*u*. var. *Reedii*.
    - Flowers 15–17 mm. long; calyx 9–12 mm. long.
      - Plants low, 8–15 cm. tall, the stems and branches short and usually widely spreading. 6*s*. var. *crinitus*.
      - Plants mostly erect, 20–60 cm. tall.
        - Banner rounded or truncate at apex; lower lip of calyx two-toothed, the middle tooth vestigial or wanting. 6*q*. var. *palustris*.
        - Banner acute or distinctly contracted apically; calyx three-toothed. 6*r*. var. *stanfordianus*.
  - Lower calyx-lip straight or nearly so, indistinctly or not at all bent and subsaccate near base.
    - Banner rounded or truncate at apex, 6 mm. wide; calyx 8–9 mm. long, two-toothed; plant densely villous. 6*v*. var. *trichocalyx*.
    - Banner mostly angled at apex.
      - Banner 11 mm. long, 5 mm. wide; calyx 8 mm. long, lower lip three-toothed, upper lip less than 2 mm. long. 6*w*. var. *barbatissimus*.
      - Banner 12–15 mm. long; calyx 10–13 mm. long, upper lip usually 3–4 mm. long.
        - Banner gradually contracted into an undifferentiated claw; wings naked or nearly so. 6*y*. var. *scopulorum*.
        - Banner contracted into a well-defined broad claw; wings ciliate at the upper basal angle.
          - Lower lip distinctly three- (rarely four-) toothed; leaflets conspicuously ciliate on the margins and midrib below. 6*r*. var. *stanfordianus*.
          - Lower lip two-toothed, the median tooth vestigial or wanting; leaflets not conspicuously ciliate. 6*x*. var. *austrocollium*.

DENSIFLORI

6*a*. LUPINUS DENSIFLORUS Benth. (typical).

Pubescence less than 1 mm. long; verticils six to nine; calyx about 8 mm. long, with short inconspicuous appressed pubescence, lower lip barely 3 mm. wide, acute, the two slender teeth with a very narrow sinus; petals white, tinted or veined with violet or rose, banner 14 mm. long, 8 mm. wide, keel 12 mm. long, relatively slender. Seed not seen.

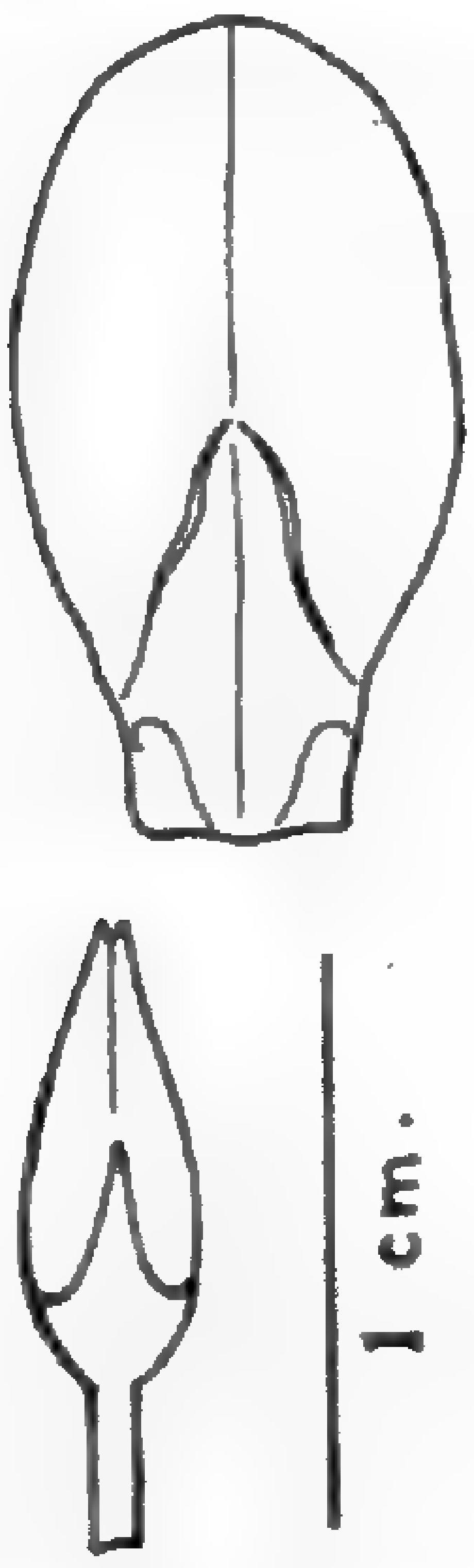

FIG. 18. LUPINUS DENSIFLORUS Benth. *A. A. Heller 5630* (US 416650).

CALIFORNIA. Sonoma County: Santa Rosa, 2 June, 1902, *A. A. Heller 5630* (DS, US, PA, NY, G). Napa County: Conn Valley, Napa River Basin, 1 May, 1894, *W. L. Jepson* (UC). Santa Clara County: Stanford University, 5 May, 1895, *Cloud Rutter 173* (UC 308269, middle and right-hand specimens only). County not given: Taylor Mountain, 20 Apr., 1898, *M. S. Baker* (UC).

6*b*. **Lupinus densiflorus stenopetalus** var. nov. [FIG. 19.]

Vexillo gracillimo, 13–14 mm. longo, 6 mm. lato, ungue gracili prope 2 mm. lato, contracto; calyce 8 mm. longo, labio inferiore bidentato, sinu lato dentis vestigio instructo, dentibus curvis; semina non vidi.

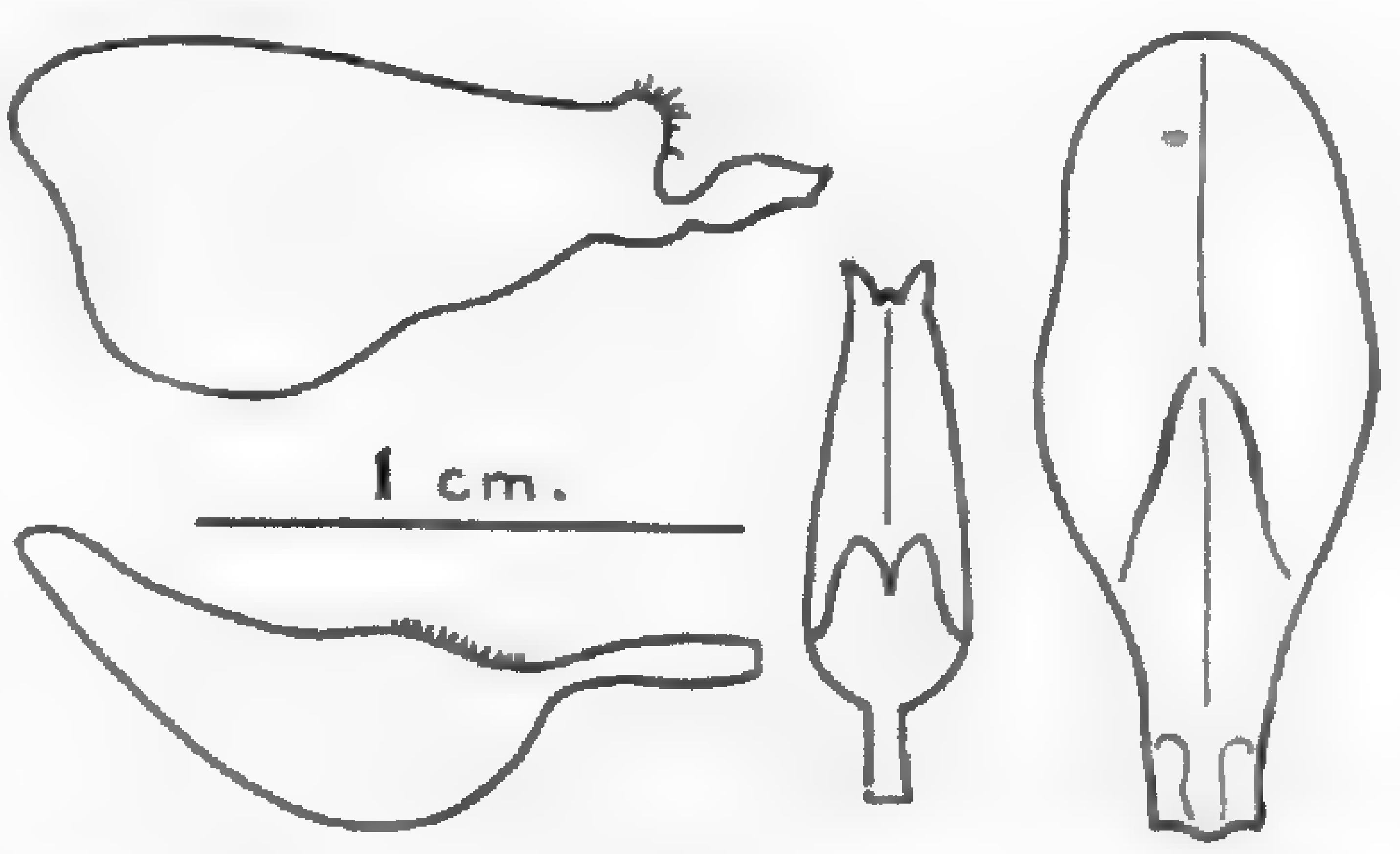

FIG. 19. LUPINUS DENSIFLORUS STENOPETALUS C. P. Smith. *A. A. Heller 7385* (US 468403).

Petals white, more or less rose-purple edged, the banner unusually narrow, about 6 mm. wide, with the claw only 2 mm. wide; lower lip of the calyx two-toothed, the teeth curved and a vestigial median tooth usually present. Seed not seen.

CALIFORNIA. Santa Clara County: Los Gatos, 7 May, 1904, *A. A. Heller 7385* (TYPE, US 468403; type-duplicates, PA, NY, G). San Mateo County: San Francisquito Canyon, 27 May, 1905, *F. Grinnell* (US).

Stenopetalus, Greek for "slender petal," refers to the very narrow banner.

6c. **Lupinus densiflorus perfistulosus** var. nov. [FIG. 20.]

Ramosus plerumque aliquantum super basin quamquam interdum eramosus, 25–60 cm. altus; caule manifeste et ramis pedunculisque plus minusve fistulosis, minute laxe pubescentibus vel levibus; foliis patentibus; petiolis longissimis, 10–20 cm. longis; foliolis 6–10, 20–40 mm. longis, oblanceolatis acutis arcuatis paulo dense appresso-pubescentibus vel levibus subter; pedunculis elongatis, plerumque folia excedentibus; verticillis plurimum 6–12 vel pluris, appositis vel distantibus subter; floribus pandentibus, 15–19 mm. longis; pedicellis 3–4 mm. longis, prope 1 mm. latis; bracteis humillimis 12–15 mm. longis, breve-pubescentibus vel levibus; calyce 11–12 mm. longo, ebracteolato, appresso-pubescenti vel levi, labio superiore 2–4 mm. longo, emarginato, inferiore manifeste inflato, prope 4 mm. lato, 2-dentato, sinu gracili vel latiore dentis vestigio instructo; petalis diverse roseo- vel purpureotinctis, interdum luteis; vexillo 15–17 mm. longo, 9 mm. lato, apice rotundato paullatim contracto in unguem rigidum inflatum 5–6 mm. latum saepe retrorse dilatatum, labium superiore calycis repellentem; alis 13–15 mm. longis, ad basin superne ciliatis, 7 mm. latis, apicibus conspicue truncatis; carina 11–14 mm. longa, manifeste arcuata: legumina seminaque non vidi.

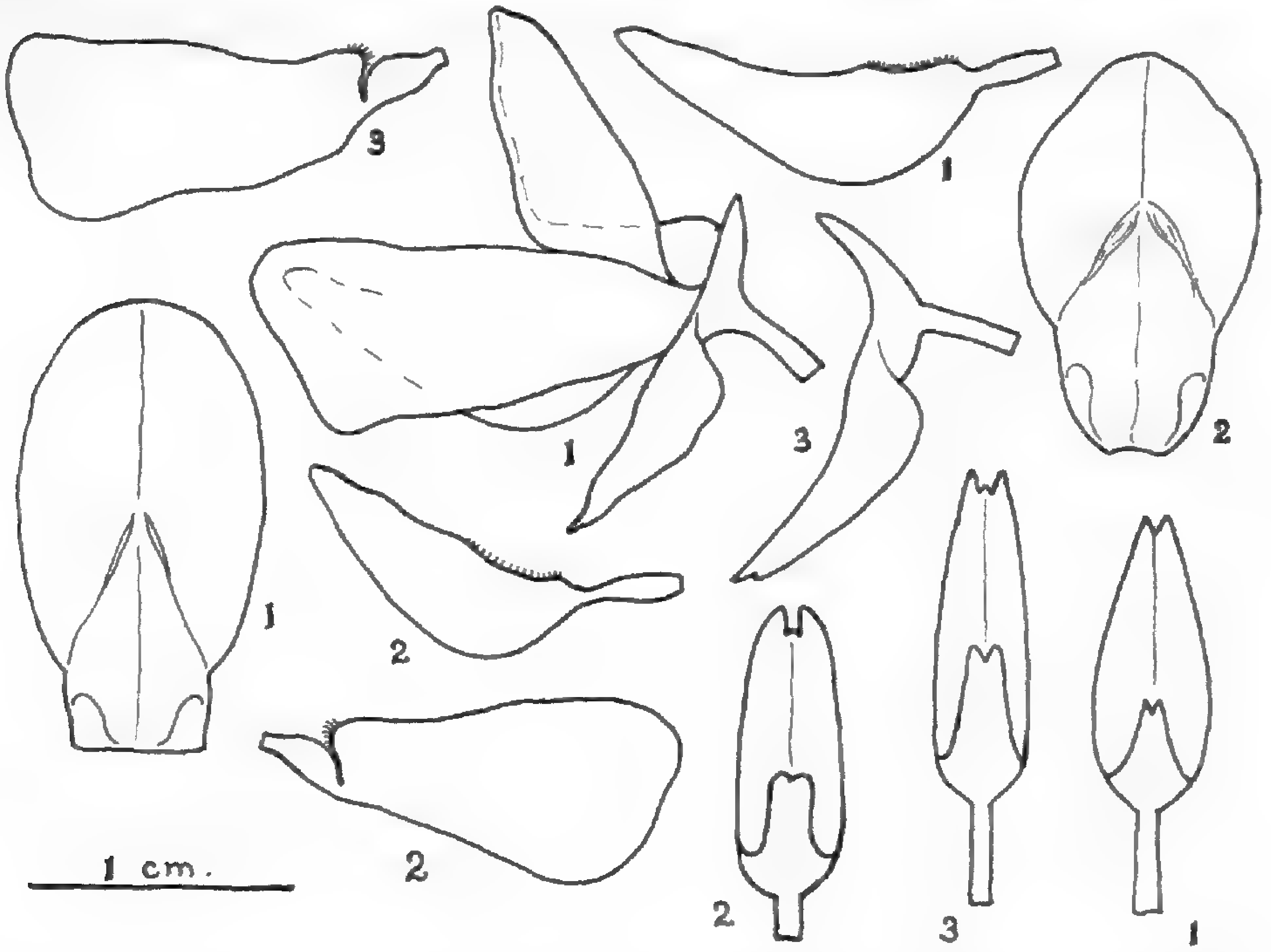

FIG. 20. LUPINUS DENSIFLORUS PERFISTULOSUS C. P. Smith. 1. *Heller & Brown 5376* (US 413708); 2. *W. H. Brewer 483* (US 321138); 3. *Heller & Brown 5381* (US 413713).

The most robust and largest-flowered variety of the species, unless equalled by var. *palustris;* often 60 cm. tall, stem usually fistulose; flowers 15–19 mm. long, banner 15–17 mm. long, rounded at the apex, the claw inflated and stiff, sometimes pushing back the upper calyx-lip, wings conspicuously truncate at the apex, lower calyx-lip strongly subsaccate and bent downward; pods and seeds, probably the largest of the species.

CALIFORNIA. County not given: 1868–9, *Kellogg & Harford 187* (TYPE, US 20645). Solano County: near Fairfield, 26 Apr., 1902, *Heller & Brown 5376* (US, G, NY, DS, PA); Gates Canyon, near Vacaville, 27 Apr., 1902, *Heller & Brown 5381* (US, PA, G); Vallejo, 11 May, 1874, *E. L. Greene 171* (G); Wolfskill, 2–6 May, 1891, *W. L. Jepson* (UC). Contra Costa County: Muir Station, July, 1904, *Charlotta Case* (UC). Yolo County: Rumsey, 7 May, 1903, *C. F. Baker 3070* (US, G); Woodland, 16 May, 1893, *J. W. Blankinship* (G). Butte County: "fields," May, 1898, *Mrs. C. C. Bruce 2033* (NY). Lake County: Burns Valley, Apr., 1902, *Agnes M. Bowman 146* (DS). San Luis Obispo County: San Luis Obispo, 27 Apr., 1861, *W. H. Brewer 483*, Geol. Sur. Cal., (US); May, 1893, *Mrs. Blochman* (UC).

Two other specimens that perhaps should have been listed above are: Little Oak, Solano County, 2–6 May, 1891, *W. L. Jepson* (UC), and Brighton, Sacramento County, Apr., 1884, *K. Brandegee* (UC). These, and also the Contra Costa plant listed, have a much denser pubescence than I have attributed to this variety and would probably not be easily traced here by the use of the key on pages 171–173. The last-mentioned plant is also a pathological individual, having leafy branches and one raceme developed from raceme-buds that normally should have produced flowers. Seeds with Jepson's "Little Oak" specimen are dull yellowish brown, finely and sparsely speckled with dark brown, 6 x 5 mm., decidedly flattened.

6*d*. **Lupinus densiflorus Menziesii** (Agardh) comb. nov. [FIG. 21.]

Lupinus Menziesii Agardh, Syn. Gen. Lup. 2. 1835.

Lupinus Menziesii aurea Kell. Proc. Cal. Acad. Sci. **5**: 16. 1873.

Agardh's description will be found on page 168, included in my general discussion of *L. densiflorus*, so will not be repeated here. The description of Kellogg's variety is as follows:

> Collected by Kellogg and Samuel Brannan, Jr., in Deer Valley, near Antioch, San Joaquin River, April 22d, 1869; chiefly differing from the accepted description of the species—if we include also *L. densiflorus*—in the 2-toothed lower lip, relative length of leaves, and the entire scarious tube of the calyx, etc.
>
> Stem fistulose, branching from near the axi[a]l summit, leaflets about 10, one third the length of the petiole, glabrous above, pubescent beneath, stipules and bracts scarious, setaceously long acuminate, persistent; calyx tube scarious, upper lip 2-toothed, deflexed, somewhat saccate; vexillum short, rounded outline, pubescent on the back at the base, and along the claw above. Legumes hirsute, minute, 2-seeded.

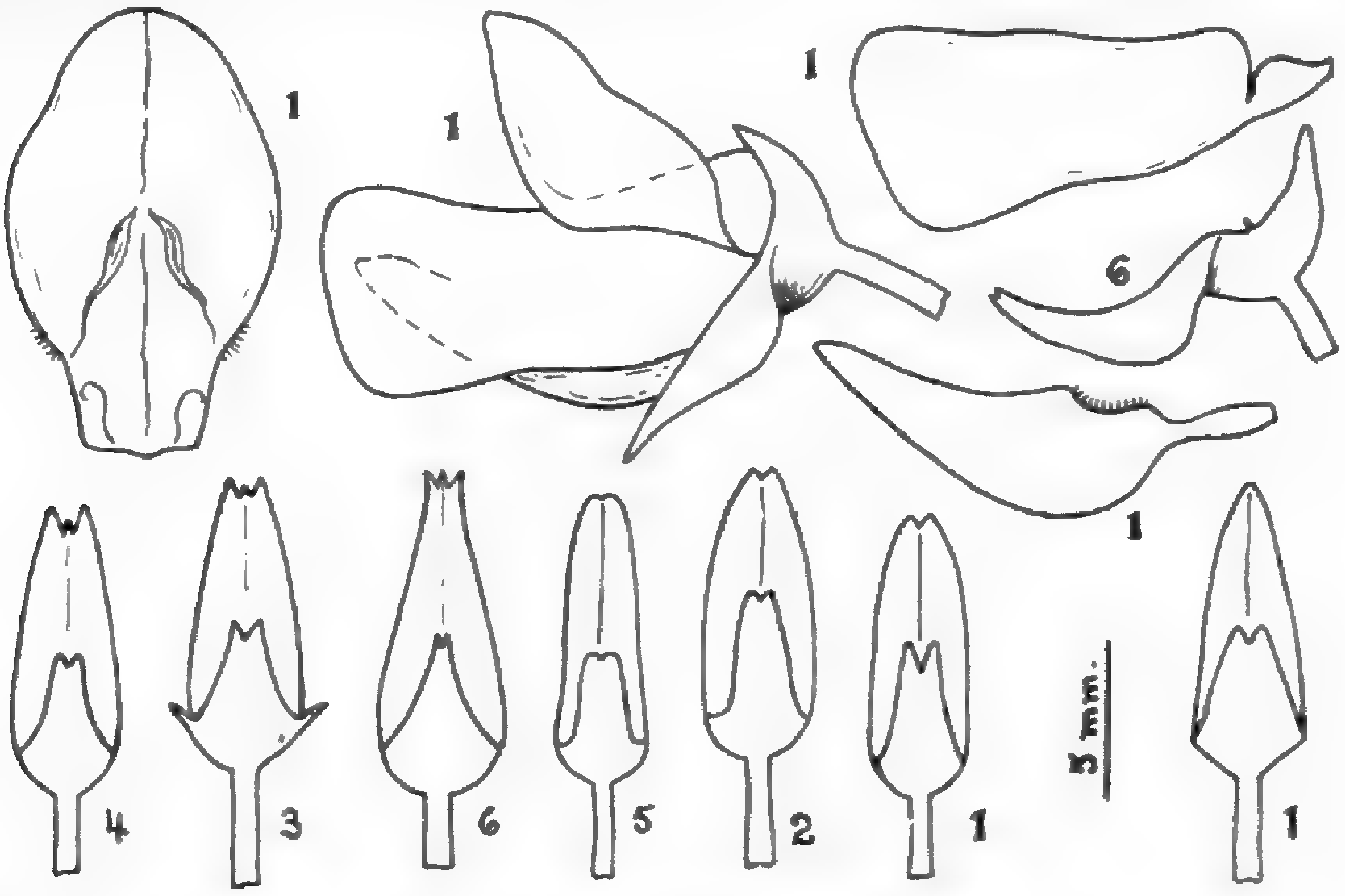

FIG. 21. LUPINUS DENSIFLORUS MENZIESII (Agardh) C. P. Smith. 1. *C. P. Smith 1456*; 2. *A. A. Heller 7311* (US 468336); 3. *A. A. Heller 7439* (US 468453); 4. *C. P. Smith 1484*; 5. *A. D. E. Elmer 4791* (US 665678); 6. *H. A. Walker 2526* (US 669625).

As I have stated in the foregoing pages, I agree with others that *L. Menziesii* is not specifically distinct from *L. densiflorus;* but, on the other hand, I consider it a readily recognizable variety, from which I do not feel justified in trying to separate Kellogg's var. *aurea*. The following description is supplementary to those given by others:

Flowers 14–15 mm. long; calyx rarely (*Heller 7439*) bracteolate, commonly 9 mm., rarely 10 mm. long, upper lip variable in form, 2.5–3.5 mm. long, lower lip acute or rounded at the tip and entire or two- to three-toothed, the teeth mostly less than 1 mm. long; petals bright yellow or paler, the apices and margins often washed with some shade of reddish purple; banner 12–14 mm. long, 7–8 mm. wide, rather abruptly contracted into a claw 4 mm. wide;

wings 11–12 mm. long, 6 mm. wide; pods conspicuously secund; seeds about 4.5 x 4 mm. long, yellowish brown, speckled with darker brown, the dark "lateral lines" enclosing a paler area about the hilum, plump or somewhat flattened.

CALIFORNIA. County not given: *D. Douglas* (T, G); *T. Bridges 59* (T, Col. U, NY, G, US). Sacramento County: Elk Grove, May, 1882, *E. R. Drew* (UC). Contra Costa County: Port Costa, 8 June, 1892, *T. S. Brandegee* (DS, NY); Antioch, 3 May, 1893, *A. Eastwood* (G); Antioch, 5 May, 1907, *K. Brandegee* (UC 155195, as to specimen in center of sheet); near Point Isabel, 8 July, 1911, *H. A. Walker 2526* (US, G). Marin County: Ross Landing, Aug., 1877, *H. Edwards* (NY). Alameda County: between Mission San Jose and Livermore, 13 Apr., 1904, *A. A. Heller 7311* (US, UC, PA, G); Mission San Jose, June, 1909, *R. J. Smith 7* (UC); Oakland, 1875, *G. R. Vasey* (US). Santa Clara County: Evergreen, 11 Apr., 1893, *J. B. Davy* (UC); Gilroy, May, 1903, *A. D. E. Elmer 4791* (US); Mt. Hamilton road, fourteen miles from San Jose, 20 May, 1904, *A. A. Heller 7439* (US); Mt. Hamilton road, Halls Valley, 1950 ft. alt., 17 June, 1908, *C. P. Smith 1484* (CPS). Santa Cruz County: along Southern Pacific Railway, east of Ellicott, 4 June, 1908, *C. P. Smith 1456* (CPS). San Luis Obispo County: open hills near sea, 1 Mar., 1883, *Mrs. R. W. Summers* (G); near boundary line of Santa Barbara County, 8 May, 1896, *A. Eastwood* (G); Newhall Ranch, 8 May, 1900, *J. H. Barber* (G).

6*e*. **Lupinus densiflorus latilabrus** var. nov. [FIG. 22.]

Caule ad basin ramoso, ramulis foliisque congestis; foliolis 5–8, 10–25 mm. longis, 2–3 mm. latis; verticillis 3–5, floribus 13–15 mm. longis, pedicellis brevibus; calyce bracteolato 8 mm. longo, pilis subappressis 0.5 mm. longis, labio inferiore 4 mm. lato apice obtuso

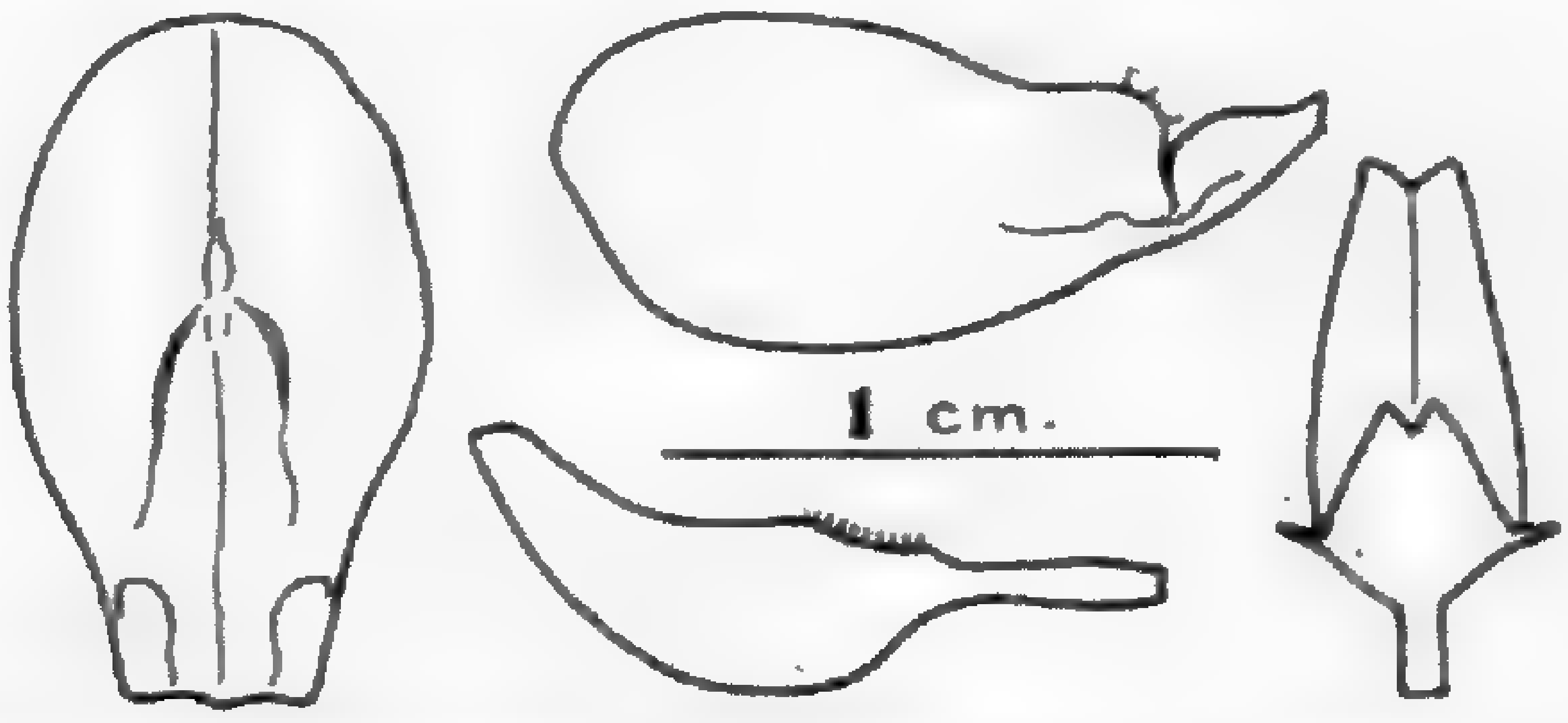

FIG. 22. LUPINUS DENSIFLORUS LATILABRUS C. P. Smith. *E. Braunton 1081* (US 469834).

2-dentato, dentibus latis brevibusque, sinu brevissimo; petalis ad dimidia terminata roseo-purpureis, ad basin pallidis; vexillo prope 12 mm. longo, 8 mm. lato, apice rotundato; alis 11 mm. longis, vix ciliatis ad basin superne; carina 9–10 mm. longa, paulo curvata; leguminibus prope 14 mm. longis; semina matura non vidi.

Differs from var. *Menziesii* in the stem being branched at the base, the branchlets and foliage congested; whorls few and pedicels short and stout; calyx with bractlets, the lower lip relatively wide at the blunt apex, the two teeth short and wide; keel not much curved; terminal half of petals a dark rose purple when dried.

CALIFORNIA. Amador County: vicinity of Ione, 200–500 ft. alt., June, 1904, *E. Braunton 1081* (TYPE, US 469834; type-duplicates, NY, UC).

Latilabrum is Latin for " broad lip."

6*f*. **Lupinus densiflorus Tracyi** var. nov. [FIG. 23.]

Caule ramosissimo ad basin foliis congestis; labio inferiore calycis apice acuto bidentato, dentis sinuque gracilibus; petalis pallido-carnosis, ad anthesin atro-caeruleis cum siccatis; vexillo 12 mm. longo, 8 mm. lato, ungue non claro; alis carinaque latis: legumina seminaque non vidi.

Much branched at the base with the foliage congested; lower calyx-lip acute, the two teeth and their sinus narrow; petals pale flesh-colored when fresh (according to the label), largely a rich blue in the preserved specimen; banner 12 mm. long, 8 mm. wide, the claw not well defined; wings and keel relatively broad.

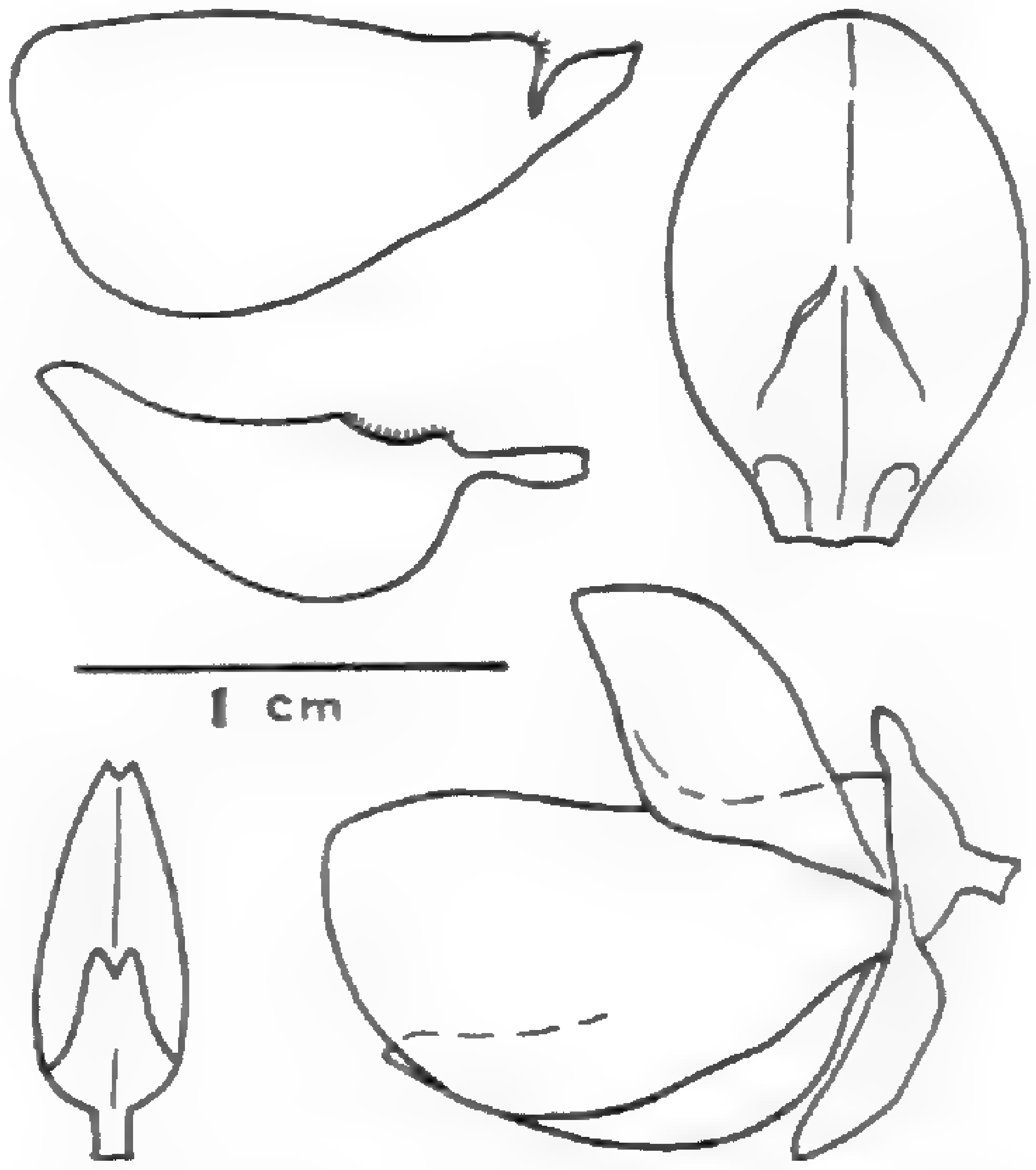

FIG. 23. LUPINUS DENSIFLORUS TRACYI C. P. Smith. *J. P. Tracy 3280* (UC 161546).

CALIFORNIA. Humboldt County: gravel bar of Willow Creek, Trinity River Valley, 4 July, 1911, *J. P. Tracy 3280* (TYPE, UC 161546), labelled " *L. microcarpus.*"

6g. **Lupinus densiflorus glareosus** (Elmer) comb. nov. [FIG. 24.]
Lupinus glareosus Elmer, Bot. Gaz. **39**: 53. 1905.

I quote from Elmer's description, as follows:

> An almost acaulescent annual, 3–5 dm. high, somewhat succulent though readily curing: stem very short, rather thick and hollow, terminated by a spicate inflorescence; branches with a soft short brownish pubescence, chiefly from the stem, the outer ones curved upwards from the middle . . . leaflets 10 . . . sparsely pubescent on both sides, soft and fleshy . . . the older ones with a very peculiar dead scarious margin: spikes cylindrical . . . 10–15 cm. long, erect and exceeding the leaves . . . flowers in whorls of 5, upon short pubescent pedicels . . . calyx . . . pubescent; lower lip rather broad, 7 mm. long, obtuse, 3-nerved; upper one thinner, 3 mm. long, notched; banner broadly elliptic, 12 mm. long . . . keel at least 12 mm. long, falcate . . . with the margin of the aperture densely ciliate . . . seeds . . . smooth, compressed.
>
> Griffin's Postoffice, Ventura County, California, July, 1902. Type specimen, no. 3588, in Herb. Stanford University.
>
> It is wholly confined to dry gravelly soil along water courses, hence its name.

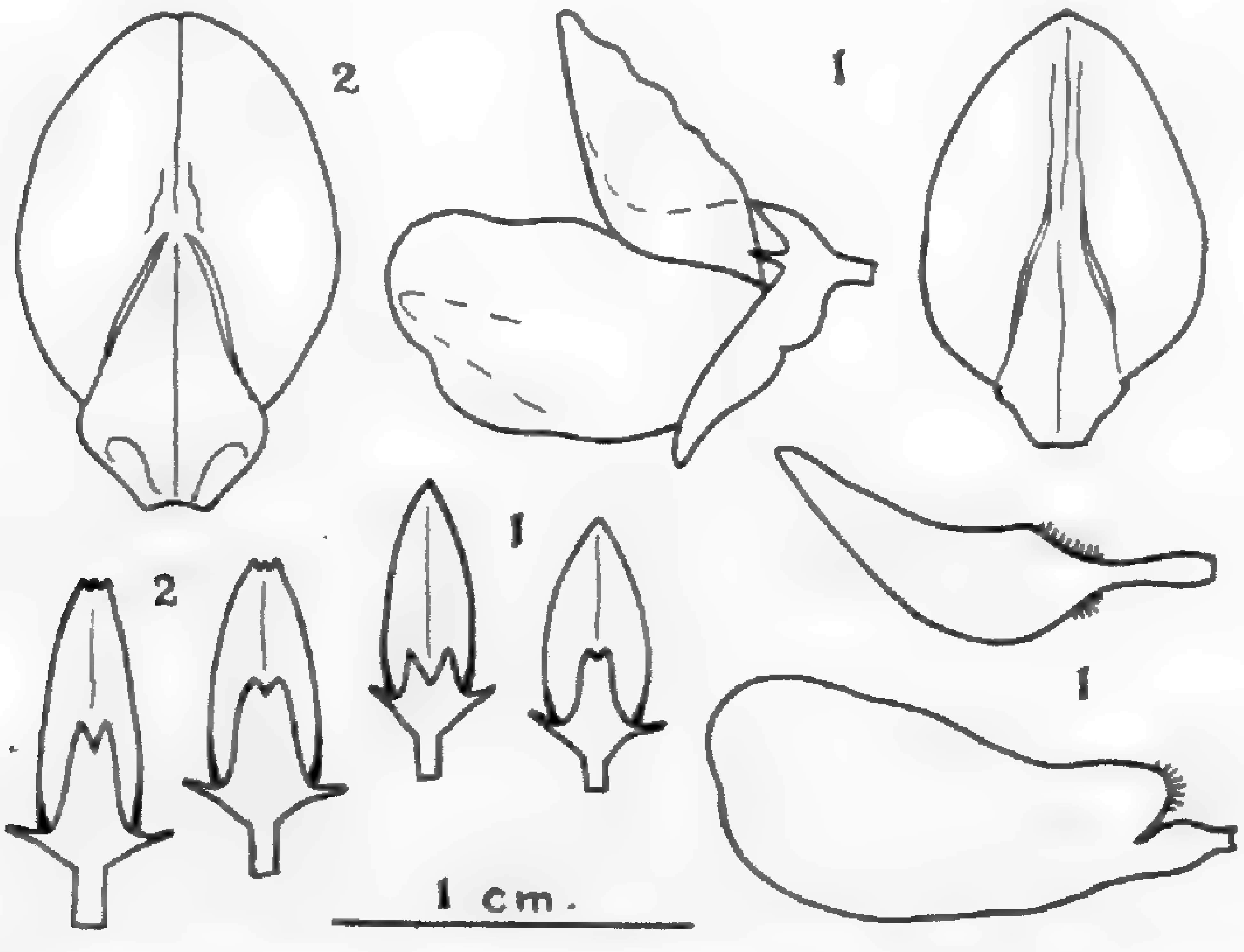

FIG. 24. LUPINUS DENSIFLORUS GLAREOSUS (Elmer) C. P. Smith. 1. *A. D. E. Elmer 3588* (US 465791); 2. *Abrams & McGregor 262* (US 613146).

I consider this one of the most extreme variations of *L. densiflorus*, and I would have upheld it as a species but for the evidence presented by Abrams & McGregor's collection listed below. The following characters should also be mentioned.

Foliage blackening in drying; verticils crowded or distinct, six to twelve or fewer; flowers spreading in anthesis, becoming secund later, 13–14 mm. long; calyx bracteolate, 6.5–8 mm. long, very shortly and almost sparsely appressed-pubescent, upper lip a little more than 1 mm. long and cleft, or 2–3 mm. long and emarginate, lower lip entire and acute or minutely three-toothed, about 3 mm.

wide; petals (according to Dr. Hall's labels) light blue, the banner with a white center; banner 12–14 mm. long, 8–9 mm. wide, ovate to "broadly elliptic," obtusely angled, truncate, or rounded at the apex, the basal inflation much thickened and stiff; seeds pale yellowish brown, sparsely mottled with dark brown, the considerably paler hilum area marked off by prominent V-shaped lines.

CALIFORNIA. Ventura County: Griffin's Postoffice, June, 1902, *A. D. E. Elmer 3588* (DS, US, NY); Griffin, Mt. Pinos, 20 June, 1905, *H. M. Hall 6334* (G, UC); near Frazier borax mine, Mt. Pinos, 12–14 June, 1908, *Abrams & McGregor 262* (DS, US).

While with his description Elmer gives the date of collection of his number 3588 as July, 1902, his labels give June as the month. His number 4006, however, from the same locality, is labeled as having been taken in July; but the latter is a very different plant, and has been treated by me elsewhere as *L. subvexus nigrescens* (Bull. Torrey Club **45**: 13. 1918).

LACTEI

6h. **Lupinus densiflorus lacteus** (Kell.) comb. nov. [FIG. 25.]
Lupinus lacteus Kell. Proc. Cal. Acad. Sci. **5**: 37. 1873.
Lupinus arenicola Heller, Muhlenbergia **2**: 75. 1905.

Kellogg's description of *L. lacteus* is, in part, as follows:

> Stem annual, fistulous, the elongated central peduncle from a mere depressed crown, mostly solitary, spike 4 to 8 inches long, lateral radicle branches 2 to 6 inches long, with secondary clusters of leaves and (when present) shorter spikes, soft pubescent throughout, with white hairs. Leaves mostly clustered at the base . . . leaflets . . . silky-pubescent beneath. . . . Flowers large, white, somewhat distant, verticillate . . . calyx ebracteolate, hirsute . . . upper lip 2-cleft (rarely entire) about ⅓ the length of the lower lip, lower lip straight, herbaceous, 2-toothed . . . vexillum . . . ciliate at the marginal juncture of the claw . . . banner, wings and keel about equal, wings oblong . . . margins ciliate at the base or origin of the claw; keel ciliate at the upper inside margin toward the base.
>
> In habit and general appearance this species resembles *L. brevicaulis*, but is rather more robust, the flowers much larger and not "deep blue," but quite *white*, . . . It is closely allied to *L. Menziesii*. . . . Specimens collected by Mr. S. Brannan, Jr., on Oak Creek hillsides, Kern County, 14 miles from Tejon Pass.

Extracts from Heller's description of *L. arenicola* follow:

> Branches several, ascending, commonly only the middle one floriferous . . . flowers in 1 to 3 whorls, merely ascending, whitish or rose color, 1.5 cm. long . . . calyx with broad acutish lower lip 7 mm. long, 5 mm. wide at base, the apex minutely 2-toothed; upper lip ovate . . . the apex 2-toothed, the teeth 1 mm. long, slightly spreading; banner turned back . . . keel . . . little curved, ciliate on the lower half, . . . seeds large, 4 mm. in diameter, white or whitish.

> The type is no. 7609, collected April 7, 1905, near the first crossing of the creek west of Caliente, Kern county, California, growing in sandy soil on steep banks near the railroad. It also occurs on the bluffs of Kern River above Bakersfield.

Heller, writing some five years later (Muhlenbergia **6**: 70. 1910), says:

> It gives me great pleasure to reinstate this long unrecognized species [*L. lacteus*], even at the expense of one of my own names. The species was barely published before it was suppressed by Watson in Proc. Am. Acad. 8: 542, November, 1873. He there puts it down as a synonym of *L. densiflorus*, but evidently never saw the plant itself, for he does not mention it in the list of specimens examined. During the course of five years he came to another conclusion, for in the Bibliographical Index, published in 1878, it is said to be the same as *L. microcarpus*, a less satisfactory disposition than the first, for it is clearly more related to *L. densiflorus* than it is to the narrow-flowered *L. microcarpus*.
>
> The type of *L. arenicola* shows a bractlet in the sinus between the calyx lobes, whereas Kellogg says it is not present.

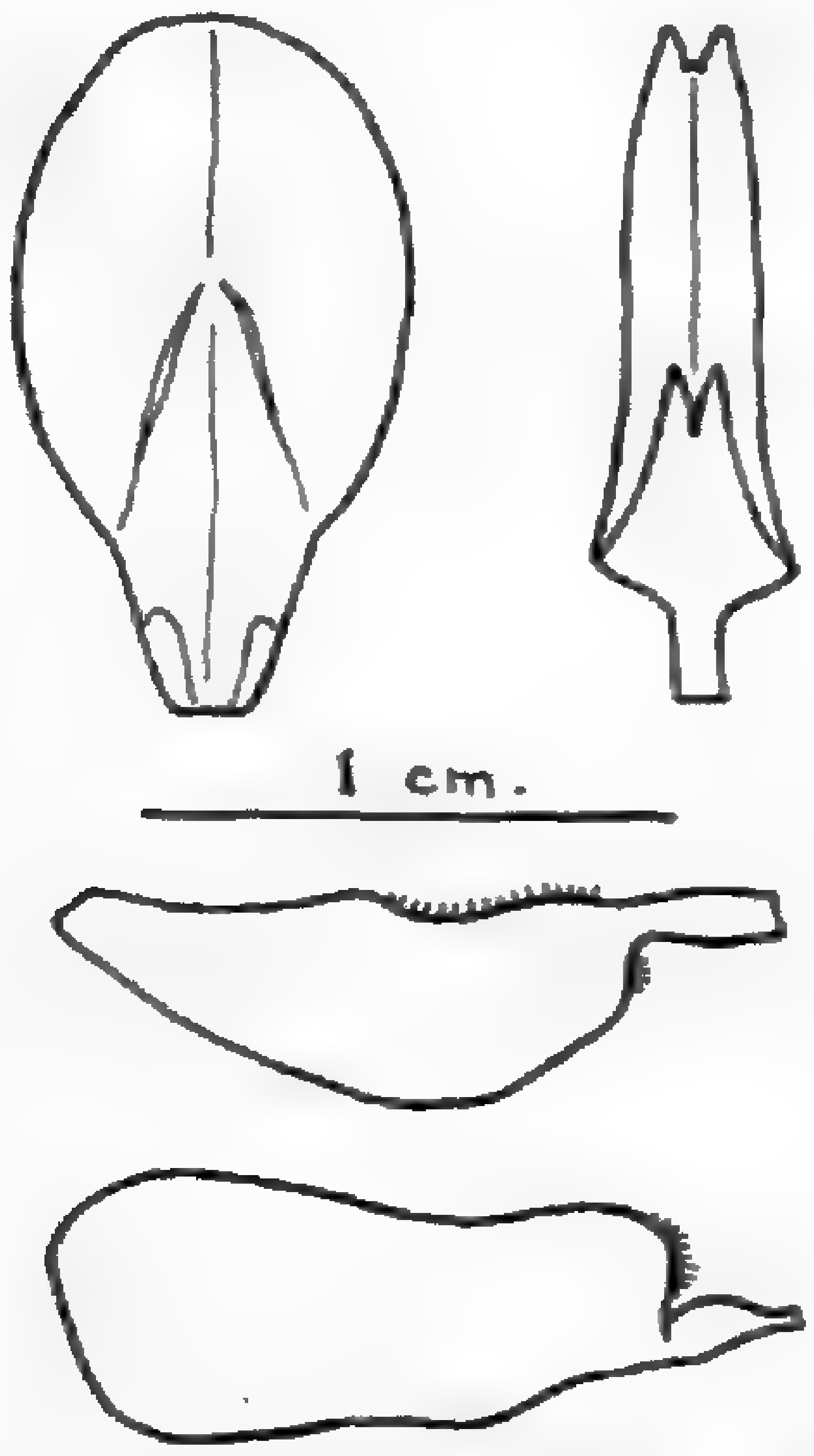

FIG. 25. LUPINUS DENSIFLORUS LACTEUS (Kell.) C. P. Smith. *C. A. Purpus 5301* (US 328676).

CALIFORNIA. Kern County: near Caliente, *A. A. Heller 7609* (US, G, NY, PA); Bakersfield, 26 Apr.–30 May, 1896, *J. B. Davy 1716* (G). Ventura County: Ojai and vicinity, 25 Apr., 1866, *S. F. Peckham* (US); Ojai Valley, 18 Apr., 1896, *F. W. Hubby 34* (UC). Tulare County: North Tule River, May, 1896, *C. A. Purpus 1733* (UC); North Tule River, May–Oct., 1896, *C. A. Purpus 5694* (UC); "Southeastern Cal."; hillsides, Erskin Creek, Apr.–Sept., 1897, *C. A. Purpus 5301* (US, G, UC). Riverside County: near San Jacinto, 9 Mar., 1898, *J. B. Leiberg 3134* (US). San Diego County: Coyote Canyon (Colorado Desert), Apr., 1902, *H. M. Hall 2853* (UC).

While not recognizing *L. lacteus* as of specific rank, I accept it as a well-marked variety of *L. densiflorus*. As to the calyx bracteoles, the discrepancy between Kellogg's and Heller's descriptions is not a critical point, for my studies have shown me that these bractlets may or may not be present in different flowers of a particular raceme. I find them to be usually absent in the specimens listed above. The pubescence in this variety is quite variable, some specimens being nearly smooth.

Kellogg's Napa specimen in the Gray Herbarium (Napa, dry barren hillsides, 1 Apr., 1870), though distributed by Kellogg as *L. lacteus,* cannot be referred here. It is possibly a diminutive specimen of var. *perfistulosus* of this paper.

6*i*. **Lupinus densiflorus sublanatus** var. nov. [FIG. 26.]

Erectus, eramosus vel ramosus, 10–40 cm. altus, caule et cetera dense conspicueque villoso, pilis plusculum 1 mm. longis: bracteis calycibusque saepe sublanatis: verticillis 5–9; floribus pandentibus ad anthesin et postea: calyce bracteolato vel ebracteolato, labio superiore 3–4 mm. longo, gracile, acuto integroque vel bifido, inferiore recto vel ad basin paulo inflato 2-dentato, dentibus 1 mm. longis parallelis, sinu cum vestigio vel sine eo: corolla alba vel tincta; vexillo 13–15 mm. longo, 7–9 mm. lato, apice rotundato vel interdum obtuse angulato; alis superne ad basin ciliatis, interdum subter paulo; carina recta vel curva: fructus seminaque non vidi.

CALIFORNIA. Kern County: Water Canyon, Tehachapi Mountains, 26 June, 1908, *Abrams & McGregor 485* (TYPE, DS 9584; type-duplicates, US, NY, G); Tehachapi, June, 1911, *K. Brandegee* (UC); vicinity of Fort Tejon, 16–17 June, 1908, *Abrams & McGregor 310* (DS, US, NY, G); vicinity of Fort Tejon, 1857–8, *L. J. X. de Vasey 21* (US); Tehachapi, 1891, *Coville & Funston 1119* (*F. W. Koch*) (US); Bakersfield, 26 Apr.–30 May, 1896, *J. B. Davy 1708* (UC); Keene Station, 1 May, 1905, *A. A. Heller 7798* (DS, US, PA, G, NY); vicinity of Havilah, 15 June, 1905, *F. Grinnell 295* (US); Johnson Canyon, Walker Basin, 3 June, 1905, *F. Grinnell 51* (US); Caliente Creek, 1 June, 1905, *F. Grinnell 4* (US); near Caliente, May, 1909, *K. Brandegee* (UC).

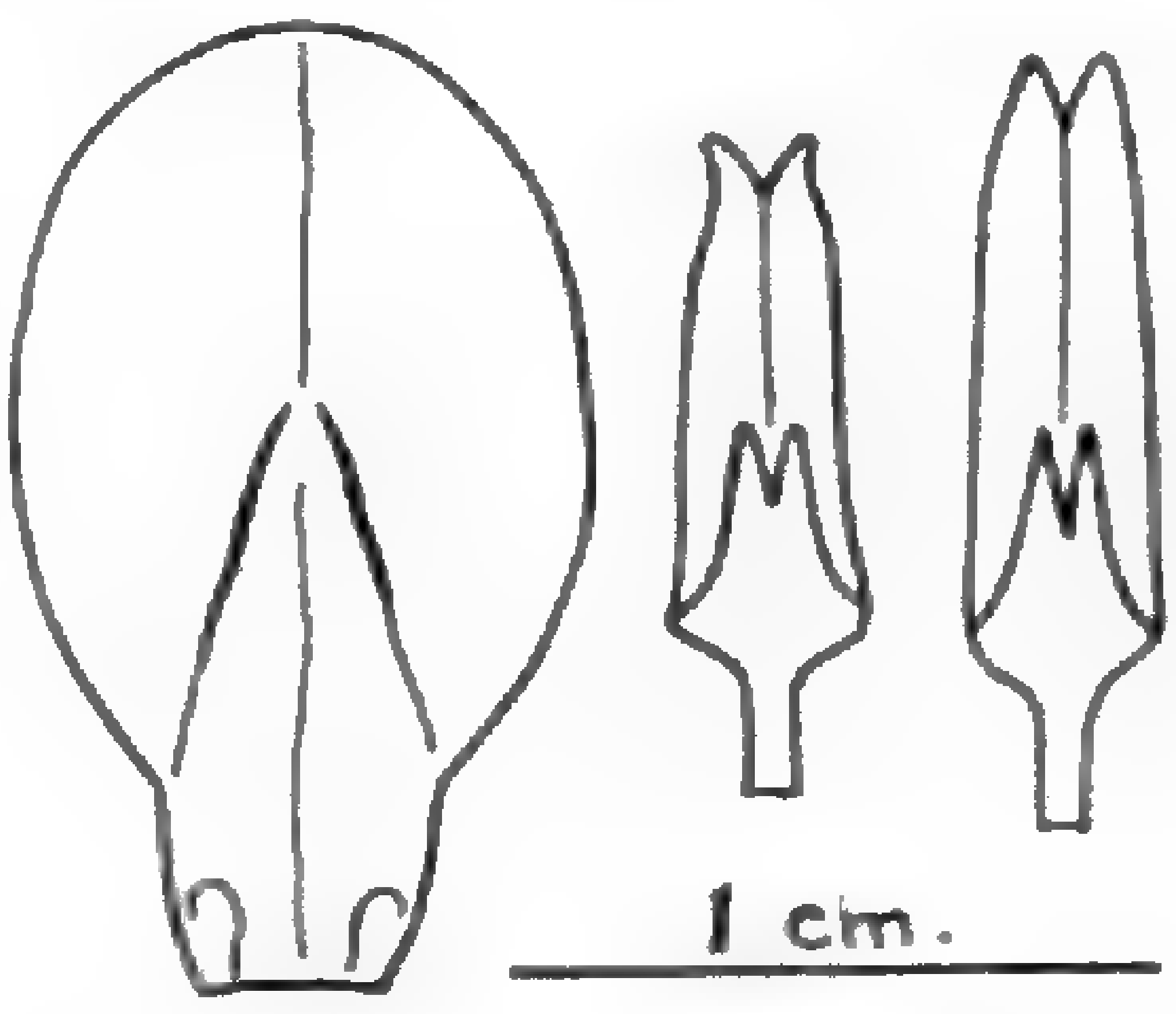

FIG. 26. LUPINUS DENSIFLORUS SUBLANATUS C. P. Smith. *Abrams & McGregor 485* (DS 9584).

Probably most closely related to var. *lacteus*, from which it would seem to be easily distinguished by the caulescent habit and the numerous racemes. It is noteworthy, however, that most of the specimens cited above were collected in June, while the types of both *L. lacteus* and *L. arenicola* were taken in April. It would therefore be an interesting study for some student to locate, if possible, the type station of Heller's *L. arenicola* and Mrs. Brandegee's station at Tehachapi, say in April, and follow both through until all the seed is matured and the season's growth is evidently completed. Cultural studies would also be of interest; but great care would be very necessary in the selection and identification of the seed to be used.

Sublanatus, "almost woolly," refers to the general pubescence of the typical phase of the variety, as represented by the type-collection and Mrs. Brandegee's Tehachapi plant. However, the specimens referred here show quite a range of variation in density of pubescence, the "least lanate" extreme being well represented by Abrams & McGregor's No. 310. This collection I had selected as the type of an additional variety, but later decided that this variation was not supported by other characters and, evidently, was in itself too inconstant to be reliable. In the upper San Joaquin Valley, as at Bakersfield, where the two varieties overlap, the nearly straight lower calyx-lip with retrorse-spreading hairs should readily distinguish var. *sublanatus* from the related var. *versabilis*, in which the lower lip is decidedly subsaccate and pubescent with subappressed hairs about 0.5 mm. long.

Some other specimens, not placed elsewhere, which may have some affinity to the above are: Nacimiento Canyon, San Luis Obispo County, 8 May, 1900, *J. H. Barber* (UC); Knights Ferry, Stanislaus County, 9 Apr., 1895, *F. W. Bancroft* (UC); Linden, San Joaquin County, May, 1896, *F. W. Gunnison* (UC).

6*j*. **Lupinus densiflorus McGregori** var. nov. [FIG. 27.]

Erectus, super basi prope 10 cm. ramosus, ramis paucis suberectis, caule ramisque gracilibus nequaquam fistulosis, laxe pubescentibus, pilis pandentibus 1–1.5 mm. longis: foliolis prope 20 mm. longis, cuneatis, apice rotundatis vel emarginatis pallido-viridis, pilis brevibus albescentibus subter: racemis brevibus, verticillis 2–3, distantibus; floribus parvis, 12–13 mm. longis, pandentibus ad anthesin; pedicellis 1.5–2 mm. longis, gracilibus; bracteis 2–5 mm. longis, inconspicuis: calyce ebracteolato, 7 mm. longo, villoso inferne, pilis prope 1 mm. longis, pandentibus vel retrorso-pandentibus; labio superiore 2 mm. longo, inferiore obtuso, paulo plus 2 mm. lato, 2-dentato, dentibus prope 0.5 mm. longis: corolla alba vel pallida; vexillo 11 mm. longo, 6 mm. lato, apice rotundato paulo abrupte contracto in unguem gracilem 2 mm. latum; alis 10 mm. longis, 4 mm. latis, non ciliatis; carina 10 mm. longa, recta: leguminibus 15 mm. longis, pallido-stramineis; seminibus 4 mm. longis, 3.5 mm.

latis, pinguibus, paulo acute angulatis, dense atro-cinereis maculatis.

Erect, branched about 10 cm. above the base, the branches nearly erect, slender, and somewhat fistulose; leaflets about 20 mm. long, cuneate, the apex rounded or emarginate, pale green, whitened below with conspicuous short subappressed hairs; whorls two or three, flowers small, 12–13 mm. long, spreading in anthesis; calyx only 7 mm. long, the hairs spreading or retrorse-spreading and about 1 mm. long, lower-lip two-toothed; banner 11 mm. long, 6 mm. wide, wings not ciliate, keel straight, all the petals white or pale: pods pale straw-colored; seeds about 4 x 3.5 mm., plump, somewhat acutely angled, densely spotted with dark gray.

CALIFORNIA. Los Angeles County: Rock Creek, desert slope of the San Gabriel Mountains, 2–4 July, 1908, *Abrams & McGregor 551* (TYPE, DS 9585; type-duplicates, US, NY, G).

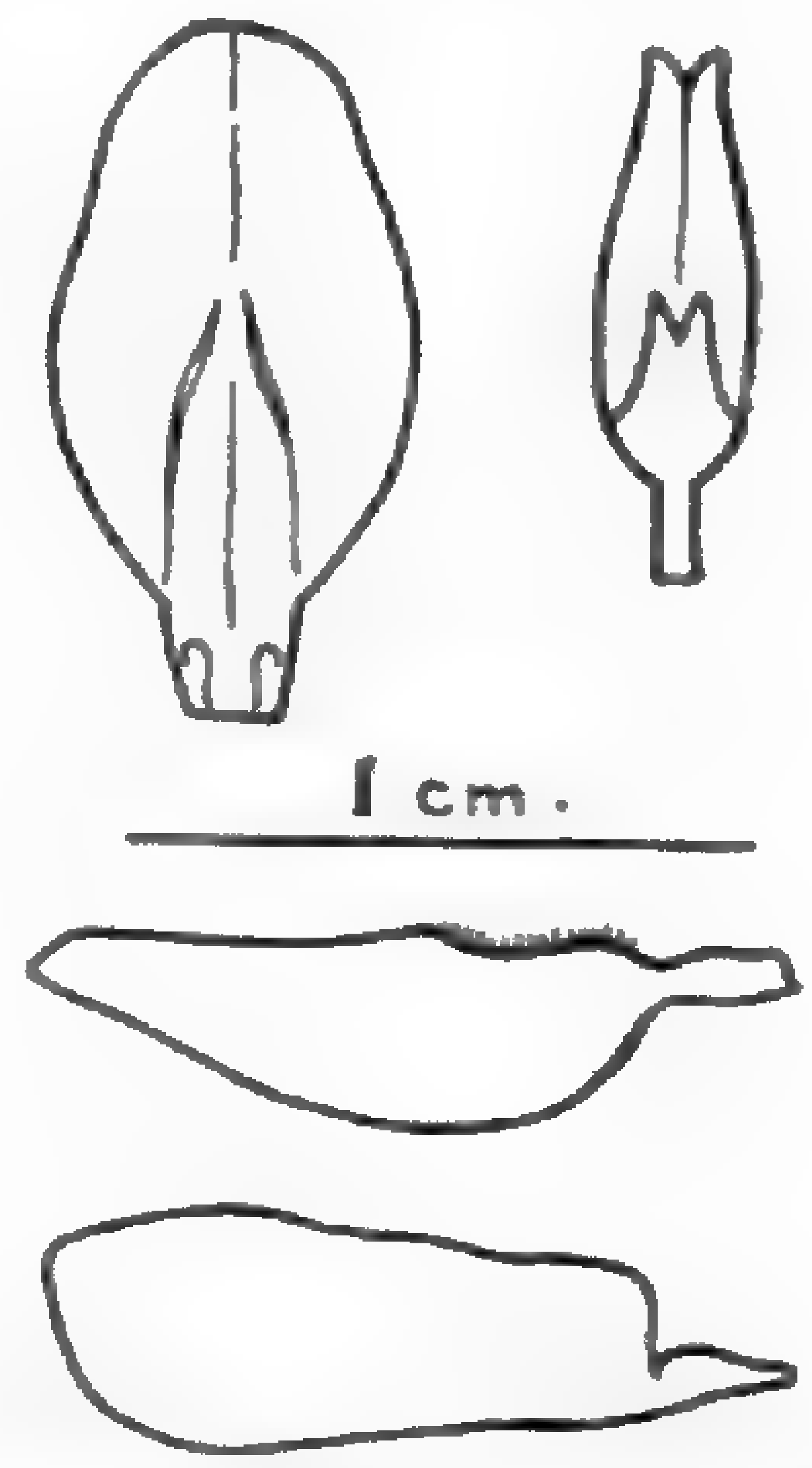

FIG. 27. LUPINUS DENSIFLORUS MCGREGORI C. P. Smith. *Abrams & McGregor 551* (DS 9585).

Apparently this form has a number of unique characters. Specimens collected in late May or early June would be interesting. Named for one of the collectors, my friend Ernest Alexander McGregor.

6*k*. **Lupinus densiflorus altus** var. nov. [FIG. 28.]

Ramosus, 30–60 cm. latus, ramis pedunculisque elongatis, caulibus ramisque laxe villosis et pedunculis petiolisque dense villosis, pilis 1 mm. longis: petiolis 10–20 cm. longis; verticillis 6–7, distinctis; floribus 14 mm. longis, pandentibus; calyce ebracteolato, 8 mm. longo, subter dense pandento-pubescenti, labio inferiore recto, paulo inflato, 3 mm. lato, 2-dentato, dentibus 1 mm. longis, sinu dentis vestigio plus minusve instructo: petalis albis; vexillo 13 mm. longo, 7 mm. lato, apice rotundato, paullatim contracto in unguem; alis 12 mm. longis, dense ciliatis ad basin superne; carina curvata: legumina seminaque non vidi.

Branched above the base, 30–40 cm. tall, the branches and peduncles elongated, branches loosely villous, the peduncles and petioles densely villous with hairs 1 mm. long; whorls six or seven, distinct; flowers spreading, 14 mm. long; calyx ebracteolate, densely pubescent below with spreading hairs, the lower lip straight, but slightly inflated, two-toothed, with or without the interstitial vestigial tooth; petals white, the banner rounded at the apex and gradually contracted into a poorly defined claw, wings densely ciliate at the free edges above, keel evidently curved; pods and seeds not seen.

CALIFORNIA. Los Angeles County: Manzana, Antelope Valley, 9–24 May, 1896, *J. B. Davy 2505* (TYPE, UC 130329).

The collector's label gives generic determination only; but an annotation label calls the specimen an "undescribed sp."

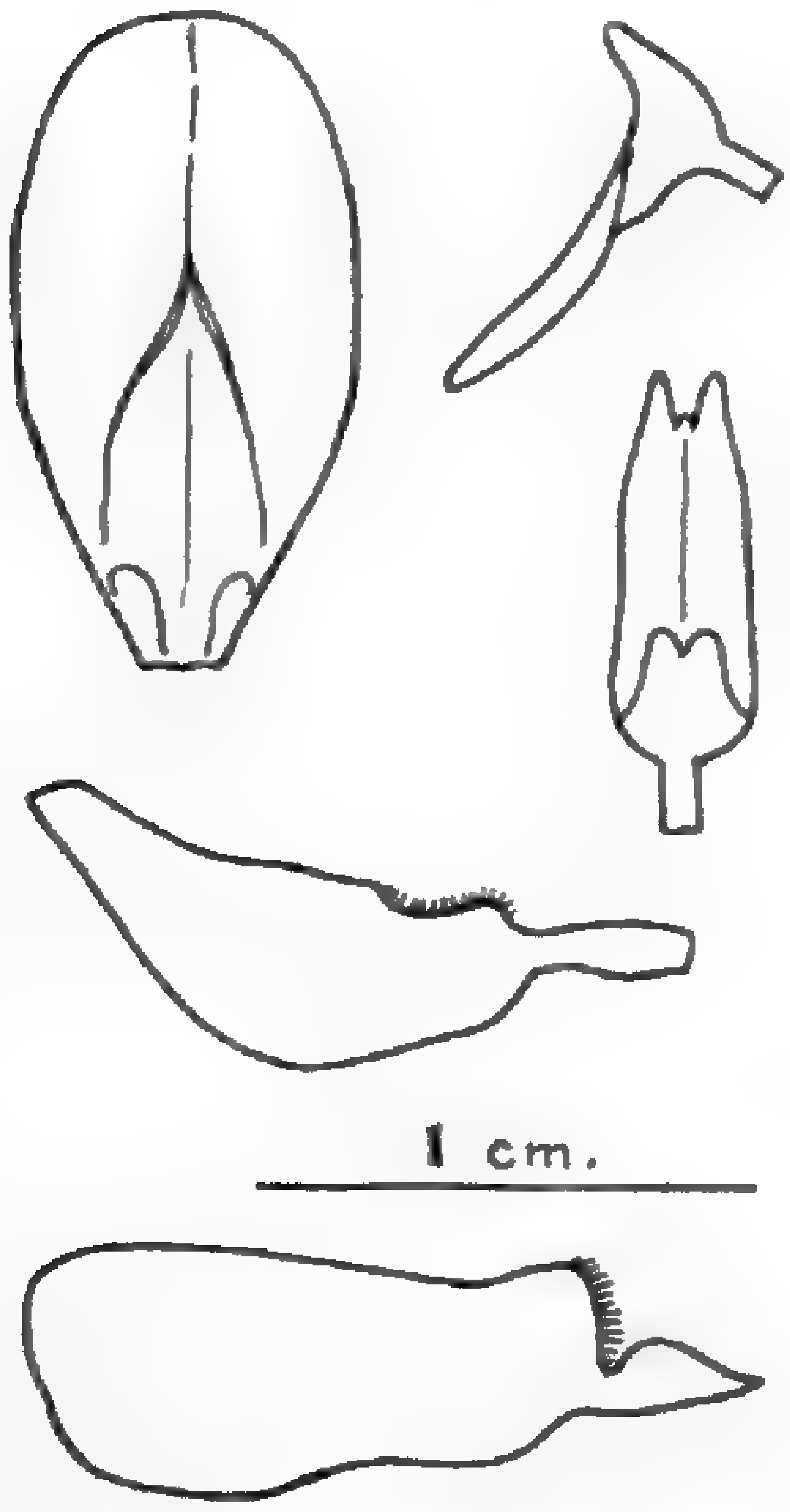

FIG. 28. LUPINUS DENSIFLORUS ALTUS C.P. Smith. *J.B.Davy* 2505(UC 130329).

6*l*. **Lupinus densiflorus vastiticola** var. nov. [FIG. 29.]

Acaulescens, eramosus vel ramosus, 9–18 cm. altus: foliolis 10–20 mm. longis, 4–5 mm. latis, oblanceolatis, acutis, laxe villosis superne: pedunculis brevibus, dense villosis, subrufis vel purpureis; verticillis prope 4–5, distantibus; floribus pandentibus, prope 13 mm. longis; pedicellis brevibus, robustis; bracteis calyces multo brevioribus: calyce ebracteolato, 8 mm. longo, pilis pandentibus prope 1 mm. longis, labio superiore 2 mm. longo, inferiore paulo inflato ad basin, 3 mm. lato, 2-dentato, dentibus plusculum 0.5 mm. longis, sinu dentis vestigio instructo vel sine eodem; colore corollae incerto; vexillo apice rotundato, paullatim contracto in unguem, 11 mm. longo, 5–6 mm. lato; alis prope 10 mm. longis, 5 mm. latis, ciliatis ad basin superne; carina curvata, maxima 11 mm. longa, 4 mm. lata, acumine brevi latoque: legumina et semina non vidi.

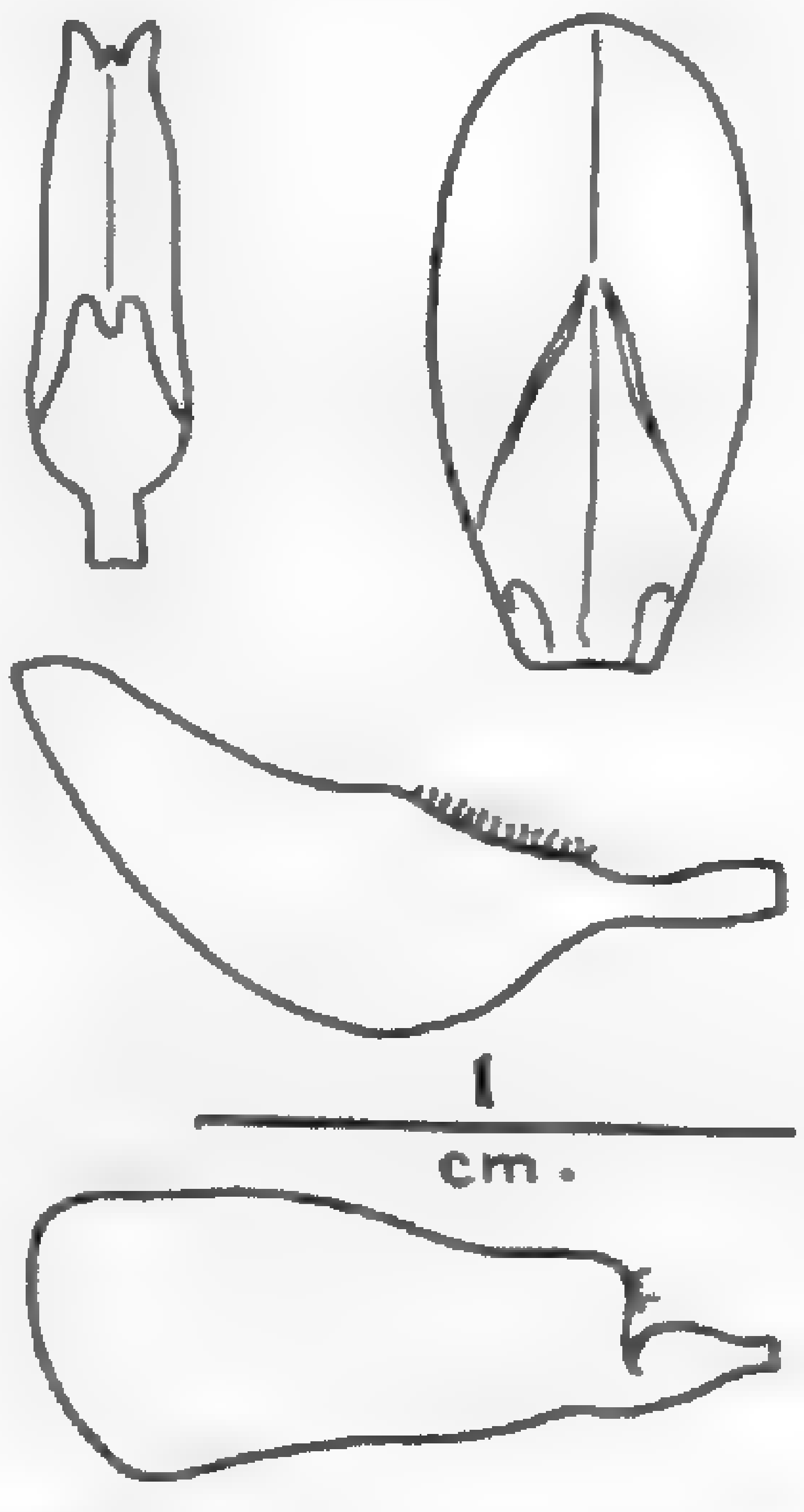

FIG. 29. LUPINUS DENSIFLORUS VASTITICOLA C. P. Smith. *C. G. Pringle* (US 20638).

Simple or branched at the base, 9–18 cm. tall; peduncles short, reddish or purplish, densely villous; whorls about four or five, distant; flowers spreading, about 13 mm. long; calyx ebracteolate, 8 mm. long, its hairs spreading and about 1 mm. long, lower lip somewhat inflated near the base, 3 mm. wide, two-toothed, with or without a vestigial median tooth; color of the corolla uncertain; banner rounded at the apex, gradually contracted into a poorly defined claw; wings ciliate at the base above; keel curved, comparatively large, the point short and wide; fruit and seeds not seed.

Vastiticola is Latin for "waste inhabiting."

CALIFORNIA. "Mojave Desert," 12 May, 1882, *C. G. Pringle* (TYPE, US 20638; type-duplicate, PA).

VERSABILES

6*m*. **Lupinus densiflorus versabilis** var. nov. [FIG. 30.]

Eramosus vel ramosus, 20–40 cm. altus, plus minusve fistulosus cum super basi ramosus, pubescens, pilis brevibus, paulo densis, plurimum retrorso-pandentibus, vix 1 mm. long; petiolis laxe pubescentibus vel sublevibus, 6–18 mm. longis; foliolis 6–10, 20–35 mm. longis, subrectis vel arcuatis, oblanceolatis, acutis, subter specie levibus, quamquam minute appresso-pubescentibus, medio-costis marginibusque ciliatis; pedunculis paulo brevibus vel elongatis, verticillis 4–10 appositis vel distantibus; floribus ad anthesin et postea pandentibus, 14–16 mm. longis; pedicellis prope 2 mm. longis, paulo gracilibus; bracteis verticilli humillimi vix 10 mm. longis, marginibus ciliatis; calyce frequenter bracteolato, 9–10 mm. longo, aliquantum dense pubescente, pilis brevibus laxe appressis, 0.5 mm. longis, labio superiore diverso, 2–3 mm. longo, inferiore inflato 2–3 mm. lato, 2-dentato, dentibus 0.5–1 mm. longis; corolla alba, diverse roseo- vel violaceo-tincta; vexillo apice rotundato, 14–16 mm. longo, 7–8 mm. lato, paulatim contracto ungue rigido, 4–5 mm. lato; alis 12–14 mm. longis, prope 6

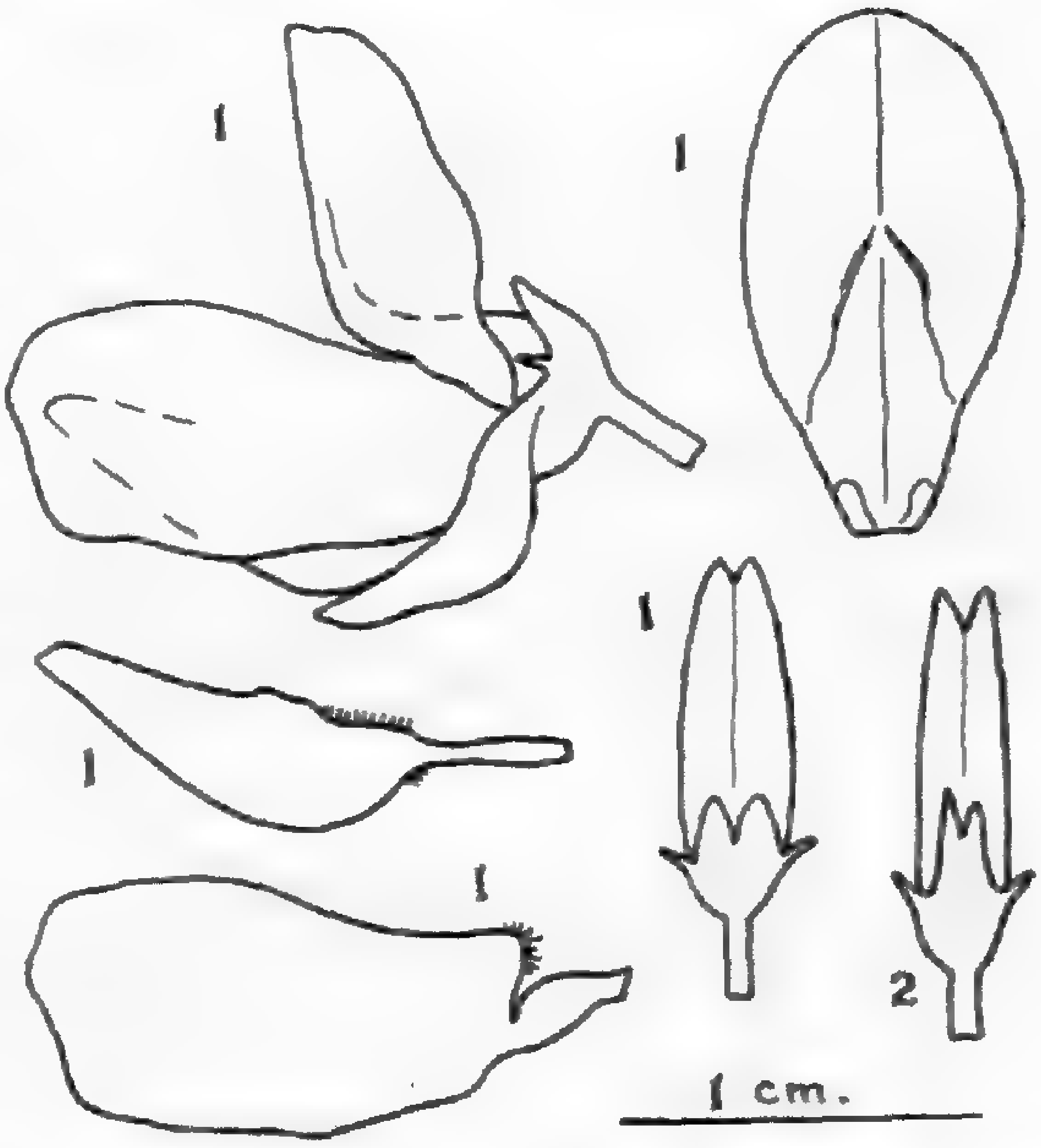

FIG. 30. LUPINUS DENSIFLORUS VERSABILIS C. P. Smith. 1. *A. A. Heller 8174* (DS 9593); 2. *A. A. Heller 7638* (CPS).

mm. latis, ad basin subter manifeste ciliatis; carina subrecta, vel paulo curvata 11–12 mm. longa.

This variety of the San Joaquin Valley and adjacent foothills of the Sierras differs from var. *Dudleyi* in the shorter pubescence of the calyx, the usually more richly tinted corollas, and the decided prevalence of interstitial bracteoles. While seeds of var. *Dudleyi* have not yet been seen by me, I have no doubt but that such will be found to differ considerably from those of var. *versabilis*. Seeds with the San Joaquin County plant, cited below, are milky-white, unmarked, rather smooth and plump, about 5 x 4 mm.

CALIFORNIA. Fresno County: Fresno, 13 Apr., 1906, *A. A. Heller 8174* (TYPE, DS 9593; type-duplicate, US). Kern County: near Bakersfield, 10 Apr., 1905, *A. A. Heller 7638* (DS, US, CPS). Madera County: Madera, 22 Apr., 1897, *W. A. Setchell* (UC); North Fork and vicinity, 30 May–8 June, 1903, *D. Griffith 4622* (US). Amador County: Jackson Gate, May, 1892, *G. Hansen 1314* (DS, UC); Stony Creek, 26 May, 1896, *G. Hansen 1674* (US). San Joaquin County: Tracy, 10 Apr., 1900, *B. Cobb* (UC).

Versabilis is Latin foı "changeable" and refers to the variation in the tinting of the petals.

6*n*. **Lupinus densiflorus latidens** var. nov. [FIG. 31.]

Habitu notisque var. *versabilis*, a ipso differt pilis pandentibus plurimum laxe vix 0.3–0.5 mm. longis; labio calycis inferiore interdum integro vel 2–3-dentato, dentibus plurimum latioribus quam longis; leguminibus secundis prope 15 mm. longis.

Differing from var. *versabilis* in the somewhat shorter pubescence, in the paler tinting of the petals, as a rule, and the lower calyx-lip being entire or with very wide short teeth. It seems to be local in the general vicinity of San Bernardino.

CALIFORNIA. San Bernardino County: vicinity of San Bernardino, 20 May, 1896, *S. B. Parish 4165* (TYPE, US 279032; type-duplicates, NY, G, UC); Redlands, May, 1890, *S. B. Parish* (US); vicinity of San Bernardino, 11 May, 1901, *S. B. Parish 4783* (DS). Riverside County: Temicula, 1880, *G. R. Vasey 96* (US). County not given: *J. M. Biglow* (Whipple's Exploration of the 35th Parallel), 1853 (US); foothills, May, 1887, *S. B. Parish* (UC).

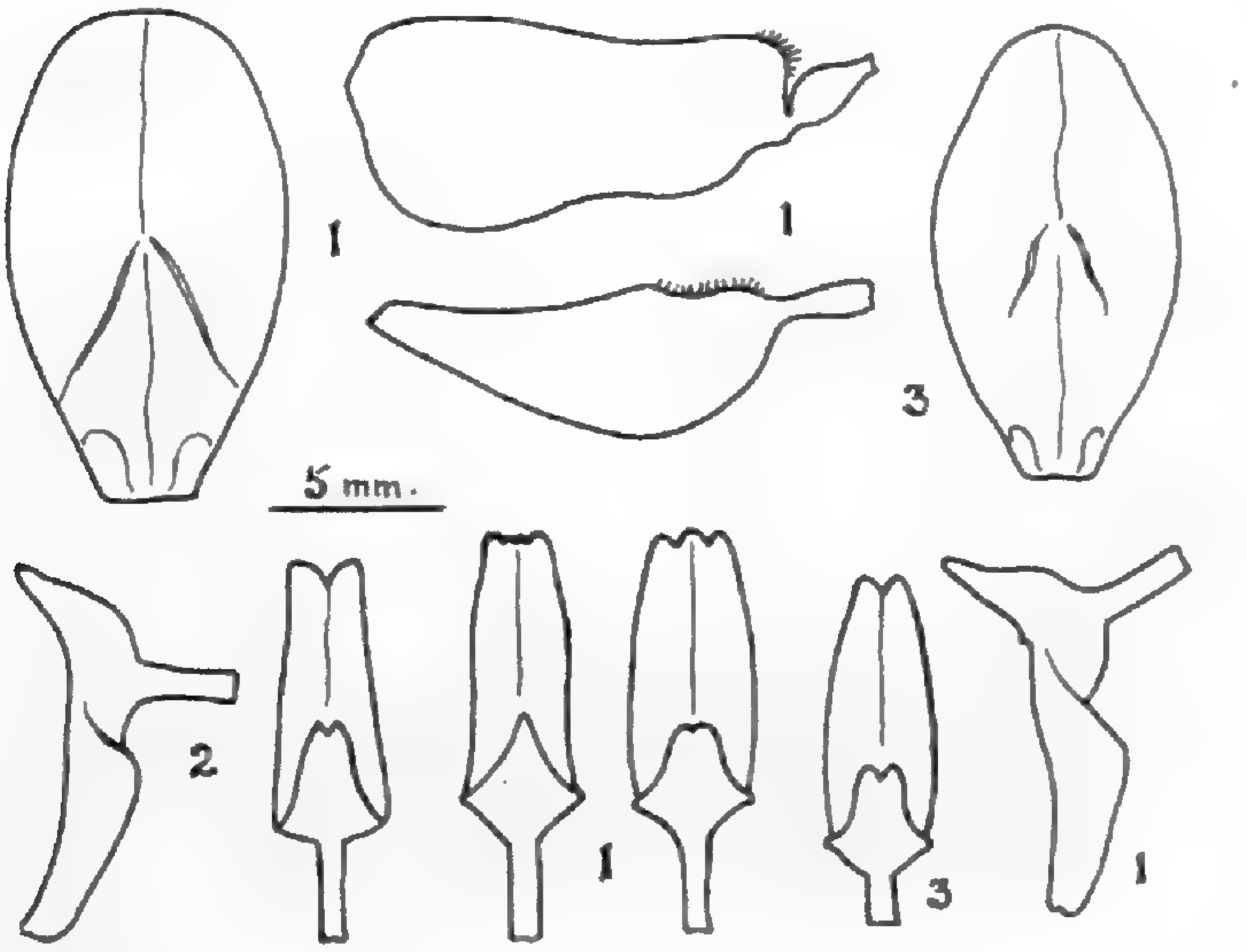

FIG. 31. LUPINUS DENSIFLORUS LATIDENS C. P. Smith. 1. *S. B. Parish 4165* (US 279032); 2. *J. M. Bigelow* (US 20644); 3. *S. B. Parish* (US 480801).

60. **Lupinus densiflorus Dudleyi** var. nov. [FIG. 32.]

Ramosus, prope basin manifeste pubescens, pilis retrorso-pandentibus prope 0.5 mm. longis; racemis pluribus, verticillis 5–10 vel pluribus, plus minusve appositis; floribus 15–16 mm. longis; bracteis humilioribus, calyces excedentibus longitudine; calyce interdum bracteolato, plerumque ebracteolato, 10 mm. longo, subter laxe villoso, pilis pandentibus, 0.5–1.5 mm. longis, labio superiore 2.5–3 mm. longo, inferiore plerumque inflato prope 3 mm. lato, bidentato, sinu dentis vestigio instructo, dentibus 0.75–1.5 mm. longis; petalis albis vel pallido-roseis; vexillo apice rotundato, 14 mm. longo, prope 8 mm. lato, paulo abrupte contracto ungue 4 mm. lato; alis 12–13 mm. longis, apice prope 7 mm. latis, ad basin superne ciliatis; carina 10–11 mm. longa, acumine subvexo; leguminibus secundis, 15 mm. longis: semina non vidi.

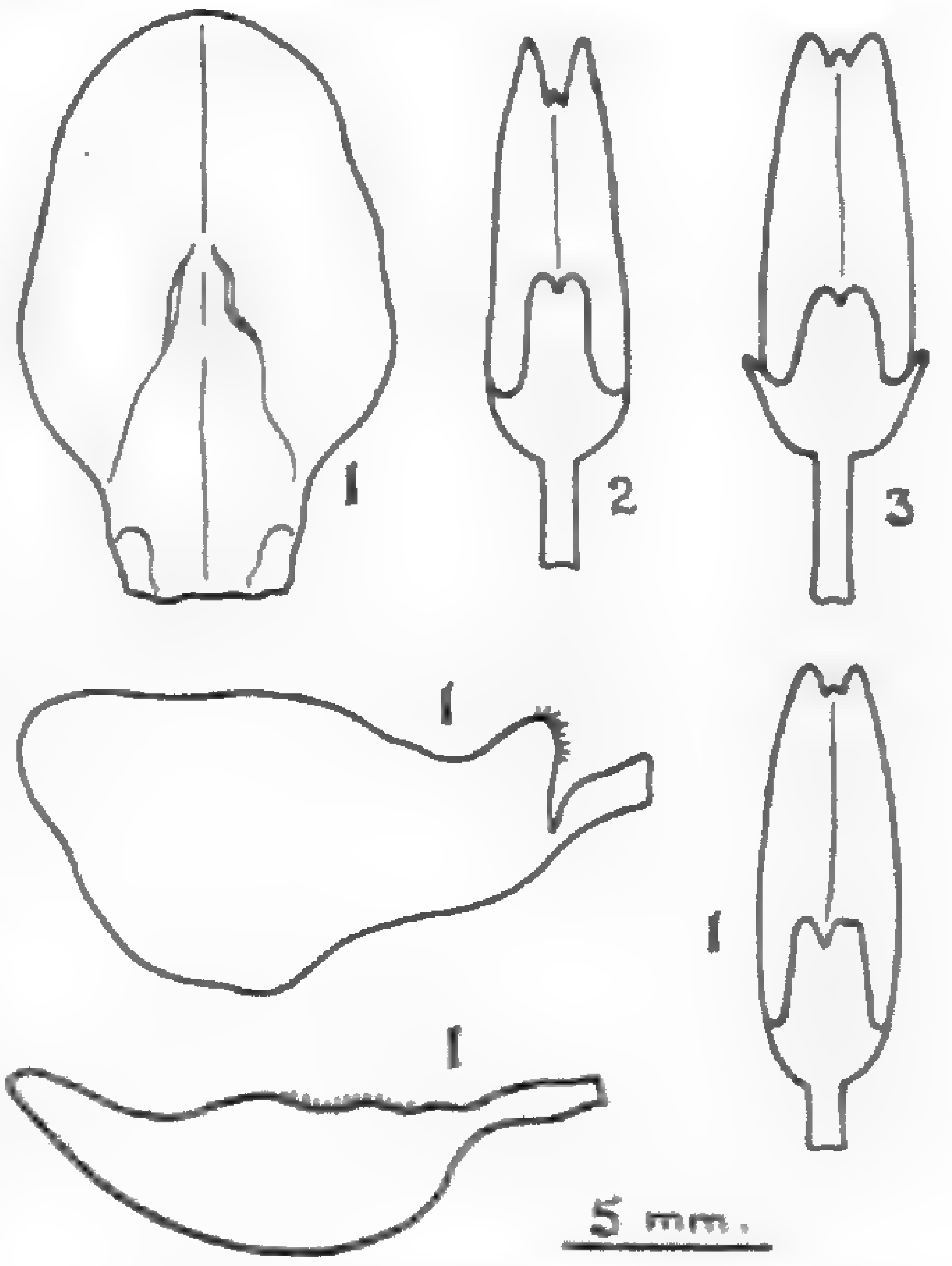

FIG. 32. LUPINUS DENSIFLORUS DUDLEYI C. P. Smith. 1. *C. P. Smith 1442*; *C. F. Baker 850* (US 440513); 3. *A. D. E. Elmer 4847* (US 665734).

The rounded banner and the short retrorsely spreading pubescence distinguish this quite local variety of the San Francisco peninsula, etc. The flowers are white or tinted with rose-pink, commonly large and showy. The pods are conspicuously secund.

CALIFORNIA. San Mateo County: serpentine rock west of San Mateo, 26 Mar., 1894, *W. R. Dudley* (TYPE, DS); Pilarcitos Lake and Canyon, 21–23 June, 1893, *J. B. Davy 1151* (UC); Crystal Springs Lake, 1 May, 1902, *C. F. Baker 850* (US); near San Mateo on the Half Moon Bay road, 23 May, 1907, *A. A. Heller 8561* (DS, US); Lake San Andreas, June, 1903, *A. D. E. Elmer 4847* (US, NY); San Mateo Canyon, 31 May, 1908, *C. P. Smith 1442*. Marin County: without definite locality, 4 June, 1895, *I. Tidestrom* (UC).

6*p*. **Lupinus densiflorus persecundus** var. nov. [FIG. 33.]

Humilis, 5–15 cm. altus, ramis brevis subpandentibus, pedunculis eorum plerumque plus pandentibus; foliis congestis, viridis, peculiaribus; petiolis 3–8 cm. longis, pilis 1 mm. longis, laxe pandentibus; foliolis 6–8, prope 20 mm. longis, 4–6 mm. latis, acutis, superne sublevibus, inferne laxe pubescentibus: pedunculis foliis aequantibus vel ea excedentibus, laxe pubescentibus, racemis aliquantum deflexis; verticillis 1–4, distinctissimis, floribus manifeste secundis, prope 16 mm. longis; pedicellis 1.5–2 mm. longis; calyce ebracteolato, 9 mm. longo, 4–5 mm. lato, laxe pandentibus pubescente, pilis vix 1 mm. longis, labio superiore 3 mm. longo, emarginato, inferiore 3-dentato, dento medio lateralibus minore interdum vestigio; petalis atro-purpureis, praesertim ad dimidia externa; vexillo 12 mm. longo, 10 mm. lato, apice rotundato, abrupte con-

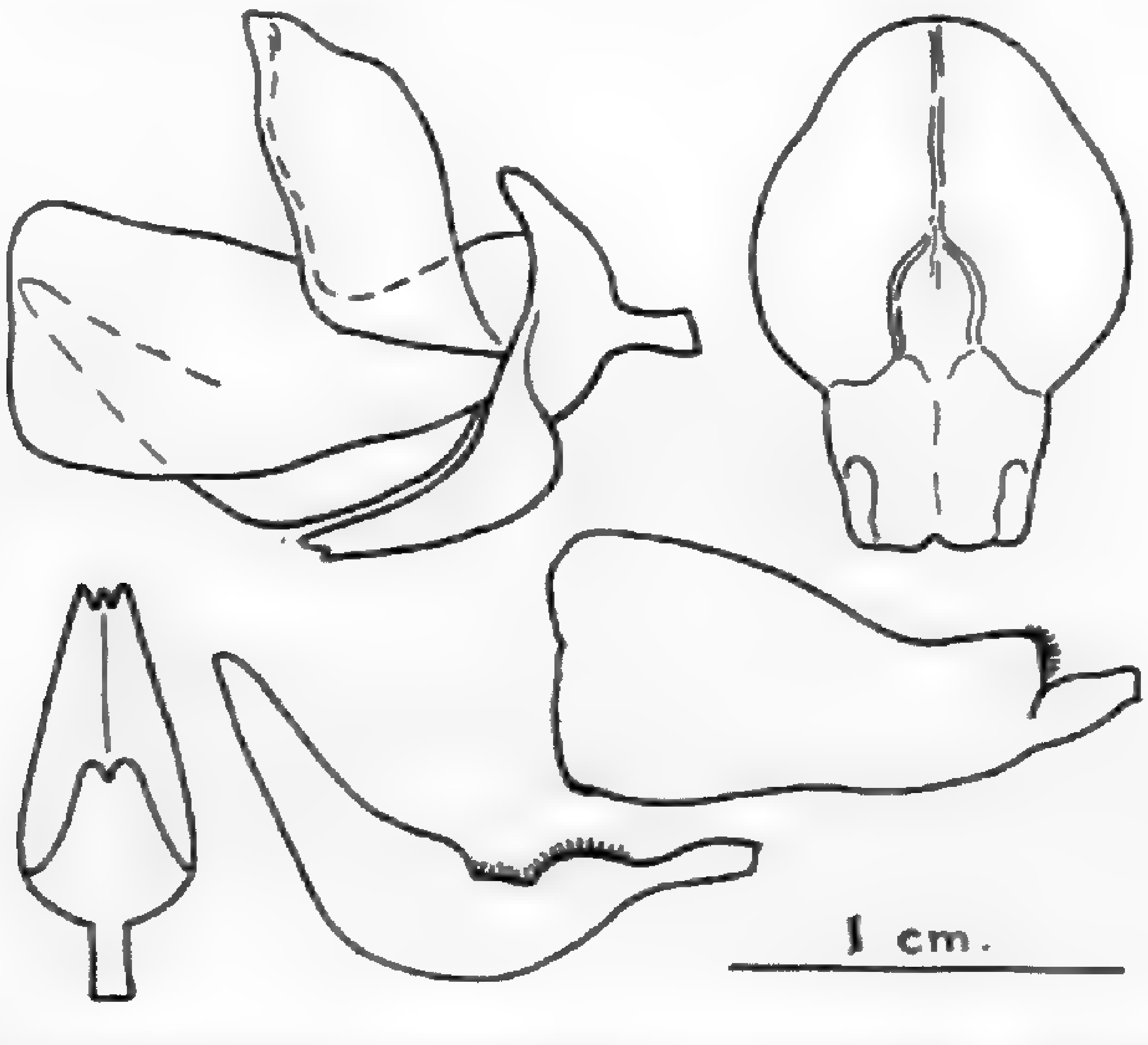

FIG. 33. LUPINUS DENSIFLORUS PERSECUNDUS C. P. Smith. *M. E. Jones 3320* (US).

tracto ungue inflato 6 mm. lato superne, 4 mm. lato basi; alis 13 mm. longis, ciliatis ad basin superne; carina 12 mm. longa, curvatissima, acumine longissimo gracile; fructibus manifeste secundis, specie usitatibus: semina non vidi.

Low, 5–15 cm. high, the branches more or less spreading with usually more widely spreading peduncles; whorls one to four, remote, the flowers secund and largely dark purple in color, about 16 mm. long; calyx ebracteolate, 9 mm. long, its pubescence spreading, about 1 mm. long, the lower lip mainly three-toothed; banner 12 x 10 mm., abruptly contracted into an inflated claw which is 6 mm. wide above; keel 12 mm. long, much curved and with a long slender apex; fruits strongly secund, otherwise apparently not distinctive; seed not seen.

CALIFORNIA. Sonoma County: Duncans Mills, 17 July, 1882, *M. E. Jones 3329* (TYPE, US; type-duplicates, NY, Utah Agr. Col.); cliffs near Bodega Bay, 30 June, 1907, *K. Brandegee* (UC). Marin County: Dillons, Dec., 1898, *R. E. Gibbs* (UC).

Persecundus is used in the sense of "strongly secund" and refers to the position of the flowers and fruits on the rachis. The type collection is labelled *L. microcarpus*.

PALUSTRES

6*q*. **Lupinus densiflorus palustris** (Kell.) comb. nov. [FIG. 34.]

Lupinus densiflorus Agardh, Syn. Gen. Lup. 1835.

Lupinus palustris Kell. Proc. Cal. Acad. Sci. **5**: 16. 1873.

Agardh's description, in part, will be found on page 169, with the general discussion of *L. densiflorus* Benth.

Kellogg's description of *L. palustris*, somewhat abridged, follows:

> Stem stout, annual, fistulose . . . often . . . branching . . . beyond the main axis and its elongated terminal spike; long, soft, silky, pubescent, or subglabrous, with barely very minute villi . . . leaflets . . . glabrous above, subpubescent beneath . . . spike 6 to 12 inches; flowers large, violet-blue, pinkish or verging to white, pedicellate, subverticellate or verticellate . . . subscarious calyx bracteolate or ebracteolate hirsute . . . slightly saccate; upper lip 2-toothed, lower herbaceous lip mostly 2-toothed, seldom sub-entire; wings very broad, obtuse, with a rhomboidal outline; petals equal. Legumes very appressed, (silvery?) hirsute, compressed, an inch or more in length, about 8-seeded.
>
> Collected by Kellogg and Bloomer on the San Joaquin River, April 7th, 1869. Differs from *Menziesii*—a 2-seeded species,—whereas this has 8 or more; also one var. (deep purple-blue flower) has very distinct bracteoles.

This description has been a puzzle to me since I first studied it in 1910, and no solution to the matter suggested itself until recently, when it was my pleasure to examine, at the Gray Herbarium, one of Kellogg's specimens distributed by himself as his *L. palustris*, and collected in April, 1869. This is in flower only, but it is the same as *L. densiflorus* Agardh, and agrees with Kellogg's description, as far as same applies at all to a *Platycarpos* species. It may be that Kellogg's type-collection included some very peculiar pathological specimens; but I am more inclined to believe that he actually confused flowering specimens of this variety of *L. densiflorus* with fruiting specimens of a quite different species, perhaps the robust annual now known as *L. affinis* Agardh.

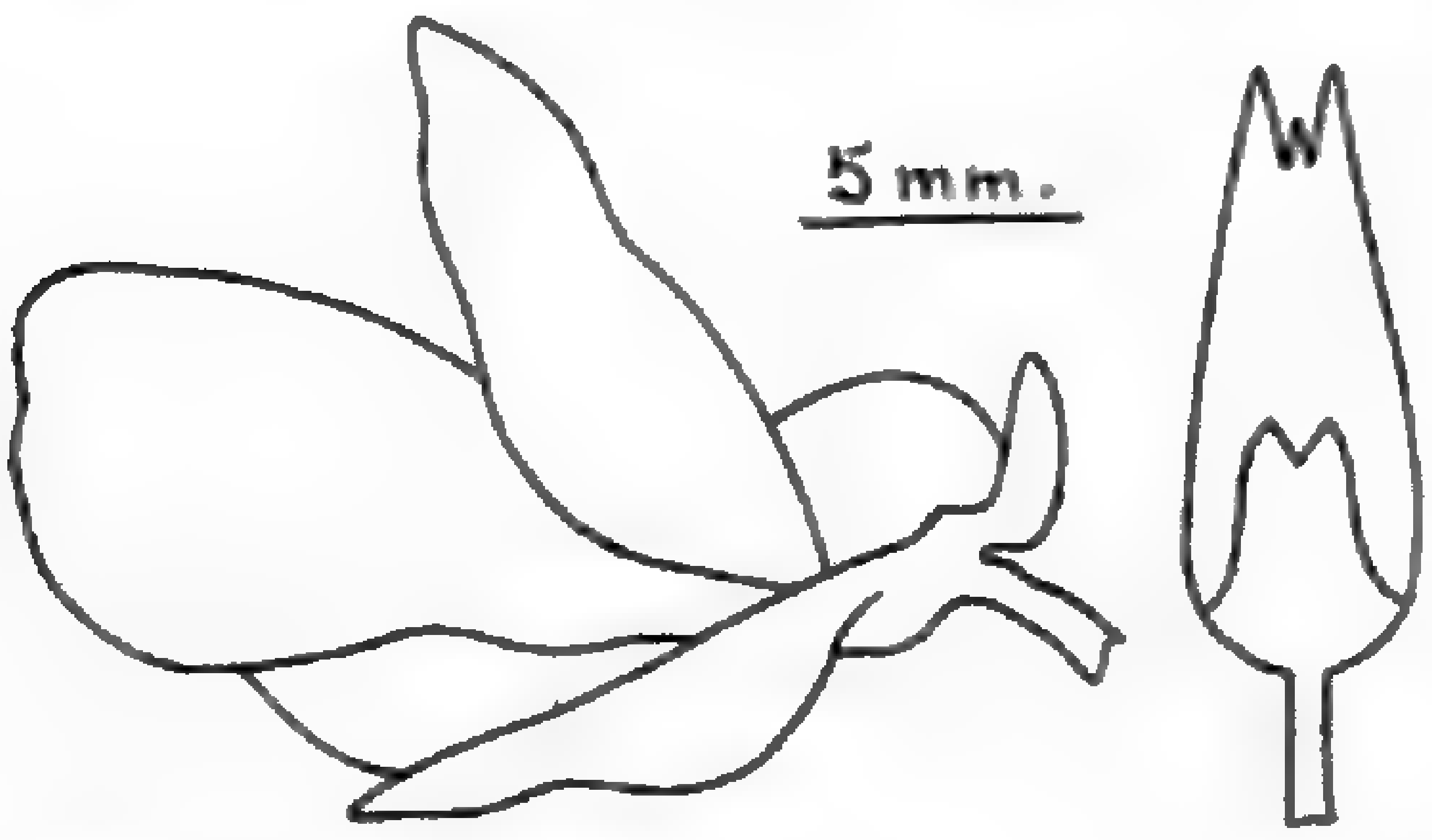

Fig. 34. Lupinus densiflorus palustris (Kell.) C. P. Smith. *A. Kellogg*, Apr., 1869 (G), not dissected.

However, as attested by Bentham himself, Agardh's *L. densiflorus* can not be accepted as the typical form of the species, and it seems to me that this easily recognizable form, as a variety, should bear Kellogg's name.

Another specimen in the Gray Herbarium calls for special attention, said specimen being the one labelled "*L. Menziesii*, var. *aurea*, Kellogg and Brannan. Jr., San Joaquin River, 22 April 1870." As may be seen by referring to the original description (see page 177), Kellogg's type is said to have been taken at "Deer Valley, near Antioch, San Joaquin River, April 22, 1869." One might easily assume that the discrepancy in date, 1869 *vs.* 1870, is a mere clerical error, overlooked by the person who wrote out the label in question. The specimen, however, according to the descriptions, is not Kellogg's var. *aurea*, but is the same as his *L. palustris*. As to the locality, Antioch and vicinity, my citations will show that Davy also collected var. *palustris* at Antioch in 1895, and that Miss Eastwood and Mrs. Brandegee each collected *L. Menziesii* (probably var. *aurea*) at Antioch in 1893 and 1907, respectively. Still a third variety of *L. densiflorus* and also the typical *L. subvexus* have been taken at Antioch. I accordingly wonder if this particular specimen was not labelled on the basis of the collectors and part of the date (22 April), rather than with careful regard to the description of var. *aurea*.

Var. *palustris* shares with typical *L. subvexus* a pronounced tendency toward a covering of long loose hairs, those of the calyx, especially, being 2–4 mm. long. The "*palustris* varieties" of *L. densiflorus*, however, may be distinguished from the varieties of *L. subvexus* by the position of the flowers soon after anthesis, the flowers soon turning up in *L. subvexus*, without becoming secund, as is so frequent in many varieties of *L. densiflorus* as the fruits develop. Some of the extreme "*palustris* variations" are below designated as separate varieties, most of which have commonly been labelled as *L. microcarpus*. One of these, however, has been named, but not described, by Miss Eastwood.

To supplement Kellogg's and Agardh's descriptions, I would mention the following diagnostic points:

Flowers spreading in anthesis and later; calyx usually ebracteolate, 12–13 mm. long, bushy-villous below, especially on the cup, the hairs 2–4 mm. long, upper lip various but usually large, about 3 mm. long, lower lip inflated near base, 3–4 mm. wide, two-toothed, with or without an interstitial vestige; petals white or tinted with pink or purple; banner rounded apically, 15–17 mm. long, 8 mm. wide, rather abruptly contracted at base, the basal inflation more or less saccate, pressing the upper lip backward; wings 13–15 mm. long, sometimes ciliate at the free edges above; keel 11–13 mm. long, slightly to considerably arcuate; pods 14–16 mm. long; seeds probably dull yellow, sparsely speckled with dark brown, about 5 x 4 mm. (DS 9588).

CALIFORNIA. County not given: San Joaquin River, Apr., 1869, *A. Kellogg* (G); San Joaquin River, 22 Apr., 1870, *A. Kellogg & S. Brannan, Jr.* (G); no data (DS 9588). Contra Costa County: Antioch, Apr., 1895, *J. B. Davy* (UC). Alameda County: vicinity of Berkeley, May–June, 1906, *H. A. Walker 173* (UC); Berkeley, June, 1894, *W. S. Blasdale* (US). Santa Cruz County: Watsonville coast, 13 Apr., 1902, *C. F. Baker 3009* (US, NY, G). Monterey County: Monterey, *T. Hartweg 1692* (G); Monterey, *J. G. Cooper* (US); dry ravine, Monterey, May, 1850, *C. C. Parry* (T).

6r. **Lupinus densiflorus stanfordianus** var. nov. [Fig. 35.]

A var. *palustri* differt labio inferiore calycis 3-dentato, dente medio plerumque amplo; corolla pallido-luteolo-alba vel pallido-rosea; vexillo apice acuto vel abrupte contracto ungue rigido; seminibus 4 x 5 mm., asperibus, atro-fulvis maculis non claris.

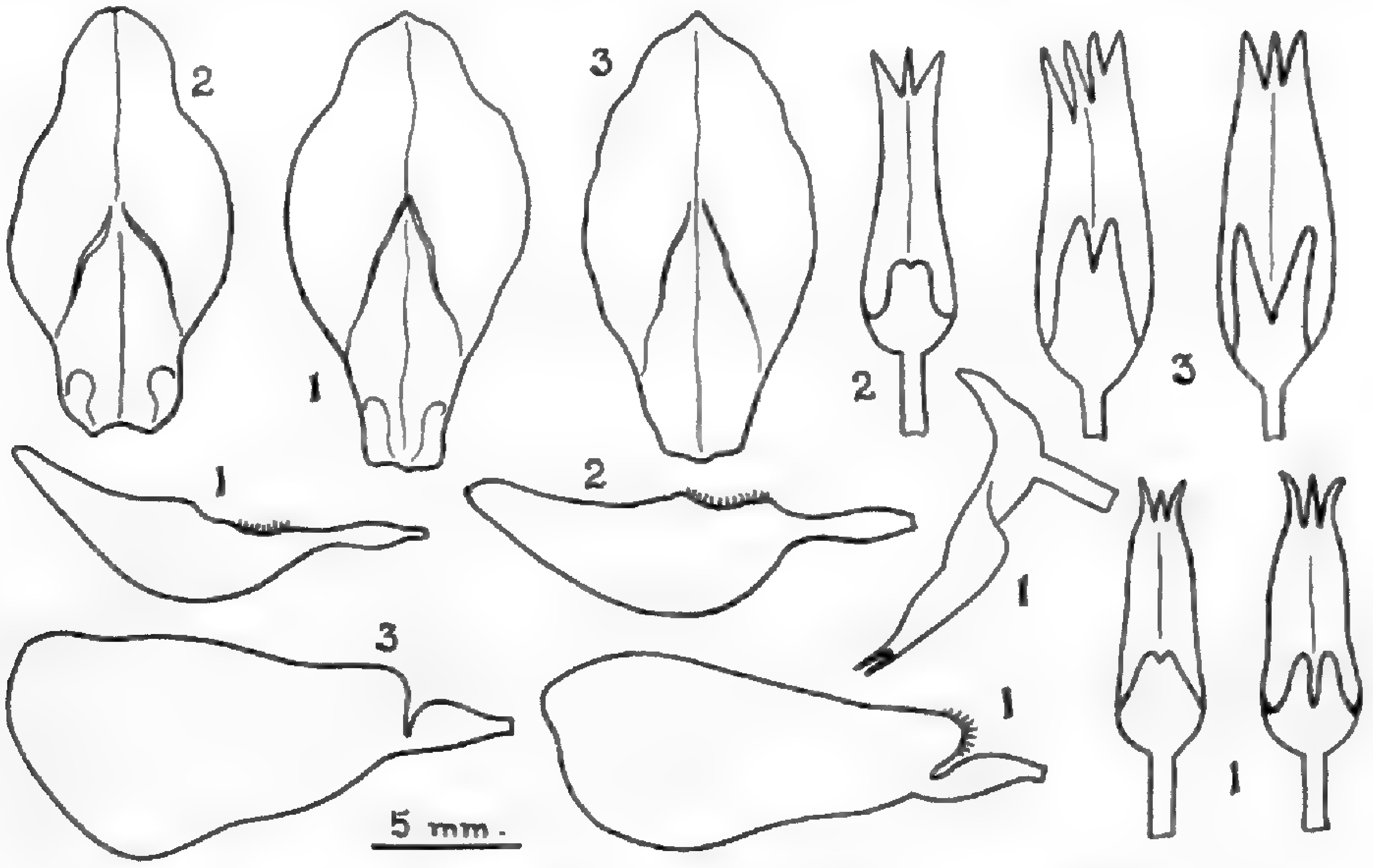

Fig. 35. Lupinus densiflorus stanfordianus C. P. Smith. 1. *C. P. Smith 791*; 2. *A. D. E. Elmer 2190* (US 655041); 3. *W. F. Wight 140* (US 467702).

Lower lip of the calyx three-toothed, the median tooth being well-developed; petals creamy or rose-tinted, the banner acute or abruptly contracted at the apex, the claw stiff; seeds rough, dark brown with indistinct specks; leaflets conspicuously ciliate on the midribs and margins.

California. Santa Clara County: Stanford University, base of foothills, 9 Apr., 1905, *C. P. Smith 791* (Type, CPS); 16 Mar., 1900, *W. F. Wight 140* (US); Stanford University, Apr., 1900, *W. A. Atkinson* (DS); west of road near Rocy House, 6 Mar., 1900, *W. A. Atkinson* (DS); near Stanford University Apr., 1900, *A. D. E. Elmer 2190* (US); foothills, Stanford University, 8 Apr.–4 May, 1902, *C. F. Baker 475* (US, DS, NY, G). San Mateo County: Stanford University, by road from county bridge to Basaltic Rocks, 10 May, 1897, *W. R. Dudley* (DS); Los Trancos road, near Stanford University, 1 Apr., 1905, *C. P. Smith 727* (CPS); Stockfarm bridge, near Stanford University, 13 Apr., 1908, *C. P. Smith 1401* (CPS).

6*s*. **Lupinus densiflorus crinitus** Eastwood, var. nov. [FIG. 36.]

Humilis, 8–15 cm. latus, villosissimus, pilis 3–5 mm. longis, caule ramisque brevibus plerimum laxe pandentibus; foliis congestis; pedunculis plus minusve decumbentibus vel deflexis, folia excedentibus praesertim ad fructum; verticillis 2–4 distantibus, floribus prope 14 mm. longis, pedicellis brevibus robustis; calyce ebracteolato, 10 mm. longo, 4 mm. lato, dense villosissimo, pilis 2–3 mm. longis, labio superiore 3 mm. longo, emarginato, inferiore 2-dentato, dentibus 1 mm. longis et 1 mm. latis basi, sinu lato; corolla plurimum atro-purpurea, vexillo 13 mm. longo, 8 mm. lato, apice rotundato abrupte contracto in unguem prope 4 mm. latum; alis 11 mm. longis, 6 mm. latis, basi ciliatis; carina 10 mm. longa, subrecta; leguminibus magnis, 15–18 mm. longis; seminibus angulatis, luteofulvis, dense minuteque maculatis maculis fulvis.

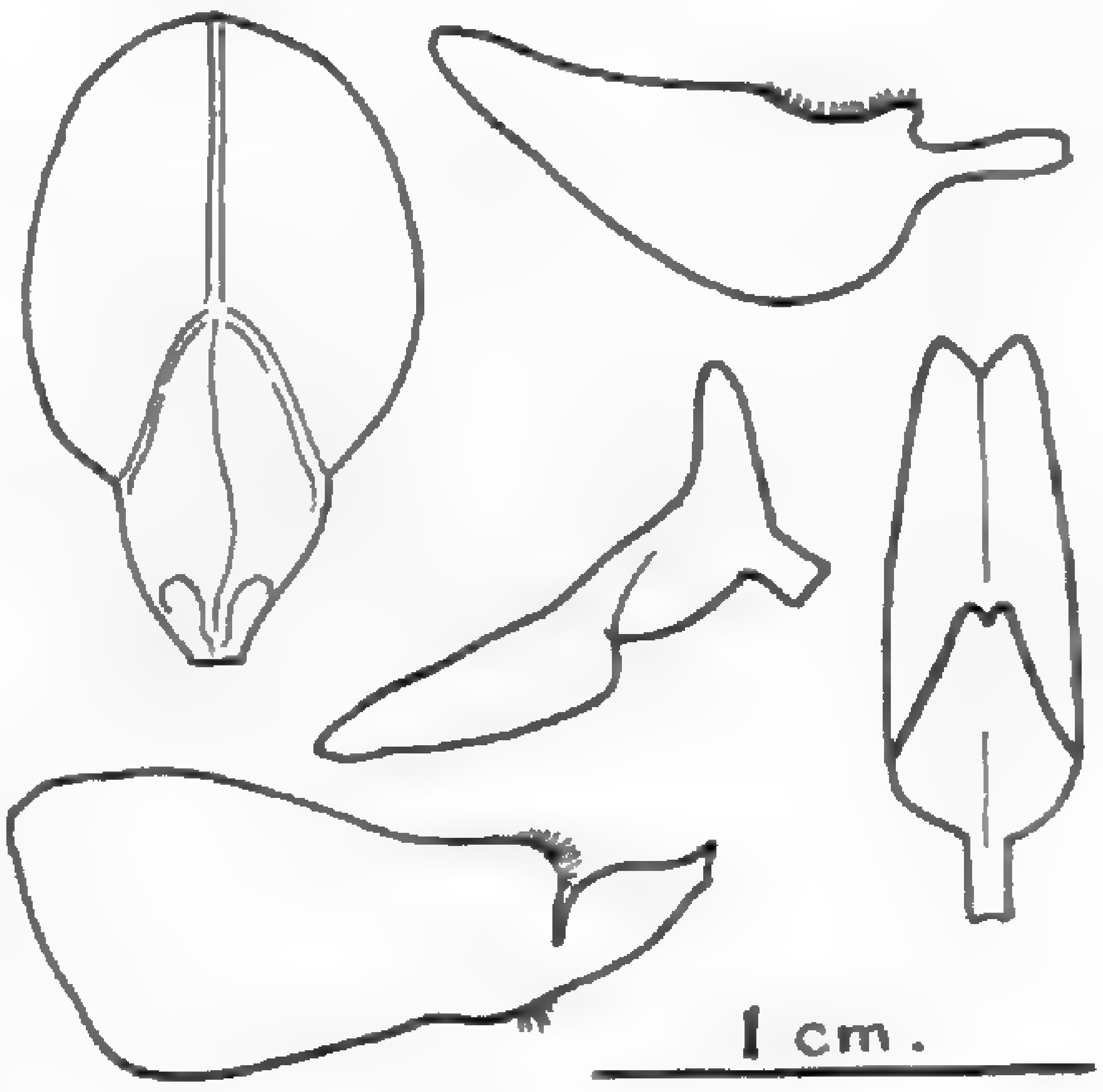

FIG. 36. LUNPIUS DENSIFLORUS CRINITUS Eastwood. *A. Eastwood* (G).

Low, 8–15 cm. tall, very villous with hairs 3–5 mm. long, stem and branches short and usually loosely spreading with the peduncles more or less decumbent or deflexed, exceeding the foliage at time of fruiting; verticils two to four, distinct, flowers about 14 mm. long; calyx ebracteolate, 10 mm. long, very densely villous with hairs 2–3 mm. long; corolla mostly dark purple, the banner 13 mm. long, rounded at the apex and abruptly contracted into a wide claw, wings ciliate, keel nearly straight; pods large; seeds angular, yellowish brown, densely and minutely spotted with brown.

CALIFORNIA. Sonoma County: Bodega Point, *A. Eastwood* (TYPE, G; type-duplicate, UC); Bodega, 25 May, 1900, *H. P. Chandler 686* (UC).

The type sheet is labelled "*Lupinus crinitus* n. sp.," but an annotation, in pencil, calls it *L. densiflorus*, var. *crinitus*. It seems to be a local and well-marked variation of the "*palustris* group" and peculiar to the coast line; while var. *persecundus* (page 190), of similar general appearance, but very different pubescence, is evidently nearer typical *L. densiflorus* and is found both near the coast and also up in the mountains of the same local region This region is not readily accessible to botanists; but I surmise that it would prove to be an especially interesting locality to taxonomists of ecological bent.

6*t*. **Lupinus densiflorus curvicarinus** var. nov. [FIG. 37.]

Eramosus vel super basi ramosus, 25–30 cm. altus, laxe villosus; foliolis subter specie levibus sed vero pubescentibus, pilis laxe appressis brevibus, medio-costis marginibusque ciliatis; verticillis 2–17, plurimum distantibus, floribus laxe pandentibus, 13–14 mm. longis, pedicellis 2 mm. longis, gracilibus, bracteis verticillorum humiliorum 15 mm. longis; calyce 8 mm. longo, subter laxe villoso, pilis 1.5–2 mm. longis, labio superiore emarginato, prope 2 mm. longo, inferiore lanceolato-ovato, inflato, bidentato, dentibus sinuque, gracilibus, 1 mm. longis; corolla pallido-rosea vel purpurea, vexillo 12 mm. longo, 7 mm. lato, apice rotundato, alis 11 mm. longis, carina curvatissima ad basin ciliata; leguminibus pallido-stramineis, 12 x 8–13 x 9 mm.; seminibus asperibus, atro-fulvis, maculis non claris.

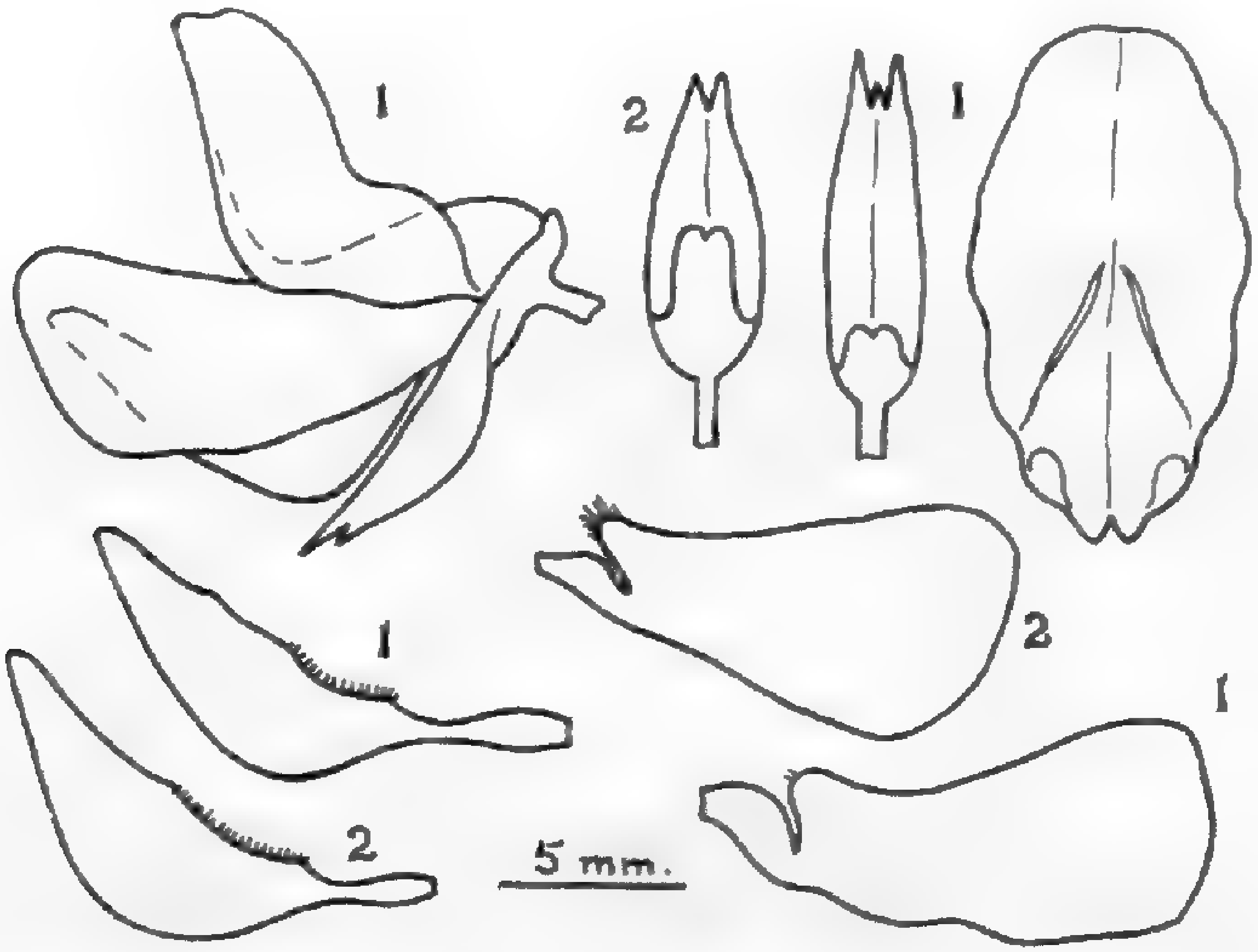

FIG. 37. LUPINUS DENSIFLORUS CURVICARINUS C. P. Smith. 1. *K. Brandegee* (UC 155195); 2. *C. P. Smith 1460.*

Loosely villous, 25–30 cm. tall, branched above the base or simple; leaflets apparently glabrous below, but in reality pubescent with loosely appressed short hairs, the margins and midribs often ciliate; flowers loosely spreading, 13–14 mm. long; calyx 8 mm. long, loosely villous below with hairs 1.5–2 mm. long, upper lip emarginate, about 2 mm. long, lower lip lance-ovate, evidently bent and subsaccate, the two teeth and the sinus slender; petals pale rose or purple, banner 12 mm. long, 7 mm. wide, rounded at the apex, keel decidedly curved, ciliate; seeds rough, dark brown, the markings indistinct.

CALIFORNIA. Yolo County: Woodland, 20 May, 1893, *J. W. Blankinship* (TYPE, G). Contra Costa County: Antioch, 5 May, 1907, *K. Brandegee* (UC 155195, except as to the specimen of var. *Menziesii* in center of sheet). Alameda County: Livermore, 16–17 May, 1891, *W. L. Jepson* (UC). Santa Clara County: Stanford University, 5 May, 1895, *C. Rutter 173* (US 308269, specimen on left only); Stanford University, 8 June, 1908, *C. P. Smith 1460* (CPS).

Curvicarinus is Latin for "curved keel."

6*u*. **Lupinus densiflorus Reedii** var. nov. [FIG. 38.]

Eramosus, humilis, 4–10 cm. altus, villosus; petiolis 1–4 cm. longis, foliolis 1–2 cm. longis, villosis; pedunculis folia excedentibus, verticillis 2–6, distantibus, floribus pandentibus, prope 13 mm. longis, pedicellis gracilibus, prope 2 mm. longis; calyce ebracteolato, 8 mm. longo, pilis densis, prope 1.5 mm. longis, labio superiore emarginato, vix 2 mm. longo, inferiore manifeste inflato, 2 mm. lato 3-dentato, dentibus 1 mm. longis, medio graciliore; colore corollae non claro, vexillo 12 mm. longo, 7 mm. lato, apice rotundato, carina 9 mm. longa, comparate brevi; legumina seminaque non vidi.

Simple and low, 4–10 cm. tall, villous; verticils two to six, distant, flowers spreading, about 13 mm. long; calyx ebracteolate, 8 mm. long, upper lip emarginate, lower lip manifestly bent and inflated near base, three-toothed, the median tooth more slender; color of corolla not evident, banner 12 mm. long, 7 mm. wide, rounded at the apex, keel comparatively short, 9 mm. long; pods and seeds not seen.

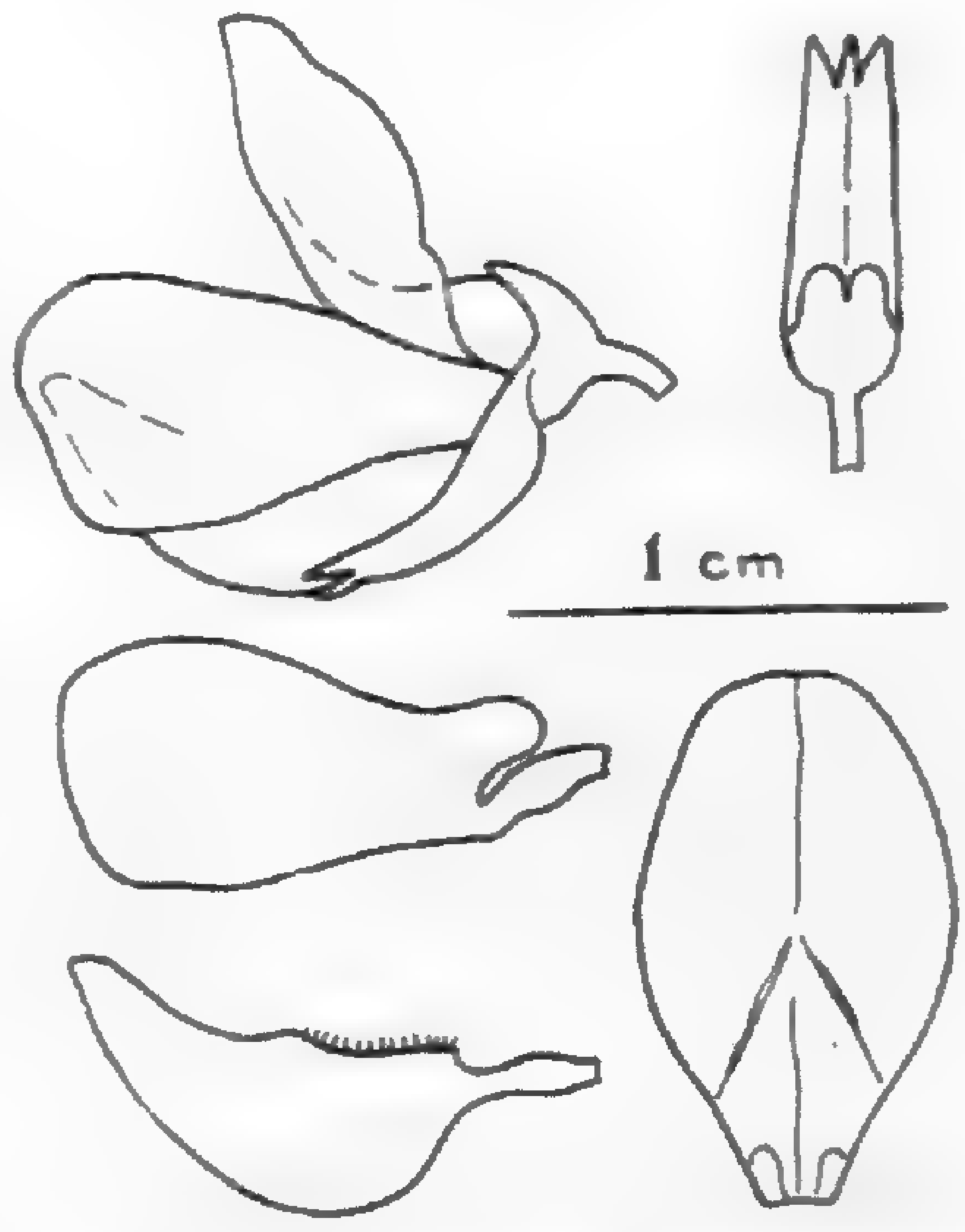

FIG. 38. LUPINUS DENSIFLORUS REEDII C. P. Smith. *E. C. Reed*, Concepcion (G).

CHILE: Concepcion, *E. C. Reed* (TYPE, G).

The sheet bears two plants. The flowers are well pressed, but the color of the petals is not preserved. *L. microcarpus* is the determination given, to which Miss Eastwood has added, "not typical."

6*v*. **Lupinus densiflorus trichocalyx** var. nov. [FIG. 39.]

Eramosus vel basi ramosus, 20–30 cm. altus, dense villosus; petiolis 10–14 cm. longis, foliolis maximis, 30 mm. longis, subter manifeste villosis; pedunculis prope folia aequantibus, verticillis prope 7, distantibus, floribus ad anthesin et specie postea pandentibus, 12 mm. longis, pedicellis prope 1 mm. longis, robustis, bracteis brevibus; calyce ebracteolato, 8 mm. longo, subter dense villoso pilis 2 mm. longis, labio superiore bipartito, inferiore lanceolato, bidentato, dentibus 1 mm. longis, parallelis, gracilibus; colore corollae non claro, specie purpureo, vexillo 12 mm. longo, 6 mm. lato, apice rotundato ungue lato, alis 10 mm. longis ad basin superne ciliatis, carina 9 mm. longa, curvata: legumina seminaque non vidi.

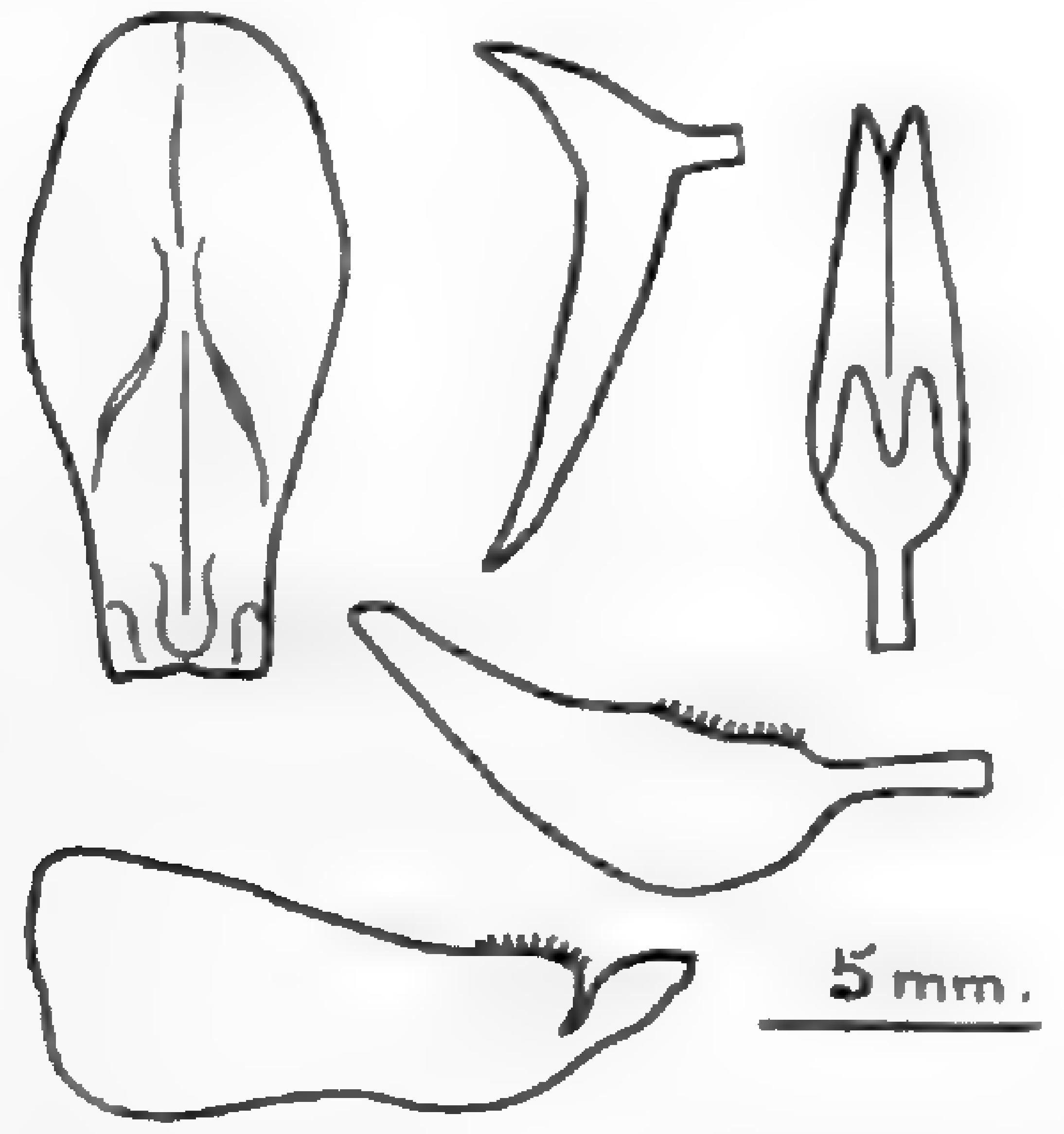

FIG. 39. LUPINUS DENSIFLORUS TRICHOCALYX C. P. Smith. *D. Douglas* (G).

Densely villous, 20–30 cm. tall, simple or branched at the base; verticils about seven, remote, flowers spreading in anthesis and seemingly later, 12 mm. long, pedicels short and stout and bracts short; calyx ebracteolate, bushy villous below with hairs 2 mm. long, upper lip two-parted, lower lip lanceolate, the two teeth about 1 mm. long, slender and parallel; color of the corolla not certain but probably purplish, banner 12 x 6 mm., rounded at the apex and with a broad claw, wings ciliate at the free edges above, keel curved: pods and seeds not seen.

CALIFORNIA. County not given: 1829, *D. Douglas*, ex. Herb. Lindley (TYPE, G); Saucelito, 21 May, 1874, *J. G. Lemmon 46* (G).

Perhaps related to this, but not at all typical, are the following: near Tulare Lake, July, 1878, *J. G. Lemmon 124* (G); Cuyama River, 27 May, 1896, *A. Eastwood* (G); Arroyo Grande, May, 1895, *M. Alice King* (UC).

The Douglasian plant upon which this variety is primarily based is probably one of the collection referred by Agardh to *L. microcarpus*,—in his words, "Etiam e California retulit Douglas." An annotation on the type sheet states that this is the *L. microcarpus* of Torrey & Gray's Flora of North America. If, as is very probable, the "Saucelito" of Lemmon is the same as the town now called Sausalito, in Marin County, such might have been the locality of Douglas's collection of "*L. microcarpus*." It seems to me more probable, however, that these plants came from Santa Barbara or San Luis Obispo County.

6*w*. **Lupinus densiflorus barbatissimus** var. nov. [FIG. 40.]

Ramosus, prope 10 cm. super basi, 25–35 cm. altus, villosus, ad basin fistulosus; petiolis longissimis, 12 cm. longis, foliolis 20–30 mm. longis, superne laxe villosis; verticillis prope 10 appositis, floribus prope 12 mm. longis, pandentibus, pedicellis prope 2 mm. longis, paulo gracilibus, bracteis villosissimis; calyce ebracteolato, 8 mm. longo, subter villosissimo, pilis 2 mm. vel plus longis, labiosuperiore prope 1 mm. longo, emarginato, inferiore manifeste inflato, 2 mm. lato, 3-dentato, dentibus 1 mm. longis, medio gracillimo; colore corollae non claro, specie roseo vel purpureo, vexillo11 mm. longo, 5 mm. lato, apice acuto, paullatim contracto in unguem non clarum, carina prope 8–9 mm. longa, acumine brevissimo: legumina seminaque non vidi.

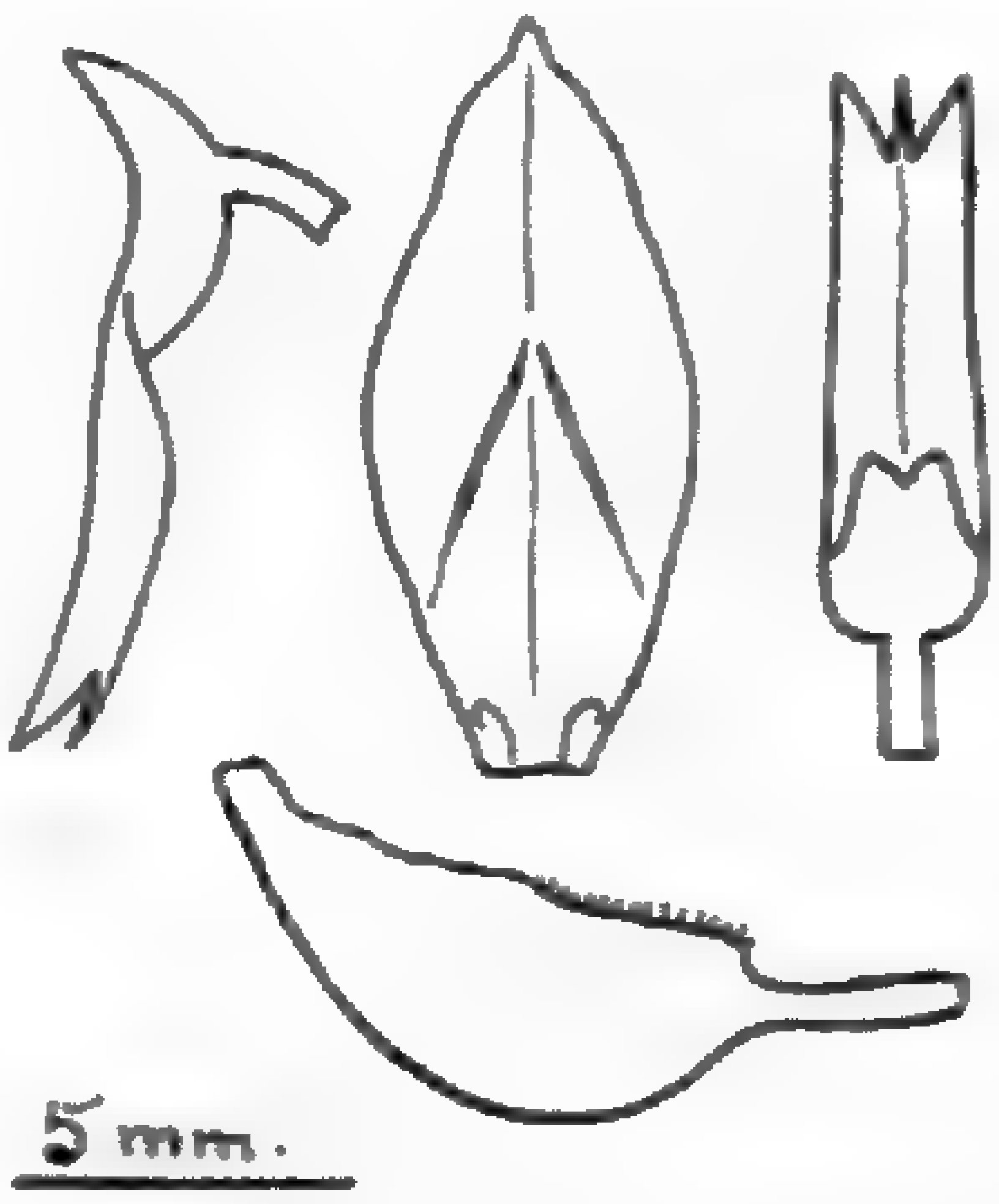

FIG. 40. LUPINUS DENSIFLORUS BARBATISSIMUS C. P. Smith. *James Macrae* (G).

Branched above the base, 25–35 cm. tall, fistulose at the base, villous; whorls about ten, approximate, flowers spreading, about 12 mm. long, bracts very villous; calyx ebracteolate, strongly bearded below with hairs 2 mm. or more long, upper lip emarginate, about 1 mm. long, lower lip manifestly subsaccate, tridentate, the median tooth slender; corolla apparently rose or purple, banner 11 x 5 mm., acute at the apex, slightly contracted into an indistinct claw, keel about 8–9 mm. long, with a short apical point: pods and seeds not seen.

CHILE. Bath of Collina, Andes, *James Macrae* (TYPE, G).

The sheet bears the following annotations:

L. microcarpus ? β barbatus Gray in Hb. Kew.

Part fr. Hb. Hook. The plant which Agardh, from Hb. Lindl., under *L. microcarpus*, refers to as 'huic proximum,' and identifies with Dougl. Calif.

Thus it is evident that neither Agardh nor Gray considered this plant to be typical *L. microcarpus.* The name "*barbatus*" is not now available, as it has been applied by Henderson to an Oregon lupine of the *Polyphylli.*

Barbatissimus, "very much bearded," refers to the very shaggy calyx, etc.

6*x*. **Lupinus densiflorus austrocollium** var. nov. [FIG. 41.]

A var. *palustri* differt labio inferiore calycis subrecto vix inflato; floribus 13 mm. longis, vexillo plurimum apice acuto, 11–13 mm. longo, 6–7 mm. lato, alis 11 mm. longis, ad basin ciliatis; leguminibus 13–16 mm. longis: semina matura non vidi.

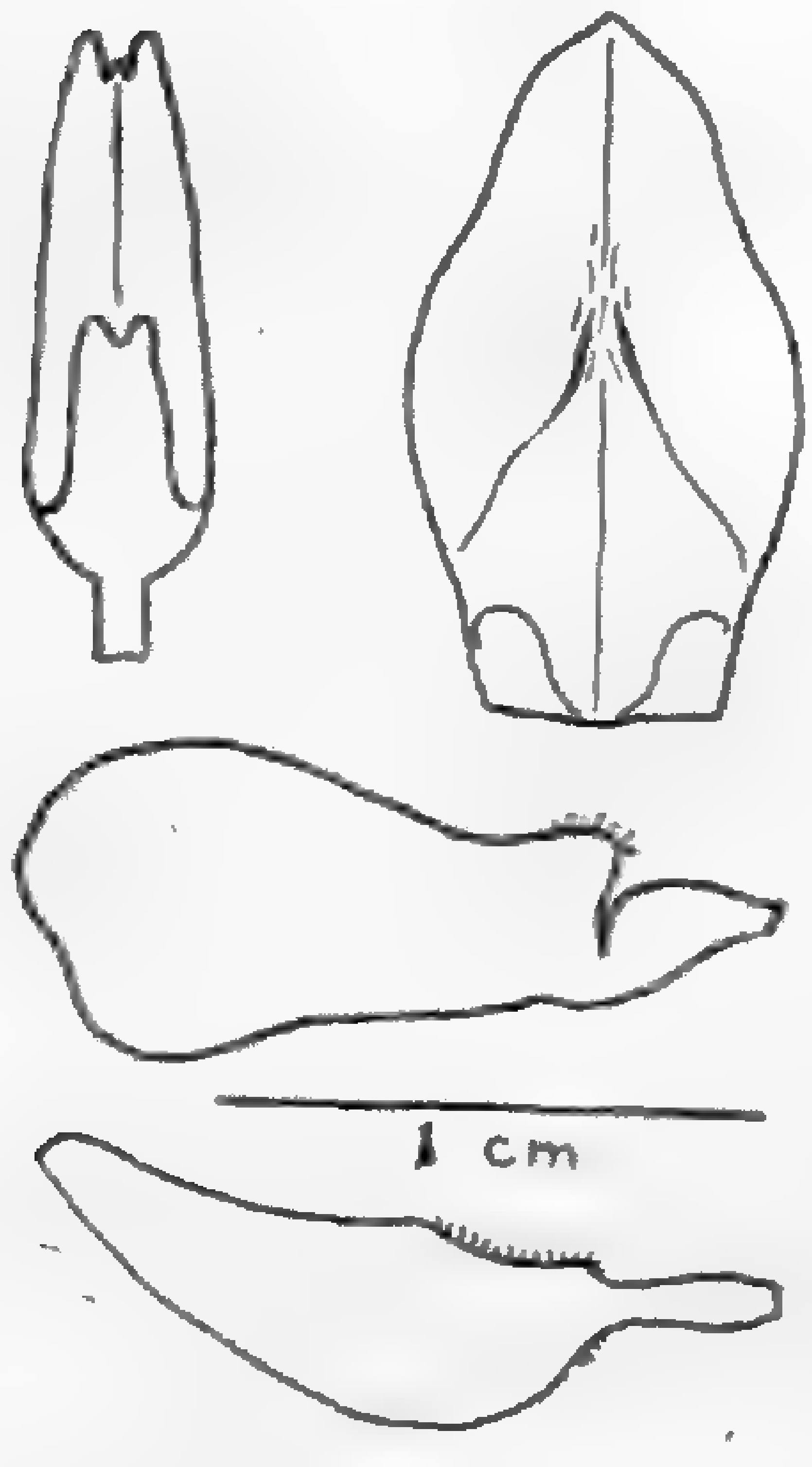

FIG. 41. LUPINUS DENSIFLORUS AUSTROCOLLIUM C. P. Smith. *L. R. Abrams 3465* (US614007).

Differs from var. *palustris* in the lower lip of the calyx being nearly straight and hardly inflated; flowers 13 mm. long, banner usually acute at the apex, 11–13 x 6–7 mm. long, wings 11 mm. long; pods 13–16 mm. long; matured seed not seen.

CALIFORNIA. San Diego County: near St. Mary's hospital, San Diego, 12 May, 1903, *L. R. Abrams 3465* (TYPE, DS9 579; type-duplicates, US, PA, NY, G); San Diego, May, 1852, *G. Thurber 579* (NY,G); San Diego, 22 Apr., 1885, *C. R. Orcutt* (Col U); San Diego, 1876, *W. G. W. Harford 185* (NY); Harbison Canyon, Sweetwater Valley, 6 May, 1888, *G. C. Deane* (G); San Ysabel, 12 May, 1893, *H. W. Henshaw 21* (US); El Cajon, 8 Apr., 1894, *T. S. Brandegee* (UC); San Diego hills, June–July, 1895, *S. G. Stokes* (DS); Canyon Road, San Diego Park, May,1905, *K. Brandegee* (UC); San Diego, May, 1906, *Brandegee* (NY).

Apparently confined to the foothills about San Diego. It is probable that all the specimens listed above should not be included under one and the same name. Considerable variation exists and it is possible that none of them should be included in the *L. densiflorus* series. Some are labelled "*L. densiflorus*," others "*L. microcarpus*." Careful field work is needed here.

Austrocollium, "of the southern foothills," is from the genitive plural of *collis*, "foothill," and *australis*, "southern."

6*y*. **Lupinus densiflorus scopulorum** var. nov. [FIG. 42.]

Ad basin ramosus et superne subramosus, caule 20–30 cm. alto, villoso, pilis 2–3 mm. longis; petiolis 4–8 cm. longis, conspicue villosis, foliolis 15–25 mm. longis, oblanceolatis, apice rotundatis vel angulatis, subter laxe villosis; pedunculis folia excedentibus vel brevioribus, verticillis 3–5, appositis, floribus ad anthesin et postea pandentibus, prope 15 mm. longis, pedicellis 2 mm. longis, gracilibus, bracteis villosissimis, cito reflectentibus marescentibusque; calyce ebracteolato, prope 11 mm. longo, labio superiore 2–3 mm. longo, diverso, interdum integro, inferiore villosissimo ad anthesin recto ad fructum subinflato, 3–4 mm. lato, 2-dentato, sinu lato dentis vestigio instructo; petalis pallido-luteolo-albis, vexillo 14 mm. longo, 6 mm. lato, medio maculato paullatim contracto, apice acuto et ungue gracili non claroque, alis 12 mm. longis, 6 mm. latis, non ciliatis, carina 10 mm. longa, subrecta; leguminibus prope 14 x 10 mm.: semina matura non vidi.

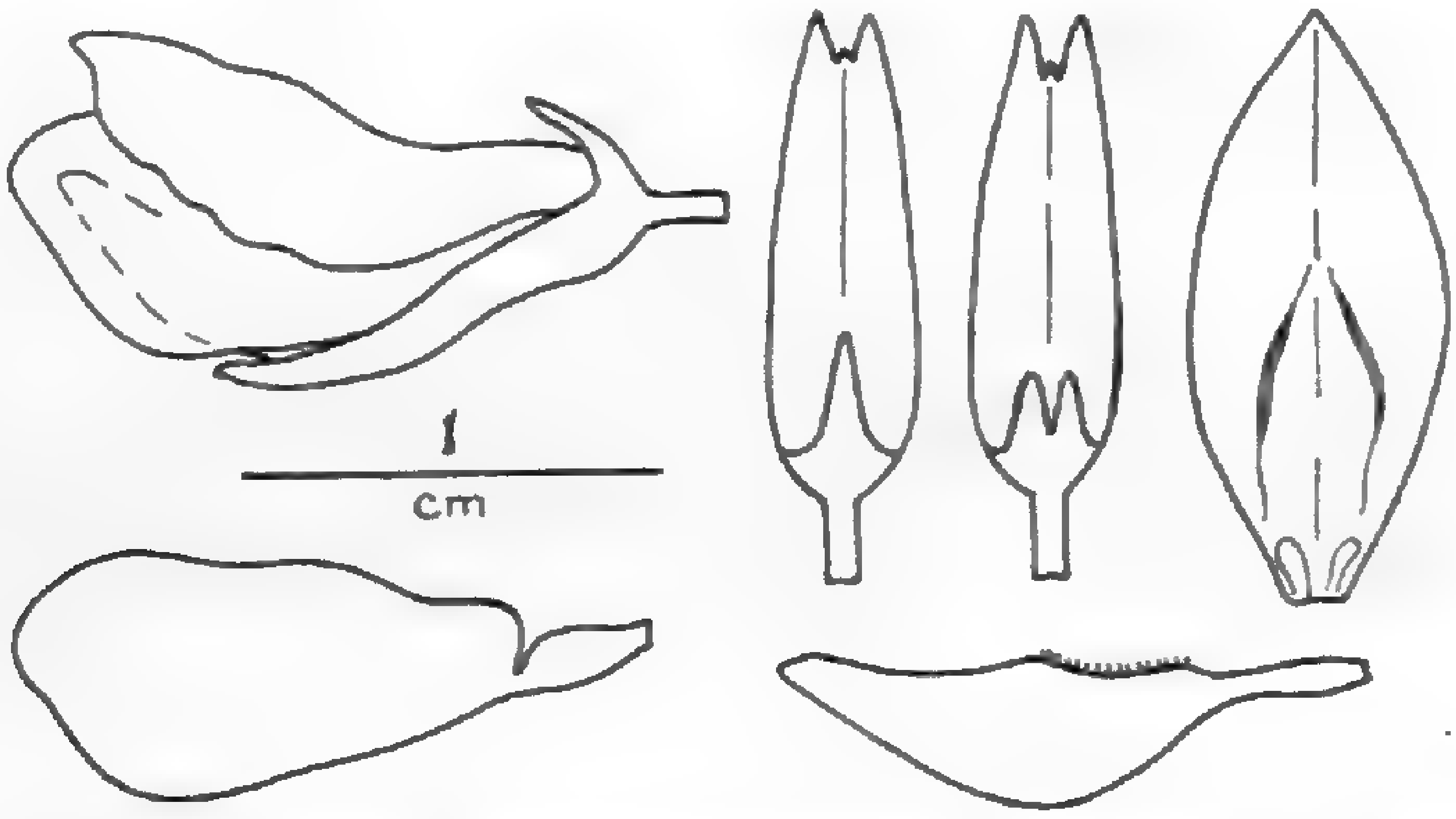

FIG. 42. LUPINUS DENSIFLORUS SCOPULORUM C. P. Smith. *J. Macoun* (US 20837).

Branched at the base and subbranched above, 20–30 cm. tall, villous with hairs 2–3 mm. long; verticils three to five, approximate; flowers spreading in anthesis and later, about 15 mm. long; bracts soon reflecting and withering; calyx without bracteoles, about 11 mm. long, upper lip 2–3 mm. long, entire or variously toothed, lower lip very villous, straight in anthesis, slightly inflated in fruit, two-toothed, the sinus wide with a vestigial tooth present; petals pale yellowish white, banner 14 x 6 mm., gradually contracted into an acute apex and an ill-defined slender claw, wings 12 x 6 mm., non-ciliate, keel nearly straight: mature seed not seen.

BRITISH COLUMBIA. Vancouver Island: sea cliffs, Beacon Hill, 4 July, 1889, *J. Macoun 21* (TYPE, US 20837; type-duplicates, T, G); Aug., 1873, *H. Edwards* (NY); cliffs by sea, Beacon Hill Park, Victoria, *A. J. Pineo* (UC).

WASHINGTON. Island County: Whidby Island, *N. L. Gardner* (UC).

While this form and the var. *austrocollium* may not be properly included in *L. densiflorus*, they certainly are less closely related to typical *L. microcarpus;* and var. *scopulorum* is certainly specifically distinct from its nearest neighbor, the Yakima Valley form I have called var. *fluviatilis* of *L. subvexus*.

Scopulorum, "of the cliffs," is the genitive plural of *scopulus*.

More extended and much more careful field study of these forms should contribute both taxonomic and ecological data. Interesting genetical data should also be obtainable from garden cultures; but one would have to devise first a suitable method of treating the seed in order to obtain proper germination, for the "hard-seed problem" would probably be the first stumbling stone to success in cultural studies—at least that has been my experience.

The collection and identification of seeds should be pursued with especial care, as one may often carelessly, though unintentionally, mix in collecting, at one time and locality, seed of more than one species or variety.

To the many friends who have generously assisted me in many different ways my full appreciation is herewith acknowledged. Listing of all of them will not be attempted here; but I cannot refrain from mentioning Drs. B. L. Robinson, H. M. Hall, and P. A. Rydberg, Professors H. H. Bartlett and L. R. Abrams, and Mr. Sidney F. Blake. Mr. Blake, while in England, looked up the old material of *L. microcarpus*, *L. densiflorus*, etc., and gave me certain valuable information.

COLLEGE PARK,
MARYLAND

Studies on the vegetation of New York State—II. The vegetation of a glacial plunge basin and its relation to temperature *

Loren C. Petry

(with three text figures)

A striking feature of the topography of the region immediately about Syracuse, New York, is the occurrence of numerous plunge basins produced by waterfalls during the later stages of the glacial period. The recently established Clarke State Reservation near Jamesville contains several of these basins; Green Lake in the Reservation occupies the bottom of a large typical one. Some of these are known to botanists acquainted with this region as the habitat of certain rare ferns, especially *Botrychium Lunaria* (L.) Sw. (*B. onondagense* Underwood) and *Scolopendrium vulgare* Sm. Maxon† and others have noted that these stations for *Scolopendrium* are always quite cool in summer. Some of these plunge basins show such remarkably low summer temperatures and display a vegetation so distinctly northern in character that a preliminary study of one of them was made during the summers of 1916 and 1917.

The basin studied lies near White Lake, six miles southeast of Syracuse. It is a natural amphitheater, elliptical in shape, with sloping sides; at the top or rim it measures about six hundred feet in length and four hundred fifty feet in width, and has a maximum depth of about ninety-five feet. Along part of the rim there are cliffs five to fifteen feet in height, and the slope begins at their foot; elsewhere the slope begins at the rim and descends at an angle of approximately thirty degrees until the opposite slope is met. The longer axis of the basin lies on an east-west line, and

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* The first of this series is a general discussion of the outstanding features of the vegetation of New York state as a whole; the citation to this is as follows:

Bray, W. L. The development of the vegetation of New York State. N. Y. State Coll. Forestry, Syracuse, N. Y. Tech. Pub. 3, 1915.

† Maxon, W. R. On the occurrence of the Hart's Tongue in America. Fern-wort Papers 30–46. Dec. 1900.

the bottom presents the appearance of a ravine running in that direction. The outlet of the basin lies to the southeast, where there is a notch about fifty-five feet in depth in the rim; this lowest point of the rim is forty feet above the bottom of the basin, which lies at an altitude of about six hundred ten feet above sea level.

The basin lies in rather thick-bedded limestone for its entire depth, and the slopes are formed of debris of this material. Throughout this region the rock is extensively fissured and it is probable that the underlying bedrock here is traversed by crevices, since water does not collect in the basin. Except on a considerable portion of the north side, where there is a rock slide, the slopes are covered by a thin layer of nearly pure humus. Under the conditions which occur here this soil is always moist and plant growth in the basin is not restricted by lack of available water.

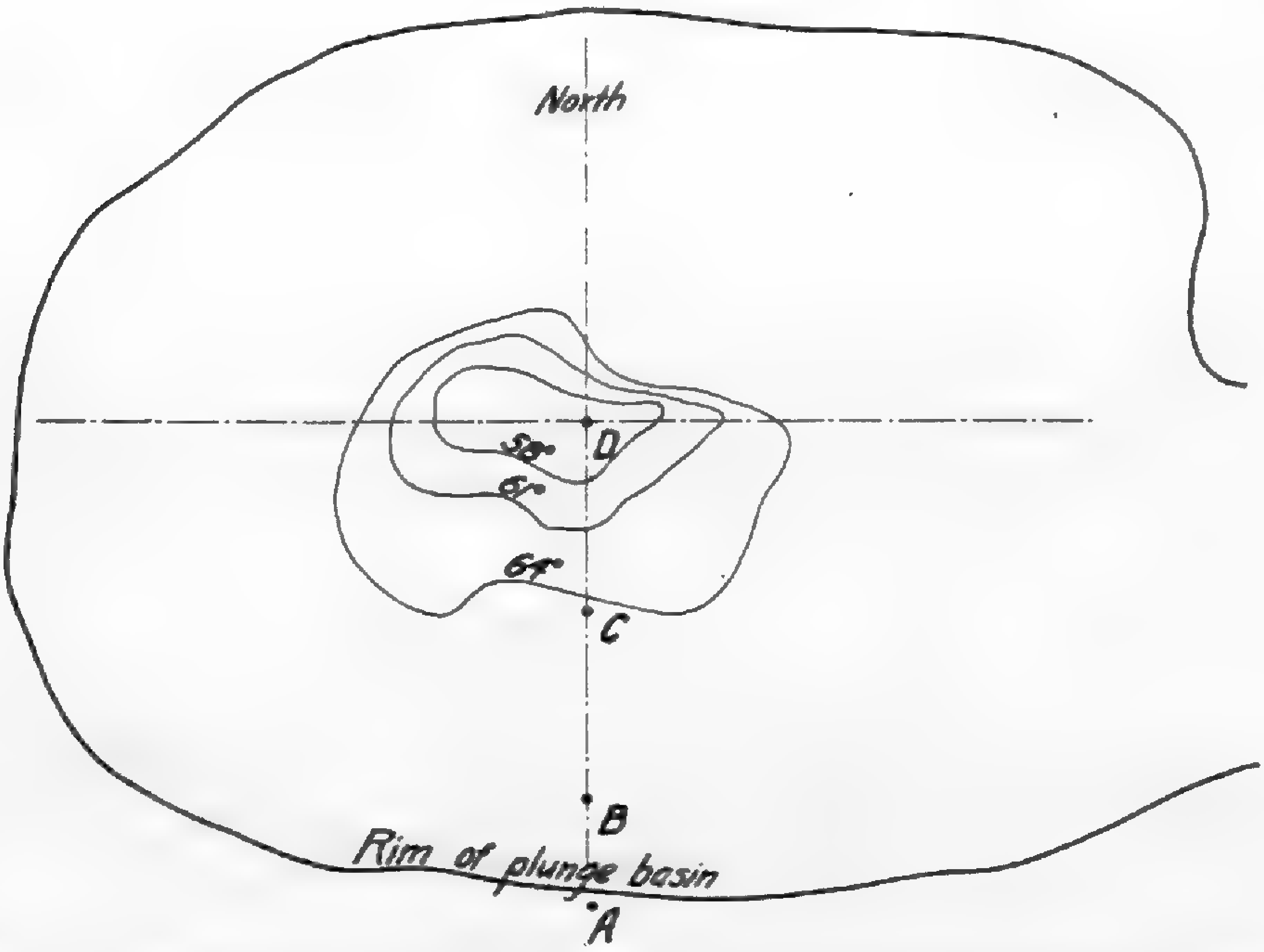

FIG. 1. Map of plunge basin, with isotherms of air temperatures (Fahr.) at 1 in. from the ground, at noon, September 12, 1916. *A, B, C* and *D* indicate location of stations referred to in the text. Scale, 1 in. = 160 ft.

The basin lies in a forest which has been somewhat disturbed by cutting. The interior of the basin itself is heavily wooded with *Tilia, Thuja, Betula lutea,* etc. The outlet is a narrow notch which extends only half the depth of the basin. As a result of these conditions, the bottom is completely free from air currents due to winds; even on a day when the local weather bureau station reported a wind velocity of thirty-five miles per hour, no movement of the air was perceptible half way down the slope of the basin. This absence of air currents is of prime significance in the explanation of the striking conditions of temperature that occur here.

Four stations for the securing of data on temperature and humidity were established in the basin. The first of these (FIG. 1, *A*) is six feet back from the rim, on the south side; it is in a forest of *Tilia* and *Acer saccharum*. The second station (*B*) is fifty feet down the slope from *A*; *Tilia, Scolopendrium* and *Impatiens* are the characteristic plants. Station *C* is one hundred feet further down the slope, while *D* is at the bottom of the basin, about one hundred feet below *C*. Temperature and humidity readings were made at each of these stations several times during the summer of 1916 and once during 1917; the data obtained on August 22, 1916, the hottest day of the year, are given in TABLE I.

TABLE I

TEMPERATURE AND HUMIDITY DATA AT STATIONS IN PLUNGE BASIN. AUGUST 22, 1916, 2.30–4.30 P.M.

Station	Temperatures (Fahr.)				Humidity (%)	
	3 ft. above ground	6 in. above ground	1 in. in soil	6 in. above ground	4 ft. above ground	6 in. above ground
A...	94.7	90.6	81.5	72.5	32	30
B...	90.0		76.6	75.2	32	37.5
C...	90.0	78.0	73.0	68.5	39	43
D...	63.5	59.7	51.3	42.5	73	71

The remarkable character of the conditions in the plunge basin is sufficiently shown by the data obtained at station *D*, where air temperatures were thirty degrees below those of station *A*, and where the soil temperature at a depth of six inches was only ten and one half degrees above freezing point. Readings made on other dates gave data similar to those of TABLE I, but in no case were any of the temperatures at station *D* higher than those given above. Similarly, the humidity at *D* varied from 75 to 85 per cent. but was at no time found to be below that recorded in TABLE I.

The cause of the low temperatures in the bottom of the basin is not clear, but is probably to be found in the accumulation of ice in underlying fissures. In the basin itself ice persists in the spring about a month after it has disappeared elsewhere. It is possible that a sufficient amount of ice accumulates in large crevices or fissures under the loose rock of the basin to maintain the low temperatures through the summer season. Some such localization of the areas of lowest temperature is indicated by the data on soil temperatures given in FIG. 2.

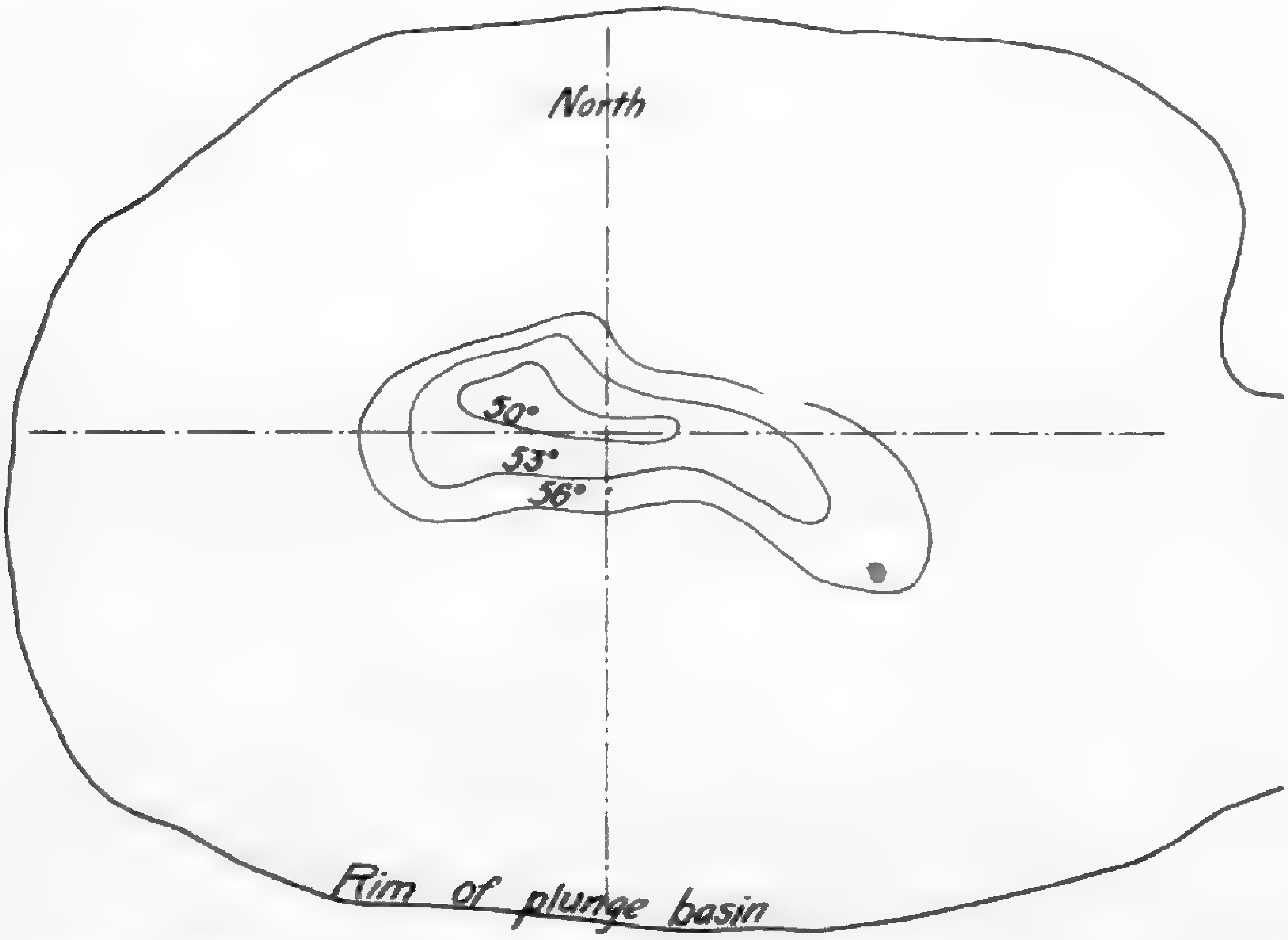

FIG. 2. Map of plunge basin with isotherms of soil temperatures (Fahr.) at depth of 1 inch at noon, September 12, 1916. Scale, 1 in. = 160 ft.

In order to determine with exactness the temperature conditions over the entire bottom of the basin, a system of twenty stations, at distances of thirty-five to fifty feet from each other, was established; these covered an irregular area extending about three hundred feet along the axis of the basin, some ninety feet up the south slope and about seventy feet up the northern slope. Two thermometers were placed at each station, one, completely shaded, at one inch from the ground, the other with the center of the bulb in the soil to a depth of one inch; after thirty minutes all the thermometers were read simultaneously.

When the temperature data are plotted on a map of the basin, isotherms can be drawn to represent the temperature conditions. FIG. 1 shows air isotherms representing the conditions existing between 11:30 A. M. and 12 M. on September 12, 1916, when the temperature at three feet from the ground at station *A* (on the rim) was 73° F.; Fig. 2 shows the soil isotherms of the same date. These are typical of the results obtained; charts made from the data obtained on other dates show that the isotherms vary but little in shape, only moving up and down the slopes within narrow limits with changes of temperature outside the basin. When the outside temperature falls below that within the basin the system of isotherms is of course destroyed.

As mentioned, *Scolopendrium* occurs abundantly in this basin, which is a typical habitat for it, associated with *Impatiens pallida* Nutt., *Asarum canadense* L., *Rubus odoratus* L., *Aspidium marginale* (L.) Sw., *Cystopteris bulbifera* (L.) Bernh., etc.; this association is restricted to the upper third of the south slope of the basin and is therefore outside the region of very low temperatures. The greater part of the basin is occupied by an association in which *Thuja occidentalis* L., *Betula lutea* Michx. f., and *Acer spicatum* Lam. are the dominant members; ground forms are few, mostly *Cystopteris bulbifera, Aspidium marginale* (L.) Sw., *A. spinulosum* (O. F. Müller) Sw. var. *intermedium* (Muhl.) D. C. Eaton, and *Thuidium* spp. The tree members of this association extend to the bottom of the basin but are less abundant there than farther up the slopes.

The forest floor association of the bottom area is the striking feature of the vegetation of the basin; a list of the species follows.

Dominant species

Cornus canadensis L.
Lycopodium annotinum L.
Dalibarda repens L.
Coptis trifolia (L.) Salisb.
Phegopteris Dryopteris (L.) Fée.
Pyrola asarifolia Michx.
Ribes lacustre (Pers.) Poir.

Incidental species

Lycopodium lucidulum Michx.
L. obscurum L. var. *dendroideum* (Michx.) D. C. Eaton
Aspidium marginale
A. spinulosum var. *intermedium*
Aralia nudicaulis L.
Tiarella cordifolia L.
Streptopus roseus Michx.
Actaea rubra (Ait.) Willd.
Diervilla Lonicera Mill.

Of these species, Bray, in the first paper of this series, lists three of the dominant ones as indicators of the Canadian zone—characteristic of the Adirondacks above 3,500 ft.—and four others as occurring abundantly in the Canadian Transition zone—characteristic of the higher Catskills and of the Adirondacks up to 3,500 ft.; and Cooper* lists four of the dominant species as characteristic of the climax forest of Isle Royale, Lake Superior. In addition, the manuals indicate a northern distribution for all the remaining species. These citations are sufficient to indicate the distinctively northern character of the plant association of the bottom of the basin.

Without entering into a discussion of the general questions of discontinuous distribution, it is evident that this may be considered to be a typical relict association, left behind at the final recession of the ice sheet. In this interpretation, certain conditions exist in this plunge basin which have caused or permitted the maintainance here of a plant association characteristic of more northerly regions or areas of higher altitude. That low temperature is the controlling factor of these conditions is the immediate and obvious conclusion from the data given above. This conclusion is strongly supported by further analysis of conditions in the basin.

During the work in the basin it was early noticed that the characteristic species of the bottom association are restricted to a common region of limited area and irregular shape; that is, the conditions which caused or permitted the maintenance of the association in the basin exist only in a small area of its bottom. As already described, the conditions of soil moisture, humidity, wind, etc., vary but slightly within the basin and cannot be controlling factors. The growing season in the bottom area is considerably shorter than in the upper part of the basin, due to the late melting of accumulated snow; the frostless period is probably about one hundred twenty-five days—an average period for the Canadian-Transition zone of Bray. This short growing season cannot however be effective in preventing the spread of the bottom association up the slopes of the basin, for not only do most of the

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* Cooper, W. S. The climax forest of Isle Royale, Lake Superior, and its development. Bot. Gaz. 55: 1–44, 115–140, 189–235. 1913.

species of the association spread readily by vegetative propagation, but ripe spores or seeds are also produced by most of them. On the other hand, the short season cannot be effective in preventing the invasion of plants of the higher parts of the slope, since these species have a longer season in which to mature spores or seeds, and every facility for their distribution into the bottom area.

With regard to the temperature conditions, however, the case is different. Casual observation indicated that the characteristic species of the bottom association do not occur outside the region of noticeably low temperatures. To verify this observation the exact distribution within the basin of five of the dominant species was determined and plotted. The maps of the distribution areas are remarkably alike; that for *Ribes lacustre*, given in FIG. 3, is typical. By comparison with FIG. 1 it will be seen that the distribution area is only roughly that of low air temperatures, being extended farther along the axis of the basin. A comparison of FIGS. 2 and 3, however, shows a remarkable similarity between the outline of the distribution area of *Ribes* and the soil isotherm of 56° Fahr.; and the maps of the distribution areas of the other species show an equally close resemblance. This coincidence of the areas of low soil temperature and of distribution of five of the dominant

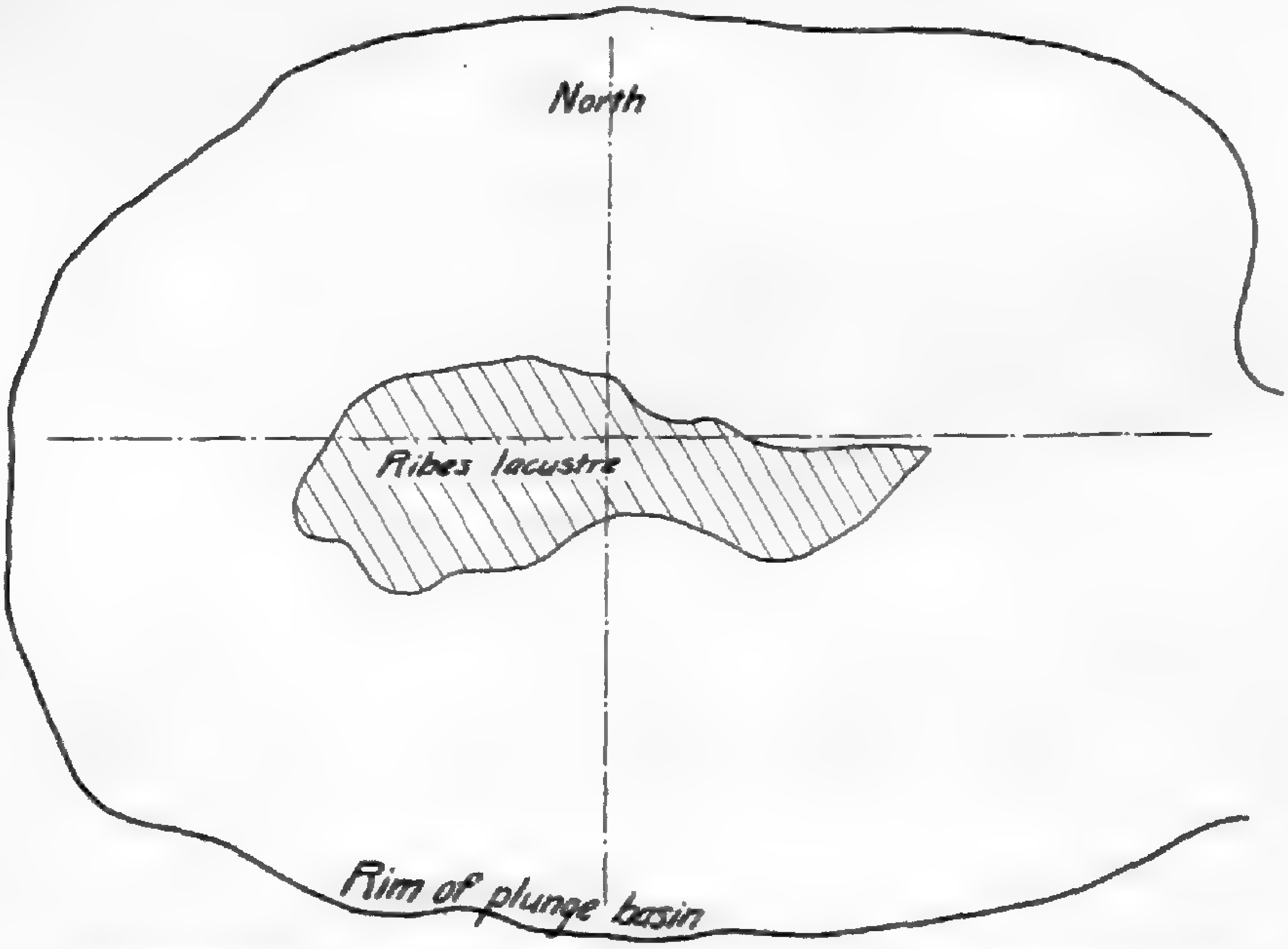

FIG. 3. Map of plunge basin showing distribution of *Ribes lacustre* (Pers.) Poir. Scale, 1 in. = 160 ft.

species is held to indicate a direct causal relationship between the two. The writer is of the opinion that we have here a case in which the control of distribution of a plant association by the single factor of temperature is demonstrable; and that the plunge basin offers an exceptionally favorable opportunity to determine experimentally the mechanism of this control. Work is now in progress along this line.

SUMMARY

1. In the bottoms of certain plunge basins near Syracuse, New York, low temperatures prevail throughout the year. Data of air and soil temperatures are given for one such basin whose bottom lies at an altitude of six hundred ten feet above sea level; an area of some thousands of square yards in it remains throughout the year at a temperature below 70° Fahr.

2. The bottom area of this basin is occupied by an association of plants characteristically Canadian in distribution. Analysis of the conditions in the basin demonstrates that temperature is the factor controlling their distribution in this area.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1912-1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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A carrier of the mosaic disease

MAKOTO NISHIMURA

(WITH PLATE 7)

INTRODUCTION

The symptoms and general character of the mosaic disease of tobacco and other solanaceous plants are becoming very well known through the work of Mayer (1886), Sturgis (1900), Woods (1899, 1902), Lowe (1900), Iwanowski (1903), Hunger (1905), Clinton (1908), Westerdijk (1910), Peters (1912), Allard (1914, 1915, 1916, 1917), Chapman (1913, 1916), Jensen (1913), and Freiberg (1917).

The disease has been observed on all varieties of *Nicotiana Tabacum*, on several of the more distinct varieties of tomato, on *Petunia violacea*, on *Physalis* (two distinct garden species), on *Datura Stramonium* and *D. Tatula*, on *Hyoscyamus niger*, on *Solanum nigrum* and *S. carolinense* and on several of the more distinct varieties of *Capsicum*. It has been transferred to all these from infected *N. Tabacum*. To this list should be added now *Solanum aculeatissimum*, the apple of Sodom, an infected plant of which was brought from Florida to the greenhouse of Columbia University in the winter of 1915.

According to Allard (1914) the following symptoms are characteristic of different phases of the disease at one or another stage in the infection: (1) partial or complete chlorosis, (2) curling of the leaves, (3) dwarfing and distortion of the leaves, (4) blistered or

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"Savoyed" appearance of the entire plant, (5) mottling of the leaves with different shades of green, (6) dwarfing of the entire plant, (7) dwarfing and distortion of the blossoms, (8) blotched or bleached corollas (in *N. Tabacum* only), (9) mosaic sucker growth, (10) death of tissue (sometimes very marked in *N. rustica*). To these should be added the narrowing of the leaves or frenching and their sometimes uniformly lighter or more yellowish green color.

In attempting to infect the alkekengi or bladder cherry (*Physalis Alkekengi*) I have found that although this plant when inoculated does not show any of the above visible symptoms, it may, nevertheless, become a carrier of the disease in the fullest sense, for I have infected *N. Tabacum* and the apple of Sodom with the juice of plants of the alkekengi which appeared to be entirely free from mosaic.

Allard reports (1914) that he has readily transferred the disease from tobacco to two distinct garden species of *Physalis*, which then showed the general symptoms of the disease, but he does not tell us what species of *Physalis* he used.

As grown by me the alkekengi certainly shows none of the ordinary symptoms, the plants remaining healthy in appearance for indefinite periods, after inoculation with the juice of diseased tobacco or apple of Sodom.

Allard (1917) reports some very interesting experiments on the behavior of the mosaic disease in *N. glauca*. He inoculated this species from diseased plants of *N. Tabacum* and found that the symptoms were confined to a sparse and indistinct mottling along the veins of some of the leaves. This mottling in some instances was too faint to be detected readily, except in transmitted light. Eight of these plants which showed these symptoms more clearly were tested by injecting the expressed sap of each into a series of plants of *N. Tabacum*. The sap of all proved exceptionally virulent, producing in most instances 100 per cent. of infection in each lot of ten plants. After the initial expression of the disease in *N. glauca*, Allard reported that the symptoms gradually became more attenuated, until they were barely distinguishable. In July three of these plants were cut back severely and were immediately transplanted to the field. Growth was resumed, but no symptoms of the mosaic disease whatever could be detected. However, inoculation tests demonstrated that the sap of these plants contained the infective principle of the disease. These plants were again taken from the field and transplanted into the greenhouse for the winter. Although growth appeared normal and symptoms of the mosaic disease could not be detected with certainty, experiments showed repeatedly that the infective principle of the disease was still present in the expressed sap. Allard further shows that when scions of the immune species, *N. glutinosa*, are grafted upon mosaic-diseased plants of *N. Tabacum* the infective principle of the disease may pass into *N. glutinosa* without the subsequent development of symptoms in it.

These experiments bear an interesting relation to my own observations on the alkekengi as a carrier of the disease. A so-called carrier of the disease is, first, an organism which through acquired toleration continues to harbor the germ or virus after recovery from the diseased condition; or second, one which through natural toleration may acquire and transmit the germ or virus without itself showing any symptoms or suffering in any way from the disease. A third type of carrier is found in those organisms which are immune, but may passively transmit a disease (as does *Abutilon arboreum* in Baur's grafting experiments), without necessarily becoming a seat for the multiplication of the germ or the increase of the virus. See Baur (1906).

MATERIAL AND METHODS

I have used two species of plants as a source of the mosaic disease, namely:

1. Apple of Sodom (*Solanum aculeatissimum*). The first plant of this species showing the mosaic disease was brought from Florida by Professor Harper in December, 1915. So far as I am aware this plant has not hitherto been reported as showing mosaic, though there is of course every reason to suppose that most of the species of *Solanum* are susceptible. The symptoms in apple of Sodom include all those enumerated above.

2. Tobacco (*Nicotiana Tabacum*). I have used the juice of mosaiced plants of the tobacco, kept as stock cultures in the greenhouse of Columbia University.

The juice for inoculation was procured by crushing the leaves. The inoculations were made in several different ways as follows:

No. 1. One stab in each node. In addition to the puncture the four upper leaves were rubbed on both surfaces with the same inoculum used for the needle stab.

No. 2. Five stabs on stem in the following places: one at the tip, one at the base, and three at equal distances between tip and base. Besides these punctures the five upper leaves were rubbed on both surfaces with the same inoculum as used for the stabs.

No. 3. Four stabs: one in the growing tip of stem, and three additional punctures on each in the base of the three upper young leaves near the midrib.

No. 4. Four stabs: one in growing tip of stem, one in middle of stem, a third in its base, and a fourth on the youngest leaf near the midrib.

No. 5. Three stabs on the stem: one in growing tip, one in the middle, and another one near the base of the stem.

No. 6. Four stabs: one in the growing tip of the stem, another in the middle of the stem, the third and fourth on the base of the upper two young leaves near the midrib.

No. 7. One stab in the growing tip of the stem.

No. 8. Two stabs: one in the middle of the stem and another in the blade of the youngest leaf.

EXPERIMENTS

1. *Inoculation of the alkekengi with juice of infected apple of Sodom plants.*

On May 21, forty-eight young plants (3–5 inches high) of the alkekengi were transplanted into five and a half inch pots from the garden and brought into the greenhouse. These were entirely free from mosaic disease and produced fine new growths in two weeks' time.

On June 5, nine plants out of the forty-eight were inoculated with the juice of *S. aculeatissimum* having the mosaic disease. I used method No. 1 in this experiment. No symptoms of the disease appeared in any of these plants. They were entirely indistinguishable from the controls. On June 27 these same nine plants were inoculated again by the same method as before. On

July 16 each plant was examined carefully, but there was no visible evidence of the disease.

On June 25 another series of inoculations with juice of diseased tobacco plants was made on fourteen healthy plants of the alkekengi. These plants were inoculated by method No. 2. After four weeks, although growth continued normally, they showed no symptoms of the disease.

The same experiment was repeated with another series of mature plants of the alkekengi (10–12 inches high). On August 4, twenty of these plants were inoculated with the juice from diseased *S. aculeatissimum*, another series of twenty plants were inoculated with the juice of diseased *N. Tabacum*. Method of inoculation No. 2 was used. After a period of thirty days no symptoms of the disease had appeared on the plants in these two series of experiments. See FIG. 1.

2. *Transfer of mosaic from the apple of Sodom to the alkekengi and then to tobacco*

It occurred to me that the plants might carry the disease, though not showing symptoms, and I inoculated plants of *N. Tabacum* and apple of Sodom with the juice from the alkekengi plants which had been inoculated from the apple of Sodom apparently without results.

TABLE I

SUMMARY OF EXPERIMENT NO. 2

No.	Date of inoculation	First symptom	Incubation period, days	25 days after inoculation
1	July 16	July 23, mosaic on the first new leaf	7	Disease developing
2	" "			No reaction
3	" "	July 24, mosaic on the first new leaf	8	Disease developing
4	" "	July 25, mosaic on the first new leaf	9	" "
5	" "	July 24, mosaic on the first new leaf	8	" "
6	" "			No reaction
7	" "	July 23, mosaic on the first new leaf	7	Disease developing
8	" "	July 24, mosaic on the first new leaf	8	" "
9	" "	July 25, mosaic on the first new leaf	9	" "
10	" "			No reaction
11	" "	July 23, mosaic on the first new leaf	7	Disease developing
12	" "			No reaction
13	" "			" "

On July 16 thirteen young healthy plants of *N. Tabacum* (six- to ten-leaf stage) were inoculated with the juice of the *P.*

Alkekengi which had been inoculated on June 5 and June 27 with the juice of mosaiced leaves of apple of Sodom. In this experiment inoculation method No. 3 was used. July 23, experimental plants 1, 7 and 11 showed mosaic on the first new leaves which were just appearing. July 24, plants 3, 5 and 8 also showed mosaic on the first new leaves. Finally on July 25, plants 4 and 9 exhibited mosaic on the first new leaves and these plants continued diseased, but plants 2, 6, 10, 12 and 13 did not show any symptoms whatever. Eight plants were left as controls and at the end of twenty-five days they showed no symptoms of mosaic· See TABLE I and FIG. 2.

3. *Transfer of mosaic from the tobacco to the alkekengi and then back to the tobacco*

I next tested plants of the alkekengi of the series which had been inoculated with mosaic from diseased tobacco plants with respect to their power to infect tobacco.

July 22, six young healthy tobacco plants (six- to eight-leaf stage) were inoculated with the juice of the alkekengi which showed no symptoms of the disease, although they had been inoculated with the juice of diseased tobacco on June 25. This inoculation was made by method No. 3. July 28, plant 3 showed mosaic on the first new leaf. July 29, plant 1 showed mosaic on the first new leaf. July 30, plants 2 and 5 showed mosaic on the first new leaf, but plants 4 and 6 did not show symptoms of the disease. For this experiment six control plants were kept, which after twenty-five days showed no mosaic.

The experiment was repeated in the period from August 8 to September 2.

August 8, twelve young healthy tobacco plants (six- to ten-leaf stage) were inoculated by method No. 4. August 15, plant 10 showed mosaic on the first new leaf. August 16, plants 7 and 14 showed mosaic on the first new leaves. August 17, plants 9, 11, 15 and 16 showed mosaic on the first new leaves. August 18, plants 12 and 18 showed mosaic on the first new leaves. August 19, plant 17 showed mosaic on the first new leaf.

All of the inoculated plants developed the disease except plants 8 and 13 which did not show any symptoms. In this experiment twelve plants were kept as controls and after twenty-five days they were found to be free from any symptoms of mosaic. See TABLE II.

TABLE II

SUMMARY OF EXPERIMENT NO. 3

No.	Date of inoculation	First symptoms	Incubation period, days	25 days after inoculation
1	July 22	July 29, mosaic on the first new leaf	7	Disease developing
2	“ “	July 30, mosaic on the first new leaf	8	“ “
3	“ “	July 28, mosaic on the first new leaf	6	“ “
4	“ “			No reaction
5	“ “	July 30, mosaic on the first new leaf	8	Disease developing
6	“ “			No reaction
7	Aug. 8	Aug. 16, mosaic on the first new leaf	8	Disease developing
8	“ “			No reaction
9	“ “	Aug. 17, mosaic on the first new leaf	9	Disease developing
10	“ “	Aug. 15, mosaic on the first new leaf	7	“ “
11	“ “	Aug. 17, mosaic on the first new leaf	9	“ “
12	“ “	Aug. 18, mosaic on the first new leaf	10	“ “
13	“ “			No reaction
14	“ “	Aug. 16, mosaic on the first new leaf	8	Disease developing
15	“ “	Aug. 17, mosaic on the first new leaf	9	“ “
16	“ “	“ “ “ “ “ “ “ “	9	“ “
17	“ “	Aug. 19, mosaic on the first new leaf	11	“ “
18	“ “	Aug. 18, mosaic on the first new leaf	10	“ “

4. *Inoculation of the tobacco with juice of healthy alkekengi plants*

To prove that the juice of uninoculated plants of the alkekengi will not produce the disease in tobacco twelve healthy young *N. Tabacum* plants (ten- to eleven-leaf stage) were inoculated on September 10 with the juice of the leaves of healthy *P. Alkekengi* by method No. 3, the same which was used in experiment No. 2. After thirty days two new leaves or more appeared on each plant but did not show any symptoms of the disease.

5. *Comparison of inculation periods*

To compare the length of the incubation period in my transfers through *P. Alkekengi* with the ordinary incubation period when tobacco is inoculated with juice from diseased tobacco, a series of inoculations was made using methods Nos. 4, 7, and 8; twenty plants of *N. Tabacum* were used in each of the three series. The first series were inoculated on March 28 by method No. 8, the plants having eight to ten leaves. The second series were inoculated on April 5 by method No. 7, the plants having five to seven leaves.

The third series were inoculated on August 10 by method No. 4, the plants having seven to eight leaves. Forty-eight of these showed the symptoms of disease. The incubation period was from six to seven days in each of the series. The mosaic symptoms always appeared on the first or second new leaves that were formed after inoculation. Fifteen controls were kept in each experiment and after twenty-five days they were found to be in a healthy condition. The incubation period is seen to be much the same in all the experiments:

In experiment No. 2, from 7 to 9 days;
In experiment No. 3, from 7 to 11 days;
In experiment No. 5, from 6 to 10 days.

This result agrees with the observations of other authors on the length of the incubation period. In each experiment the mosaic was observed on the first or second new leaf which appeared after inoculation.

The appearance of the mosaic leaves of apple of Sodom and tobacco, infected through the alkekengi, is the same in design and coloring (i. e., distribution of the dark green with relation to the vein, etc.) as in direct infection from tobacco to tobacco.

There can be no question that the virus induces the same symptoms after passing through the apparently immune plant as when transferred directly from one susceptible plant to another. The affected plants developed the disease on all new leaves which appeared after inoculation.

6. *Transfer of mosaic from the apple of Sodom to the alkekengi and then back to the apple of Sodom*

The transfer through *P. Alkekengi* from apple of Sodom to apple of Sodom is equally easy.

June 23, ten young healthy plants of apple of Sodom (3–4 inches high) were inoculated with the juice from the leaves of the same plants of *P. Alkekengi* (inoculated from apple of Sodom) which were used in experiment No. 2 as a source for the inoculation of tobacco. I used method No. 5 for this inoculation. June 30, plants 2 and 6 showed mosaic on the first new leaves. July 1, plant 4 showed mosaic on the first new leaf. July 2, plants 7 and

10 showed mosaic on the first new leaves. July 3, plant 1 showed mosaic on the first new leaf. These six plants developed the disease, but plants 3, 5, 8 and 9 showed no symptoms.

On July 20, the same experiment was repeated with another series of ten young healthy plants of apple of Sodom 4–5 inches high. July 29, plant 12 showed mosaic on the first new leaf. July 30, plants 11 and 13 showed mosaic on the first new leaves. July 31, plants 14 and 16 showed mosaic on the first new leaves. August 1, plants 19 and 20 showed mosaic on the second new leaves. Plants 15, 17 and 18 showed no symptoms.

Ten plants were kept in each experiment as controls and after twenty-five days they were found to be in healthy condition.

TABLE III

SUMMARY OF EXPERIMENT NO. 6

No.	Date of inoculation	First symptom	Incubation period, days	25 days after inoculation
1	June 23	July 3, mosaic on the first new leaf	10	Disease developing
2	" "	June 30, mosaic on the first new leaf	7	" "
3	" "			No reaction
4	" "	July 1, mosaic on the first new leaf	8	Disease developing
5	" "			No reaction
6	" "	June 30, mosaic on the first new leaf	7	Disease developing
7	" "	July 2, mosaic on the first new leaf	9	" "
8	" "			No reaction
9	" "			" "
10	" "	July 2, mosaic on the first new leaf	9	Disease developing
11	July 20	July 30, mosaic on the first new leaf	10	" "
12	" "	July 29, mosaic on the first new leaf	9	" "
13	" "	July 30, mosaic on the first new leaf	10	" "
14	" "	July 31, mosaic on the first new leaf	11	" "
15	" "			No reaction
16	" "	July 31, mosaic on the first new leaf	11	Disease developing
17	" "			No reaction
18	" "			" "
19	" "	Aug. 1, mosaic on the second new leaf	12	Disease developing
20	" "	Aug. 1, mosaic on the second new leaf	12	" "

7. *Inoculation of the apple of Sodom with the juice of healthy alkekengi plants*

To prove that the juice of uninoculated plants of *P. Alkekengi* will not produce the disease in the apple of Sodom, twelve healthy young plants of apple of Sodom (5–6 inches high) were inoculated on September 12 with the juice of the leaves of healthy *P. Alke-*

kengi by the method used in experiment No. 6. After a period of four weeks two or three new leaves had appeared on each plant but no symptoms of the disease had appeared.

8. *Transfer of mosaic from the tobacco to the alkekengi and then to the apple of Sodom*

To make the evidence still more clear that *P. Alkekengi* is a carrier, I tried an inoculation of the apple of Sodom with the juice of *P. Alkekengi* used in experiment No. 3, that is from plants inoculated from tobacco. The experiment is the reverse of experiment No. 2.

August 20, twelve young healthy plants of apple of Sodom (4–5 inches high) were inoculated with the juice of the leaves of *P. Alkekengi* which had been inoculated with the juice of mosaic leaves of *N. Tabacum*. Four punctures were made in each plant by method No. 6. August 30, plants 2, 3 and 10 showed mosaic on the first new leaves. August 31, plants 1, 9 and 11 also showed mosaic on the first new leaves. September 1, plant 5 showed mosaic on the second new leaf. September 2, plant 7 showed mosaic on the second new leaf. These eight plants developed the disease, but plants 4, 6, 8 and 12 did not show any symptoms.

TABLE IV

SUMMARY OF EXPERIMENT NO. 8

No.	Date of inoculation	First symptoms	Incubation period, days	25 days after incubation
1	Aug. 20	Aug. 31, mosaic on the first new leaf	11	Disease developing
2	" "	Aug. 30, mosaic on the first new leaf	10	" "
3	" "	" " " " " " " "	10	" "
4	" "			No reaction
5	" "	Sept. 1, mosaic on the second new leaf	12	Disease developing
6	" "			No reaction
7	" "	Sept. 2, mosaic on the second new leaf	13	Disease developing
8	" "			No reaction
9	" "	Aug. 31, mosaic on the first new leaf	11	Disease developing
10	" "	Aug. 30, mosaic on the first new leaf	10	" "
11	" "	Aug. 31, mosaic on the first new leaf	11	" "
12	" "			No reaction

In this experiment twelve controls were kept and after twenty-five days they were found to be in healthy condition. See TABLE IV and FIG. 3.

9. *Inoculation of the apple of Sodom with juice of infected tobacco plants*

Before making the above experiments with the alkekengi I had already satisfied myself as to the relation of the mosaic of tobacco to that of the apple of Sodom.

Forty young healthy plants of apple of Sodom (4–6 inches high) were used in each of the two series. The first series was inoculated on March 27 with juice from diseased apple of Sodom. The second series was inoculated on March 25 with juice from diseased tobacco. These inoculations were made by method No. 5. In the first series thirty-three plants showed mosaic. The incubation period was from eight to ten days. In the second series thirty-six plants showed mosaic. The incubation period was from seven to twelve days. In every case the mosaic symptoms appeared on the first or second new leaves that were formed after inoculation. The incubation period was much the same in all these experiments. Twenty-five controls were kept and after thirty days they were found to be in healthy condition.

The appearance of the mosaic leaves of apple of Sodom, produced by infection from the carrier, *P. Alkekengi* (which had been inoculated from apple of Sodom or from tobacco) is the same as in the case of direct infection from tobacco or apple of Sodom in the distribution of the dark green with relation to the veins, in the blistering, etc. There can be no question that the virus induces the same symptoms after passing through the apparently immune plant to another as when transferred directly from one susceptible to the disease.

10. *Reinoculation of tobacco plants*

The *N. Tabacum* plants inoculated in experiments 2, 3, and 4, which did not take the disease, were later used for further inoculations with virus from the diseased tobacco which had been inoculated from *P. Alkekengi*. September 10 the fourteen plants of *N. Tabacum* were inoculated by method No. 1. September 18, plants 3 and 5 showed the mosaic on the first new leaves. September 19, plants 7 and 11 also showed the mosaic on the first new leaves. September 20, plants 8, 10 and 12 showed the mosaic. September 21, plants 2, 6 and 9 showed the mosaic. September

22, plant 13 showed the mosaic on the second new leaf. These eleven inoculated plants developed the disease, but plants 1, 4 and 14 did not show any symptoms.

It is evident that the failure to infect these plants in the earlier inoculations was due to the uncertainties of the method of inoculation. Twelve of these same plants were kept as controls (four plants which had been used in experiment No. 2, five plants from experiment No. 3 and the other three plants from experiment No. 4). All of the controls but one remained in a healthy condition. The results show that the chances of accidental inoculations in the greenhouse where the work was carried on were very small. These control plants with one exception had remained uninfected for over two months.

11. *Reinoculation of apple of Sodom plants*

The same test was made on the plants of the apple of Sodom which had remained healthy after inoculation in the earlier experiments.

September 13, the twelve plants of apple of Sodom of experiments 6, 8 and 9, which had failed to develope the disease were inoculated by method No. 6 with juice from diseased tobacco which had been inoculated from *P. Alkekengi*. September 21, plants 8 and 11 showed the mosaic on the first new leaves. September 22, plants 7 and 6 showed the mosaic as above. September 23, plants 2, 4 and 5 showed the mosaic as above. September 24, plant 9 showed the mosaic as above. September 25, plant 12 showed the mosaic on the second new leaf.

Nine plants developed the disease, but plants, 1, 3 and 10 did not show any symptoms.

SUMMARY

Physalis Alkekengi is found to be a carrier of the mosaic disease without itself showing any symptoms. The experimental results were as follows:

1. Thirty-four healthy plants of *Physalis Alkekengi* were inoculated with juice of mosaic-diseased plants of *N. Tabacum* and showed no symptoms. To test the method of inoculation and the virulence of the disease sixty young healthy plants of *N.*

Tabacum were inoculated with juice of the mosaic-diseased tobacco and forty-eight of these plants showed the disease.

2. The same test was made with the juice of mosaic-diseased *Solanum aculeatissimum* on twenty-nine healthy plants of *P. Alkekengi*, and none showed any symptoms of the disease. Of forty healthy plants of *S. aculeatissimum* inoculated with juice of mosaic-diseased *S. aculeatissimum* thirty-three plants showed the disease.

3. Of thirty-one healthy plants of *N. Tabacum* inoculated with juice from leaves of *P. Alkekengi* which showed no symptoms of mosaic but had been inoculated from diseased tobacco or *S. aculeatissimum*, twenty-two plants showed typical mosaic disease. Of twelve young healthy plants of *N. Tabacum* inoculated with juice from leaves of *P. Alkekengi* which had not been inoculated none showed the disease.

4. Of thirty-two healthy plants of *S. aculeatissimum* inoculated with juice from leaves of *P. Alkekengi* which showed no symptoms of mosaic but had been inoculated from diseased tobacco or *S. aculeatissimum*, twenty-one plants showed mosaic also. Of twelve young healthy plants of *S. aculeatissimum* inoculated with juice from leaves of *P. Alkekengi* which had not been inoculated, none showed the disease.

5. Experiments have shown that the mosaic diseases of *S. aculeatissimum* and *N. Tabacum* are similar with respect to the symptoms and incubation periods.

6. The juice from diseased *N. Tabacum* when passed through *P. Alkekengi* to *N. Tabacum* has produced the disease in 80 per cent. of the inoculations on healthy plants of *S. aculeatissimum* or *N. Tabacum*. It is evident that there is no marked weakening of the virus by the carrier *P. Alkekengi*.

The author is especially indebted to Professor Harper of Columbia University for his kindly interest and valued supervision throughout these experiments.

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Explanation of plate 7

FIG. 1. Typical leaf of *Physalis Alkekengi*, the carrier of the mosaic disease, inoculated with the juice of the leaves of *Solanum aculeatissimum* having mosaic disease but not showing any symptoms of the disease.

FIG. 2. Typical mosaic leaf of *Nicotiana Tabacum*, inoculated with the juice of the leaves of *Physalis Alkekengi* which had been inoculated with the juice of mosaic leaves of *Solanum aculeatissimum.*

FIG. 3. Typical mosaic leaf of *Solanum aculeatissimum*, inoculated with the juice of *Physalis Alkekengi* which had been inoculated with the juice of mosaic leaves of *Nicotiana Tabacum.*

The air chambers of Grimaldia fragrans*

ALEXANDER W. EVANS

(WITH FOURTEEN TEXT FIGURES)

INTRODUCTION

In most of the Marchantiales the thallus shows a layer of green tissue with air spaces or chambers below the dorsal epidermis. These chambers exhibit many differences when the group as a whole is considered, but it is possible to refer the majority to three distinct types. To these the names of the representative genera *Riccia*, *Reboulia* and *Marchantia* may be applied.

In the *Riccia* type the chambers occupy a single layer and are in the form of canals with their long axes approximately vertical; the canals are usually narrow and bounded by only four rows of cells, but in certain cases they are broader and bounded by a greater number of cells. In the *Reboulia* type the chambers are in two or more layers (at least in the median portion of the thallus) and are in the form of irregular polyhedrons, often tending to be isodiametric; this type is sometimes complicated by cellular outgrowths into the chambers. In the *Marchantia* type the chambers are again in a single layer (as in the *Riccia* type) but are in the form of more or less flattened polygonal prisms with their longer dimensions approximately horizontal; they are further distinguished by the presence of numerous simple or branched green filaments, extending from the floors of the chambers nearly or quite to the epidermis. In all three types the chambers communicate with the outside air by means of openings in the epidermis. In the *Riccia* type these may be nothing more than continuations of the canalicular chambers, but in the two other types the openings are usually surrounded by specialized epidermal cells and form the characteristic air pores or epidermal pores of the group.

Among North American genera the *Riccia* type is restricted to *Riccia* and *Oxymitra;* the *Reboulia* type is found in *Ricciella*,

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* Contribution from the Osborn Botanical Laboratory.

Ricciocarpus, Peltolepis, Sauteria, Clevea, Plagiochasma, Reboulia, Grimaldia, Neesiella, Cryptomitrium, Asterella and *Bucegia;* while the *Marchantia* type occurs in *Corsinia, Targionia, Conocephalum, Lunularia, Preissia* and *Marchantia.* The reduced air chambers of *Cyathodium* conform best perhaps to the *Marchantia* type, in spite of the absence of green filaments, while the adult thallus of *Dumortiera* lacks air chambers altogether.

The genus *Grimaldia* Raddi, as understood by most recent writers, contains about half a dozen species. The most widely distributed of these is *G. fragrans* (Balb.) Corda, which is found in Europe, Asia and North America. Other well-known species, closely related to *G. fragrans*, are the Mediterranean *G. dichotoma* Raddi and the Californian *G. californica* Gottsche. In the eastern parts of the United States *G. fragrans* is sometimes locally abundant, preferring sunny trap ridges and growing on earth among rocks, rather than on the rocks themselves. It was in such a locality as this, on West Rock Ridge, near New Haven, Connecticut, that the material used in the present study was collected. The narrow thallus is firm and compact and produces an abundance of purple ventral scales with bleached-out appendages. The upper surface is grayish green and shows no indications of the boundaries of the air chambers beneath the epidermis. The margins, as well as the ventral surface, are more or less pigmented with purple. The species is markedly xerophytic, the margins becoming involute when dry, thus covering over and protecting the upper surface.

THE AIR CHAMBERS OF THE MATURE THALLUS

The green tissue of the thallus in *Grimaldia* has been repeatedly described, most of the observations having been based on either *G. fragrans* or *G. dichotoma.* Unfortunately the descriptions show marked discrepancies. Stephani (11), for example, states that the air chambers are densely filled with erect green filaments composed of long cylindrical cells, and K. Müller (**6**, p. 259) notes the presence of vertical plates of cells in addition to the filaments. Schiffner (**9**, p. 309) criticizes these descriptions. According to his account the chambers of *Grimaldia* undergo a secondary partitioning by means of irregular green lamellae which grow upward from the floors and lateral walls of the chambers. A spongy tissue is thus formed in which narrow air spaces run, scarcely broader than the thickness of the lamellae, and the original partitions of the chambers soon become unrecognizable. He admits that in section the plates of cells one cell thick look like filaments and that marginal cells of the plates sometimes project as teeth, but he maintains that actual filaments are never present and that this fact is at once made evident by sections of the green tissue cut parallel with the surface of the thallus. Massalongo (**5**, p. 730), on the other hand, agrees with Stephani and states that the chambers are filled with vertical uniseriate filaments, some of them reaching the epidermis. His figures not only show filaments clearly but indicate that the boundaries of the chambers are distinct, in this respect also differing from Schiffner's account.

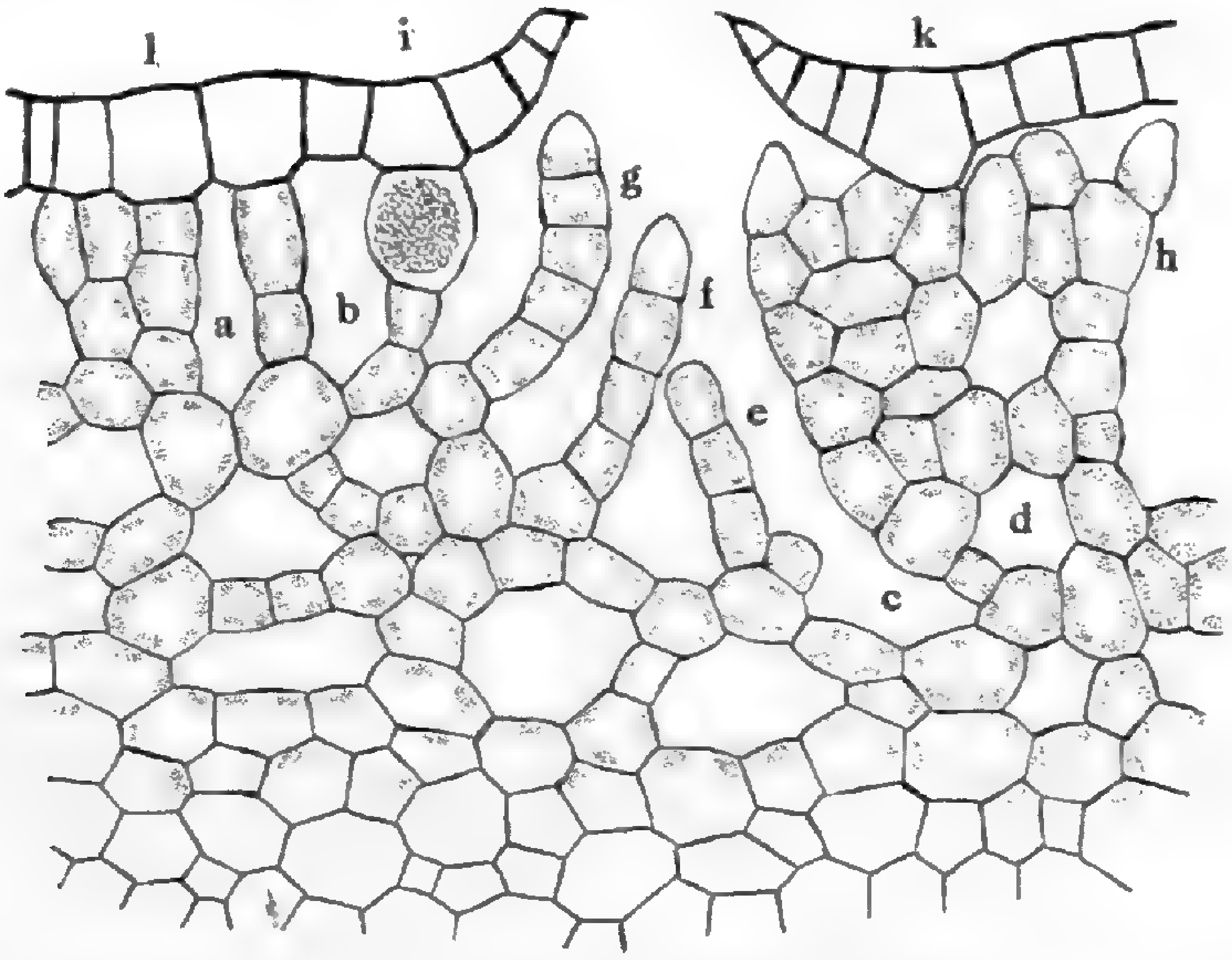


FIG. 1. Transverse section through epidermis and green tissue, × 270. *a–d*, air chambers; *e–g*, apparent filaments; *h*, plate-like outgrowth; *i*, *k*, *l*, boundaries between chambers.

The green tissue of *G. fragrans* is so compact that it is difficult to make out its true structure from ordinary hand sections. Even microtome sections are not always easy to interpret, but they give a much clearer idea of the complex arrangement of the cells and of the intricate system of aërating chambers and help to explain some of the conflicting statements in the published descriptions. In a transverse section, such as the one shown in FIG. 1, the chambers are seen to be in three or four layers in the thickened median portion of the thallus. As the margins are approached the thallus becomes thinner, and the number of layers decreases until only the uppermost layer is left. Except in this uppermost layer the chambers are usually polygonal in outline and tend to be isodiametric. In the uppermost layer they tend to be elongated vertically, as shown in the spaces *a* and *b*. That the spaces communicate with one another is also indicated in the figure. The space *c*, for example, is connected with a space nearer the epidermis, and the space *d* probably represents a passageway to a chamber in another section. The figure seems, at first sight, to confirm the statements made by Müller, that both filaments and cell plates are present. Immediately beneath the pore there are apparently three filamentous outgrowths, *e*, *f*, and *g*, and a plate-like outgrowth is clearly shown at *h*. Of course, as Schiffner intimates, apparent filaments may be nothing more than sections of cell plates. In the section drawn careful focusing does indeed show that *e* and *f* are in close contact with another apparent filament in another plane, and the same thing is true of other apparent filaments in the section. Some of the cell plates, moreover, appear to have a fluted surface, so that a section cut parallel with the surface of the plate might readily give the impression of a series of filaments. At the same time there are many apparent filaments which seem to be entirely free from one another, and it is impossible to determine their true status except by the study of other sections. It will be noted that the more deeply situated chambers are free or nearly so from outgrowths of any kind.

The figure is of further interest in showing that some of the apparent filaments and plate-like outgrowths end freely in the chamber without reaching the epidermis, this being especially true in the vicinity of the pores; others, as shown by the one between the spaces *a* and *b*, extend to the very epidermis and seem to be connected with it. It is doubtful, however, if the connection is ever anything more than a close contact, such as the free filaments in *Marchantia* and *Conocephalum* often exhibit. No instance has been observed where an outgrowth extends downward from the epidermis and ends freely in a chamber, and there is no adequate evidence that the epidermal cells themselves ever give rise to outgrowths, as Schiffner suggests may be the case. The original boundaries of the dorsal air chambers are not absolutely unrecognizable, but they are by no means as distinct as Massalongo's figure represents them. In FIG. 1 the boundaries of the chamber with the air-pore are shown at *i* and *k*, while another boundary is situated at *l*.

The longitudinal section drawn (FIG. 2) brings out the fact that many of the air chambers are more or less elongated. This is strikingly true of those most deeply situated but is also well shown by the chamber with the air-pore, although the actual boundaries of this chamber are not definitely indicated. It will be noted that the upper margin of the cell plate represented, which extends almost longitudinally beneath the pore, is distinctly dentate, some of the teeth being over a cell in length. This accords, on the whole, with Schiffner's statement that the marginal cells of the plates may project as teeth. Although some of the teeth shown are more than projecting cells, it would be a stretch of the term to describe them as filaments. The figure, therefore, presents no evidence of the occurrence of true filaments. Other sections, however, show apparent filaments, similar to those represented in FIG. 1.

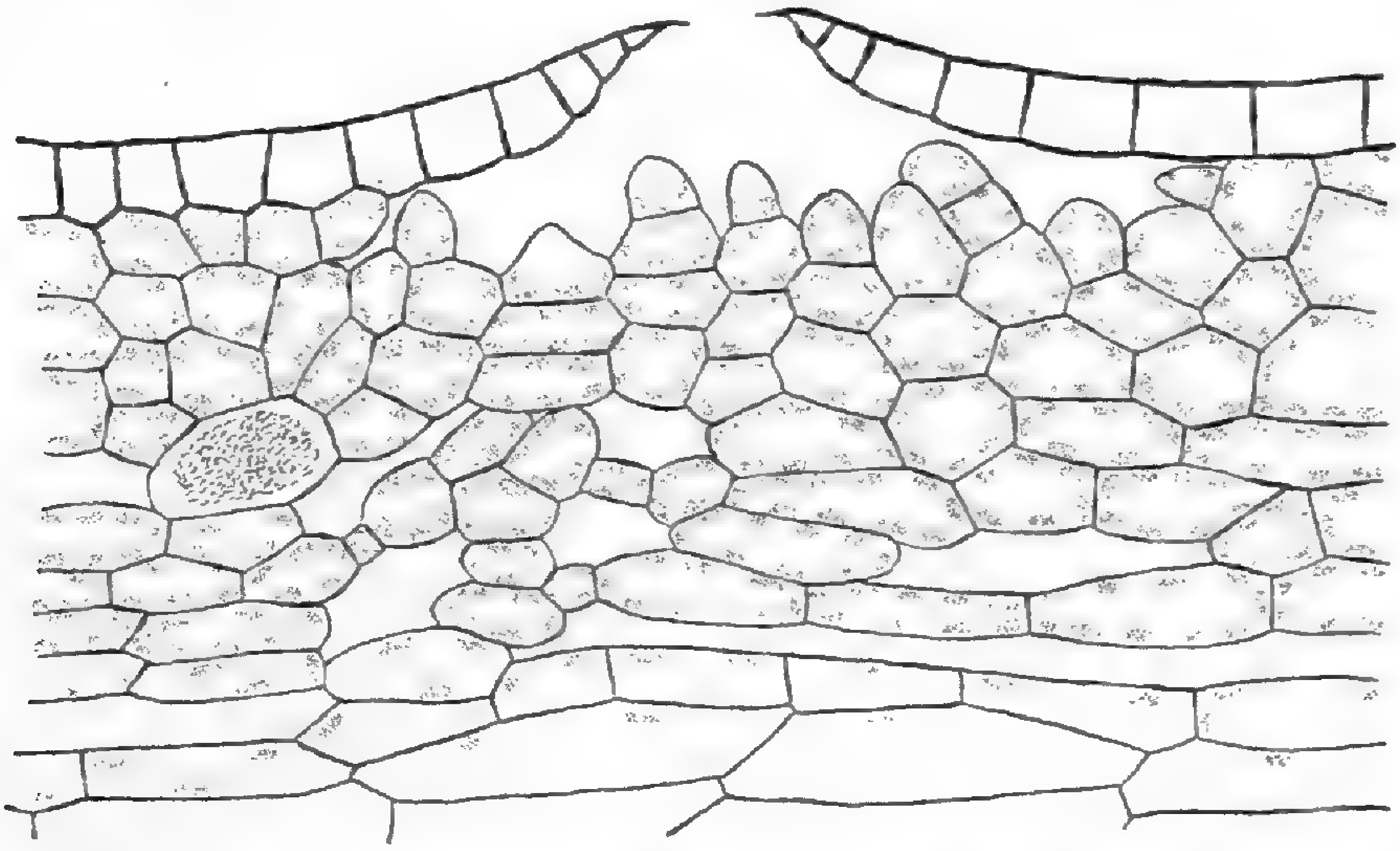
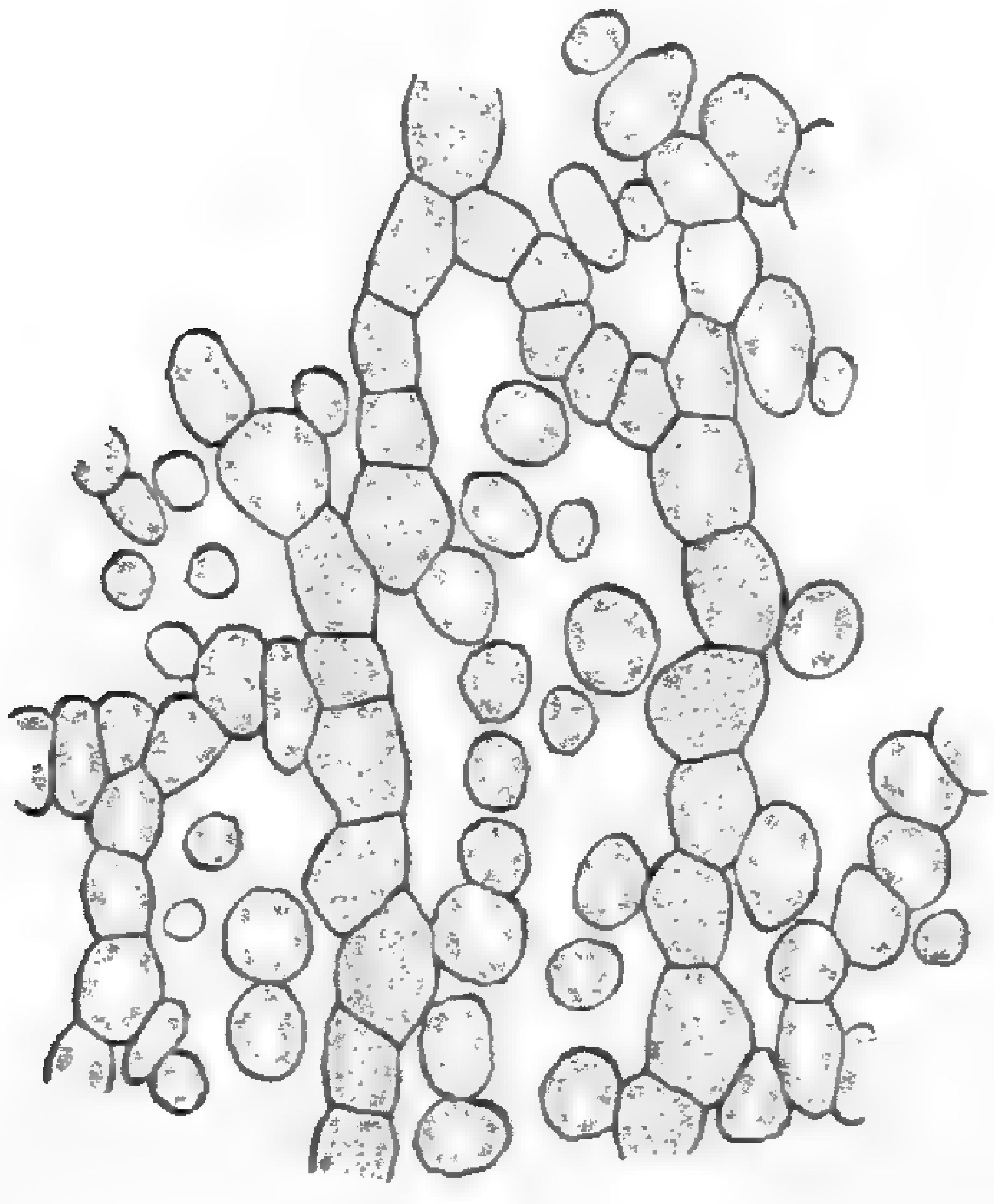


FIG. 2. Longitudinal section through epidermis and green tissue, × 270.

According to Schiffner, a section through the green tissue parallel with the surface of the thallus will at once show that the chambers are destitute of free filaments. FIG. 3 shows a part of such a section, cut immediately below the epidermis, and seems at first to belie his statement. The figure shows the partitions, almost complete, of an air chamber, the cells being distinguished by stippling. Only one end of the chamber is represented; the other end did not show because the section was slightly oblique in that region and passed through the epidermis instead of the green tissue beneath. That the stippled cells represent the boundaries of a chamber is evident from their close union and also from the fact that an epidermal pore was situated above the middle of the space which they enclose. It will be seen that the chamber contains a number of cells, circular in section and either entirely free or else loosely connected with one another or with the cells of the partitions. Similar cells are shown elsewhere in the figure, and a superficial examination would interpret them as the sections of filaments, especially if they were considered in connection with FIG. 1.



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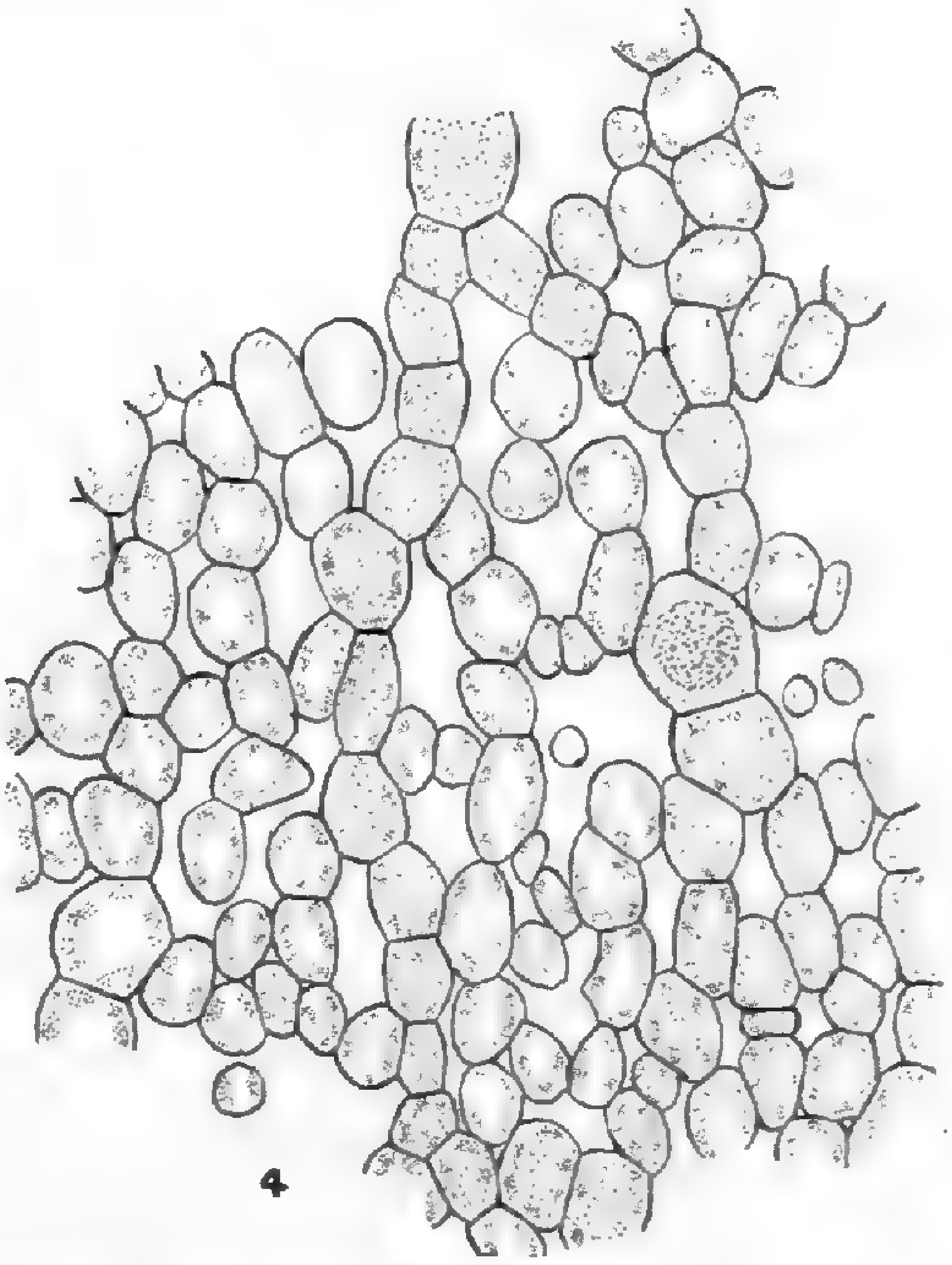

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FIG. 3. Section parallel with the surface, just below epidermis, × 270.

FIG. 4. Section a short distance below the one shown in FIG. 3, × 270.

The incorrectness of this interpretation is brought out by a comparison with FIG. 4, which shows the same chamber at a lower level, the cells of the partitions being again indicated by stippling. In this figure the complete boundaries of the chamber are shown, but the cells enclosed present a very different appearance. They are not only much more numerous but are, with a few exceptions, more or less firmly united, and the entire chamber is thus divided up into smaller chambers, some of which seem entirely cut off while others show their connections with other chambers. The seven cells shown on the right of the left-hand partition in FIG. 3 are represented in FIG. 4 by seven united cells, showing at once that these seven cells are not the cross sections of filaments but simply the cross sections of teeth, like those shown in FIG. 2. Similar conclusions would be created by comparing other apparently free cells in FIG. 3 with their representatives in FIG. 4. It thus becomes established that there are no free filaments in the chambers. It will be noted further that FIG. 4 presents a much more complicated condition than FIG. 3 and that the boundaries of the air chamber would be hardly distinguishable except through comparison with the simpler figure. It is probable that a section like the one shown in FIG. 4 was responsible for Schiffner's statements, which it certainly strongly supports.

In FIG. 5 a section from another thallus is shown, cut at a still lower level. This section shows a loose spongy tissue, two of the chambers being connected by a passageway. Cellular outgrowths are very infrequent, but a single cell, apparently free, is shown in one of the chambers, and a single short outgrowth in another. When compared with FIG. 4 the spaces are relatively larger and fewer and the tissue in consequence much less compact. Sections cut farther down show elongated spaces, similar to those represented in FIG. 2, while sections beneath these show the ventral parenchymatous tissue without spaces of any sort.

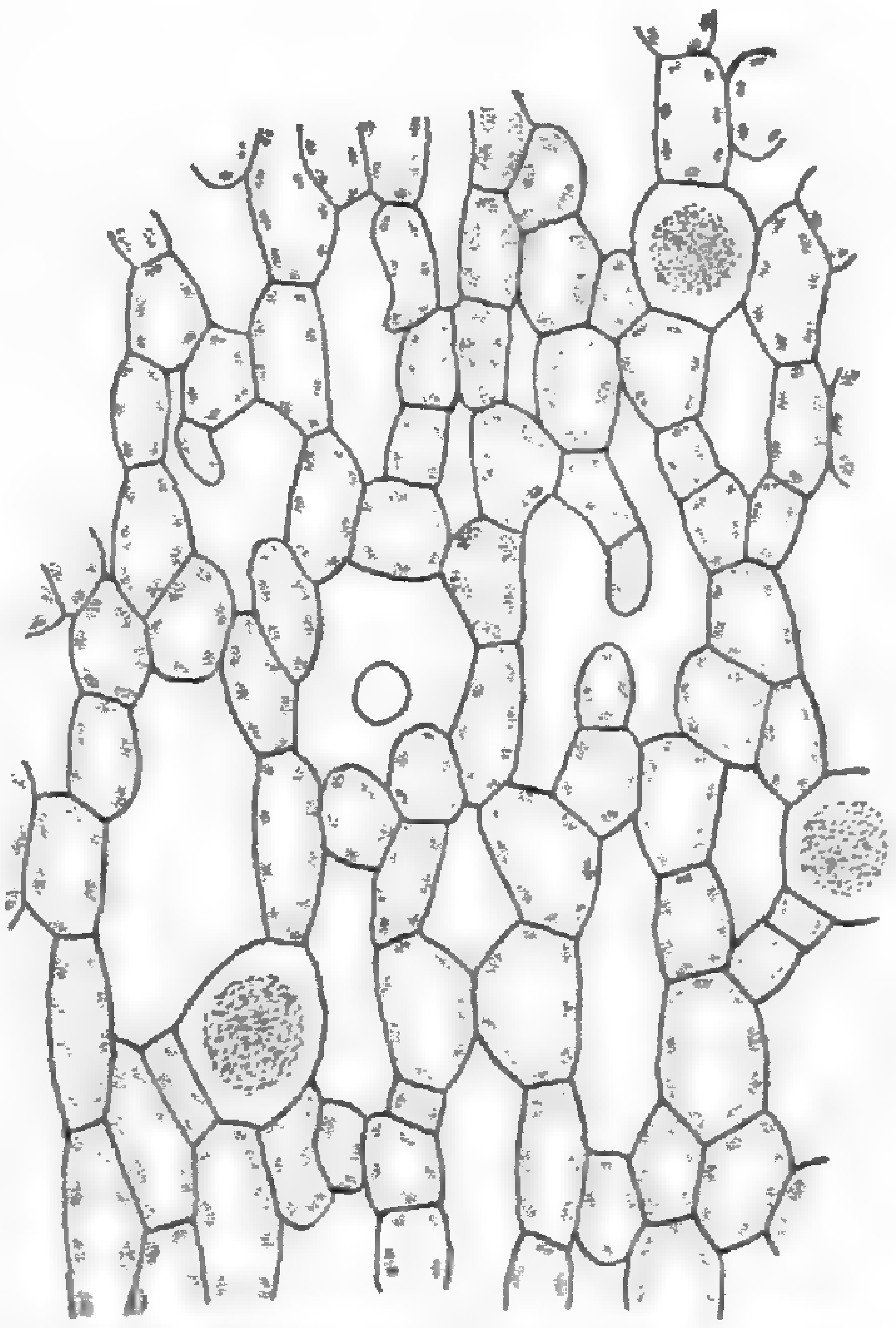


FIG. 5. Section parallel with the surface below the dorsal layer of chambers, × 270.

It is clear from a comparison of transverse, longitudinal and horizontal sections that a distinction may be made between the dorsal layer of air chambers in *Grimaldia* and the more deeply situated layers. In the dorsal layer the original chambers show a secondary partitioning by a system of more or less vertical cell plates, the free margins of which sometimes bear scattered teeth, apparently always less than two cells long. Except for these teeth the chambers lack filaments completely. In the more deeply situated layers, the chambers are much simpler and rarely show evidences of any kind of outgrowth. These conclusions show the incorrectness of certain statements made by Stephani, K. Müller, and Massalongo and the essential correctness of Schiffner's account.

The complex conditions found in the green tissue of *Grimaldia* are duplicated by *Plagiochasma* and by certain species of *Asterella*. The other genera showing the *Reboulia* type of air chamber have a much looser green tissue, the secondary partitioning being less highly developed or absent altogether.

ORIGIN AND ENLARGEMENT OF THE AIR CHAMBERS

The development of the air chambers in the Marchantiales has aroused a good deal of interest among students of the Hepaticae, and the history of the subject is fully given by Barnes and Land (1). The explanation which they advance to account for the origin of the chambers differs in certain respects from the older explanation advanced by Leitgeb and accepted by many of his successors. Leitgeb's explanation was based primarily on his study of *Riccia*, but he extended its application to the more complex genera. According to his ideas the air chambers do not originate in compact tissue, and no splitting of cell walls is involved in their formation. They arise, rather, on the surface of a young thallus and are due to a cessation of upward growth in certain limited areas, the surrounding parts growing upward vigorously. The areas where growth is supposed to cease are situated in most cases where four of the surface cells come together; they mark the lower ends of the chambers, the vertical extent of which depends upon the degree of upward growth which the surrounding parts exhibit.

According to Barnes and Land there is nothing to support Leitgeb's views. In their opinion the chambers always originate in compact tissue below the surface of the young thallus by a splitting of cell-walls and, in case the mature chamber has an epidermal pore, the splitting extends upward until the surface is reached. They based their conclusions on a study of *Ricciella* (*Riccia fluitans* L.), *Ricciocarpus* (*Riccia natans* L.), *Marchantia*, *Lunularia*, *Conocephalum*, *Dumortiera*, *Asterella* (*Fimbriaria*), and *Plagiochasma*, and assumed that they would apply as well to *Riccia* (in its restricted sense). After the chambers are once established their increase in size need not involve any further schizogenous processes. It is largely brought about by the growth of the cells surrounding the chamber, and may be wholly brought about in this way; in other words, by the surface extension of the bounding cell-walls. According to Leitgeb's ideas the increase in the size of the chambers is brought about in much the same way, except that a total absence of splitting is always assumed. It will be seen, therefore, that the most important differences between the two explanations are concerned with the very beginning of the developmental process: according to Leitgeb the chamber is superficial in origin and no splitting occurs; according to Barnes and Land the chamber is not superficial in origin and splitting does occur.

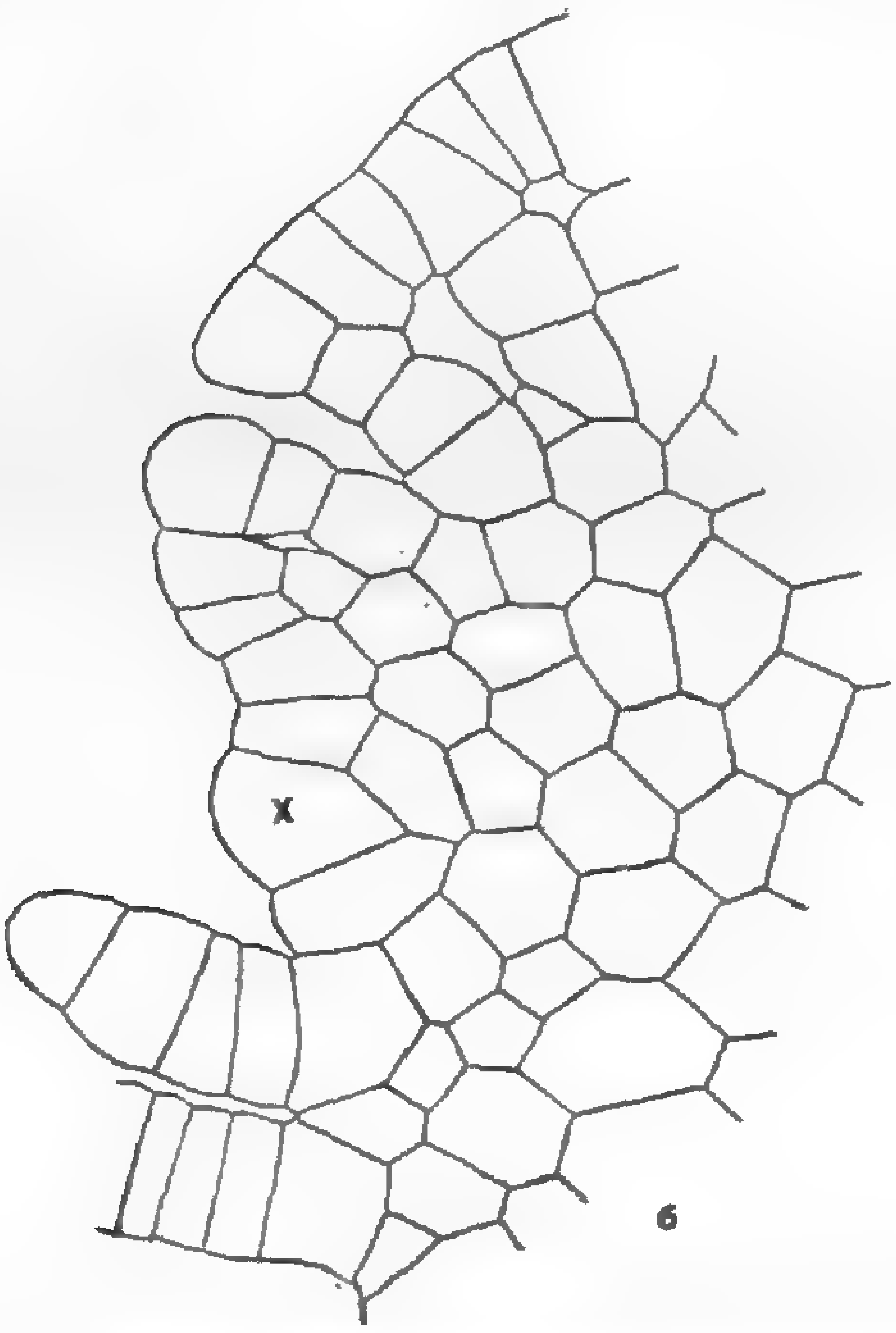
Among recent papers dealing with air chambers, those by Miss Hirsh (4), Pietsch (8), Deutsch (3), Miss O'Keeffe (7) and Miss Black (2) may be briefly noted. Miss Hirsh's work is based largely on *Ricciocarpus natans* (L.) Corda and *Riccia Frostii* Aust. She reaches the conclusion that the first of these species agrees with Barnes and Land's explanation, while the second agrees with Leitgeb's. Her figures of *R. Frostii*, however, by no means support this conclusion fully. Although they show that the chambers drawn may have been superficial in origin, they show as well that a splitting must sometimes have occurred, because some of the chambers extend below the original surface of the thallus. This is brought out clearly by her *f. 6*, upon which she lays especial emphasis. This figure, in fact, presents no convincing evidence that the chamber may not have been initiated by a schizogenous process.

Pietsch's work is remarkable for its thoroughness and accuracy. It deals with species of *Riccia* and *Ricciella*. and his account is therefore based on the group of plants from which Leitgeb drew his conclusions. Although he criticises the work done by Barnes and Land, his observations lead to similar conclusions, so far as the development of the air chambers is concerned. He finds that even in *Riccia* the chambers originate from a splitting of cell walls, the split beginning below the surface and then extending upward until the surface is reached.

Deutsch's paper, devoted to *Targionia hypophylla* L., includes an interesting observation on the development of the air chambers. He states that they arise by a splitting apart of cells close to the apical cell but maintains that the split begins on the outside and extends inward, instead of beginning below the surface and extending outward. The *f. 3*, which he cites as evidence, would be more convincing if the youngest chamber shown did not extend into the hypodermal tissues; as the figure stands it might equally well bear the opposite interpretation from the one drawn. Deutsch does not consider that his account differs in any essential respect from the explanation of Barnes and Land, in spite of the superficial origin which he assigns to the chambers. Miss O'Keeffe, who also worked on *Targionia*, fully supports Deutsch in his statements about the origin of the chambers. Fortunately, the youngest chamber which she shows (*f. 1, A, a*) seems to be conclusive; it appears in longitudinal section as a split between two superficial cells and does not extend beyond them.

Miss Black's paper deals with *Riccia Frostii*, one of the species investigated by Miss Hirsh, and the same conclusions are drawn as to the origin of the air chambers. Her *f. 6*, however, is open to the same criticism as Miss Hirsh's figures. It represents the apical region of a thallus cut longitudinally and including five young air chambers, but even the youngest of these projects below the original surface, showing that a splitting of a cell wall must have taken place. Miss Black emphasizes the fact that she observed no cases in which an intercellular space appeared below the surface and then broke through to the outside, so that her conclusion regarding the superficial origin of the chambers seems justified. At the same time her figure presents no evidence that the chambers may not have originated from splits between superficial cells, as Deutsch and Miss O'Keeffe maintain is the case in *Targionia*.

The thallus of *Grimaldia fragrans* is so complex that it is impracticable to trace the cell divisions which take place in the segments cut off from the apical cell, as Pietsch has so ably done in the case of *Riccia glauca* L. FIGS. 6–8, however, give some idea of the apical region and bring out the fact that a single apical cell with four cutting faces is present. In FIG. 6, immediately above the apical cell the meristematic tissue forms a compact mass without intercellular spaces. Between the fourth and fifth cells the first indication of a chamber appears in the form of a split a short distance below the surface. Between the fifth and sixth cells an older and longer chamber is visible, which has reached the surface, apparently through the upward extension of a similar split. The elongation and widening of the chamber have been largely due, it would appear, to the growth of the bounding cells. The still older chambers shown in the figure are not cut squarely in the middle and need not be further considered.



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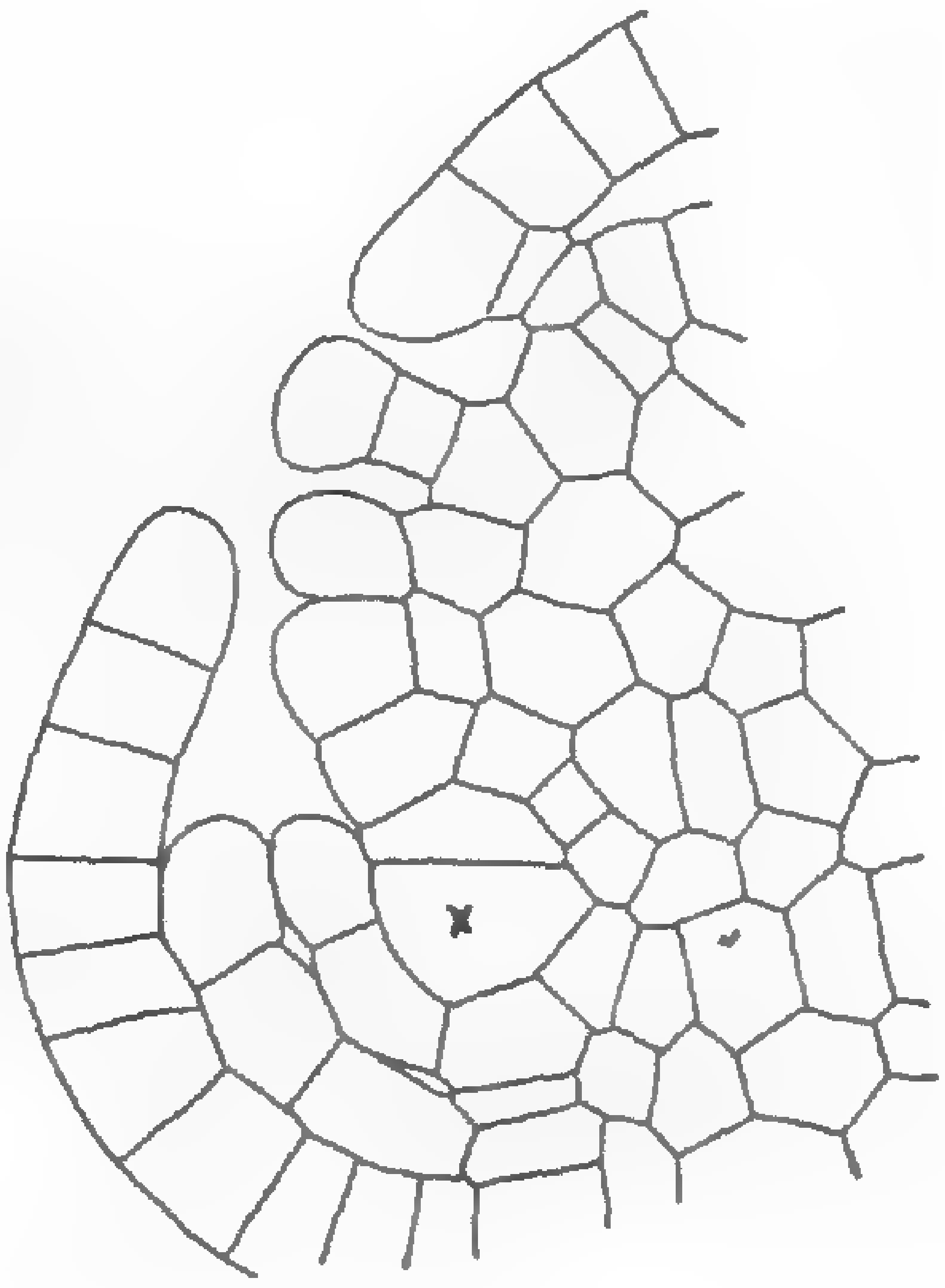

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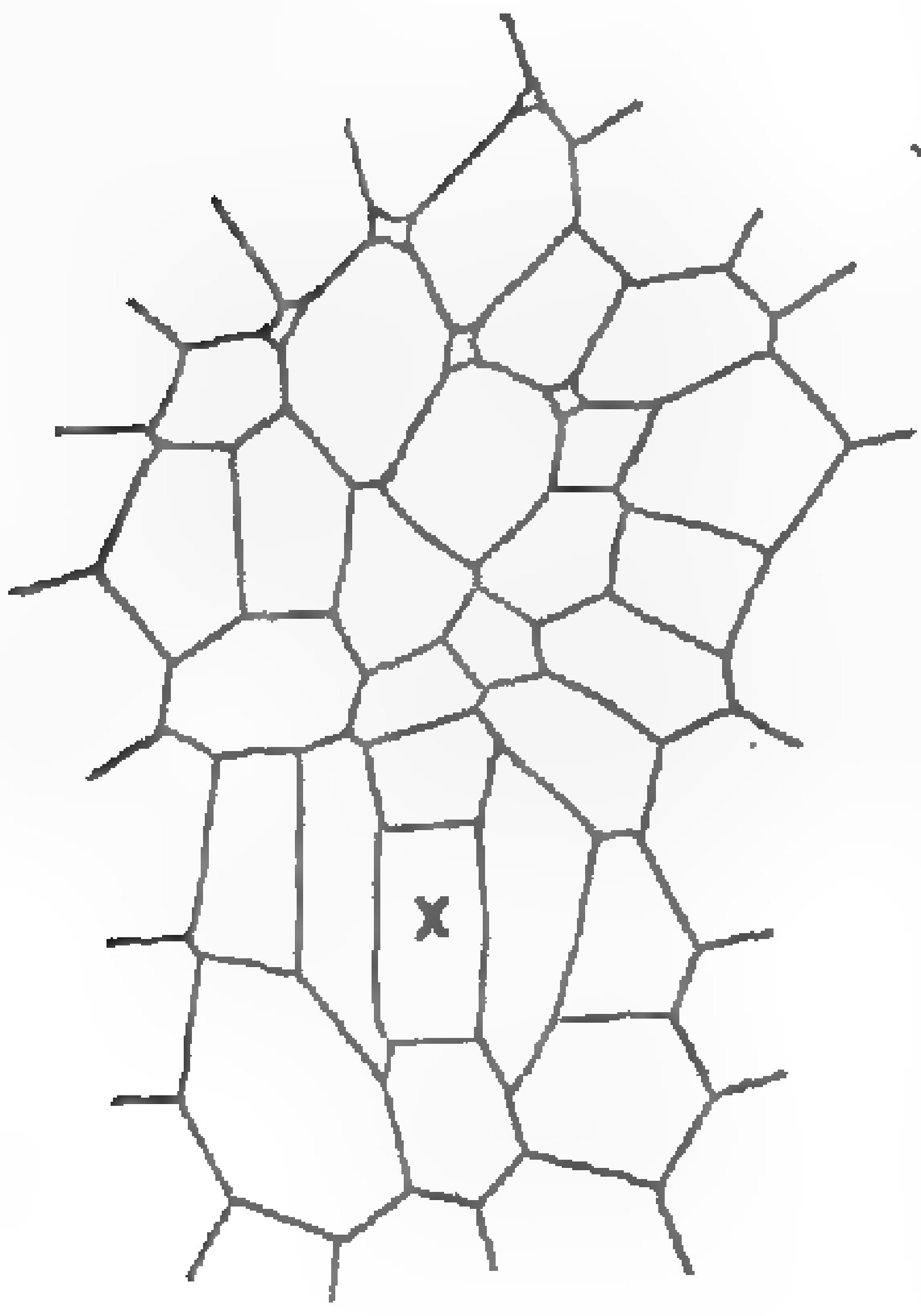
FIG. 6. Longitudinal section through a growing point, × 500. *x*, apical cell.
FIG. 7. Longitudinal section through another growing point, × 500. *x*, apical cell.

In FIG. 7, which represents the apical region of another thallus, a somewhat different condition is revealed. In this case the first indication of an air chamber appears between the third and fourth cells and is likewise in the form of a split, but this time the split evidently began on the outside and extended inward. Although the chamber is thus superficial in origin, there is no evidence that a surface area has had its upward growth arrested, as Leitgeb's explanation demands. The split clearly extends inward from the original surface. The chamber between the fourth and fifth cells is considerably deeper and broader, and it is clear that its increase in size has involved further schizogenous processes. The next chamber shown gives evidence of a further horizontal extension.

It would appear from these two figures that the air chambers in *Grimaldia fragrans* owe their origin to a splitting of cell walls, but that the place where the split first makes its appearance is not always the same. It may be below the surface and extend outward, in which case it agrees fully with the explanation advanced by Barnes and Land; it may be at the surface and extend inward, thus agreeing with Deutsch's account of *Targionia hypophylla*. In the writer's opinion the figures published by Miss Hirsh and Miss Black might be interpreted in the same way as FIG. 7, so that there still seems to be no conclusive evidence that Leitgeb's explanation ever applies.

FIGS. 8–10 yield further evidence as to the origin of the chambers; they were all drawn from a single section, cut at right angles to the long axis of the thallus, and show for the most part superficial cells. In FIG. 8 the apical cell appears in the form of a rectangle. Directly above it an air chamber reaching the surface is shown between the fourth and fifth cells, corresponding apparently with the chamber between the fourth and fifth cells of FIG. 7. The schizogenous origin of this chamber seems clear, but there is nothing to show whether the split began at or below the surface. Between the third and fourth cells no signs of a chamber can be discerned, although a superficial split may be present like the one shown in FIG. 7. The figure at any rate gives no evidence of a split beginning below the surface.

FIGS. 9 and 10 are much more conclusive. They represent a portion of the thallus to the right of the apical cell and derived from lateral segments. In drawing Fig. 9 the microscope was focused on the surface of the cells in a circumscribed area; in drawing Fig. 10 it was focused a little below the surface of the same area. Fig. 9 shows a series of cells in close union and two air chambers which have reached the surface; Fig. 10 shows the same two chambers and six additional ones. The latter clearly represent schizogenous spaces below the surface and demonstrate an origin like that of the youngest chamber in Fig. 6.



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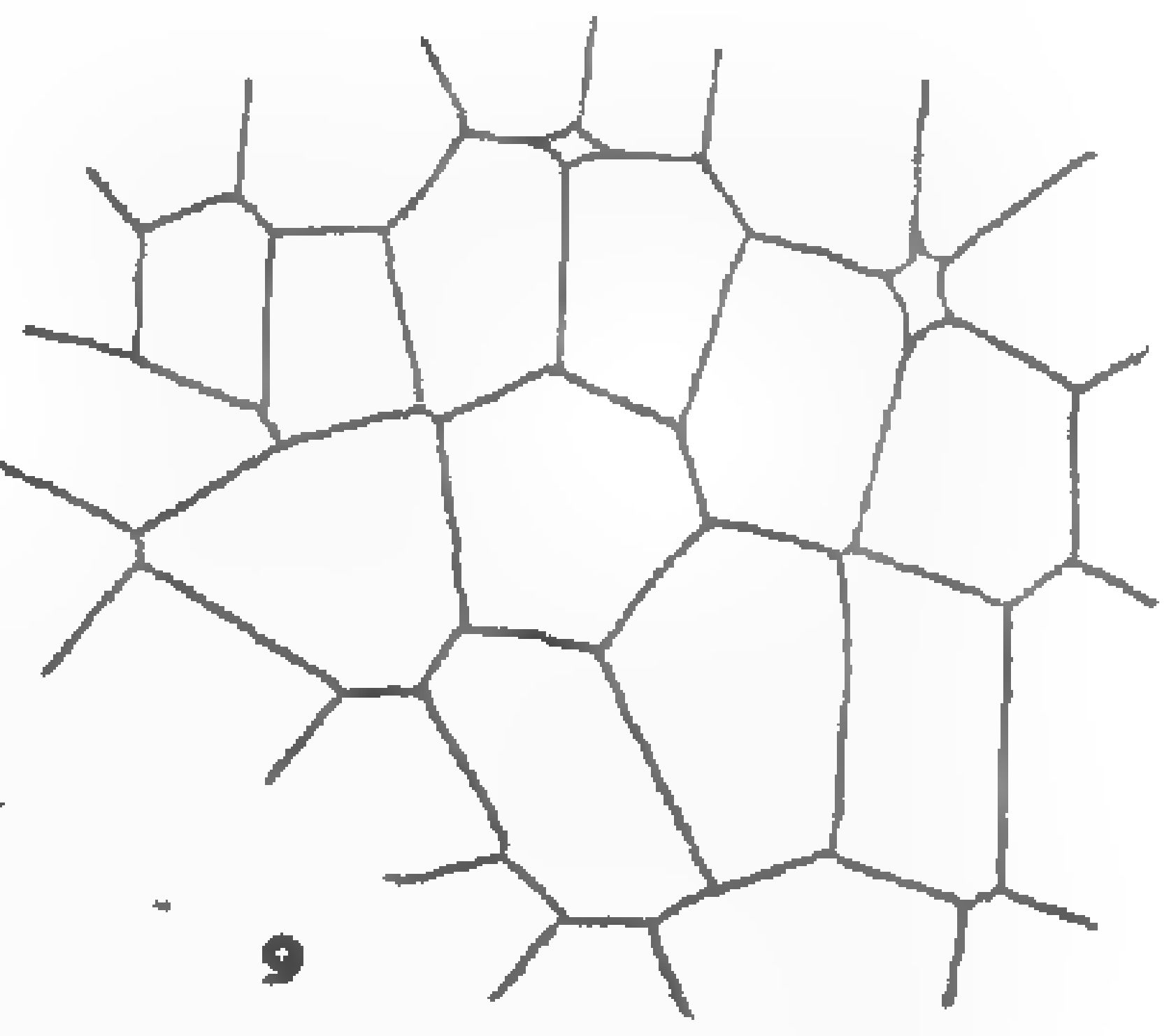
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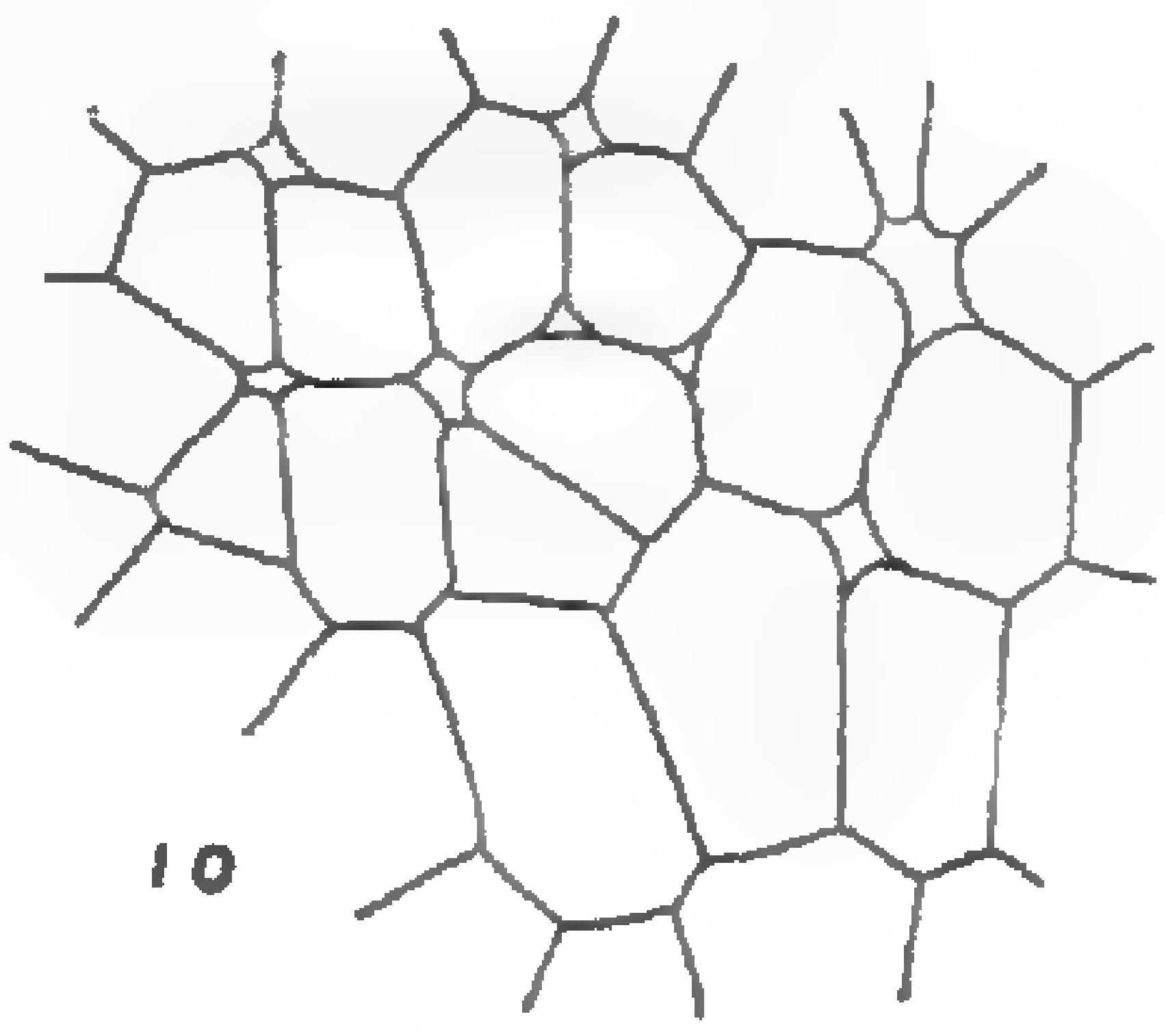
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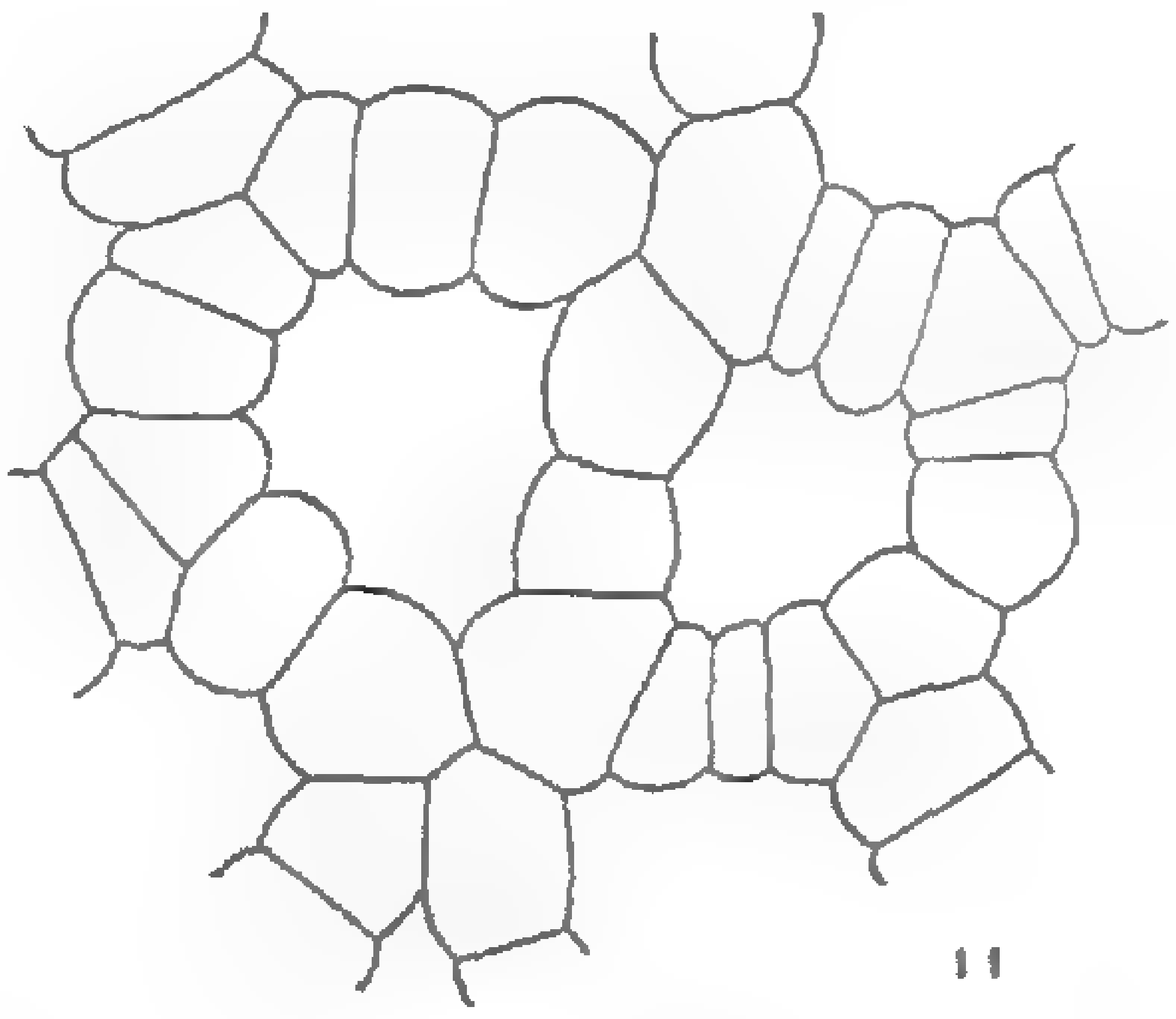
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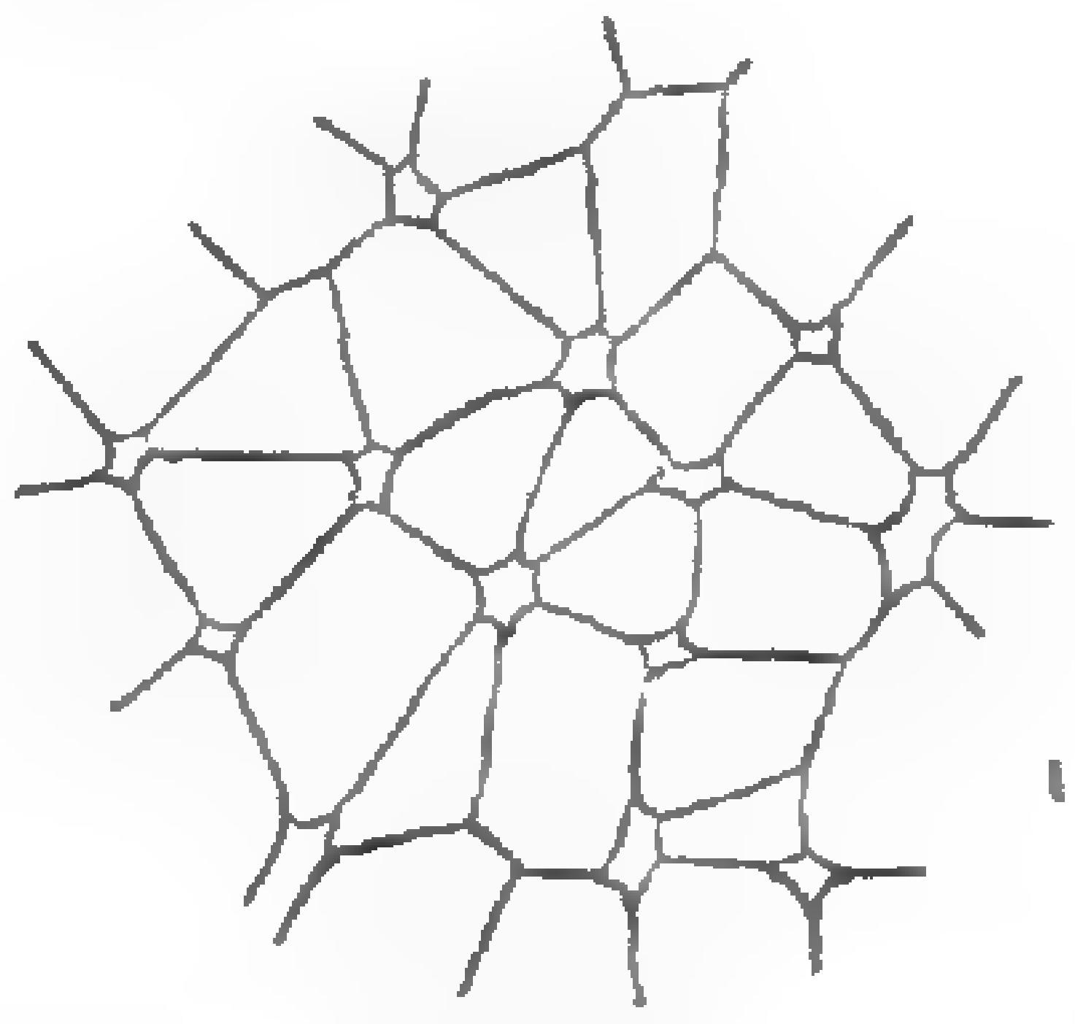
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Fig. 8. Transverse section through a growing point, × 500. *x*, apical cell.

Fig. 9. Superficial cells to the right of the apical cell shown in Fig. 8, × 500.

Fig. 10. The same region as that shown in Fig. 9, but at a slightly lower focus, more very young dorsal chambers being visible, × 500.

Fig. 11. Slightly older dorsal chambers than those shown in Fig. 10, the section parallel with the surface, × 500.

Fig. 12. Section just below the one shown in Fig. 11, the numerous intercellular spaces being the beginnings of more deeply situated chambers, × 500.

The rudimentary chambers shown in Figs. 6–10 represent the beginnings of the complex dorsal chambers shown in Figs. 1–4. The later stages in the development of these chambers and the origin and development of the more deeply situated chambers are exceedingly difficult to follow. For a while the dorsal chambers are distinct enough in sections cut immediately below the epidermis. Such a section is shown in Fig. 11, where two complete chambers and parts of six others are represented. The increase in size which these chambers show, when compared with the small intercellular spaces in FIG. 10, is due to the vigorous growth of the bounding cells, accompanied by rapid cell divisions. At this stage the partitions show no evidence of outgrowths. FIG. 12 represents the section just below the one shown in FIG. 11, the cells drawn, in part at least, forming the floors of the dorsal chambers. The figure shows many intercellular spaces, which are clearly schizogenous in origin; these spaces represent the beginnings of the more deeply situated chambers or, in some cases, the passageways leading from these chambers to the dorsal chambers.

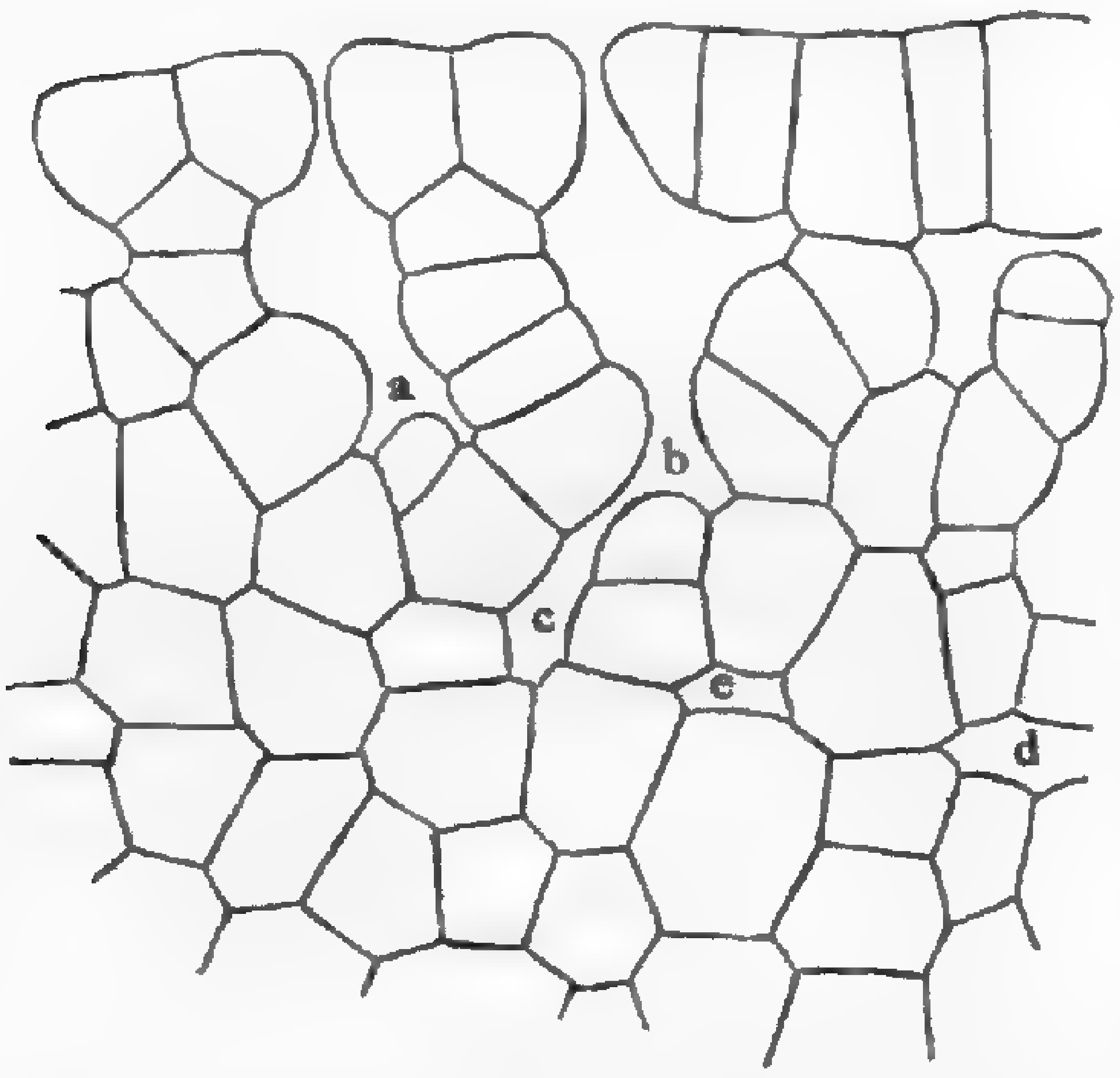

FIG. 13. Longitudinal section through young chambers, × 500. *a–e*, more deeply situated chambers.

A longitudinal section, representing about the same stages as those shown in FIGS. 11 and 12, may be seen in FIG. 13, the left-hand side of the figure being toward the apical cell. The very rapid development of the chambers is clearly indicated, and light is thrown on the way in which the deeper chambers originate, such chambers being indicated by the letters *a–e*. It will be seen that some of these chambers seem to be completely enclosed, showing that they may have originated by a splitting of cell walls in compact tissue, and that others already communicate with more dorsally situated chambers. Whether the connecting passageways are always formed subsequently to the chambers, or whether the formation of the passageways may sometimes precede that of the chambers is not altogether clear. If the older, right-hand side of the figure is compared with the younger, left-hand side, it becomes evident that the tissue with intercellular spaces has almost tripled in thickness and that the dorsal chambers have become distinctly deeper. The rapid growth involved in these changes has taken place in the original partitions of the dorsal chambers, in the cells which formed their irregular floors and in the cells immediately beneath. As the writer conceives the process, the growth of the partitions is both horizontal and vertical, the growth in the latter direction being often equalled by the upward growth (accompanied by cell division) of the cells forming the floors of the chambers; these in turn remain more or less united with one another and with the cells of the partitions and in this way form the system of united cell-plates in the dorsal chambers. At a later stage the margins of some of the plates which end freely in the chambers give rise to teeth as shown in FIG. 2.

It is difficult to secure direct evidence from the vegetative thallus that the partitions form surface-outgrowths. FIG. 14, however, which is drawn from a section of the young female receptacle, shows that such outgrowths are possible. The section was cut parallel with the upper surface of the receptacle, and the figure shows two complete chambers and parts of eight others; two of the latter contain sections of the tubular epidermal pores which hang down from the roofs of the chambers. The partitions are one cell thick but give the impression of being thicker when cut obliquely. The outgrowths originate as projections of cells which become cut off by walls and then continue their growth and cell-divisions. In the vegetative thallus such outgrowths evidently play a very minor part in the development of the green tissue.

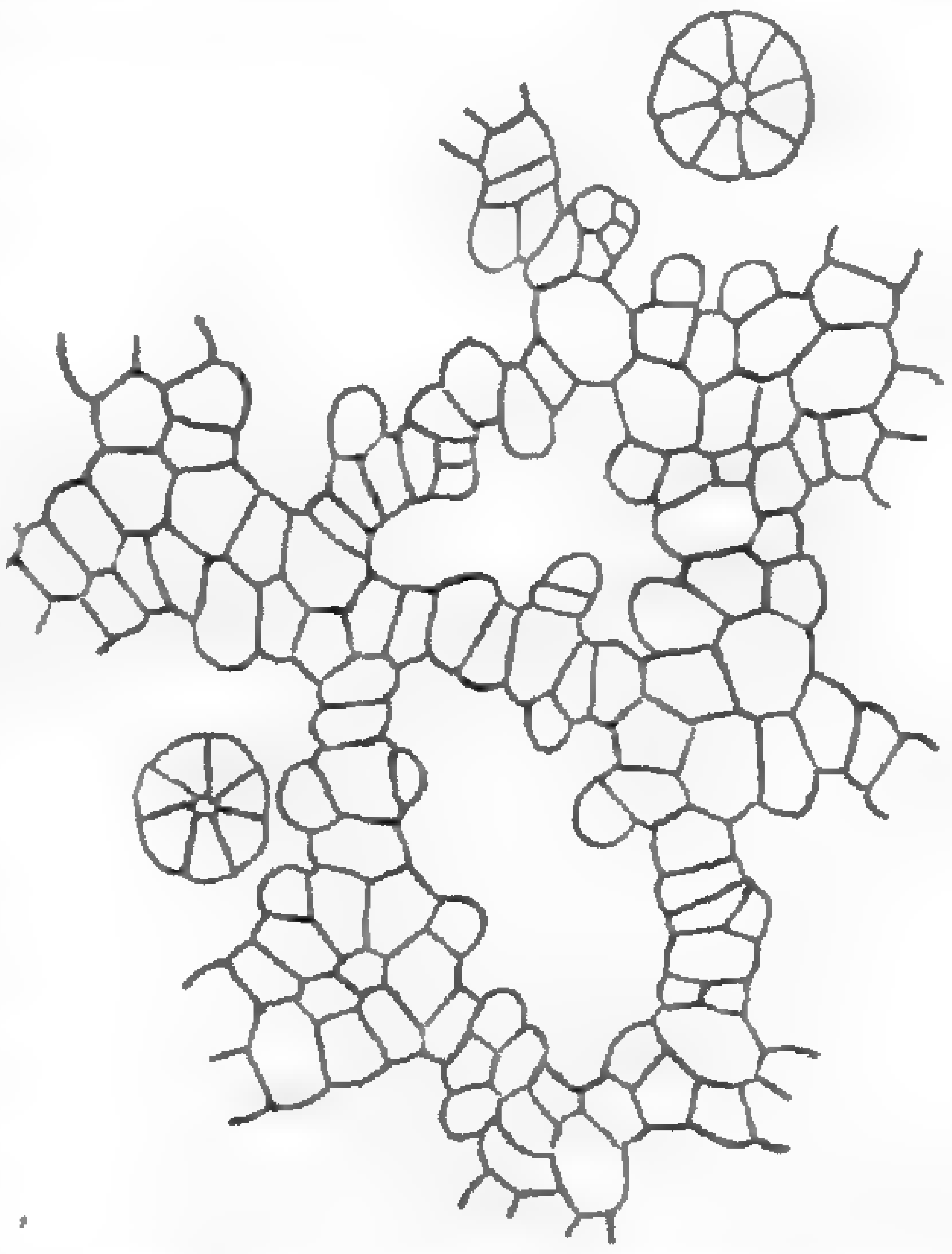

FIG. 14. Section parallel with the surface of a young female receptacle, just below the epidermis, × 270.

The chambers below the dorsal layer make their appearance very early, as seen in FIGS. 12 and 13, although they always appear later than the dorsal chambers. As the thallus becomes differentiated, these chambers increase rapidly in size through the growth of the bounding cells, but the appearance of new chambers, except in the apical region, has not been demonstrated and seems improbable. If schizogenous processes play a part in the enlargement of these chambers, it is only to a very limited extent.

The green tissue in the thallus of *Plagiochasma* bears a strong resemblance to that of *Grimaldia.* Its development has been described by Miss Starr (10), her investigation having been based on an undetermined species from Mexico. She confirms the earlier observation of Barnes and Land that the air chambers of *Plagiochasma* owe their origin to a splitting of cell walls below the surface. She notes further that the chambers are at first deep and narrow but that they soon become wide and irregular, and she ascribes the changes in size and form which they show to a "stretching and tearing of tissues between neighboring chambers." In other words she considers that schizogenous processes play a leading part in the enlargement of the chambers as well as in their origin. This conclusion is hardly supported by her *f. 11* or by the earlier figures published by Barnes and Land (1, *f. 17–22*). Although these figures indicate a schizogenous origin of the chambers, they do not disprove that the enlargement is mainly due to the growth of the surrounding cells.

SUMMARY

The air chambers of *Grimaldia fragrans* are in several layers in the thickened median portion of the thallus.

The dorsal chambers communicate with the outside by means of epidermal pores. They are subdivided by an irregular system of more or less vertical, united cell plates, enclosing narrow spaces, so that the boundaries of the chambers are difficult to distinguish. The cell plates sometimes reach the epidermis and sometimes do not; in the latter case the free margins sometimes bear scattered teeth, less than two cells in length, especially in the vicinity of the pores. Except for these teeth the chambers lack filaments completely.

The more deeply situated chambers communicate with one another and with the dorsal chambers by means of passageways; they are scarcely or not at all subdivided by cell plates.

The chambers all owe their origin to a splitting of cell walls in closely united tissue. In the case of the dorsal chambers the split sometimes begins below the surface and extends outward; sometimes at the surface and extends inward.

The dorsal chambers appear first, very close to the apical cell, but the more deeply situated chambers appear soon afterwards.

The increase in the size of the chambers is due largely to the growth of the bounding cells and only slightly to further splittings of cell walls. The system of united cell plates in the dorsal chambers and the partitions between the chambers increase in vertical height simultaneously. Direct outgrowths from the surfaces of cell plates play a very small part in the process of subdivision.

The material upon which this investigation was based was collected and prepared by Mr. John F. Logan, who expected to utilize it in his own studies. Through the pressure of other work his plans could not be realized, and his preparations were placed at the disposal of the writer for examination. The writer would therefore express his sincere thanks to Mr. Logan for his courtesy.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1911-1918

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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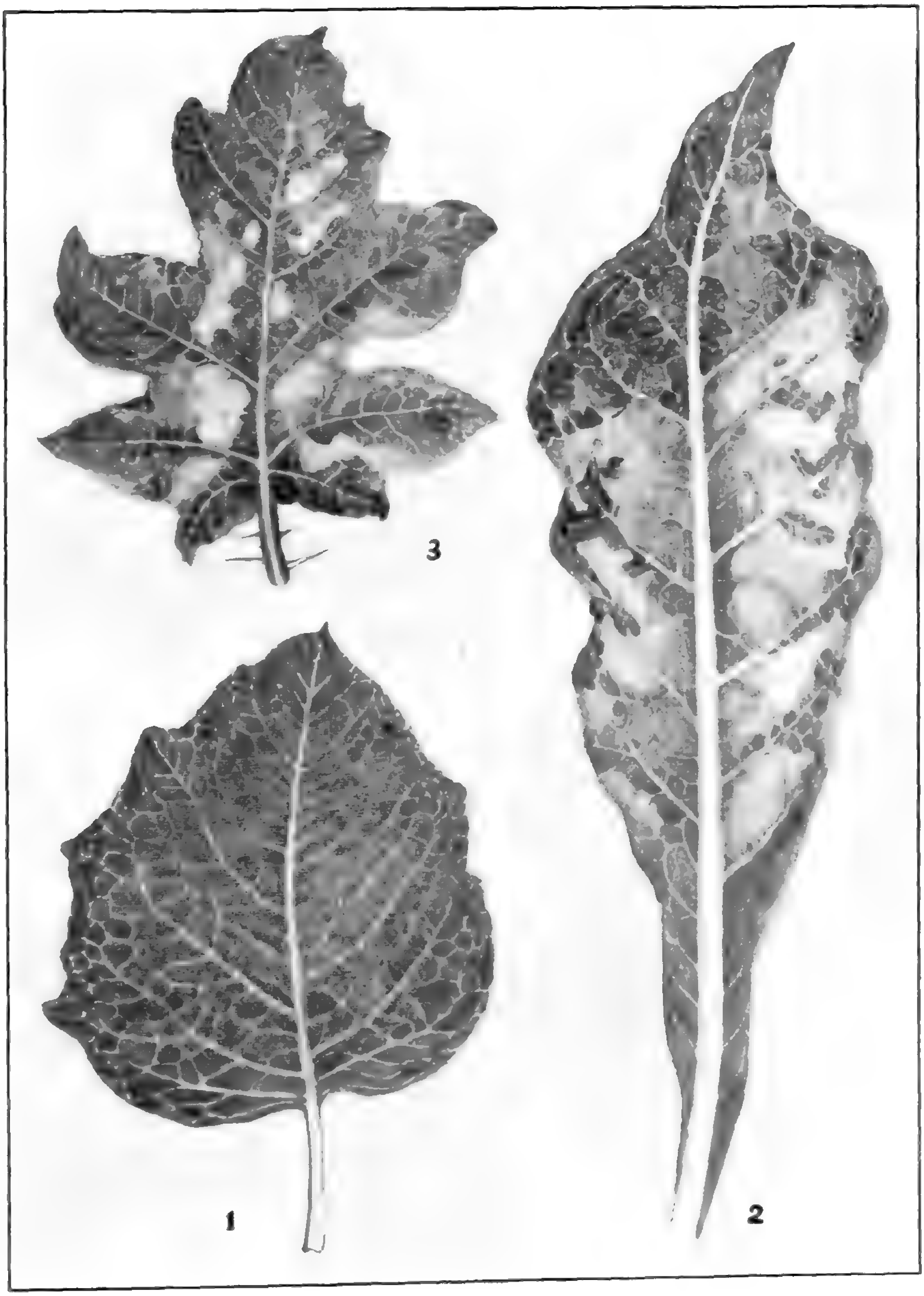

NISHIMURA: CARRIER OF THE MOSAIC DISEASE

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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The strand flora of the Hawaiian Archipelago—I. Geographical relations, origin, and composition

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GEOGRAPHICAL RELATIONS

For a long time botanists have manifested particular interest in the strand vegetation of various countries. The floras of many continental and insular strands have alike yielded significant material. There is, however, absolutely no comprehensive account of the Hawaiian littoral. Fragmentary and uncoördinated notes concerning various Hawaiian strand plants are given by Hillebrand, Wawra, Gray, Chamisso, Heller, Mann, Schauinsland, Forbes, and other botanists, who at various times during the past century have studied the Hawaiian flora. In the works of none of these investigators is the littoral flora given any special prominence or consideration. This is somewhat surprising, as much of the Hawaiian coast line is readily accessible by boat or trail, whereas the montane districts present innumerable difficulties to the explorer and collector.

Guppy ('06),* in connection with his suggestive studies of plant dispersal in the Pacific, visited the Hawaiian Archipelago and studied the strand flora with reference to the general problems of evolution and distribution. Frequent references are made to Guppy's work in the present paper. His brilliant theories will undoubtedly require more or less revision as data concerning the Pacific flora become more comprehensive and standardized.

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* The literature cited will be listed in the second paper of this series.

[The Bulletin for June (45: 219–258. *pl.* 7) was issued June 20, 1918.]

The unique position of the Hawaiian Islands, as the most northern group of the great Polynesian island series, and as a region of extreme isolation, gives *particular significance* to its strand flora. The absences from this flora are as important criteria as are the species actually present, and in many ways contribute as effectively to our knowledge of the origin and history of Hawaii's strand flora.

The attempt is here made to present a salient account of the Hawaiian littoral flora, both from the standpoint of content and dispersal, and also from the ecological viewpoint. In the latter phases of the subject the author has been particularly interested. During a residence of nine years in the islands he has made hundreds of excursions along Hawaiian strands, including the principal islands of the archipelago. The present papers incorporate the important data of these field studies.

A noteworthy feature of the littoral floras of the tropical Pacific islands is their *remarkable similarity*. As Hedley ('15) expresses it: "The same species are repeated from atoll to atoll over enormous distances across the Pacific Ocean. The identity of the vegetation possessed by tiny islets separated by thousands of miles of deepest ocean is very striking, since paradoxically they present a *greater continuity of life range than any continent can show*." Many of the more common Hawaiian littoral plants occur on practically all the islands of the archipelago, along an axis of nearly two thousand miles, whereas the montane species are highly localized.

Just as the interior mountainous districts of a high Pacific island contain the majority of the endemic species, so the strand regions are characterized by a majority of the cosmopolitan or wide-ranging species. Tansley and Fritsch ('05) find two main causes for "the striking uniformity of strand plants through the tropics—first, the great similarity of life conditions prevailing on tropical coasts, and secondly, tropical strand plants are mostly adapted for distribution by ocean currents." These factors will be considered in detail in later sections of this paper.

As will be shown later, the Hawaiian littoral flora comprises many species that occur in other parts of the Pacific, and in many other parts of the world. The mountain flora, on the contrary, is highly endemic and precinctive, and each island possesses an array of peculiar forms. The Hawaiian Islands therefore obey the general law of the cosmopolitanism of littoral constituents.

The geographic situation of the Hawaiian Islands is unique, and has a very important bearing upon the character of the strand flora. There is no other land area of equal magnitude on the earth that is so far removed from continental land areas. The Hawaiian Islands are the most isolated islands, of their size, in the world, and their flora strikingly and faithfully registers this profound and prolonged isolation. An examination of a map of the North Pacific Ocean will show the nature of this isolation. Using the island of Oahu, which is situated in the eastern part of the archipelago, as a base point, the distances to adjacent land-masses, in terms of nautical miles, to ports specified, are as follows:

San Francisco	2,100
San Diego	2,260
Panama	4,665
Callao	5,147
Cape Horn	6,488
Tahiti	2,440
Samoa	2,290
Fiji	2,700
Auckland	3,810
Sandakan	4,980
Hongkong	4,920
Yokohama	3,400
Vladivostok	4,721
Portland	2,360
Unalaska	2,106

The isolation is further emphasized by an examination of the deep-sea soundings in the vicinity of the Hawaiian Islands, which show that the islands rise from abyssal depths. The great deeps of the Pacific Ocean, which lie between the Hawaiian Archipelago and the continents, are:

Name of deep	Position with reference to Hawaii	Maximum depth in fathoms	Area in square miles
Murray	Due north	3,540	1,033,000
Supan	Due north		
Maury	Due north		
Renard	Northeast		
Wyman	Northeast		
Tanner	Northeast		
Glover	Northeast		
Agassiz	Northeast		
Bache	Northeast		
Moser	Southeast		
Gray	Southeast		
Belknap	South	3,337	165,000
Campbell	South		
Ammen	Southwest		
Brooke	West	3,429	282,000
Bailey	West	3,432	241,000
Tuscarora	Northwest	4,655	908,000

The isolation of the Hawaiian flora is reflected in the vegetation of the littoral zone by the high proportion of endemic species, 32 out of a total of 110, or 30 per cent. Nine of these belong to endemic genera. This is a remarkable showing, since littoral floras, in all parts of the world, are usually comprised almost wholly of cosmopolitan and non-endemic constituents.

South Pacific equivalents of Hawaii

In the comparisons which are likely to be made of the Hawaiian flora with those of the South Pacific islands it is important to recognize the geologic and topographic status of the various island groups. Guppy ('06, p. 14) makes the following significant observationt:

> The Hawaiian Islands, standing alone in the North Pacific, form a floral region in themselves, a region that is the equivalent not of one group in the South Pacific, such as that of Fiji or of Tahiti, but of the whole area comprising all the groups extending from Fiji to the Paumotu Archipelago.

For the purposes of this paper the islands and continental coasts of the Pacific region may be roughly divided into the following great phyto-geographic provinces, listed clockwise in and around this greatest of marine basins. These provinces are not presented as of equal biological value or range, but merely for purposes of convenience in description.

1. Northeastern Siberia and Alaska: Kamchatka, Korake, Tschuktsche, Aleutian Islands, Alaska, British Columbia, and coastal islands.
2. Pacific Coast of North America: Washington, Oregon, California, and coastal islands.
3. Pacific Coast of Mexico and Central America: Lower California, Mexico, Guatamala, Honduras, Nicaragua, Costa Rica, Panama.
4. Pacific Coast of northern South America: Colombia, Ecuador, Galapagos Islands, Peru, Chile, Juan Fernandez Islands.
5. Pacific Coast of southern South America: Chile and coastal islands; Tierra del Fuego.
6. Australasia: Australia, Tasmania, New Zealand, and adjacent islands.
7. Malaysia: Sumatra, Java, Borneo, and other Sunda Islands; Moluccas, New Guinea, Philippine Islands.
8. Southeastern Asia: China, Hai-nan, Indo-China, Cochin China, Cambodja, Siam, Malay Peninsula.
9. Pacific Coast of Central Asia: Japan, Riu-Kiu Islands, Formosa, and adjacent Asiatic coasts and islands.
10. Melanesia: Bismarck Archipelago, Louisiade, Solomon, Santa Cruz, New Hebrides, and Loyalty Islands, New Caledonia, Fiji, and intervening smaller groups.

11. MIKRONESIA: Mariana, Pelew, Caroline, Marshall, and Gilbert Islands, and intervening islands.
12. POLYNESIA—(*a*) *Nuclear Polynesia:* Samoa, Tonga, Fiji, Tokelau, Ellice Islands, etc.
    (*b*) *Central Polynesia:* Cook, Phoenix, Tubuai, Rokahanga, Tongarewa, Manahiki Islands.
    (*c*) *Southeast Polynesia:* Society, Marquesas, Taumotu, Gambier, Pitcairn, Easter, Ducie Islands, etc.
    (*d*) *Northern Polynesia:* HAWAIIAN ISLANDS.
    (*e*) *Southern Polynesia:* New Zealand and Chatham Islands.
    (*f*) *Polynesian Verge:* scattered islands between Polynesia and Melanesia, such as Ticopia.

EXTENT OF THE HAWAIIAN LITTORAL

The great length of the archipelago gives the littoral zone a much larger significance and extent than if the archipelago consisted of but a few islands situated close together. The Hawaiian littoral, ranging for nearly two thousand miles, contrasts sharply with the compact littoral of such groups as Samoa, Tonga, New Caledonia, Ellice and Phoenix. Other Pacific island groups which are extended over long axes, similar to Hawaii, are the Aleutian, Kurile, Paumotu, Marshall, Caroline, and Solomon Islands.

The Hawaiian strand occupies an island series extending from 18° 54′ to 22° 15′ north latitude, and between 154° 50′ and 160° 30′ of longitude west of Greenwich. This range should greatly increase the mathematical probability of plant dispersal, and in some measure tend to neutralize the powerful isolation-factor. The east-and-west range of the littoral naturally results in a much greater homogeneity of flora than would be the case in an archipelago with a dominant north-and-south axis. In this respect the Hawaiian Islands may be contrasted with such archipelagoes as the Philippines, and the Mariana and Maldive groups.

The great variation in the size and elevation of the several islands markedly influences the extent of the littoral. In general, the low islands have strands that extend further back into the interior than do those of the high islands; the small islands have a larger proportion of strand, relative to their total area, than do the large islands. The small, low coral islets that predominate in the western end of the archipelago are littoral throughout practically all their area; the large, high islands of Maui and Hawaii, at the eastern extremity of the archipelago, have a narrow and closely defined strand.

The following islands have *relatively wide strands:*

1. Ocean, Kure, or Cure Island: circular barrier atoll, 16 miles in circumference; area of lagoon about 38 square miles; several low sand islets in the lagoon; considerable shrubbery and other low vegetation on the largest sand islet, "Green Island."
2. Midway or Brook's Island: circular barrier atoll, 18 miles in circumference; area of lagoon about 40 square miles; several low sand islets in the lagoon; native and introduced vegetation.
3. Pearl and Hermes Reef: irregular, oval barrier atoll, 42 miles in circumference; area of lagoon about 80 square miles; numerous low sand islets in the lagoon, some with grasses and other low vegetation.
4. Lisiansky Island: low, oval isle of coral sand; two miles by three miles; lagoon empty of water; surrounded by reef which extends six or seven miles from isle; vegetation very sparse.
5. Laysan Island: elevated, oval atoll; two miles by a mile and a half; well-developed fringing reef; briny lagoon; abundant scrubby vegetation.
6. French Frigates Shoal: crescentic atoll, with numerous low sand isles, and several high, rocky volcanic isles; area of shoal about 30 square miles; extensive reefs; grasses and low vegetation on sand isles.
7. Small isles along the coasts of Oahu, most of them formerly connected with the island; sparse vegetation: Kihewamoku, Mokuaia; Pulemoku; Kukuihoolua; Mokualai; Mokolii; Kapapa; Ahuolaka; Kekepa; Mokuoloe; Mokolea Mokulua; Kaonikaipu; Mokauea; Mokuoeo; Onini; Moku Umaume; Laulaunui.
8. Small isles along the coasts of Molokai, most of them formerly connected with the island; vegetation sparse or absent: Namoku; Mokapu; Okala; Kuelo-Lepau; Mokuhooniki; Kanaha; Puukole.
9. Small isles along the coasts of Hawaii: Coconut Island, etc.

Narrow strands are characteristic of the following islands:

10. Niihau: area 97 square miles; highest point, 1,300 feet.
11. Kauai: area 547 square miles; highest point, 5,250 feet.
12. Oahu: area 598 square miles; highest point, 4,030 feet.
13. Molokai: area 261 square miles; highest point, 4,958 feet.
14. Maui: area 728 square miles; highest point, 10,032 feet.
15. Lanai: area 139 square miles; highest point, 3,400 feet.
16. Kahoolawe: area 69 square miles; highest point, 1,472 feet.
17. Hawaii: area 4015 square miles; highest point, 13,825 feet.

A number of the smaller islands of the Hawaiian Archipelago rise very abruptly from the sea, and are characterized by *steep or precipitous coasts.* The following are of this type:

18. Gardiner Island: conical rock, 700 feet in diameter, 175 feet high; cliffs 60–70 feet high on all sides; a smaller, precipitous rock nearby.
19. French Frigates Shoal: volcanic rocky islet in center of formerl agoon; 180 feet long, 45 feet wide, 120 feet high; vertical walls; barren.
20. Necker Island: remnant of volcanic crater, surrounded by reef; isle is three quarters of a mile long, 500 feet wide, and 300 feet high; scanty vegetation sea-cliffs on all sides.

21. Nihoa, Bird Island or Moku (Modu) Manu: volcanic remnant; three quarters of a mile long, one third of a mile wide, 600–900 feet high; sea-cliffs on all sides; vegetation scanty.
22. Small isles along the coast of Niihau, probably at one time connected with the island: Kaula and Lehua, small eroded cinder cones with sea-cliffs and steep slopes.
23. Small isles along the coast of Oahu: Moku Manu (two volcanic remnants); Manana (Rabbit Island), eroded crater, with sea-cliffs.
24. Small isles and rocks along the coasts of Molokai: Mokolea, Mokohola, Mokomana.
25. Small isles along the coasts of Maui: Molokini, etc.
26. Five Needles: a group of detached pinnacle rocks about 120 feet high, situated five and a half miles north of Cape Kaea, Lanai, and about the middle of the bight on the west side of the island.

The largest strand areas on any single island occur on the island of Hawaii; the smallest strands are those of the tiny islets in the westward end of the archipelago. On the whole, the Hawaiian strand, as a phytogeographic province, is *poorly developed* when compared with the Indo-Malayan or West Indian strands, or with those of numerous other archipelagoes.

SUBSIDENCE AND ELEVATION

A factor of far-reaching importance in any biological studies in the Hawaiian Archipelago is that of subsidence, i. e., the islands are but the apices of lofty and slowly-sinking submarine mountains. Physiographical evidence is accumulating to show that during previous stages in the history of the central Pacific, these islands undoubtedly stood *thousands of feet higher* than they do at present. Many stages of subsidence and erosion may be found today within the group, ranging from the large, actively volcanic island of Hawaii (nearly 14,000 feet in elevation), at one end of the chain, to the tiny coral atolls, but a few feet above sea-level, which are scattered along the other extremity.

Considering the strand zone of any given island, it is evident that through a long period of time this zone has been slowly *creeping up* the slopes of the island, and the terrestrial vegetation has been crowded into steadily diminishing areas. In other words, the total mileage of strand was formerly much greater than at present, other things being equal. Granting slow subsidence as the prevalent condition of Pacific islands (see, in this connection, an important contribution by Bryan, '16), the great strand mileage of an island like Hawaii steadily decreases until ultimately the condition exhibited by the tiny strand of Laysan or Midway is reached. In this manner the subsidence-factor, although not of especial force at any one time, has been through long periods of time a powerful influence on the strand flora.

Although subsidence has been the dominant note in Hawaii's geological history, there have been minor elevations within recent times. Raised coral reefs and beaches occur at various points along the coasts, e. g., along the southern and western shores of Oahu. The highest reef known is on the southwestern end of Mailiilii, elevated 120 feet above the sea. Just as local elevation at such points as Mokapu, Kalihi, and the Coral Plain has pushed the littoral zone seaward, so at Hanalei, Kahana, Kaneohe, and Pearl Harbor the drowning or submergence of valley-mouths has developed deep embayments, and the littoral flora extends deep into the lowland zone which surrounds it on three sides. It is evident that sufficient study and emphasis has not been given to the ecological effects of these gradual changes of land- and sea-level.

In his illuminating studies of the New Zealand flora, Aston ('12) concludes that the raised marine beaches at Cape Turakirae show that there has occurred comparatively recently, and perhaps within historic times, rapid elevation of the coast line. Violent earthquakes have so altered the physiography of the littoral as to result in some unusual ecological features.

ORIGIN

Relation of Pacific Ocean currents to the dissemination of plants of the Hawaiian littoral

The importance of ocean currents as agencies for the distribution of plants, and more particularly for the wide dissemination of beach species, has long been recognized. In a vast body of water, like the Pacific, dotted with thousands of scattered islands, the surface currents assume special significance in relation to the migrations of plants, animals, and man.

The surface circulation of the Pacific is, on the whole, notably less active than that of the Atlantic. The vertices of the rotational movements are marked by "Sargasso Seas" in the north and south basins, but these quiet areas are of small extent when compared with the well-known Sargasso Sea of the North Atlantic Ocean.

Reference should here be made to the Northern Equatorial Current, which receives important contributions from the great stream that sweeps down the North Pacific coast of America. Many of the largest and most famous of the Hawaiian double canoes were hewn from Douglas spruce (*Pseudotsuga taxifolia*) which had been carried to the shores of Niihau, Kauai, and other islands by the currents. It is a well-known fact that the natives of the Alaska islands obtain much of their fire-wood as drift from the Asiatic coast. Japanese fishing-boats, at various times in history, have drifted to the Hawaiian Islands and to the northwest coast of America.

Between the two great equatorial currents flowing westward on either side of the equator there is a narrow counter-equatorial current flowing to the east. This stream is largely assisted during the latter half of the year by the southwest monsoon, and from July to October the southwest winds prevailing east of 150° E. further strengthen the current, but later in the year the easterly winds weaken or even destroy it. The currents of the South Pacific are well shown in Schimper's ('91) monograph of the Indo-Malayan strand flora.

A feature of ocean currents as seed carriers that has not been sufficiently emphasized is the definiteness of their courses. This fact is well illustrated by the large number of tree trunks and logs from the North Pacific coast that are annually cast upon the Hawaiian coasts. These trees occur in a relatively small and well-defined region, and evidently follow a definite course across the North Pacific. Wood-Jones ('12) performed an interesting experiment to determine the course of drift material in the Indian Ocean. He cast adrift, in the Cocos-Keeling Islands, bottles containing messages. One was picked up on the beach of Brava, Italian Somaliland, after a journey of three thousand miles across the Indian Ocean, and a second one, sent out nearly a year later, was washed ashore at precisely the same place. This definiteness of course gives to the ocean currents a high potential cumulative effect as carriers, that merits more than passing mention.

Currents in the vicinity of Hawaii

The United States Coast Pilot contains data concerning the local island currents, which may be summarized as follows. The strong northeast trades begin early in March, blowing well from the northward until May, and from then until October they are more easterly. During October the trades are light with frequent calms, and occasionally a west southwest swell sets in. During November and December the trades are strong and variable, occasionally being interruped by light southerly winds. During January and February southerly and southwesterly gales often prevail. These are *konas* and are from a few hours to two or three days duration, followed by rain.

Hawaii.—Generally the currents follow the trades but occasionally they set against the wind. A current follows the coast north of Cape Kumukahi around Upolu Point; another one follows the trend of the coast offshore southwestward from Cape Kumukahi around Kalae and northward as far as Upolu Point. There is an inshore current that sets southward from Okoe Landing along the west coast around Kalae, and thence northeastward along the shore as far as Keauhou.

Maui.—Generally the currents set with the trades. A current follows the north shore of Maui westward from Kauiki Head and draws down through Pailolo Channel; the current is stronger on the Molokai side of the channel. A strong current follows the coast southward of Kauiki Head until past Kahoolawe. In the vicinity of Lahaina the current generally sets northwestward.

Molokai.—The current sets westward along the entire northerly coast, and about half the length of the southerly shore, where an easterly current prevails.

Oahu.—The currents around Oahu are variable in strength and direction, but the general movement of the water along the coast is westward or northwestward, the direction being modified by the trend of the coast.

Kauai.—Currents are very uncertain as to direction but they generally follow the winds, though frequently setting in the opposite direction during the first calms after strong trades.

A careful study of any good map which depicts the ocean currents of the North Pacific Ocean will graphically show that the Hawaiian Archipelago is practically outside the zone of influence of the great currents that would naturally bring the seeds of tropical plants to her shores. Guppy's statements ('06, pp. 75, 64) are pertinent in this connection:

> The currents of the Pacific have failed to establish the numerous beach-trees (possessing buoyant fruits) of the Pacific Islands, not only in the Hawaiian group, but also on the coast of America; and it is therefore argued that we should expect the Hawaiian group to have received through the currents its shore-plants with buoyant seeds or fruits from the tropical west coasts of America.
>
> In support of this contention it is pointed out that most of the Hawaiian strand-plants that are dispersed by the currents are found in America, and some indeed in America to the exclusion of the Old World.
>
> The arrangement of the currents in the North Pacific also favours the view that the Hawaiian Islands are more likely to receive plants by the agency of the currents from America than from the Asiatic side of the Pacific.
>
> ……
>
> Speaking generally of the extension eastward of the Indo-Malayan strand-plants over the Pacific, Professor Schimper (['91] page 195) remarks that they become fewer and fewer in number as they extend farther from their original home, their number shrinking to a very few in the most remote groups of the Marquesas and the Hawaiian Islands. . . . The number actually introduced through the currents into Hawaii in all likelihood, therefore, does not exceed ten.

IMPORTANCE OF DRIFT MATERIAL

Drift material is much more abundant along the Hawaiian windward shores than on the leeward shores. Nowhere does it attain the proportions that characterize many other regions elsewhere on the globe. Certain districts, for example, the southeast coast of Hawaii, between Honuapo and Kalae, particularly the Kamilo beach near Kaluwalu, seem to be much more favorably situated for the reception and accumulation of drift than do others.

Tansley and Fritsch ('05) describe the abundant drift on portions of the Ceylon littoral, and note the great variety of plant fragments, fruits, and seeds:

> The thickest masses of drift were very moist and quite warm to the hand, and in this natural forcing bed many different plants had germinated. The thick line of brown-black humus with the fresh green leaves of the seedlings arising from it at intervals was a most striking sight. Of these the most conspicuous were *Cerbera odollam, Calophyllum inophyllum, Bruguiera gymnorhiza, Crinum asiaticum,* and *Colocasia antiquorum* (from bits of old rhizome).

Moseley ('79, p. 367) reports from the Moluccas living epiphytic orchids and young palms as part of the drift, washed high up on the beach and growing. He states:

> We passed large quantities of leaves, fruits, and flowers, and branches of trees floated off from the shores. . . . I was astonished at the large quantities of fresh vegetable matter thus seen floating on the sea. . . . Not only are large quantities of fruits [containing seeds] capable of germinating thus transported from island to island, but entire living plants, even trees, are washed from island to island and transplanted by the waves.

Hooker ('47, p. 253) states that the majority of the littoral species of the Galapagos Islands have reached the islands through oceanic and aerial currents. There are about twenty such plants, mostly species common to warm latitudes. Some of these are: *Cissampelos Pariera*, *Tribulus cistoides*, *Tephrosia littoralis*, *Verbena littoralis*, *Avicennia tomentosa*, *Scaevola Plumieri*, *Ipomoea maritima*, *Calystegia Soldanella*, and *Heliotropium curassavicum*. Hooker attributes the following plants of the Peruvian and Chilean littoral, which occur on the Galapagos strand, to ocean currents: *Vigna oahuensis*, *Acacia Cavenia*, *Nicotiana glutinosa*, *Dictyocalyx Miersii*, *Lycopersicum peruvianum*, *Verbena littoralis*, *V. polystacha*, and *Plantago tomentosa*.

FLOTATION ADAPTATIONS OF STRAND PLANT SEEDS

In his monograph on the Indo-Malayan strand flora Schimper ('91, pp. 163–178) makes the following classification of strand plants, based upon the flotation characters:

1. Driftfrüchte und Driftsamen mit grossen luftführenden Hohlräumen. Examples: fruits of *Heritiera littoralis*, *Thespesia populnea*, *Pongamia glabra*, and *Derris uliginosa;* seeds of *Mucuna* species, *Caesalpinia Bonducella*, *Vigna lutea*, *Hibiscus tiliaceus*, *Dodonea viscosa*, *Euphorbia Atoto*, *Suriana maritima*, *Ipomoea pes caprae*, *Pangium edule* (?), *Colubrina asiatica* (?), *Morinda citrifolia*.
2. Driftsamen mit schwammigen Samenkern. Examples: many Leguminosae, such as *Sophora tomentosa* and species of *Erythrina* and *Canavalia;* embryos of *Rhizophora* and *Avicennia*.
3. Driftfrüchte und Driftsamen, deren Schwimmfähigkeit durch luftführendes Schalengewebe bedingt ist.
    - A. Schwimmgewebe peripherisch. Examples: *Clerodendron inerme*, *Carapa* species, *Cordia subcordata*, *Wollastonia glabra*, *Tournefortia argentea*, *Pemphis acidula*.
        - a. Schwimmgewebe mit grossen Intercellularräumen. Examples: *Cerbera Odollam*, *Laguncularia racemosa*, *Nipa fruticans*.
        - b. Schwimmgewege ohne oder nur mit winzigen Intercellularräumen. Examples: fruits of *Cocos nucifera*, *Barringtonia speciosa*, *B. excelsa*, *Ter-*

minalia Katappa, Conocarpus erecta, Lumnitzera racemosa, L. coccinea, Scyphiphora hydrophyllacea, Guettarda speciosa, Tournefortia argentea, Wollastonia glabra, Scaevola Koenigii, Clerodendron inerme, Cynometra cauliflora, Cordia subcordata; seeds of *Carapa moluccensis, C. obovata, Sonneratia* species, *Pemphis acidula.*

B. Das Schwimmgewebe befindet sich innerhalb einer harten Stein- oder Samenschale. Examples: fruits of *Calophyllum inophyllum* and *Ximemia americana;* seeds of *Cyas circinalis* and *Excoecaria Agallocha.*

Guppy ('06, p. 531) enumerates the following seeds or seed vessels that remained afloat after a year's flotation in sea-water: *Thespesia populnea, Mucuna gigantea, Dioclea* sp., *Strongylodon lucidum, Sophora tomentosa, Caesalpina Bonducella, Entada scandens, Morinda citrifolia, Scaevola Koenigii, Cordia subcordata, Tournefortia argentea, Ipomoea grandiflora,* and *Tacca pinnatifida.*

In Helmsley's classification of the Bermudian flowering plants ('85, p. 48) the following indigenous genera, chiefly littoral forms, are listed as having probably been conveyed to the island by ocean currents: *Cakile, Hibiscus, Suriana, Elaeodendron, Sapindus, Dodonaea, Cardiospermum, Rhus, Sophora, Vigna, Canavalia, Centrosema, Conocarpus, Rhizophora, Opuntia, Sesuvium, Rhachicallis, Chiococca, Morinda, Solidago, Borrichia, Scaevola, Tournefortia, Heliotropium, Ipomoea, Convolvulus, Avicennia, Coccoloba, Atriplex, Salicornia, Euphorbia, Croton, Ruppia, Zostera, Cenchrus, Spartina, Stenotaphrum, Sporobolus, Chloris.*

Helmsley ('84, p. 304) has also recorded the actual germination of various drifted seeds after being cast ashore. He lists *Hibiscus tiliaceus, Vitis vinifera, Sapindus Saponaria, Anacardium occidentale, Aleurites moluccana, Ricinus communis, Cocos nucifera,* and *Sagus* sp. Of *Vitis vinifera* he records the foundering of a vessel laden with a cargo of white Lisbon grapes, off the south shore of Bermuda. Many of the grapes were washed ashore, and the seeds germinated at high-water mark. Numbers of plants were taken up, out of curiosity, and transplanted, and bore fruit. Martins raised plants from seeds of *Ricinus communis* that had been floating for ninety-three days upon the surface of the sea.

Shull's ('14) extensive experiments show that the seeds of many species will germinate after four years of continuous submergence in fresh water, and that the seeds of three species were viable after seven years of continuous submergence.

Guppy ('06, p. 529) shows that of the littoral plants of Fiji and Tahiti, 75–80 per cent. have seeds or fruits that will float unharmed for two months or more, and that about 30 per cent. of this number are legumes. He says:

> In the course of the ages the plants with buoyant seeds or seed vessels have been gathered at the coast. This is indicated: (1) By the far greater proportion of species with buoyant seeds and seed vessels amongst the shore plants than among the inland plants. (2) By the circumstance that almost all the seeds or seed vessels that float unharmed for long periods belong to shore plants. (3) By the fact that when a genus has both inland and littoral species, the seeds or fruits of the coast species as a rule float for a long time, while those of the inland species either sink at once or float only for a short period.

Guppy ('06, p. 563) makes the following list of "Hawaiian plants with buoyant seeds and fruits known to be dispersed by the currents either exclusively or, as in a few species, with the assistance of frugivorous birds": *Colubrina asiatica, Dioclea violacea, Mucuna gigantea, M. urens, Strongylodon lucidum, Vigna lutea, Caesalpinia Bonducella, Scaevola Koenigii, Ipomoea glaberrima, I. Pes-caprae, Vitex trifolia* and *Cassytha filiformis.* Although many strand plants possess seeds or fruits that can float for long periods, other widely distributed species possess feeble or no flotation power. It is necessary to recognize other agencies.

TREES AND LOGS AS DISSEMINATORS

Logs and tree-trunks of various coniferous species from the Puget Sound region are commonly cast ashore upon the Hawaiian windward coasts. It is a matter of common observation that on all windy coasts, small seeds, like sand, are blown into every available cranny. In this way many lodge in the holes and cracks in drift-wood, which is floated off at high tide or during storm time, and thus the seeds or fruits may be carried to new localities. Strand seeds or fruits which do not possess special flotation devices may be carried to new shores. Moreover, the seeds of inland species may be carried by trees which have been uprooted by inundations or storms, either in the soil around the roots, or in the bark, etc.

Ernst ('08, p. 56) states that "tree stems and branches played an important part in the colonization of Krakatau by plants and animals." Hedley ('15) records a log of *Dammara australis* the New Zealand Kauri, as stranding on the windward reef of Funafuti. Wood-Jones ('05) gives an excellent account of tree-trunks and "floating islands" of storm-washed vegetation as carriers of seeds, animals, etc., to the Cocos-Keeling group. He emphasizes the importance of trees with buttressed bases as disseminators:

> These buttresses are in the form of large thin wings, which taper to the trunk above, and below form a series of compartments like stalls in a circular stable. Within these stalls much earth is held fast by the interlacing of smaller roots, and when such a tree is uprooted, and set adrift to sea, it carries its earth with it. It may carry it for very great distances, and I have seen a buttressed tree come ashore in the atoll, from whose base a wheelbarrow-load of fine red earth might have been collected.

FLOATING ROCKS AS DISSEMINATORS

The idea of floating rocks as disseminators of littoral plants might be met with incredulity, were it not for the testimony of many reliable observers. Among the volcanic islands of the East Indies large blocks of pumice float for many weeks, and are carried many hundred miles from their points of origin. The salient points—prolonged flotation of the blocks; presence of numerous kinds of seeds in the crevices and pores of the pumice; and the germination of these seeds when the block is cast upon a favorable beach-situation—have all been corroborated by careful investigators. Ernst ('08, p. 56) states that floating blocks of pumice constitute an important dispersal agency in the Sunda-Straits region.

Although there is very little pumice to be found on the Hawaiian coasts at the present time, there is abundant evidence that in earlier periods in the geologic history of the islands, repeated volcanic explosions, resulting in pumice production, have taken place. There are today extensive pumice beds around the volcano Kilauea. Therefore, although pumice blocks play little or no part in the dispersal of plants in the Hawaiian group at present, it is entirely possible that they had a more important rôle in earlier times, at least in distributing seed from island to island.

Floating masses of dead coral may also be ranked as possible seed-carriers. Wood-Jones ('15) found numerous instances of this in the Cocos-Keeling group. The innumerable air-cavities in certain kinds of coral render it buoyant. The block is cast upon a beach at storm time; it lies there for an indefinite period;

earth, sand, and seeds lodge in its many crevices; another storm sets it again adrift; and it may be cast ashore upon a distant strand. Coral blocks of this sort are infrequent on Hawaiian shores, owing to the relative paucity of fringing reef, and have probably been of minor significance in seed dispersal. They constitute, however, a possible factor, particularly on Oahu, Kauai, and the leeward isles.

COMPOSITION—A CLASSIFIED LIST OF THE HAWAIIAN STRAND PLANTS

I. True littorals

Species which occur only or chiefly within the strand zone.

Endemic littorals

Trees and shrubs

There are no endemic trees that are strictly littoral. This is a significant feature of the Hawaiian flora. The shrubs are:

Lycium sandwicense Gray
Nototrichium humile Hillebd.
Santalum Freycinetianum Gaud. var. *littorale* Hillebd.
Phyllostegia variabilis Bitter
Scaevola coriacea Nutt.
Solanum Nelsoni Dun.
S. laysanense Bitter
Wikstroemia Uva-ursi Gray

Herbaceous plants

Achyranthus splendens Mart.
A. splendens var. *rotundata* Hillebd.
Campylotheca molokaiensis Hillebd.
Fimbristylis pycnocephala Hillebd.
Kadua littoralis Hillebd.
Lepidium owaihense Cham. & Schlecht.
Lipochaeta connata (Gaud.) DC. var. *littoralis* Hillebd.
L. integrifolia (Nutt.) Gray
L. succulenta (Hook. & Arn.) DC.
Schiedea globosa Mann
S. Lydgatei Hillebd.
Sporobolus virginicus (L.) Kunth var. *phleoides* Hillebd.
Tetramolopium sp.

2. Indigenous littorals

Trees and shrubs

There are no indigenous trees that are strictly littoral. Shrubs:

Colubrina asiatica (L.) Brongn.
Gossypium tomentosum Nutt.

Heliotropium anomalum Hook. & Arn.
Scaevola Lobelia Murr.
Sesbania tomentosa Hook. & Arn.
Vitex trifolia L.

Herbaceous plants

Argyreia tiliaefolia (Desr.) Wight
Boerhaavia diffusa L.
Cressa cretica L.
Cyperus laevigatus L.
Euphorbia cordata Meyen
Heliotropium curassavicum L.
Herpestis Monnieria H. B. K.
Ipomoea acetosaefolia (Vahl) Roem. & Schl.
I. glaberrima Bojer
I. insularis Steud.
Ipomoea Pes-caprae (L.) Sweet
Lepturus repens R. Br.
Lysimachia spathulata Benth. & Hook.
Ruppia maritima L.
Scirpus maritimus L.
Sesuvium Portulacastrum L.
Sporobolus virginicus (L.) Kunth
Tephrosia piscatoria (Soland.) Pers.

3. LITTORALS INTRODUCED BY THE PRIMITIVE HAWAIIANS*

Trees

Calophyllum Inophyllum L.
Cocos nucifera L.
Cordia subcordata Lam.

4. LITTORALS INTRODUCED SINCE THE ADVENT OF EUROPEANS (1555–1778 TO DATE)

Trees and shrubs

No true littoral trees and shrubs have been introduced.

Herbaceous plants

Batis maritima L.
Polypogon littoralis (With.) Sm.

II. Pseudo-Littorals

Species which chiefly inhabit the lowlands or other zones, and which appear on the strands in the role of invaders from the interior.

1. ENDEMIC PSEUDO-LITTORALS

Trees and shrubs

Acacia koa Gray
Cassia Gaudichaudii Hook & Arn.
Chenopodium sandwicheum Moq.
Erythrina monosperma Gaud.
Myoporum sandwicense (A. DC.) Gray

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* *Thespesia populnea* Soland. should be noted here.

Herbaceous plants

- *Carex sandwicensis* Boeckl.
- *Jacquemontia sandwicensis* Gray
- *Nama sandwicensis* Gray
- *Peucedanum sandwicense* Hillebd.
- *Sicyos hispidus* Hillebd.
- *S. microcarpus* Mann

2. Indigenous pseudo-littorals

Trees and shrubs

- *Caesalpinia Bonducella* (L.) Flem.
- *Metrosideros polymorpha* Gaud.
- *Pritchardia* spp.
- *Tribulus cistoides* L.

Herbaceous plants

- *Argemone mexicana* L.
- *Cassytha filiformis* L.
- *Cenchrus calyculatus* (Spreng.) Cav.
- *Chenopodium album* L.
- *Cladium leptostachyum* Nees
- *Cyperus pennatus* Lam.
- *C. phleoides* Nees
- *Eragrostis hawaiiensis* Hillebd.
- *Erythraea sabaeoides* (Griseb.) Gray
- *Fleurya interrupta* Gaud.
- *Kyllingia monocephala* Rottb.
- *Lythrum maritimum* H. B. K.
- *Malvastrum tricuspidatum* (Ait.) Gray
- *Mucuna gigantea* (Willd.) DC.
- *Ophioglossum vulgatum* L.
- *Sida* spp.
- *Vigna lutea* (Sw.) Gray
- *Waltheria americana* L.

3. Pseudo-littorals introduced by primitive Hawaiians

Trees

- *Aleurites moluccana* (L.) Willd.
- *Hibiscus tiliaceus* L.
- *Morinda citrifolia* L.
- *Pandanus odoratissimus* L. f.

4. Pseudo-littorals introduced since the advent of Europeans

Trees and shrubs

- *Acacia farnesiana* Willd.
- *Casuarina equisetifolia* Stickman
- *Hibiscus Rosa-sinensis* L.
- *Leucaena glauca* (Willd.) Benth.
- *Prosopis juliflora* (Sw.) DC.

Herbaceous plants

Abrus precatorius L.
Achyranthus aspera L.
Cardiospermum Halicacabum L.
Crotalaria spp.
Cynodon Dactylon (L.) Pers.
Cyperus umbellatus Vahl
Datura Stramonium L.
Euphorbia pilulifera L.
Euxolus viridis Moq.
Hydrocotyle verticillata Thunb.
Indigofera Anil L.
Mesembryanthemum spp.
Portulaca oleracea L.
Salvia occidentalis Sw.
Samanea Saman (Benth.) Merrill
Xanthium echinatum Murr.

There are numerous ruderals, in addition to those indicated in the last section, that occur at random on the various beaches.

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Notes on the fern genus Clathropteris

EDWARD W. BERRY

(WITH TWO TEXT-FIGURES)

Among the more fascinating objects of paleobotanical investigation are the abundant and varied forms which have now come to be rather generally recognized as constituting two distinct families of ferns, the Matoniaceae and the Dipteriaceae, members of which are such characteristic and striking objects in Mesozoic fern floras. This interest associated with their far distant ancestry is heightened by the fact of the singular association of the few surviving representatives of these two families at a limited number of localities in the oriental tropics.

It is not my purpose, however, to attempt an elaboration of this subject in the present connection, since it has already been discussed by others* and there is, moreover, a rather extensive literature dealing with the different extinct generic types that seem to be referable to the one or the other of these families All that will be attempted in the present brief contribution will be the placing on record of certain observations on new material belonging to the genus *Clathropteris* and a discussion of its bearing on the probable habit of these ferns.

During a visit to the Richmond (Virginia) coal field during 1911 I collected for the United States National Museum a remarkably fine specimen of the so-called *Clathropteris platyphylla*, which, in so far as I recall, was the most complete specimen of this ubiquitous form that has ever been collected. This specimen was about 40 × 55 cm. and showed several dichotomies of the stipe. During its shipment to Washington the edges were broken and the surface abraded so that only a very inferior specimen remains. A counterpart of a portion of the face of this specimen

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* Seward, A. C. On the structure and affinities of *Matonia pectinata*, R. Br., with notes on the geological history of the Matonineae. Phil. Trans. Roy. Soc. Lond. B, 191 : 171–209. 1899. Seward, A. C., & Dale, E. On the structure and affinities of *Dipteris*, with notes on the geological history of the Dipteridineae. *Idem.*, B, 194 : 487–513. 1901.

was carefully brought back for the collections of the Johns Hopkins University and it is upon this fragment that the following remarks are mainly based.

The latter has maximum dimensions of about 22 × 27 cm. and shows a fragment of a large stipe 12 cm. long and 1 cm. in diameter, part of a whorl of large pinnae, and a fragment of the terminal part of a stipe with eight palmately arranged and mostly attached pinnae. Some of the marginal dentations of the pinnae are perfectly preserved, as is the peculiar netted venation. This specimen is shown in FIG. 1, one half natural size.

The genus *Clathropteris* was proposed by Brongniart[*] in 1828, the type being his *Filicites meniscioides*[†] from the Rhaetic beds of Hoer in Scania. In 1849 Brongniart[‡] transferred the *Camptopteris platyphylla* of Goeppert[§] to the genus *Clathropteris*, and these two species have usually been maintained as distinct, although Nathorst states[||] that after an examination of Brongniart's type material of *Clathropteris meniscioides* he is convinced that it is identical with *Clathropteris platyphylla*. If this is true then the former name has priority.

The genus has been discussed recently by Nathorst (*op. cit.*), Zeiller[**] and Seward[††] so that it is unnecessary to attempt to redefine it at the present time. Seward[‡‡] has advocated the merging of *Clathropteris* and the allied genus *Thaumatopteris* Goeppert (*op. cit.*) with *Dictyophyllum*, but this course has fortunately not been followed, and Nathorst (*op. cit.*) has given excellent reasons why such a consideration would be unwarranted. The last author proposes that these fossil genera should be segregated from the existing family Dipteriaceae under the family name of Camptopteriaceae and on philosophical grounds it would seem that such a course would come nearer to representing the true status of these forms since the two groups are separated by the whole time interval of the

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[*] Brongniart, A. Prodrome, 62. 1828.

[†] Brongniart, A. Ann. Sci. Nat. Bot. **4**: 200. *pl. 11.* 1825.

[‡] Brongniart, A. Tableau 32. 1849.

[§] Goeppert, H. R. Gen. pl. foss. **5–6** : 120. *pl. 18, 19, f. 1–3.* 1846.

[||] Nathorst, A. G. Kgl. Svenska Vetens.-Akad. Handl. **41** : 4. 1906.

[**] Zeiller, R. Flore foss. gîtes charbon Tonkin. Ministère trav. publ. Études gîtes minér. France, Atlas, 1902, texte, 1903.

[††] Seward, A. C. Fossil Plants **2** : 386. 1910.

[‡‡] Seward, A. C. Phil. Trans. Roy. Soc. Lond. B, **194** : 503. 1901.

Cenozoic, generally estimated at several millions of years, during which it is almost inconceivable that family boundaries did not shift. At the same time there seems to be a consensus of opinion that the existing Dipteriaceae represent the last relics of this adaptive radiation of the Camptopteriaceae, so that the question of family nomenclature is really not of great importance.

Specimens referable to *Clathropteris* and probably representing several botanical species, but not certainly distinguishable in the present state of our knowledge, have a very wide geographic and a very considerable geologic range. In this country they are found in the rocks of the Newark formation, probably of Keuper age, in Massachusetts, Connecticut, New Jersey and Virginia. They occur in the Keuper of Prussian Saxony and Switzerland. In the succeeding Rhaetic they are found in Sweden, Bornholm, Germany, France, England, Persia, China and Tonkin. In rocks referred to the lower Lias they are recorded from Hungary, Saxony, Silesia and France. Owing to the peculiar habit of these ferns and the often great length of the pinnae the specimens are usually much broken, the best foreign material probably being that described by Zeiller (*op. cit.*) from Tonkin.

As regards the habit it appears that the dichotomously forked rhizomes described by Nathorst (*op. cit.*) as *Rhizomopteris cruciata* represent the rhizomes of *Clathropteris*. The scars on these rhizomes indicate that in the Swedish region the fronds were not as crowded as they were in the allied *Dictyophyllum* growing at the same locality. The Virginia material shows that the stipes were stout and somewhat curved (in this respect suggesting *Mertensia*), as much as a centimeter in diameter, and with a longitudinally striated epidermis.

These stipes, rising for a considerable distance from the creeping rhizome, divided dichotomously at a wide angle and bore on the upper side of this fork from ten to thirty pinnae as in the genera *Dictyophyllum* and *Camptopteris*, species of both of which genera have been admirably restored by Nathorst. These pinnae are said to be fused proximad but it may be considered certain that the amount or absence of fusion was a variable feature as it is demonstrated to have been in the allied genus *Dictyophyllum*. It appears from Zeiller's Tonkin material that these primary pinnae are more inclined to separation, are more slender, have simpler margins and are more numerous than those pinnae which I propose to consider as ultimate or secondary pinnae. I regard the

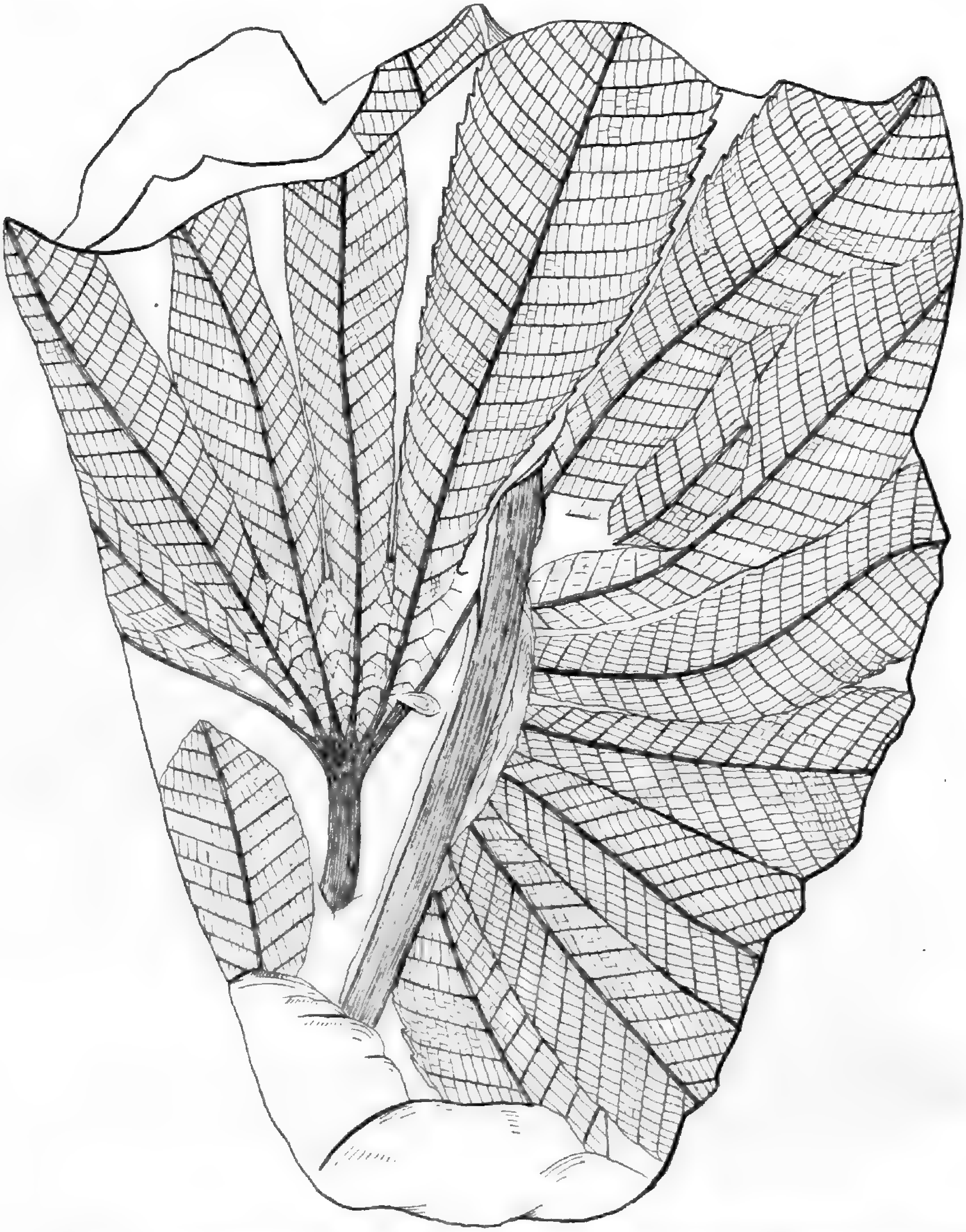

FIG. 1. Specimen of *Clathropteris platyphylla* from Triassic of Virginia, one half natural size.

palmately arranged pinnae on the right of the specimen figured (FIG. 1) as representing such primary pinnae. These are lanceolate in form, show a maximum width of 5 cm. at about one third the distance above the base, and have an indicated length of about 30 cm. They taper conspicuously proximad and are still free at a point where their width has narrowed to less than 1.5 cm. Although their extreme bases are obliterated they were evidently either entirely separate or only slightly united. The margins are not entire but the marginal teeth are very much reduced, even at a distance of 10 cm. above the base, and proximad they appear to have been entirely wanting, although the preservation is not sufficiently good to be positive on this point.

It has been assumed by most students that the *Clathropteris* frond consisted of a single dichotomy and therefore had a habit somewhat like the modern *Dipteris* and more conspicuously like the existing *Matonia pectinata*, or like that of the extinct genus *Dictyophyllum* as restored by Nathorst. It would appear from the Virginia material that, in addition to such a group of what I have called primary pinnae, arranged *en éventail*, each branch of the dichotomy continued for some distance and then expanded into palmately arranged ultimate or secondary pinnae. These were fewer in number than those that I have called primary pinnae, being eight in the preserved material. They are wider and more conspicuously toothed and are clearly united for a distance of 3–5 cm. above their bases in my material.

While this interpretation is based in the first instance on material no longer extant and is therefore to be accepted with reserve, I feel justified in calling attention to it and in offering the tentative restoration of this interesting species as shown in FIG. 2. That the fronds were sometimes much larger than I have indicated is shown by fragments in my possession and by the extremely large fragments collected by Fontaine, which according to this author showed a width of pinnae of 20 cm. and an indicated length of 60 cm.

I have seen no fertile specimens from Virginia, but certain foreign material shows, on the lower surface of the lamina, an abundance of crowded sori without indusia and made up of from five to fifteen annulate sporangia, similar to those of *Dictyophyllum* and *Dipteris*, although the annulus is said by Goeppert to have been complete—a feature that it would seem would be impossible to decide in the absence of structural material.

The venation of *Clathropteris* has always excited great interest. In the proximal region where the pinnae are fused it is somewhat irregularly anastomosing, as is admirably shown in Zeiller's restoration.* In the free portion of the pinnae the very stout midribs give off, at regular intervals and at very wide angles ap-

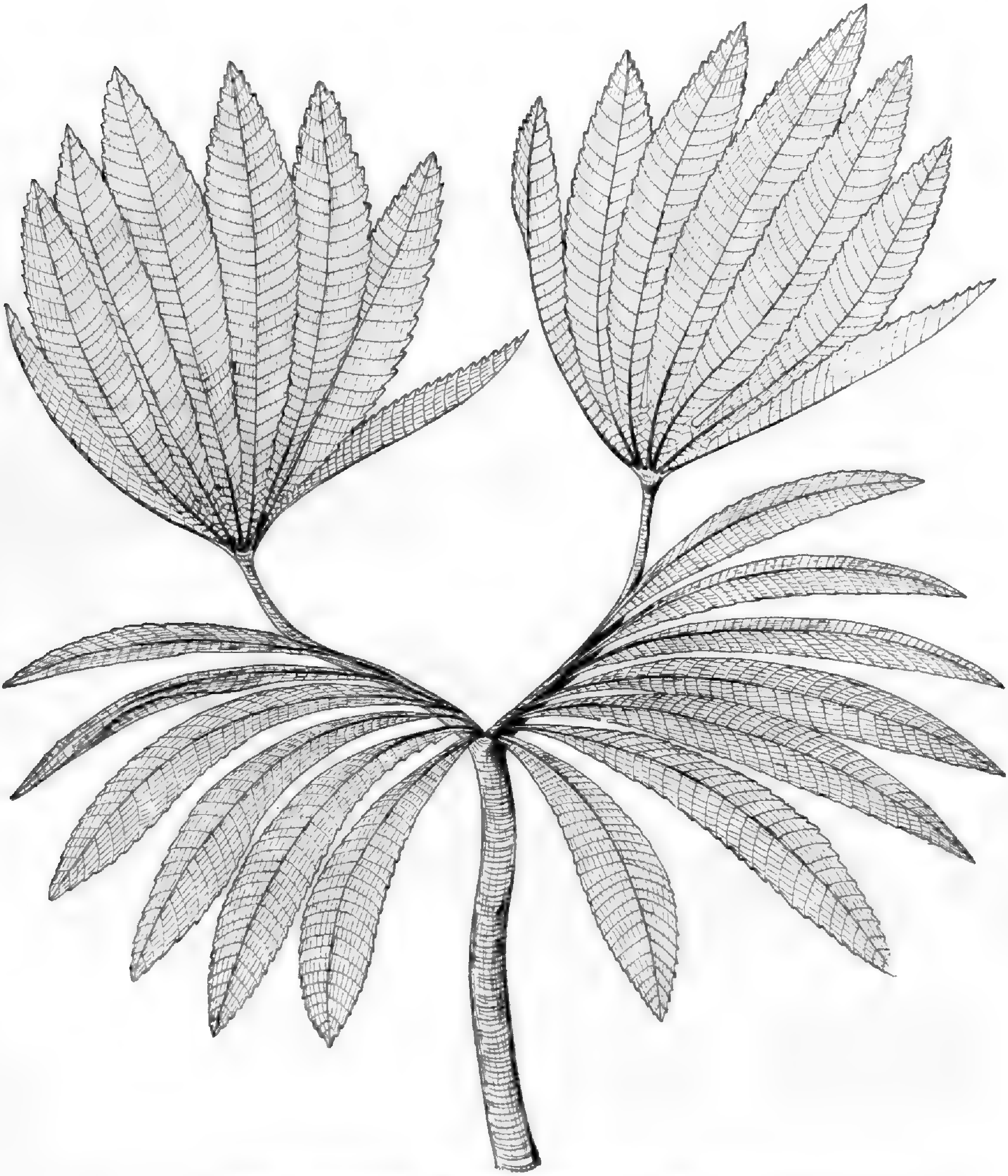

FIG. 2. Tentative restoration of *Clathropteris platyphylla*, one eighth natural size.

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* Zeiller, R. Éléments de Paléobotanique, 116, *f. 89*. 1900.

proaching 90 degrees, stout parallel secondaries. These usually alternate but not invariably. They proceed outward in almost straight courses nearly to the margin where they curve conspicuously upward, becoming rapidly much reduced in size and terminate at the tips of the marginal teeth. The secondaries are connected at approximately regular intervals by relatively stout straight percurrent tertiaries at nearly right angles to the secondaries, and subordinate divisions result in an ultimately fine rectangular areolation with blind endings.

This rectangular venation is rather consistently more regular than in the allied fossil genera and rather different from that of the existing Dipteriaceae. It is, however, approached very closely by certain existing Polypodiaceae with the so-called *Drynaria composita* type of venation. Among modern ferns that have a comparable venation might be mentioned various oriental species of Polypodiaceae, belonging to the genera *Lomariopsis*, *Dryostachyum*, *Polybotrya* and *Drynaria*. The latter genus is especially like *Clathropteris* in the form of its pinnules, in their venation and (in some of its species) in their toothed margins. *Drynaria* comprises about a dozen species of epiphytes of the oriental tropics and the species *Drynaria quercifolia* is particularly like *Clathropteris* in respect to the characters just enumerated, although the general habit is very different.

Although Schenk refers the fossil forms to the family Dictyopterideae, the venation characters, more readily ascertainable from fragmentary specimens, which are the kind usually collected, have resulted in the usual reference of the fossils to the Polypodiaceae or Acrostichaceae, as is done by Ettingshausen, although it is obvious that they constitute a unique and distinct line of forms ancestral to the modern family Dipteriaceae.

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Studies in the genus Gymnosporangium—II. Report on cultures made in 1915 and 1916

B. O. Dodge

(WITH PLATE 8)

The writer (2) reported the infection of *Chamaecyparis* with *Roestelia transformans*, and later (3) gave an account of experiments which resulted in the infection of the red cedar with *G. clavipes*, *G. macropus*, *G. globosum* and *G. nidus-avis*. Arthur's results (1) were confirmed in the case of *G. clavipes*, and it was stated that the other species required nearly two years to mature. *G. globosum* as well as *G. macropus* may develop strictly foliicolous galls. In 1917 the writer reported the infection of *Chamaecyparis* with *G. Ellisii* (4). Weimer (12) states that *G. clavipes* matures in two years, although it seems he was unable to make the infections. He also reports the development of one small gall of *G. macropus* on cedars which he had previously inoculated. The abstract of the writer's paper read at a meeting of the Botanical Society of America, 1916, has not appeared in print, and as further work has resulted in the accumulation of considerable data, a summary of the cultures of 1915 and 1916 is presented at this time.

GYMNOSPORANGIUM CLAVIPES

A red cedar eight inches high obtained from Cold Spring Harbor, Long Island, in May, 1915, had at the time a few sori of *G. clavipes* on the stem. This material was used to infect *Crataegus oxyacantha*.

Six red cedars were sprayed with aecidiospores August 1, 1915, and left in the infection frame two days. Several other cedars were growing in the same greenhouse, otherwise no controls were provided. TABLE I includes all cedars that were growing in the greenhouse at the time aecidiospores were being shed from the rust on the *Crataegus*.

The results shown in the table indicate that spores may mature the first spring after inoculation, although in some cases they do not appear until the second year. All of the plants that were inoculated became so heavily infected that by 1918 many of the branches had been killed. Those plants that became infected without inoculation through being exposed near hawthorns bearing aecidia bore only a few sori in 1917 and had about twice as many in 1918. The invasion of new regions of the host by the mycelium is not very rapid. It has, however, completely connected spaces between most of the groups of sori that were evident on the plants in 1917. In some cases small witches' brooms have been formed, and spindle-shaped swellings are beginning to appear on some of the larger branches and main stems.

TABLE I

INOCULATION OF *Juniperus virginiana* WITH AECIDIOSPORES OF *G. clavipes*

Plants inoculated August 1, 1915			Cedars exposed in the greenhouse but not inoculated by spraying, etc.		
No.	Results, 1916	Results, 1917	No.	Results, 1916	Results, 1917
401	−	+, many sori	405	−	+, 6 sori
402	−	+, " "	407	−	−
403	−	+, " "	408	−	−
412	+, 11 sori	+, " "	411	−	−
415	+, 30 sori	+, " "	938	−	−
416	+, 1 sorus	+, " "	413	−	−
			414	−	−
			417	−	−
			418	−	+, 2 sori
			590	−	−
			591	−	−
			594	−	−
			609	−	−

GYMNOSPORANGIUM MACROPUS

The life histories of the two "cedar apple" rusts have become fairly well understood through field observations made by many investigators of the gymnosporangial stages, and by cultures of the rusts on their aecidial hosts.

The cedar plants used in this work were obtained at Cold Spring Harbor, New York, February 1, 1914. Some of them bore a few galls of *G. macropus* and *G. globosum*. Spores from these galls were used to infect seedling apples and hawthorns. The galls were marked with tags for further observation. The cedars were carefully inspected during the summer of 1914 and until

July 1, 1915, and any new galls that appeared were marked with tags. The heights of the plants were taken in February, 1914, and each spring since that date. These precautions enabled me to obtain evidence relating to the length of life of the galls, especially of *G. globosum*, which has been assumed to be perennial, although records bearing on this point appear to be meager. Hawthorns bearing aecidia of *G. globosum* were grown in the greenhouse at the same time and this fact required that infections be made with teleutospore material from galls that appeared on the cedars later, since the smaller galls of *G. globosum* and *G. macropus* are not always so characteristic as to be easily distinguished. The results are given in TABLE II.

TABLE II

INFECTION OF THE RED CEDAR WITH *G. macropus*

No.	Height of cedars, inches				Date of inoculation	Results, number of galls	Spores matured
	Feb., 1914	Feb., 1915	Feb., 1916	Feb., 1917			
					1914		
401	11	16	24	38	July 13	0	
403	7	12	26	35	June 13	2	March 17, 1916
504	6	10	15	23	June 7	3	March 6, 1916
411	14	24	39	53	June 22	0	
414	16	24	39	53	June 20	2	May 18, 1916
415	9	13	?	20	June 28	2	April 2, 1916
417	16	21	34	48	June 20	0	
403	7	12	26	35	1915 July 2	3	April 14, 1917
407	12	22	35	50	Aug. 1	6	April 24, 1917
416	10	14	17	24	June 5	2	April 25, 1917
418	?	?	20	42	June 10	1	March 1, 1917

The last date upon which the plants were exposed to natural infection was in the summer of 1913. The point at which the lowest gall, for example on plant No. 403, appeared was five inches above the tip of the main stem of this plant February 1, 1914, as shown by the records of measurements. The cultures, especially those made in 1915, prove that Heald's conclusions were correct as regards the time required for the maturity of the rust. There were fourteen galls on these four plants; they were for the most part comparatively small, bearing from one to five sori.

GYMNOSPORANGIUM GLOBOSUM

The inoculations of cedars with *G. globosum* were made in 1914 and 1915 under the conditions described in the preceding experiments. The results appear in TABLE III.

TABLE III

INFECTION OF THE RED CEDAR WITH *G. globosum*

No.	Height of cedars in inches				Date of inoculation	Results, number of galls	Spores matured
	Feb., 1914	Feb., 1915	Feb., 1916	Feb., 1917			
					1914		
405	6	10	15	23	June 7	15	March 7, 1916
407	12	22	35	50	June 25	5	Feb. 28, 1916
408	11	20	30	48	June 20	0	
					1915		
401	11	16	24	38	Aug. 1	0	
402	14	?	26	37	Aug. 1	0	
403	7	12	26	35	Aug. 1	2	March 10, 1917
405	6	10	15	23	Aug. 1	1	April 4, 1917
416	10	14	17	24	Aug. 1	0	

The first indications of infection were discovered August 1, 1915; there were two small green galls on plant No. 407. The writer is rather inclined to disregard these galls, especially as they were on the lower branches and grew to considerable size like those one finds in nature. There were no sorus-scars such as we should expect to see if the plants had been infected in nature in 1913. The other galls were clearly the result of inoculation as most of them developed at points on the plants represented by new growth since they had been brought in. None of the fifteen leaf galls on plant No. 405 developed sori a second time. The ones on No. 407 matured spores two seasons. Most of the large galls on naturally infected plants, so far as observed, bore sori three years in succession. There is no record of one bearing four crops of spores. It was impossible to inspect the cedars thoroughly during July and August, so that it is uncertain at just what time the galls made their first appearance. Most of them were visible in September, although some of the galls of *G. globosum* were so small that they might have been overlooked. In some cases there is very little hypertrophy of the leaf tissue upon which they appear. Weimer (11) has very adequately described these small galls.

Gymnosporangium Ellisii

Fromme (6) connected *Gymnosporangium Ellisii* with *Aecidium myricatum.* Dodge and Adams (5) found the aecidium on *Comptonia asplenifolia.* Attempts were made to infect *Comptonia* in 1915 and 1916 without success. The plants brought in March 25, 1917, leaved out in about two weeks and were inoculated April 12. The spermogonia appeared April 1 on several leaves. By May 14 the peculiar ram's horn twist of the leaves was very striking. Absence prevented further observation of the infected plants but at least two of them matured aecidia.

Certain seedling plants of *Chamaecyparis* were sprayed with aecidiospores from *Myrica* in 1915 and others in 1916. The cedars in the first lot showed no signs of infection in 1916, three years after they had been exposed to natural infection. The second lot consisted of small seedlings, one to three inches high. The results of these experiments are given in Table IV.

TABLE IV

Infection of *Chamaecyparis thyoides* with *G. Ellisii*

A. *Inoculation, 1915*

No.	Date of inoculation	Results			Controls
		1916	1917	1918	
345	June 21	−	+ 5 Infec.	+	Eighteen other plants were exposed in the same greenhouse several weeks where aecidiospores were being shed, but they were not sprayed and kept in moist chambers. Only one plant, No. 431, became infected. One sorus developed on young growth of a branch.
349	June 21	−	−	−	
400	June 21	−	+ 4 “	+	
404	June 21	−	−	−	
406	June 21	−	+ 2 “	+	
410	June 21	−	+ 1 “	+	
420	June 21	−	+ 14 “	+	
426	June 21	−	−	−	
433	June 21	−	+ 1 “	+	
436	June 21	−	−	−	

B. *Inoculation, 1916*

906	April 24	−	−	+	Eighty-four similar plants were exposed, but not sprayed in the infection frame. No infection has appeared on these plants.
907	April 24	−	+	+	
908	April 24	−	+	+	
909	April 28	−	+	+	
914	May 4	−	−	+	
915	May 4	−	−	+	
916	May 4	−	−	+	
918	May 17	−	−	+	
953	June 1	−	Plant died		
954	June 1	−	−	−	
955	June 1	−	−	+	
956	June 1	−	−	+	
957	June 1	−	−	+	
958	June 1	−	−	+	

The table shows that eighteen of the twenty-four plants inoculated became infected, one of them in fourteen different places. Sori matured about twenty months after inoculation, except in the case of plants Nos. 907, 908, and 909, where sori developed the year following inoculation. It is possible that in some cases this species may mature in one year especially where inoculations are made as early as April 24.

In many cases there is but little hypertrophy or distortion of the leaves or twigs when the sori are first formed. There is a slight bending of the tip of the branch and a cushion-like swelling is developed beneath the sorus. After another year a witches'-broom of considerable size is formed, or if the main stem is infected a slight spindle-shaped swelling occurs. Sori may be foliicolous with the primordia in the leaf tissue, but in all cases the mycelium penetrates into the wood of the branch.

GYMNOSPORANGIUM CLAVARIAEFORME

The telial stage of G. *clavariaeforme* was obtained from New Haven, Connecticut, through the courtesy of Dr. Clinton and Dr. Nichols. Several plants of *Amelanchier* and other pomaceous hosts were inoculated May 9–13, 1916. The most abundant aecidia were produced on *Amelanchier canadensis* and *A. intermedia.* If spores are floated on water in damp chambers the percentage of germination is ordinarily about 95 per cent.

Five plants of *Juniperus communis* had been obtained from a nursery in New Jersey in 1915. They were about one foot high. Six smaller plants, three to six inches high, came from Glen, New Hampshire. Nine of these junipers were sprayed with spores in June, 1916. They were taken from the cold frame March 7, 1917. Two plants from New Hampshire were used as controls and showed no signs of being infected. Minute sori were discovered on three plants in April. No further inspection was made from May 14 until September 10. At this time slight swellings along the stems of two of the infected plants could be distinguished. Three of the nursery plants died before January 7, 1918. The results of these inoculations are given in TABLE V.

TABLE V

INFECTION OF *Juniperus communis* WITH *G. clavariaeforme*

No.	Date of inoculation	Results noted March 7 to May 14, 1917	Results January 7, 1918
	1916		
925	June 10	Plant died 1916.	
926	June 6	No infection.	Plant died 1917.
931	June 6	One infection.	Two infections.
932	June 6	No signs of infection.	Plant died 1917.
933	June 6	" " " "	One infection.
959	June 29	Two infections, lost many leaves.	Three infections.
960	June 29	No signs of infection.	One infection.
961	June 29	One infection.	Two infections.
962	June 29	No infection.	No infection.

There were nine separate infections in all. One of the plants from New Hampshire was not infected. The two control plants remained uninfected. Sections of three of the swollen stems were made January 17, 1918, ten days after the plants had been taken from the cold frame. It was found that teleutospores were being formed, although the sori had not yet broken through the bark. In sections even at the lowermost points of the swellings there appeared only two annual rings of wood. There were at first no signs of infection but minute sori with a few spores each developed on three of the plants during the last of April, 1917. The fact that sori formed the first year may be so small as not to break through the cork or epidermis, and therefore not be detected, should always be considered. Sections made the next year will show the cork callus at the point where the sorus was located. The infection of these plants undoubtedly occurred on the new growth of the spring of 1916. These cultures do not furnish much evidence that, as Plowright maintains (**9**), sori are not produced the spring following the year of infection. Tubeuf (**10**) gives a detailed and quite convincing account of his cultures of the species and there is no doubt that the incubation time may vary. This period does not appear to be absolutely fixed in the case of the infection of the red cedar with *G. clavipes* and *G. Ellisii*, which the writer has previously noted, and it will be shown later that the incubation time varies when cedars are infected with *G. nidus-avis*.

GYMNOSPORANGINM JUVENESCENS

The telial stage of *G. juvenescens* was obtained from Dr. J. J. Davis, Madison, Wisconsin, in April, 1916. Sori were present in the axils of the acerose leaves, but the witches'-broom effect was not pronounced. Three or four plants of *Amelanchier intermedia* and *A. spicata* that were in bloom at this time were inoculated. Infection was evident in five days. Aecidia matured in abundance on fruit and leaves as early as May 1.

Nine red cedars were inoculated in 1916. No infection appears to have followed these inoculations; there are as yet, April, 1918, no indications of swellings or the development of sori.

GYMNOSPORANGIUM NIDUS-AVIS

The red cedars on Long Island and in the vicinity of New York are badly infected with a *Gymnosporangium* which, if the infections are due to a single species, is certainly multiform in its manifestations. *Amelanchier* and *Malus* have been infected with spores taken from each of the following forms, although the inoculations were not made in each case with a single sorus: (1) Sori in the axils of densely crowded acerose leaves; (2) sori caulicolous, large branches forming coarse witches'-brooms; (3) trunk infections, sori appearing in deep fissures in the thickened bark. There is perhaps another form recognized by the presence of long parallel cork ridges, about one centimeter in width, that mark the location of sori of former years.

Several apple seedlings had been infected with spores from material resembling the second type mentioned above. A considerable number of aecidia matured. Spores from these aecidia were sowed on a red cedar, No. 418, in June, 1914. No infection was discovered on this cedar in 1915, but two sori developed on the main stem in May, 1916. In 1917, even on this small plant, the swollen sori coalesced in masses two inches long. The infection has spread over five inches vertically during the past three years. Old and new branches growing from the infected portion of the stem appear not to be infected at all. It is a typical trunk infection, and slightly fusiform. *Amelanchier* and *Malus* have been infected with spores from a single sorus two years in succession and there can be no doubt that both the shad bush and the apple are host plants for this form of *G. nidus-avis*.

Twelve red cedars were sprayed with spores from *G. nidus-avis* on *Amelanchier* in 1916. Only three of the plants have become infected, one of these in five different places. Cedar No. 414 was inoculated with spores from *Amelanchier* No. 878, June 11, 1916. Three small tongue-shaped sori were found among the young leaves of a side branch on April 5, 1917. This branch has since died. Cedar No. 929 had not been exposed to infection since 1913. The original teleutospore material with which the experiment was begun was obtained at Fort Lee, New Jersey, May 10, 1916. The infected branch, about two inches in diameter, had a very rough appearance and was covered with corky mounds and swellings. The sori when swollen were tremella-like and about an inch long. *Amelanchier "canadensis"* No. 878 was sprayed May 14. Spermogonia appeared on the leaves May 21, and aecidia were fully matured on the fruits June 9. Only a few aecidia developed on the leaves, although they had previously borne a great many spermogonia. No. 929 cedar was then sprayed with aecidiospores June 9; it was put in the cold frame October 22 and taken out March 7, 1917. A swelling and distortion of the main stem at the tip was plainly visible about November 1, although no sori had been noticed during the early months of spring. This plant was brought back to the green house again January 6, 1918. Sections of the swollen region were made January 17, 1918 and showed two annual rings of wood and two developing sori. No callus scars have been found on these sections, showing that a sorus had developed in 1917. In this case the resulting infection was just about of the type we should expect, and we can imagine it might have in years come to look much like the original infection with which we started. Photographs and specimens of all stages have been preserved.

The history of the infection of cedar No. 609 is more interesting. The teleutospore material was obtained from the largest infected red cedar on the grounds of the New York Botanical Garden. The trunk of this tree is heavily infected for a distance of several feet and has developed a large spindle-shaped swelling three feet long about ten feet above the ground. *Amelanchier "canadensis"* No. 886 was sprayed May 17, 1916. Spermogonia appeared May 26 and aecidia ripened on the fruit June 12. Red cedar No. 609

(six inches high June 6, 1915) was inoculated June 21, 1916. On March 22, 1917, twenty-one days after it had been taken from the cold frame, one very light-colored orange-yellow sorus developed in the axil of the leaf. This was supposed to be a sorus of *G. clavipes* that resulted from accidental infection in 1917. The little branch was marked with a tag. The plant was taken from the cold frame again January 7, 1918. On February 15, there were two light-colored sori in the axils of the leaves of the tagged branch. February 19 two more sori were discovered in the axils of leaves of another branch, and two strictly foliicolous sori on opposite leaves of another branch. March 5 another foliicolous sorus appeared on another branch, and at the base of a larger branch a small brown sorus was found, upon removing a piece of loose cork. All of the leaf sori were very light colored and looked like *G. clavipes*. The mycelium has been traced from the infected leaves down into the branches for about two centimeters. The infected branches are all on parts of the plant that have grown since it could have been exposed to natural infection. I have proved by the examination of spores, by sections of infected leaves and branches and by infection of the shad bush that this cedar was infected in 1916 with *G. nidus-avis*. Some of the infections appeared one year after inoculation, while it undoubtedly required two years for other sori to mature. This is the fourth species of *Gymnosporangium* which I have found requiring either one or two years in which to mature the teleutospores. Under favorable conditions the rust may develop in one year.

GYMNOSPORANGIUM TRANSFORMANS AND G. FRATERNUM

Kern (8) describes *G. fraternum* as an annual species. The writer (3) called attention to the fact that there are two leaf forms of this genus on *Chamaecyparis*, both of which are frequently perennial, and in another paper (4) showed how the two forms could be distinguished by the character of the buffer cells that precede the teleutospores in the sori of each.

Blueprints were made of infected branches so that leaves bearing sori could be located on the prints. In many cases it was found that sori developed a second and third year on the same leaves.

To prove that the species were distinct, spores from individual sori were germinated and smeared on selected leaves of both *Amelanchier* and *Aronia*. Slide mounts of the spores were then preserved and photographed. A few of the photographs are shown in PLATE 8. TABLE VI, A and B, is arranged to show the effect of inoculating both trial hosts with spores from the same sorus.

TABLE VI

PARALLEL INOCULATIONS OF *Amelanchier* AND *Aronia* WITH INDIVIDUAL SORI FROM LEAVES OF *Chamaecyparis*, 1916

A. *G. fraternum*

Date	Amelanchier	Result	Aronia	Result	Source of sorus
Feb. 22	491	+	642	−	435·3*
Ap. 18	558	+	806	−	721.1
Ap. 18	556	−	808	−	721.10
Ap. 18	651	−	809	−	721.5
Ap. 18	807	+	344	−	721.8
Ap. 18	810	−	256	−	721.4
Ap. 18	485	+	250	−	721.11
Ap. 20	820	+	818	−	721.3
Ap. 20	554	+	819	−	721.2
Ap. 20	821	+	822	−	721.7
May 8	864	+	456	−	746.1
May 8	484	+	470	−	746.2

B. *G. transformans*

Feb. 22	441	−	465	−	435·2
Feb. 26	438c	−	452	+	423·1
Feb. 22	503	−	643	−	435·2
Feb. 26	552	−	452	+	423·2
Mch. 1	553	−	454	+	424·2
Mch. 7	649	−	518	+	400.2
Mch. 3	430*a*	−	645	−	424·1
Ap. 27	653	−	457	+	701.0
Ap. 7	653	−	652	−	437·1
Ap. 7	651	−	650	−	437·2
My. 10	654	−	808	+	710.1
My. 17	800	−	806	+	738.1

Referring to the table it can be seen under "A" that *G. fraternum* infected nine of the twelve amelanchiers inoculated, while the aronias were not infected. Under "B" where the thicker-walled teleutospores, *G. transformans*, were used seven Aronias were infected, five gave no results, and none of the amelanchiers was infected. In addition to the cultures shown in the table, 32 amelanchiers have been heavily infected by spraying with care-

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* Means that the sorus used was sorus No. 3 from plant No. 435.

fully chosen sori of *G. fraternum* and 50 aronias with *G. transformans* without the infection of control plants used in either case.

So far as color, size and thickness of walls are concerned, one finds sori made up of intermediate types of spores not so easily identified. Compare FIGS. 3 and 5 (*G. transformans*) with FIG. 7 (*G. fraternum*). On the contrary, such types as are shown in FIG. 6 (*G. transformans*) and FIG. 8 (*G. fraternum*) are easily distinguished. Spores of *G. biseptatum* are shown in FIGS. 9 and 10 for comparison. *G. fraternum* does not become *G. biseptatum* when grown in the greenhouse.

INFECTION OF CHAMAECYPARIS WITH G. TRANSFORMANS

The ninety-eight seedling plants of *Chamaecyparis* described in connection with cultures of *G. Ellisii* (Table IV, B) were used for this work. None of them developed rust in 1916. Most of them had no branches and only subulate leaves when brought in (1915). All new growth could be determined readily. Twenty-four plants were inoculated and seventy-four were kept in another greenhouse as controls. The results of these experiments are given in TABLE VII.

TABLE VII

INFECTION OF *Chamaecyparis* WITH *G. transformans* IN 1916

No.	Dates of inoculation	Results, number of sori, March–April, 1917.	Controls
615	May 2, Aug. 28	5	Plants numbered 610–614, 616, 620, 625, 629, 790–798, 906, 908, 909, 914–921, 948–958, 963–992, 1012, 1014–1016: remained entirely free from this rust in 1917 and 1918
617	June 1, Aug. 28	11	
618	June 1, Aug. 28	2	
619	July 16, Aug. 28	1	
621	June 1, Aug. 28	1	
622	Apr. 24, Aug. 28	1	
623	July 23, Aug. 28	5	
624	Apr. 24, Aug. 28	3	
626	Apr. 24, Aug. 28	2	
627	Apr. 24, Aug. 28	1	
628	July 16, Aug. 28	12	
788	June 1, Aug. 28	Plant died.	
789	May 7, Aug. 28	0	
900	Apr. 26, Aug. 28	0	
901	Apr. 24, Aug. 28	1	
902	Apr. 24, Aug. 28	21	
903	Apr. 24, Aug. 28	0	
904	Apr. 24, Aug. 28	1	
905	Apr. 24, Aug. 28	1	
907	Aug. 28	0	
910	May 2, Aug. 28	0	
911	May 2, Aug. 28	11	
912	May 2, Aug. 28	Plant died.	
913	May 2, Aug. 28	0	

Sixteen of the twenty-four plants inoculated gave positive results, showing seventy-nine separate infections. Six plants were not infected, two died. The time required for the full development of this species is only nine or ten months.

The endeavor to infect *Chamaecyparis* with *G. fraternum* and *G. biseptatum* has not as yet resulted in success.

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Explanation of plate 8

The photographs of spores were made from sori used in making the inoculations reported in TABLE VI. Magnification, about 350.

GYMNOSPORANGIUM TRANSFORMANS

FIG. 1. A typical spore of this species showing a germ pore at the apex of each cell. The cell wall is comparatively thick.

FIG. 2. A three-celled spore, the lower cell showing two germ pores near the septum.

FIG. 3. A comparatively long spore of the type that is difficult to distinguish from such spores of *G. fraternum* as are shown in FIG. 7. The germ pore at the apex of the terminal cell, shown in FIG. 3, appears to be a very characteristic feature. Spores of *G. fraternum* frequently germinate at the apex but the germ pore is not plainly marked.

FIG. 4. Small spores comparatively short. Both cells of three of them have already germinated.

FIG. 5. A group of very thin-walled spores shaped very much like spores of *G. fraternum*. The three-celled spore shown is easily distinguished by its shape from the three-celled spores of *G. biseptatum* shown in FIG. 10.

FIG. 6. Large, broad, dark brown spores, none of which has germinated.

GYMNOSPORANGIUM FRATERNUM

FIG. 7. Spores from a dark brown sorus. The spore wall of the upper cell is much thickened at the apex.

FIG. 8. Spores from a light rusty-orange-colored sorus. The pore at the apex of the upper cell is visible in one of the spores at the right. The spore walls are very thin.

GYMNOSPORANGIUM BISEPTATUM

FIG. 9. Spores from a sorus taken from the infection mentioned in another paper (Dodge, 4). This is the youngest infection I have been able to find in nature. The spores have from four to seven cells. There are very few three-celled spores.

FIG. 10. Spores from a sorus on a large burl about eight inches in length and two inches in diameter. Nearly every spore is three-celled.

INDEX TO AMERICAN BOTANICAL LITERATURE

1916-1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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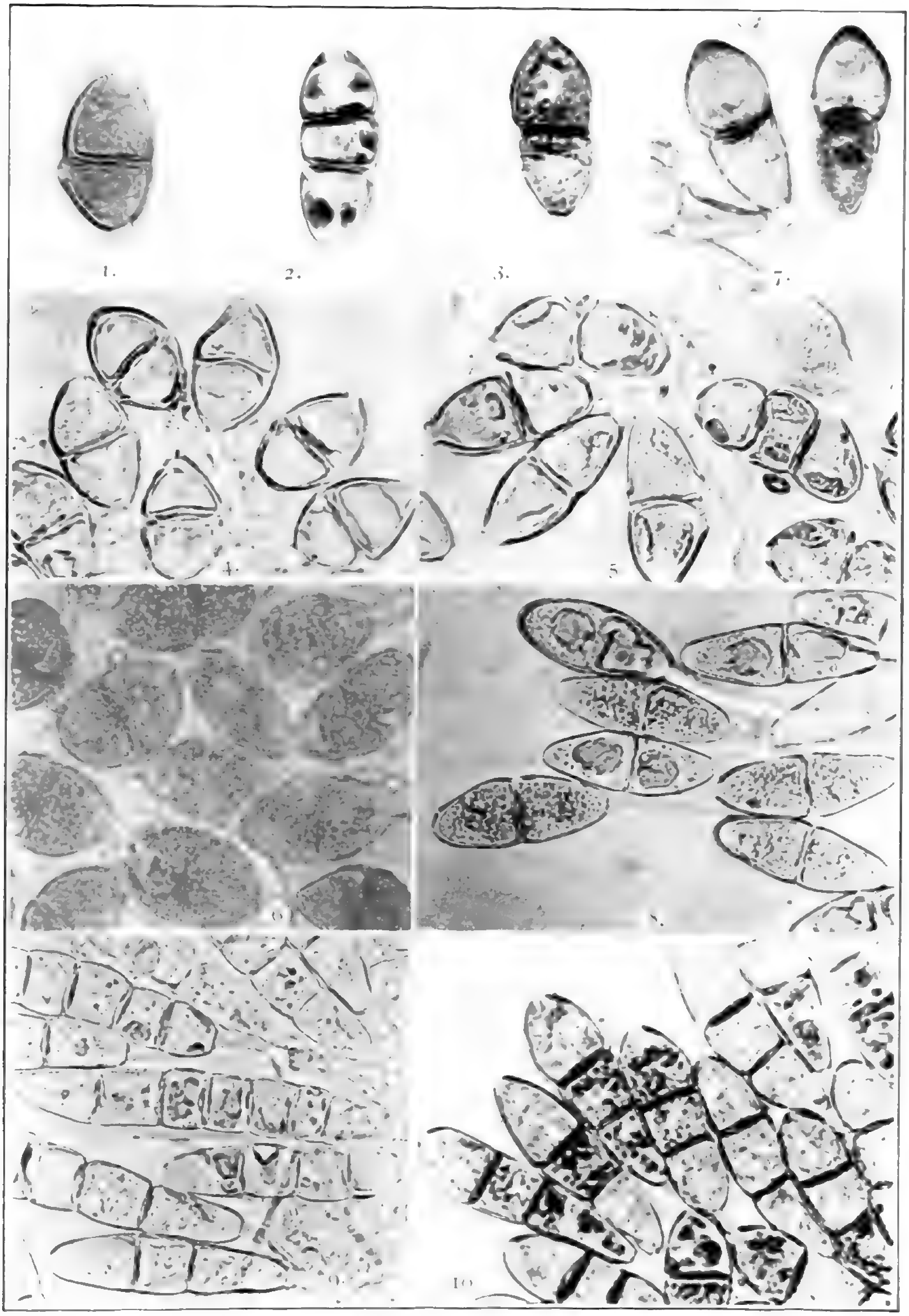

DODGE: STUDIES IN THE GENUS GYMNOSPORANGIUM

Vol. 45 No. 8

BULLETIN

OF THE

TORREY BOTANICAL CLUB

AUGUST, 1918

The evolution of maize

Paul Weatherwax

(WITH THIRTY-SIX TEXT FIGURES)

The ancestry of Indian corn, the place of its origin, and its relation to other plants of its family have been the subjects of extensive study and discussion. As a New World contribution to science and agriculture, the maize plant found, after a time, its present systematic position, and it has made its way into a place of prime importance in the economic life of the world.

When first seen by the civilized explorers of this country, maize was a cultivated plant; and no wild form of it has ever been found. Theories maintaining that it was of Old World origin have been shown to lack sufficient proof, and it is now very generally believed to have originated somewhere in the plateau region of Mexico or Central America.

Concerning the ancestry of maize a number of different theories have been advanced. In 1892 Bailey (**1**) expressed the opinion that *Zea canina*, which had been described a short time previously, was the progenitor of maize. Harshberger's work (**17**), published in 1893, was also based upon the assumption that this was the primitive maize plant. The latter authority and others have since shown that *Zea canina* is a hybrid between teosinte and ordinary maize. In 1911 Harshberger (**20**, pp. 51–52) described, as the theoretical ancestor, a plant whose inflorescence would resemble that of *Tripsacum;* and in 1912 he suggested (**21**, p. 399) that

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[The Bulletin for July (**45**: 259–308. *pl. 8*) was issued August 9, 1918.]

"our maize is of hybrid origin, probably starting as a sport of teosinte, which then crossed itself with the normal ancestor, producing our cultivated corn." Characterizing these earlier theories is Häckel's suggestion, made (**16**, p. 20) as early as 1889, that the female spike of corn was evolved by monstrous fasciation, from a number of parts like the lateral branches of the male inflorescence. In 1906 Montgomery (**24**) described a theoretical ancestor of maize and pointed out the fact that the ear is not the fasciated homologue of the lateral branches but the equivalent of the central spike of the tassel. Mrs. Kellerman had given a similar interpretation of the case in 1895, but her article (**22**) seems not to have been available to many botanists. In 1912 Collins made the point (**9**, p. 525) that the homology between the ear and the central spike of the tassel is inconclusive, because the central spike of the tassel is as anomalous and as hard to explain as is the ear. He discussed two theories as to the structure and origin of these organs and favored the idea that they are the results of fasciation. According to his theory, ordinary maize originated as a hybrid between teosinte and some plant possessing the characters of pod corn. In 1912 East (**12**) discussed the origin of maize and said that he agreed, in a way, with both Collins and Montgomery.

These are the more comprehensive discussions of the subject, but the discovery of an abnormal ear or tassel, a new variety, or an unusual habitat for the plant has, from time to time, been enough to provoke a new theory or a modification of an old one.

The present status of the question may be summarized as follows: most of the evidence concerning the evolution of maize has come from a comparison of its gross morphology with that of its near relatives, and from a study of hybrids between maize and teosinte; the ear of corn is generally supposed to be a fasciated structure; two theories are now held as to the origin of the plant—(1) that maize and teosinte have descended along slightly different lines from a common ancestor, and (2) that maize originated in a cross between teosinte and some closely related grass.

But in a detailed examination of maize and its near relatives, we meet with many inconspicuous but significant organs which have not thus far been considered in any theory of the evolution of the plant. The writer has made a thorough study of many varieties of corn, probably representing the full range of variability of the species, and other species of the Maydeae have been examined in detail by way of comparison. As a result of these studies, a theory is here proposed, which is believed to explain, in a manner more consistent with known facts, the evolution of maize.

Acknowledgment is here made of valuable assistance received in this study from a number of sources. The investigation is an outgrowth of a problem suggested to me five years ago by Professor D. M. Mottier, who has since then also aided me with many suggestions and criticisms. American consuls in several cities of Central and South America have assisted me in getting seeds of many varieties of corn; and very material assistance of the same kind has been given me by a large number of friends in this country. The Bureau of Plant Industry has supplied me with seeds of corn and teosinte. Rhizomes of *Tripsacum* were obtained from the Missouri Botanical Garden. The late Mr. Juan J. Rodriguez, of Guatemala, sent me rhizomes of a species of *Tripsacum* and seeds of a number of varieties of corn; he also told me of many interesting observations that he had made on the grasses of Guatemala. Mr. George F. Will, of Bismarck, North Dakota, supplied me with seeds of thirty varieties of corn collected from Indian reservations. Mr. A. Heinisch, of Clarcona, Florida, sent me seeds and morphological material of teosinte, aided me in making observations in his teosinte fields in the summer of 1917, and gave me the benefit of many observations that he had made as a grower of the plant.

CLASSIFICATION

The tribe Maydeae includes a number of grasses characterized by unisexual spikelets, the male being above the female, in the same or in different inflorescences. The seven genera of the tribe fall naturally into two classes. *Zea*, *Euchlaena*, and *Tripsacum* bear evidences of close relationship and are all native of America. Having the same general characteristics as these, but differing from them somewhat in appearance and detailed structure, are four genera, *Coix*, *Chionachne*, *Sclerachne*, and *Polytoca*, which are all native of southeastern Asia and the neighboring islands. An anomalous American genus, *Pariana*, has been included in this tribe by some authorities, but its natural position seems to be in another group.

The best evidences concerning the immediate ancestry of maize come from a comparative study of the three American genera of the Maydeae. The Asiatic species are probably much less closely related to those of America than they are to each other; and, for present purposes, they will not be considered in detail.

Zea and *Euchlaena* are sufficiently closely related to cross readily, and there is a record of at least one case of hybridization of *Euchlaena* and *Tripsacum;* but I have found no record of any hybrid between *Zea* and *Tripsacum.*

FIG. 1. A variety of corn from an Indian reservation; this plant may be considered the type of the species, which is today essentially the same as when first seen by the white man.

MORPHOLOGY OF ZEA

The genus *Zea*, represented by the single species, *Zea Mays* L., comprises all the varieties of maize. Being the best known species of the Maydeae, it is taken as the basis for comparison. It is a very variable species, but its variability is mostly quantitative in character. Good general descriptions of the plant have been available for a long time, but some significant details have not thus far been included in any of these. A complete working description makes necessary here the repetition of some well-known facts as a proper background for new details.

The aerial part of the typical maize plant (FIG. 1) consists of a tall, jointed stem, provided with distichous leaves, and bearing in the axil of each leaf, except possibly some of the upper ones, a potential branch. Some of these branches do not normally develop, and microtome sections are sometimes necessary to disclose their rudiments. One or more near the middle of the stem develop into ear-bearing shoots. The lowest branches, arising at or below the surface of the ground, become the well-known "suckers" or "tillers." The main stem terminates in a male inflorescence.

FIG. 2. A typical male inflorescence of corn.

Male inflorescence.—The terminal panicle of spikelets (FIG. 2) is made up of a number of simple or branched lateral organs attached to a central axis which terminates in a spike. The spikelets are borne in pairs, one pedicelled and the other sessile (FIGS. 3, 5). Occasionally in all, and very regularly in a few varieties, groups of three or more are found (FIG. 4), instead of pairs of spikelets, and in such a group one is usually pedicelled. Both of a pair or all of a larger group are occasionally sessile. In the typical

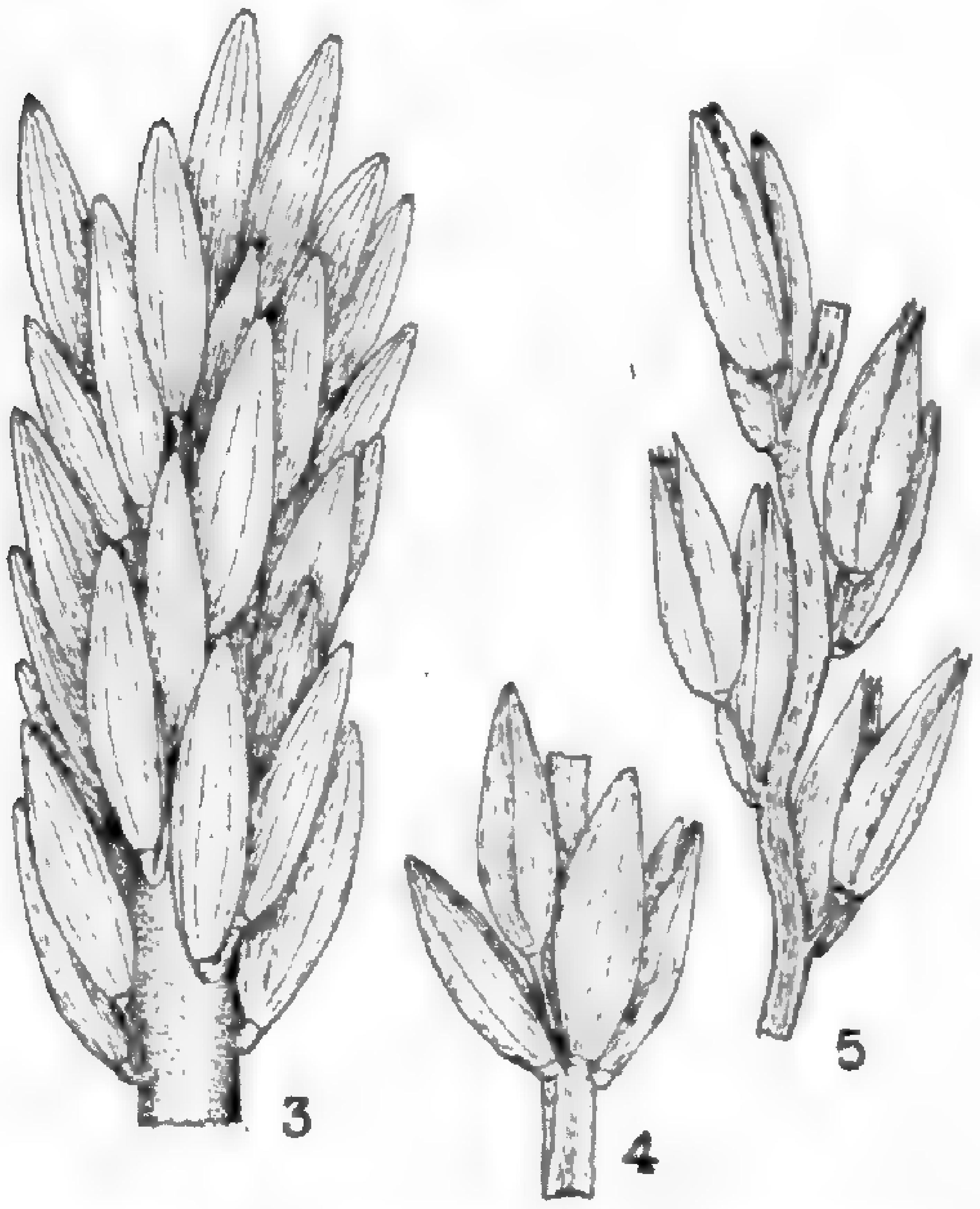


FIG. 3. Portion of the central spike of a corn tassel. FIG. 4. A group of spikelets, such as often occurs instead of a pair. FIG. 5. Spikelets on the lateral rachis of a corn tassel.

case, where the spikelets are paired, the pedicelled ones are arranged symmetrically in a horizontal plane along the sides of the lateral rachis, and the sessile ones are ventral to these on the rachis, giving the structure a definite dorsoventral aspect (FIG. 5). The central spike is symmetrical with respect to the pairs of spikelets, which are arranged in several longitudinal rows upon it (FIG. 3).

The spikelets have been described in detail elsewhere (**25**, **26**). Each has two flowers and a full complement of glumes, palets, and lodicules. Only the male essentials are functional, but each flower has a rudimentary pistil. A superabundance of pollen is produced, and it depends upon gravity and the wind for distribution. The flowering period of an individual plant is limited to two or three weeks, depending upon weather conditions and the size of the inflorescence.

Female inflorescence.—The ear-bearing branch has the same general structure as the main stalk, except that its inflorescence is female; and the shortness of its axis enables the leaf sheaths to cover the inflorescence and mature fruit. In some cases the laminae and ligules of these prophylla are present (FIG. 6), but often they are lacking (FIG. 7). In the axil of each prophyllum is a bud which may develop into an ear-bearing shoot (FIG. 8). This behavior is common to some varieties, and it seems possible to bring it about in any variety by subjecting the plant to proper physiological conditions. The clusters of ears formed in this way and occurring in ordinary maize (**6**, *f. 96, 97*) or in teosinte-maize hybrids (**17**, *pl. 1*) are not at all to be confused with branched ears of maize (FIG. 9). They have much the same appearance to the casual observer, but they have a different origin and a different

FIG. 6. An ear of corn whose husks have laminae.

FIG. 7. An ear-bearing shoot of a high-grade dent corn. The prophylla have lost their laminae and ligules. FIG. 8. An ear branch bearing small lateral ears.

meaning. When these secondary branches develop far enough, buds are formed in the axils of their prophylla, indicating the possibility of tertiary branches.

The female spikelets are borne in pairs, sessile or almost so, on a thickened axis, the whole structure being the "ear." The "cob" is the axis of the mature ear after the grains have been removed. Each row of pairs of spikelets is responsible for two rows of grains on the ear, thus accounting for the fact that an ear always has an *even* number of rows. The spikelets are two-flowered and have the same parts as those of the male inflorescence; but the whole lower flower of each is aborted, the lodicules are present only in early stages of development, and the stamens are aborted. The pistil of the upper flower is usually the only functional organ of either flower, but occasionally in any plant, and as a fixed characteristic of some varieties, the pistil of the lower flower may also

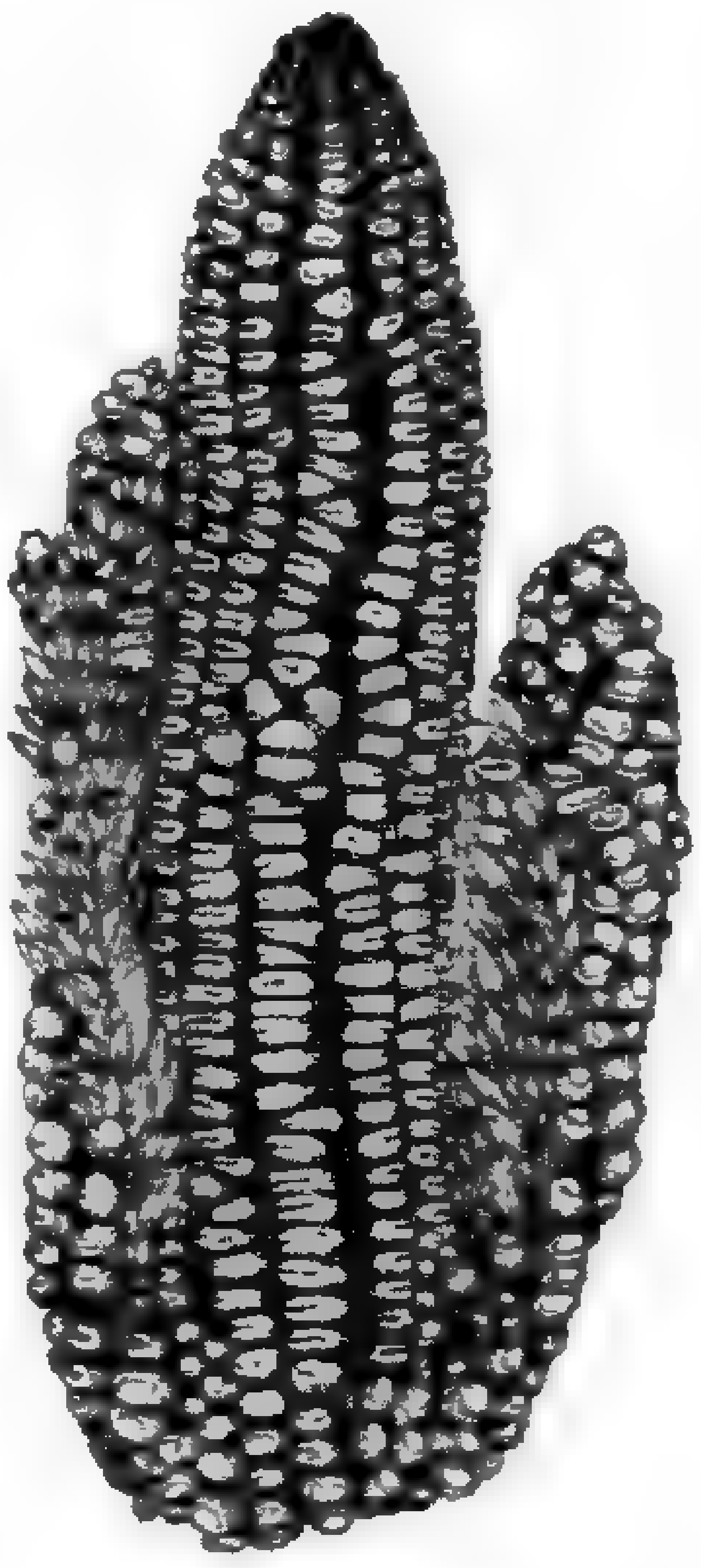


FIG. 9. Ateratological ear suggesting the relationships between the normal ear and the central spike of the tassel.

function. The pistil is characterized by the greatly elongated "silk," which reaches beyond the husks of the ear. I have given in other papers (**25**, pp. 131–137, and **26**, pp. 488–493) a detailed description of the parts of the female spikelet.

As has already been noted, the normal ear is doubtless the homologue of the central spike of the tassel. Every part of either can be identified in the other, and they bear identical relations to the other parts of the shoots which they terminate. The apparent difference between the two is one of development. Teratological forms (FIGS. 9, 10) and the inflorescences of suckers (FIGS. 11–13) suggest connecting links between the two organs.

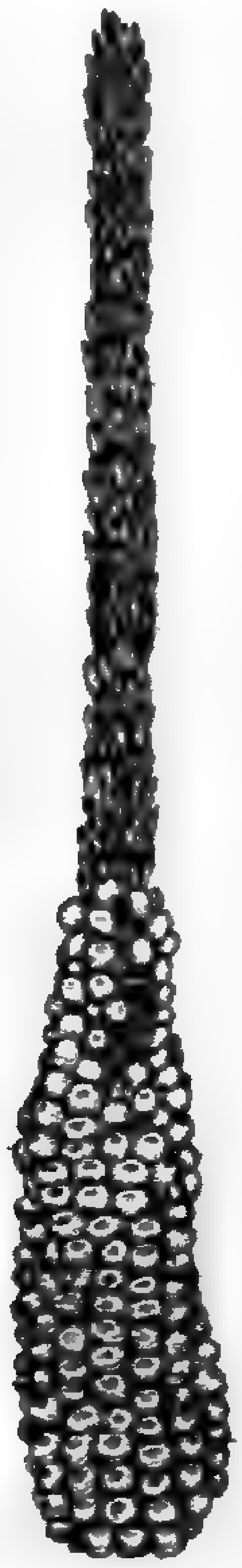
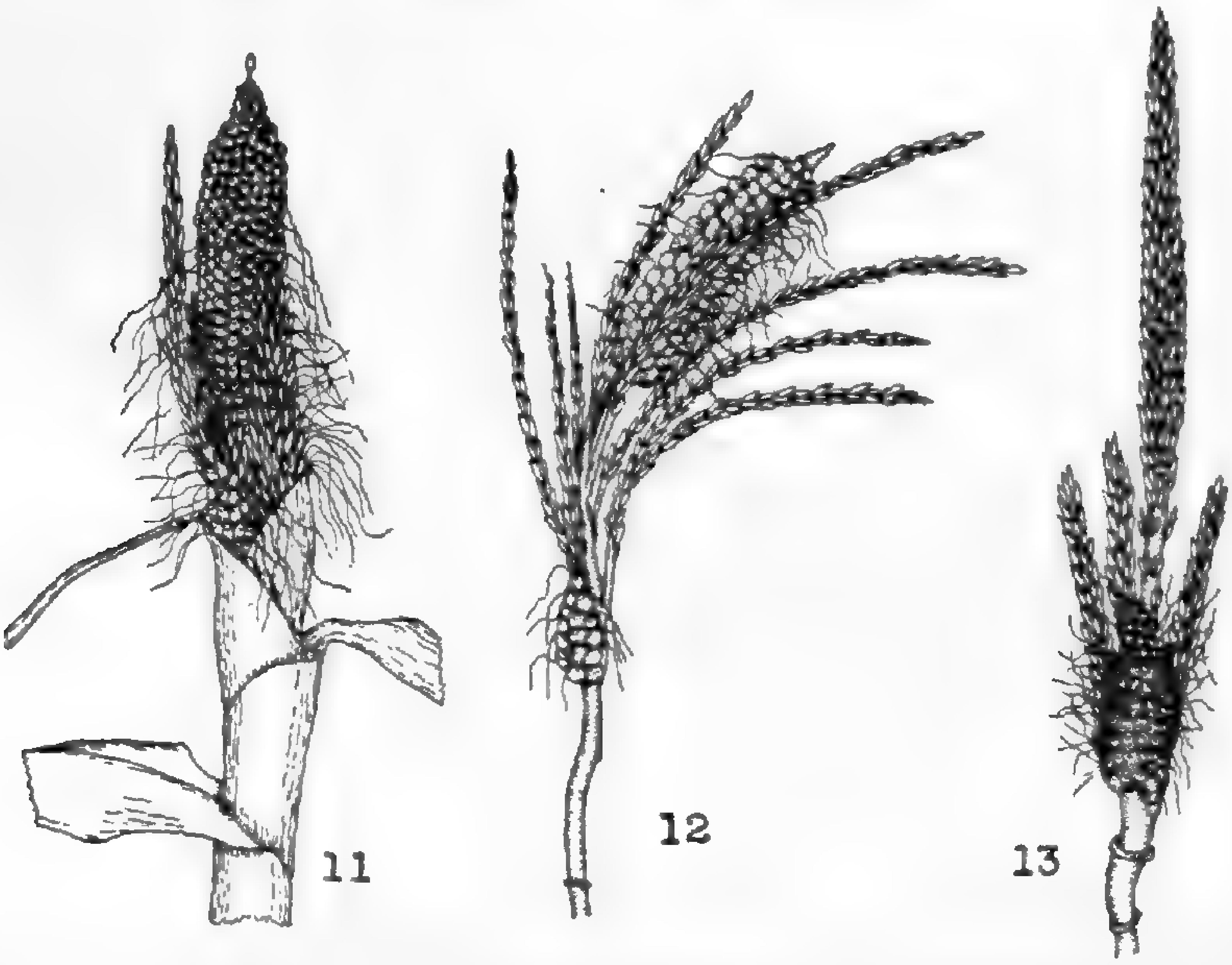


FIG. 10. A teratological ear having the upper part metamorphosed into a male spike.

Suckers.—The sucker branches may arise singly or two or more from one node (FIG. 1), an appearance of the latter condition often being the result of secondary branching. Most of the suckers develop root systems more or less independent of that of the main plant. Some suckers have all the appearance of ears growing low on the stalk; others grow tall and become structurally and functionally the same as the main stalks; and still others have characteristics intermediate between these two extremes. These intermediate types, while they have axillary buds, usually develop only terminal inflorescences, which may represent any possible gradation between an ear and a normal tassel (FIGS. 11–13). The most ear-like of these have, no doubt, been made the subject of many of our popular articles on freak ears. The figure given by Mrs. Kellerman (**22**) and some of Montgomery's photographs (**24**) look suspiciously like sucker inflorescences. Many freak ears given to me by non-technical collectors have turned out, on close inquiry, to have been taken from suckers. Their value as evidences of evolution are none the less for this; but they must be interpreted in a different way, for they are not in any way teratological.

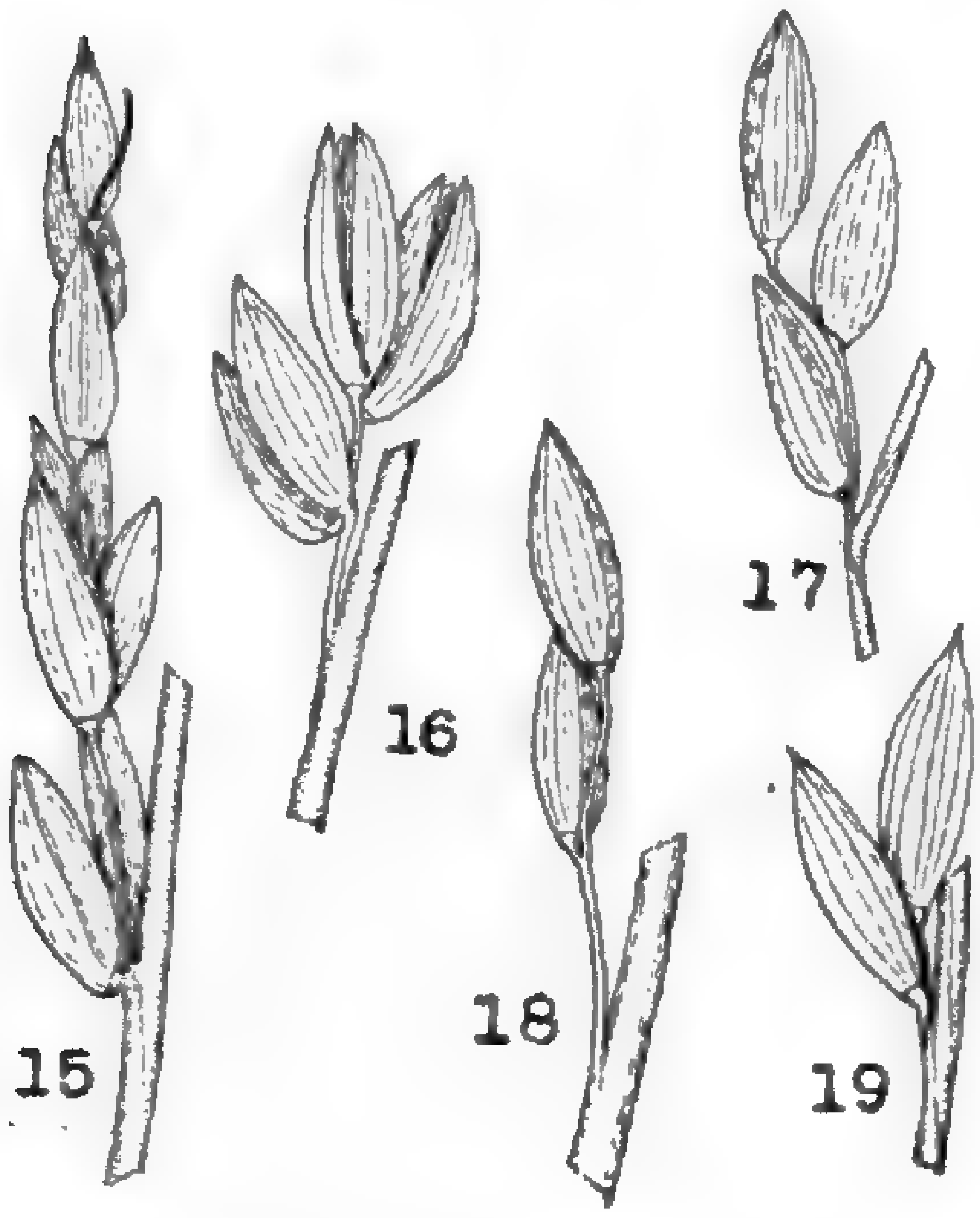
Variations.—Anomalous inflorescences are common, however, and there are several more or less definite varieties of maize which do not agree with the general description just given. A well-known variation is found in pod corn, each mature grain of which is covered by the enlarged glumes of the female spikelet. Many plants of pod corn have perfect or female flowers in their tassels and produce fruits there, and some of these plants have a tendency to become earless; but no independent earless variety has ever been isolated. Other varieties of maize occasionally produce female flowers in the tassel, probably as a result of physiological conditions. It is significant that silks produced in the tassel are usually fasciated like those of the normal female flower, but bipartite silks have been seen in a few cases. Most female spikes of maize have sterile tips, and these are often re-



FIGS. 11–13. Normal terminal inflorescences of suckers, having characteristics of both the ear and the tassel.

FIG. 14. A tassel of Gernert's Branch Corn.

placed by staminate spikes (FIG. 10). Emerson (**13**, p. 83) has isolated a dwarf variety which has perfect flowers in the ear. Gernert (**15**) has isolated from a yellow dent variety a strain in which the ear is a loose panicle like that of one of the sorghums. The tassel is also branched more than in the typical variety (FIG. 14), and many groups of spikelets are borne on peduncles instead of being in sessile groups (FIGS. 15–19). A common type of variation consists of a normal ear bearing a whorl of small, four-rowed branches around the base (FIG. 9). Ears variously divided or branched at the tip are also of common occurrence.



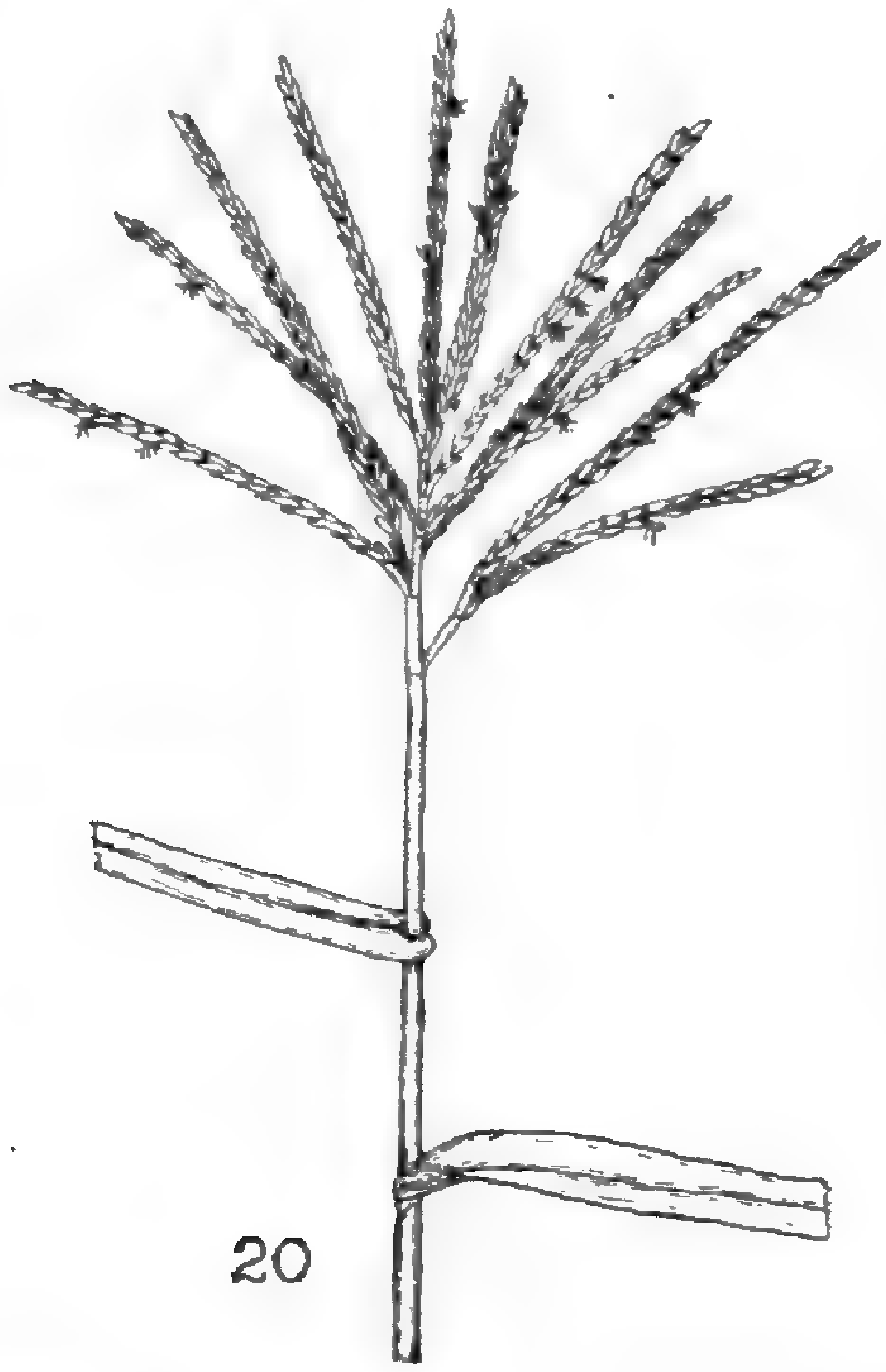
FIGS. 15–19. Peduncled groups of spikelets from Branch Corn, showing the probable steps in the evolution of the pair of spikelets.

MORPHOLOGY OF EUCHLAENA

Without discussing the systematic treatment of *Euchlaena*, we may take *Euchlaena mexicana* Schrad. (synonymous with *Euchlaena luxurians* Dur. and *Reana luxurians* Dur.) as the type of the genus. It is the well-known teosinte, an annual forage plant of the warmer parts of America. The species is much less variable than maize.

Teosinte has much the same general appearance as maize, especially since the casual observer's mental picture of the latter is obtained from seeing two or three plants growing in a clump. It has the same sort of leafy stem, and the same potential branches in the axils of its leaves; but the branches arising from the base of the plant—ten to sixty or more in number—grow as tall as the main stem and resemble it in every way. These continue to branch indefinitely, a branch being possible at practically every node; generally speaking, a branch has about as many nodes as the main stalk above the point of branching. The main stalks and some of the higher branches are terminated by male panicles. At the top of any stem, the branches tend to be male, while the lower ones of the same order tend to be female.

The plant makes a very ready response to conditions of soil and climate, and herein lies the main cause of its variability.



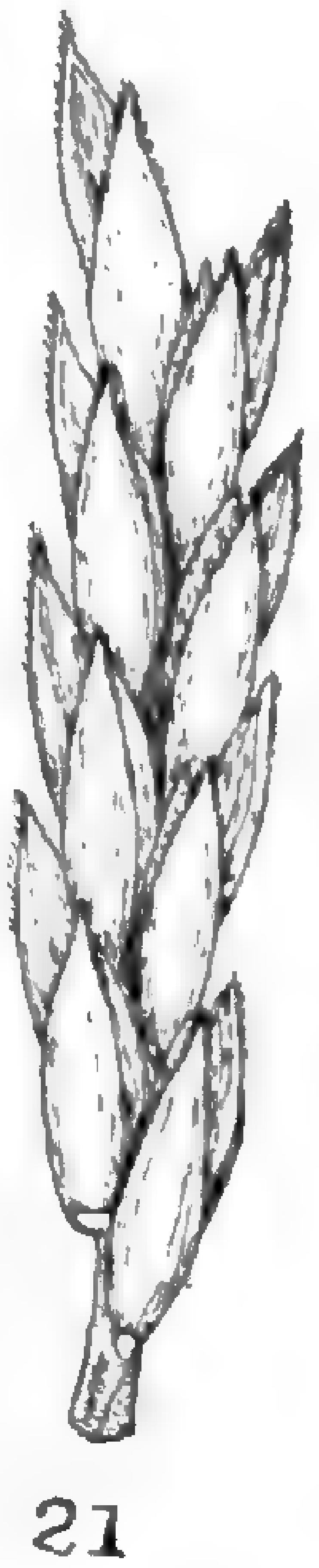


FIG. 20. Tassel of teosinte FIG. 21. Portion of a spike of a teosinte tassel.

Rich, wet soil and warm weather are most favorable for luxuriant growth. Plants are not injured by standing for some time in water a foot deep. Under favorable conditions the stems often

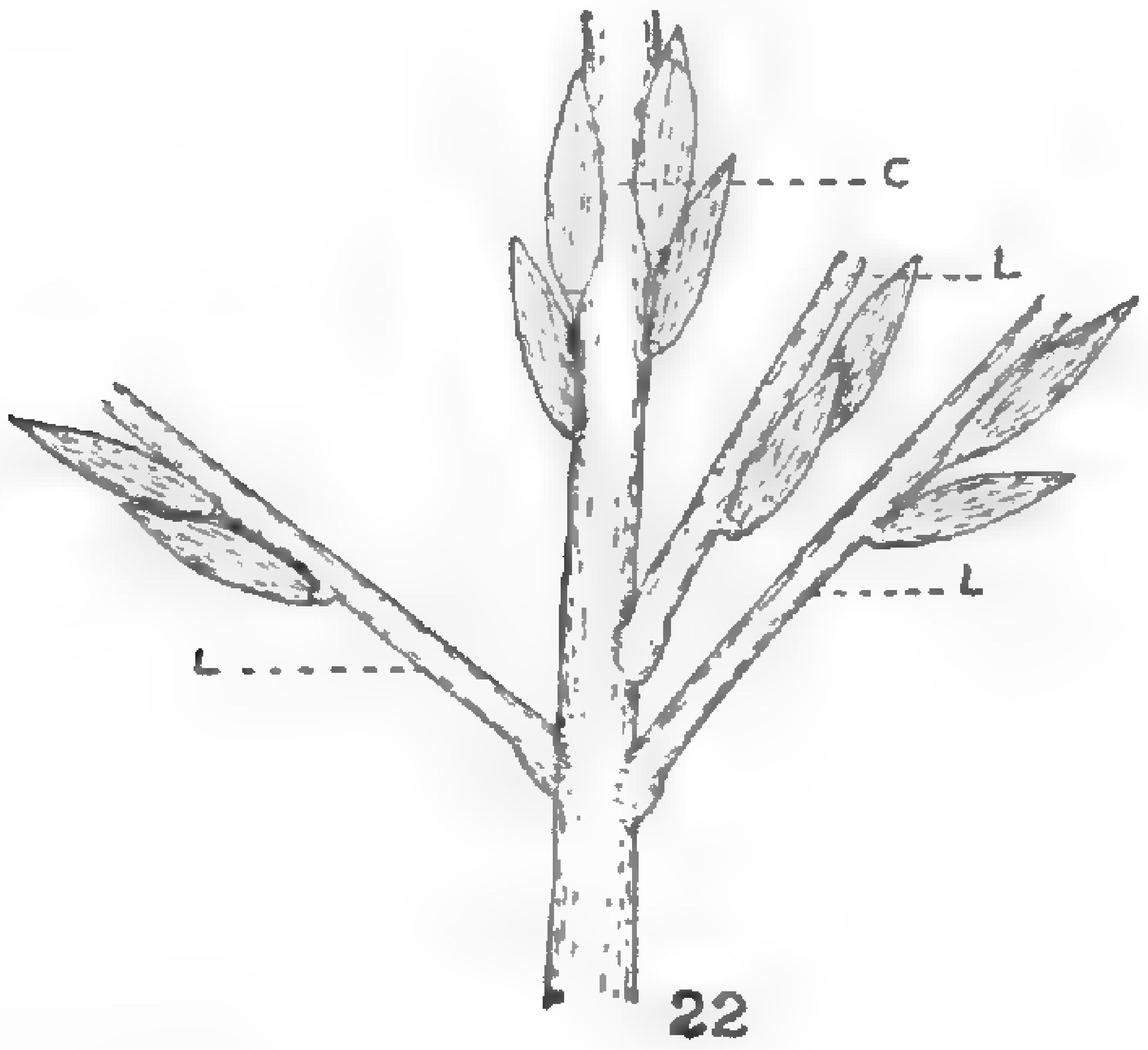


FIG. 22. Portion of a corn tassel. The lateral spikes, *LL*, are jointed to the main axis, which continues into the central spike, *C*. FIG. 23. Part of a tassel of teosinte; all the spikes are jointed to the main axis.

fall prostrate, take root at the nodes, and send up branches, becoming almost if not quite perennial at times.

Male inflorescence.—The male panicle (FIG. 20) resembles that of maize in appearance. The lateral spikes are so much alike in the two that a close examination is necessary to reveal any difference; but the central spike, which is characteristic of maize, is lacking in teosinte. All the branches (FIG. 21) of the teosinte tassel are dorsoventral, and it is probable that they are all morphologically lateral, the true end of the axis being not in any one rachis but between the bases of the uppermost two. This is further supported by the fact that all the tassel branches, including that (or those) apparently occupying a central position, are jointed at their bases (FIG. 23), which is not true of the central spike of the tassel of maize (FIG. 22). This organ seems merely to have failed to develop in teosinte. Following anthesis, the rachids become brittle, easily separating at the nodes.

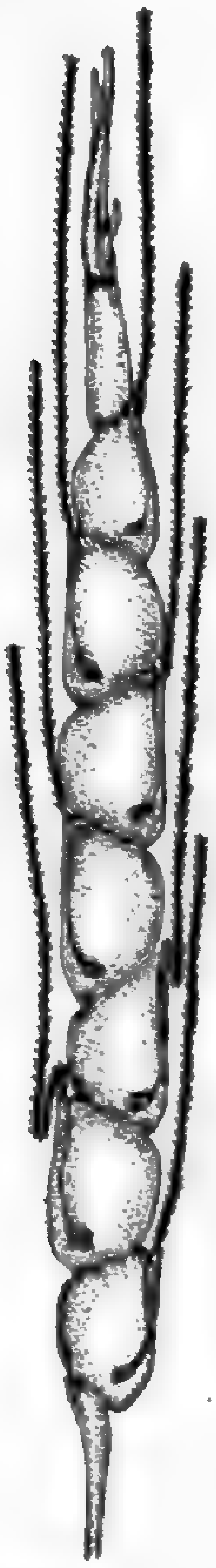


FIG. 24. A female spike of teosinte.

The male spikelet is much like that of maize. The same parts are present, including the rudimentary pistils, and, in so far as has been observed, there is no significant difference in the development or the final form of the two. The pollen and pollination are as in maize.

Female inflorescence.—The female inflorescence is usually a single spike (FIG. 24), enclosed in the sheath of a single leaf, which often has a ligule and a short lamina (FIG. 25). Many of these shoots, each borne on a short stem in the axil of a leaf, may be enclosed in the sheath of a larger leaf of the main stem, and the silks, protruding from the sheath, give the whole the appearance of a young ear of maize (FIG. 26). This whole structure is the equivalent of an ear-bearing shoot of maize, having branches of the third, fourth, or higher orders, but with the characteristic female spike of teosinte, instead of an ear, borne on each branch.

The female spike has received the most unsatisfactory treatment of any part of the plant. As a typical instance of misinterpretation of its structure may be cited a statement in a recent textbook (**2**, p. 137), where it is spoken of as being made up of kernels fastened end to end, the whole structure having nothing to correspond to the cob in maize. Collins's description (**9**, p. 525) of the spike as "one-rowed" is equally misleading.

This spike is made up of two rows of functional spikelets borne alternately in alveoli in the rachis; by the side of each of these spikelets there is a small rudimentary structure (FIGS. 27, 28) which represents the other spikelet of the pair. Structurally, then, the spike has four rows of spikelets. It will be remembered that in the male spike the pedicelled spikelets are symmetrically arranged on the rachis, with the sessile ones below them; but, in the female spike, the fully developed sessile spikelets occupy the symmetrical positions, and the rudimentary pedicelled ones have been crowded up to a dorsal position (FIGS. 34, 35). In teosinte somewhat mixed with maize the rudimentary spikelet is sometimes replaced with a sterile or male, pedicelled one, and a little further contamination with maize produces two functional female spikelets side by side. Paired female spikelets are also occasionally found in pure teosinte. These facts indicate that the female spike is the homologue of one of the branches of the tassel, and it probably does not morphologically terminate the shoot of which it is a part.

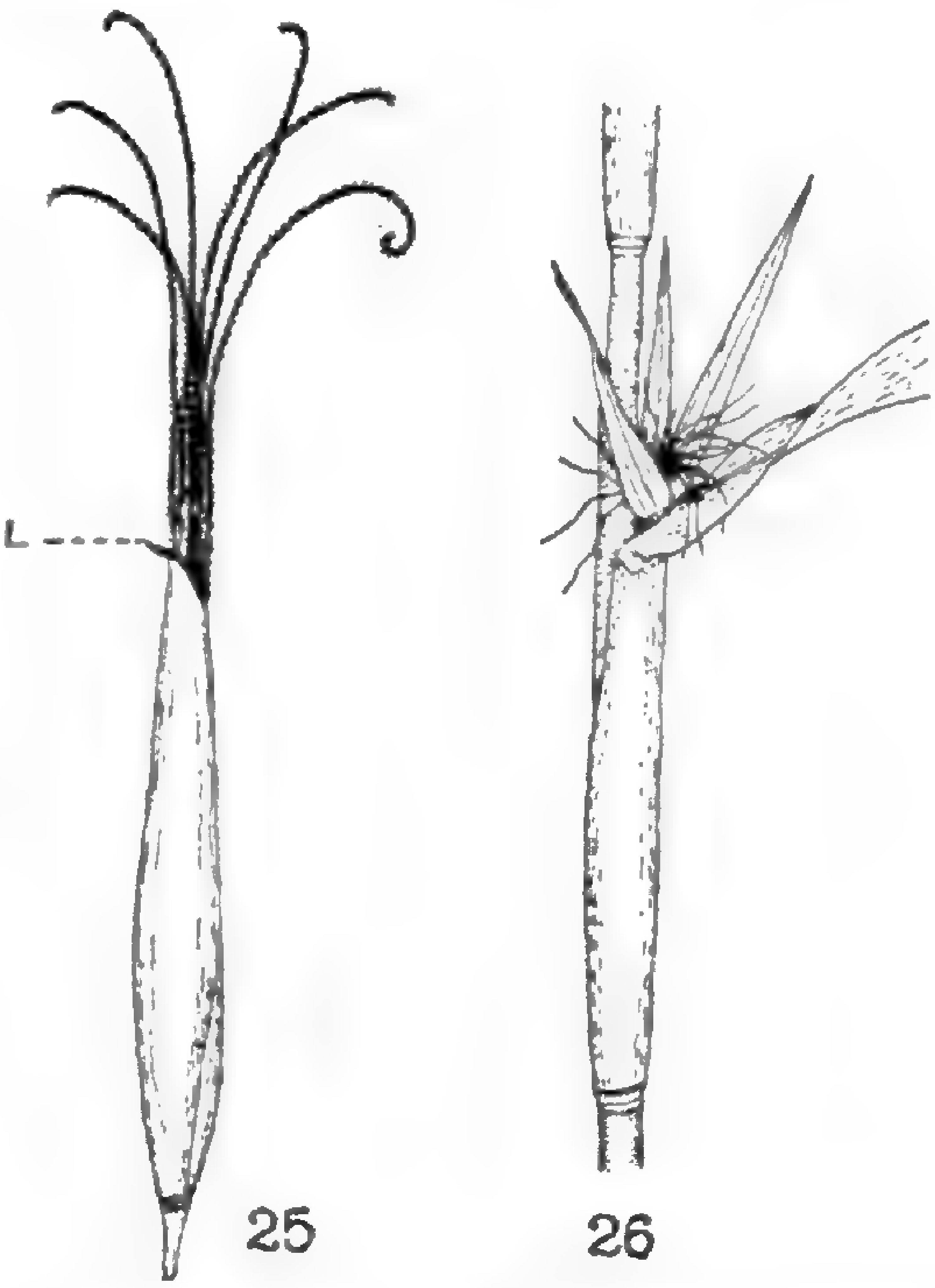
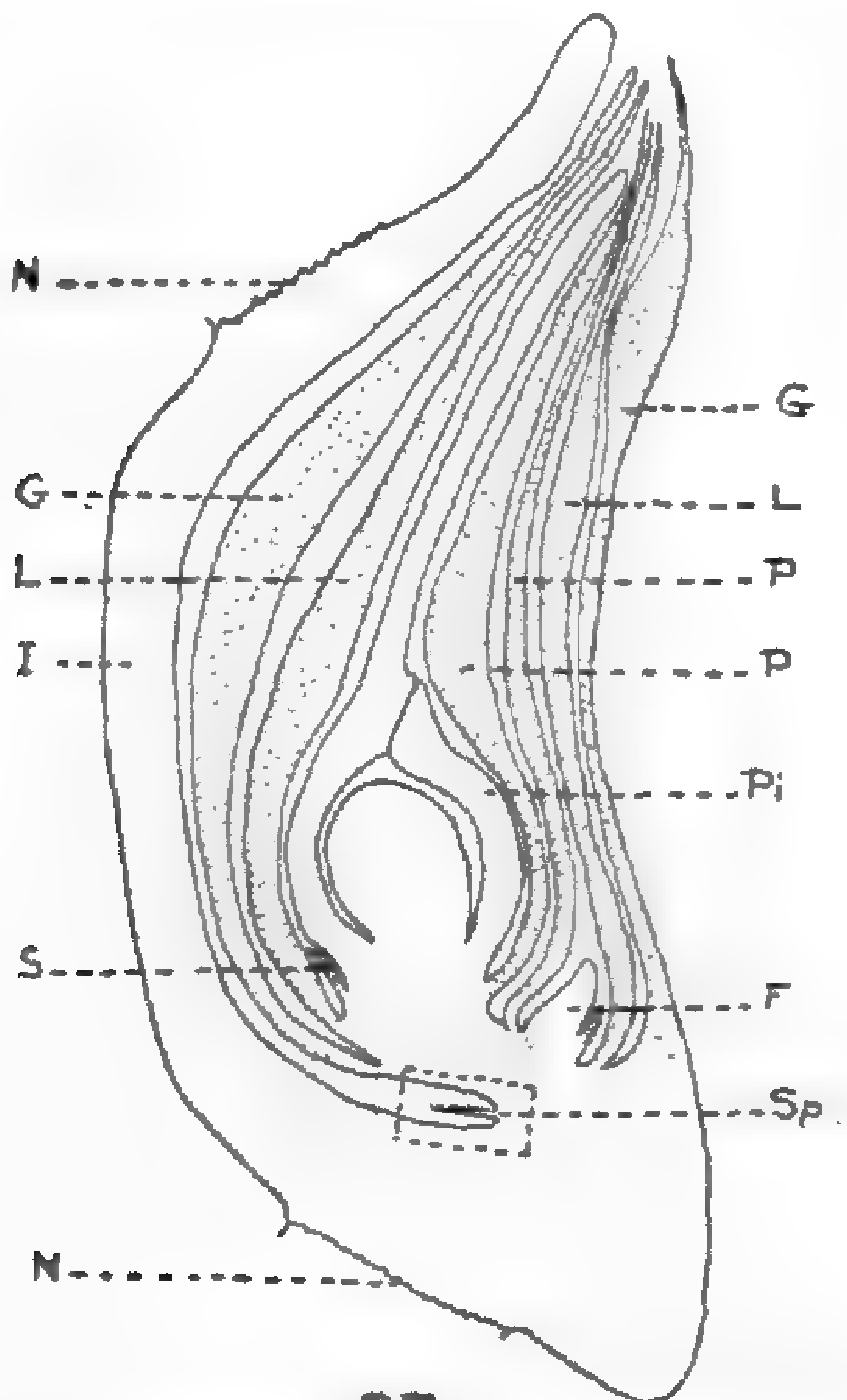


FIG. 25. An "ear" of teosinte, covered by its single husk, which has a rudimentary lamina, *L*. FIG. 26. Portion of a stem of teosinte bearing a cluster of female spikes.

The female spikelet consists of the same parts as that in maize. The lower flower is aborted, rudimentary stamens are present, and the development of no part shows any significant difference except for the indurated outer glume. The silk has much the same structure as in maize, but it is shorter.

Because of the large number of inflorescences, the flowering period of a teosinte plant is much longer than that of a maize plant, and the chances for self-pollination are better. When the seeds are mature, the female spike separates at the nodes, each internode bearing a spikelet and its enclosed fruit.



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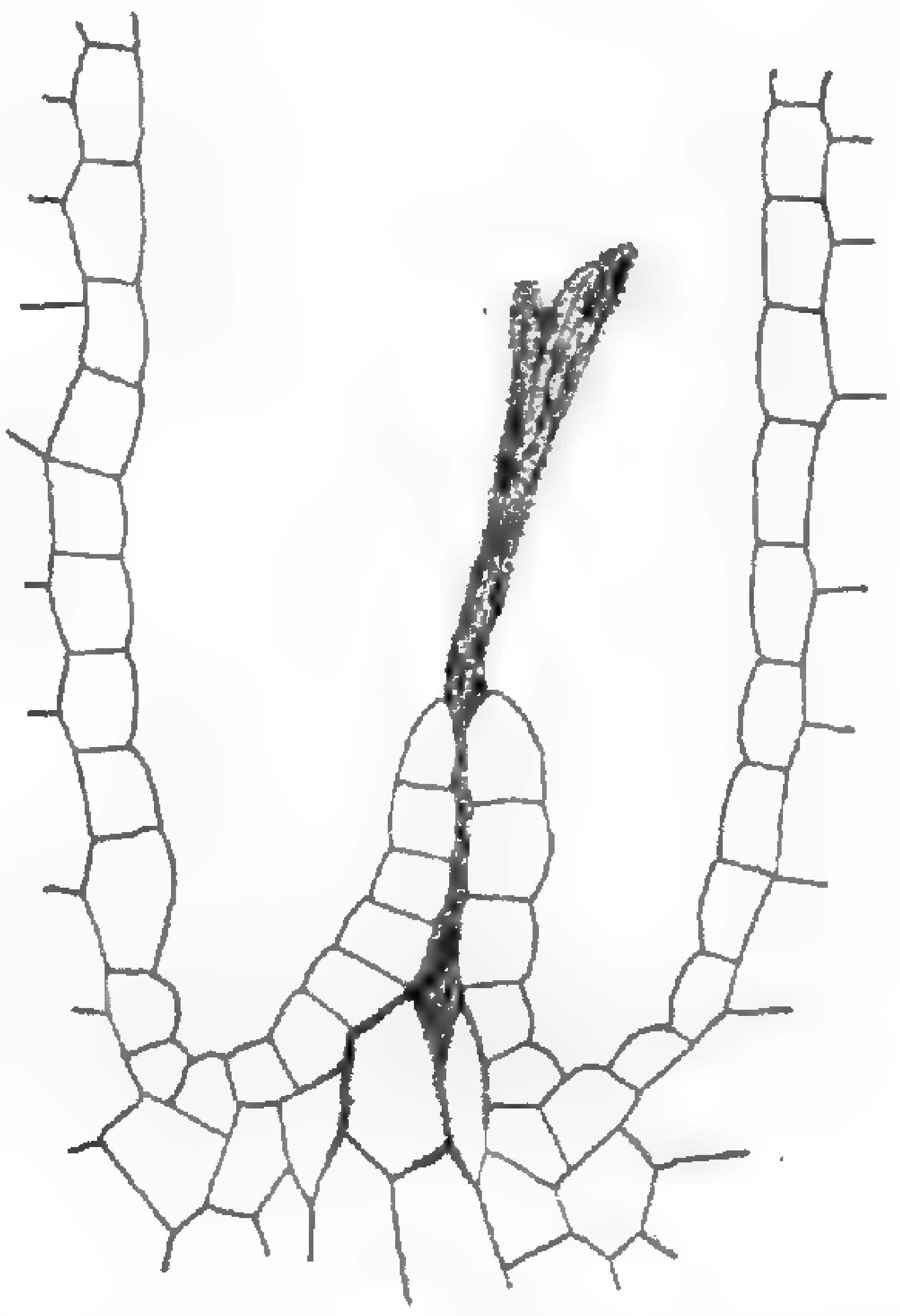

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FIG. 27. Diagram of a longitudinal section of an internode and its spikelet in the female spike of *Euchlaena* or *Tripsacum*. *NN*, nodes; *I*, internode; *GG*, glumes; *LL*, lemmae; *PP*, paleae; *S*, rudimentary stamen; *F*, rudimentary flower; *Pi*, functional pistil; *Sp*, position of the rudimentary spikelet, which does not appear in a median section. FIG. 28. The rudimentary spikelet shown in the dotted rectangle in FIG. 27.

Mixed inflorescences.—The homologies suggested between the male and female inflorescences are further indicated by the occurrence of mixed inflorescences. In male tassels, functional female spikelets have several times been observed near the base of one or more of the branches; and the sterile tip of the female spike, as in maize, is often replaced by a short staminate portion (FIG. 29). Some single spikes are so much like those of *Tripsacum*, to be described later, that it would be hard to determine whether it is a case of male spikelets being in a female inflorescence, or vice versa. In such a mixed spike, each male spikelet is usually accompanied by another male or sterile one; and each female spikelet is characteristically alone, has an indurated outer glume, and is sunken into the rachis. No functionally bisexual spikelets have been seen, but it must be emphasized that all are structurally so.

FIG. 29. A mixed spike of teosinte.

MORPHOLOGY OF TRIPSACUM

A number of species of *Tripsacum* are native of various parts of America, but the best known is *Tripsacum dactyloides* L., the gama grass of swamps and stream banks of the central and southern parts of the United States. Being the only species available for my work, it is the basis of my conclusions for the genus.

Tripsacum dactyloides (FIG. 30) is perennial by means of a branched rhizome, from the nodes of which arise the aerial shoots. Many of these are sterile, and their stems are so short that only the leaves appear above the ground. In early summer, however, some of the shoots elongate for flower bearing and show the adult structure. These stems attain the height of four to six feet and resemble somewhat those of maize or teosinte. The flowering period continues for two or three months. The main stem bears a branch at each node, and this has secondary and even tertiary branches. The main stem is terminated by a panicle, and each branch by a spike or a panicle. Erect or curving until after flowering, the stems are, by means of some growth-mechanism near the base, caused to lie prostrate by the time the seeds are mature.

Inflorescence.—The male spikelets occupy the terminal and the female the basal part of the same spike (FIG. 31). The mode of branching of the panicle is similar to that in the male inflorescence of *Euchlaena*. There is no evidence of any central spike, all the branches being much alike.

There is a very evident tendency for the highest inflorescence, that is, the one terminating the main stem, to be male, and the lower ones, terminating the branches, to be female. Counts of male and female spikelets in a number of inflorescences showed in those of the main stem a ratio of 1 female to 18.5 male; in those of the primary branches the ratio was 1 to 7.5; and on secondary branches the ratio was still higher. No unisexual inflorescence has been observed, however, on any plant.

FIG. 30. Habit of *Tripsacum dactyloides.*

Male spikelets.—The male spikelets are arranged on the rachis in two rows of pairs; and the male portion of the spike, even where there is but one spike in the inflorescence, has the same dorsoventral appearance as in maize or teosinte (FIG. 32); one spikelet of a pair sometimes has a short pedicel, but both are usually sessile. The rachis of the male part of the spike becomes brittle soon after the pollen is shed.

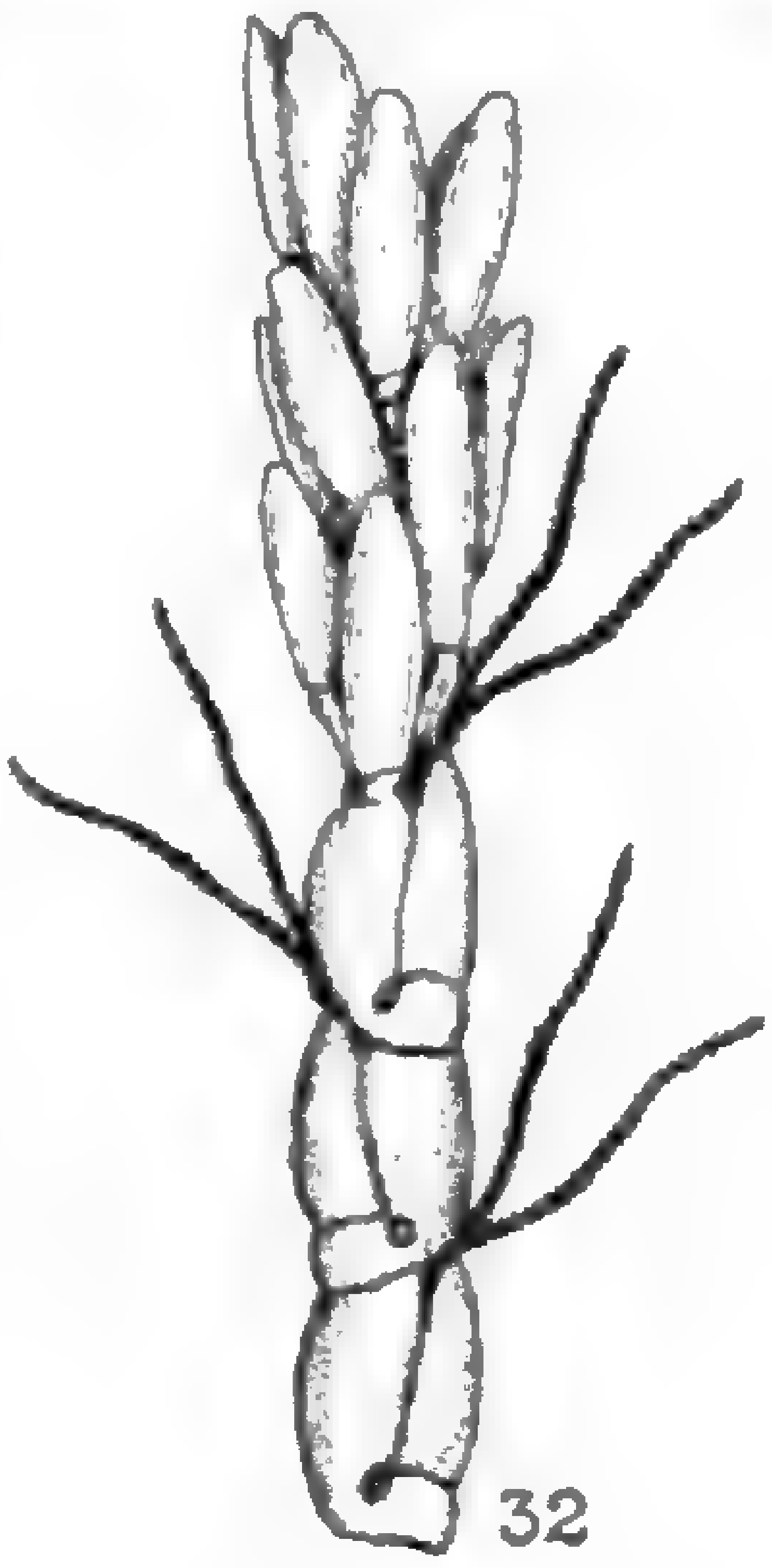
FIG. 31. Terminal inflorescence of *Tripsacum dactyloides.*

The outer glume of the male spikelet is somewhat thickened and hardened, but otherwise the bracts, lodicules, stamens, and rudimentary pistils are essentially the same as those of maize or teosinte.

Female spikelets.—The female portion of the spike (FIG. 32) is similar to that of teosinte, but there is usually more or less external evidence of dorsoventrality. The spikelets are alternately imbedded in alveoli in the rachis, forming two rows arranged almost symmetrically or along one side of the rachis. But the real four-rowed structure is clearly indicated, as in teosinte, by the presence of a rudimentary spikelet (FIGS. 27, 28) near the base of each functional one. This rudiment is sometimes replaced by a functional spikelet, which may be either male or female (FIG. 33). As in teosinte, the female portion of the spike easily separates at the nodes when the seeds are mature.

The female spikelet has the same parts as that of teosinte, and they are arranged in the same way. The stigma is bipartite (FIGS. 32, 33), in contrast with that of *Zea* or *Euchlaena*.

Seeds.—The plants that I have grown ordinarily set seeds in only a few flowers, and these do not germinate well. Mr. Rodriguez has informed me that *Tripsacum laxum*, a Central American species, has never been known to produce seeds. The morphological basis of this peculiarity has not been determined, but it is doubtless correlated with the perennial habit.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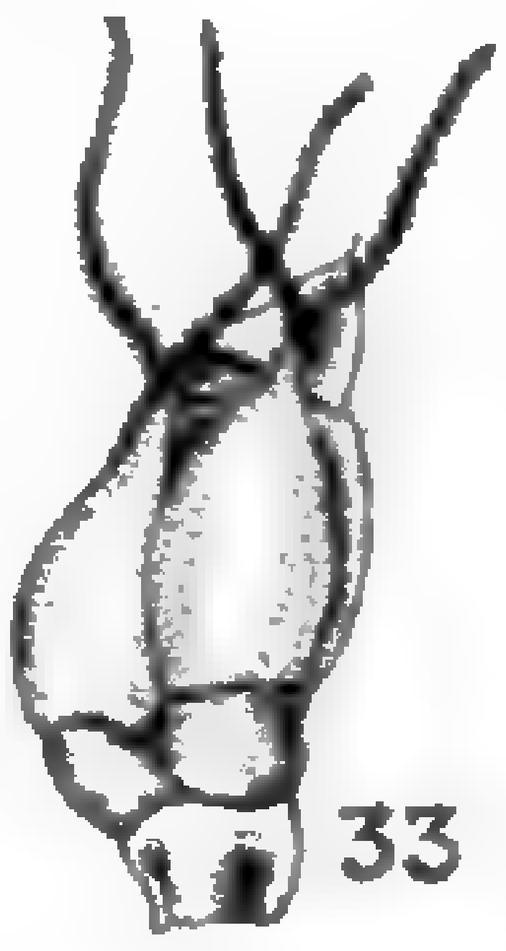
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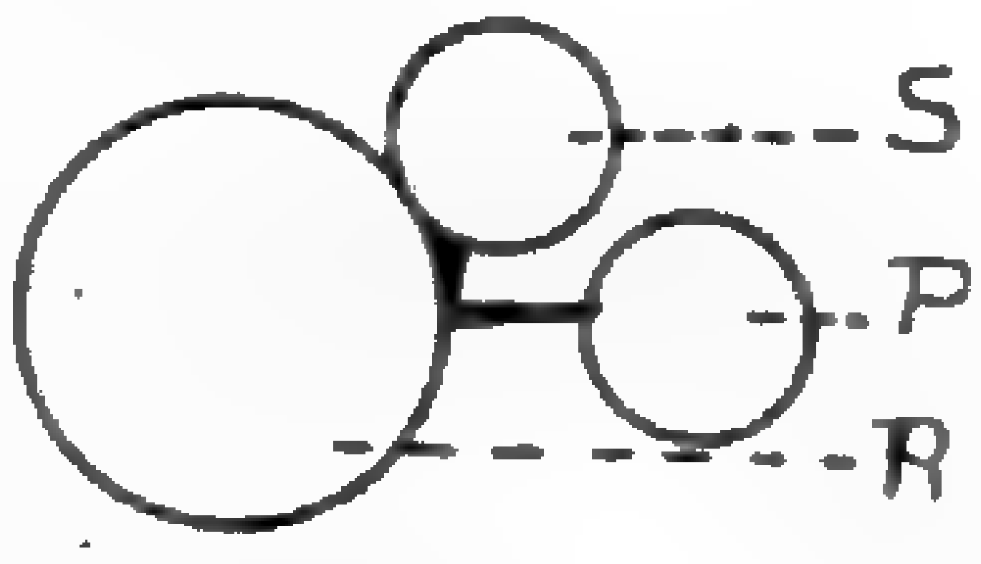
FIG. 32. Portion of a spike of *Tripsacum*, showing paired male and solitary female spikelets. FIG. 33. Pair of female spikelets sometimes found in *Tripsacum*.

SUMMARY OF MORPHOLOGY

As is evident from the foregoing descriptions, these genera are identical in structural plan; for every significant organ in any one of them, there is a homologue, fully developed, rudimentary, or indicated, in each of the others.

Common to all three is the jointed vegetative stem, bearing a leaf or a leaf rudiment at each node and a branch or a bud in the axil of almost every leaf. Buds, representing undeveloped shoots, bear no indication of giving rise to branches, because their nodes have ordinarily not developed far enough; but practically every fully developed node has a bud.

Some of the stems of *Tripsacum* live underground, thus making the plant perennial, a condition which, in some of the species at least, is associated with the swamp habitat and limited seed production. When *Euchlaena* grows in a swampy place, it has a tendency to assume the perennial habit by means of prostrate stems rooting at the nodes; its seed production, however, seems in no way impaired by this habit. Maize produces a large number of viable seeds and has no tendency to become perennial.



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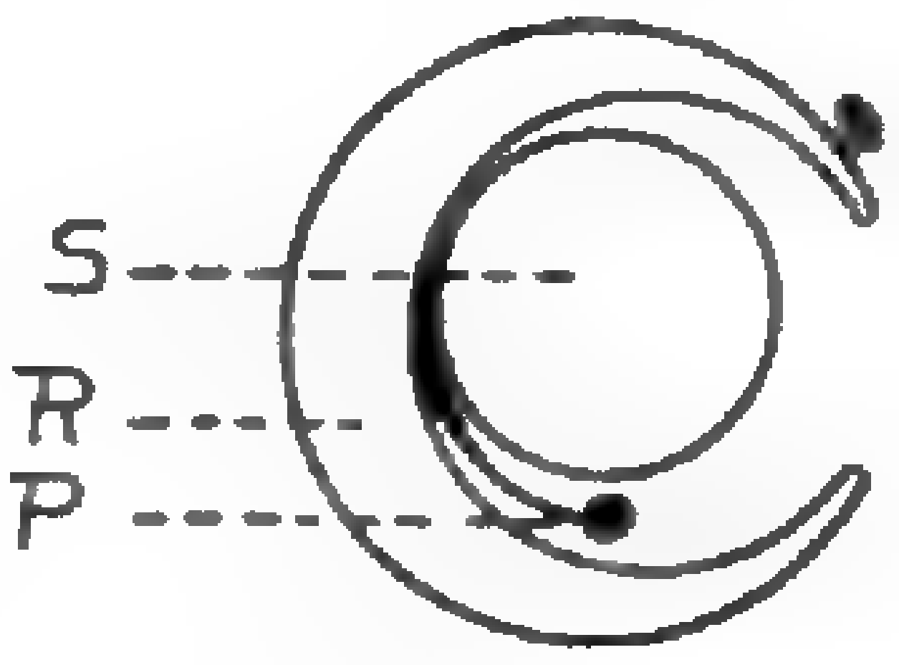

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FIG. 34. Diagram of a cross section of one internode of a male spike of maize or teosinte, showing the rachis, *R*, with one sessile, *S*, and one pedicelled, *P*, spikelet. FIG. 35. Section of an internode of a female spike of *Tripsacum* or *Euchlaena*, showing a functional sessile, *S*, and a rudimentary pedicelled, *P*, spikelet imbedded in the rachis, *R*.

The general inflorescence of the group is a panicle with a central spike and lateral branches, like the tassel in maize. In most of the inflorescences some parts of this general structure are lacking; in the maize ear it is the lateral branches, and in the teosinte tassel and the inflorescence of *Tripsacum* it is the central spike; in the female spike of *Euchlaena* all that is present is a single lateral branch. The spikelets occur usually in pairs, but sometimes in larger groups, in all the inflorescences.

The spikelet has two glumes and two florets. Structurally the flowers are as in the typical grass, but the regular suppression of some of the essentials makes all the flowers functionally unisexual. *Tripsacum* has two feathery stigmas, but the homologue of these in *Zea* and *Euchlaena* is the silk, a fasciated organ divided at the tip.

THEORIES OF THE EVOLUTION OF MAIZE

As has been noted by way of introduction, several theories have been advanced to explain the origin of the maize plant or some of its parts; and it is appropriate here to examine in a critical way some of the more prominent of these.

Origin of the ear.—Most of the attempts to explain the structure and origin of the ear of corn have been based upon Hackel's idea (**16**, p. 20) that it has resulted from the union of several organs like the lateral branches of the tassel. Harshberger at first supported this theory (**17**, pp. 75–83); after describing the ear and some of its teratological variations, he says: "These structural and teratological arrangements point to the probable union of several spikes into a thick, fleshy axis, with grains on the circumference, each paired row limited at the sides by a long, shallow furrow, a row corresponding to a single spike of *Euchlaena* or *Tripsacum*." Gernert (**14**, p. 37) agrees with Harshberger in support of the fasciation theory and gives some additional evidences, most of which, however, are irrelevant or obviously open to objection. Mrs. Kellerman (**22**) and Montgomery (**24**) object to this theory and point out that the ear is the homologue of the central spike of the tassel; and later (**20**, p. 51) Harshberger apparently agrees with the former. Collins (**9**, p. 525) removes all doubt of this homology and shows that the central spike of the tassel is as anomalous and as much in need of explanation as is the ear. He thinks it probable that both have resulted from fasciation. One of the latest discussions of the structure of the ear is that given by Worsdell (**28**, p. 58). Due to a special definition of terms, he does not call this a case of fasciation; but, as the following statement indicates, he is in accord with most of the others in his interpretation of the structure and origin of the ear: "It consists of the fusion of numerous spikes with flattened rachis, each bearing two rows of female spikelets, to form the thick female inflorescence usually termed the 'cob.'" (The word "cob" is a misnomer; he is evidently talking about an ear.) A new term, "disruption," is proposed to cover the *abnormality*, which "consists in the appearance of a 'cob' as a copiously-branched paniculate inflorescence, closely resembling, in its extreme form, the male inflorescence; and is due to the dissolution of the compound organ into its separate parts."

In spite of the apparent consistency of this widely accepted theory of the formation of the ear, it is untenable at least in its present form. There can be no reasonable doubt of the homology between the ear and the central spike of the tassel. Ears terminated by male spikes (FIG. 10), ears with small female or mixed branches attached (FIG. 9), and perfect ears replacing the central spikes of sucker tassels (FIG. 12) all give indication of this. Moreover, the early development of the two organs is the same except that in the case of the normal ear no side branches are developed. But the idea that either or both of these organs is fasciated is inconsistent with some important morphological facts. Carefully prepared microtome sections fail to show any evidence of fasciation, the development in either case being essentially the same as that of any ordinary floral or vegetative shoot. The only kind of organ of which we have any knowledge, the like of which could have united to form an ear, is the lateral branch of the tassel, and this involves a mathematical difficulty. The rows of grains on an ear are paired because the spikelets are borne in pairs. If a lateral spike of the tassel should contribute to the formation of an ear anything in terms of paired spikelets, it would be responsible for *four* rows, and this would make impossible an ear of ten, fourteen, or eighteen rows; but the fact remains that such ears are common. Harshberger's idea that each pair of rows of grains corresponds to a spike of *Euchlaena* or *Tripsacum* is of no avail in getting around this difficulty; they bear two rows of functional spikelets, but not at all because of the presence of paired spikelets, for one spikelet of each pair is rudimentary. It may be noted, too, that although Worsdell has the ear formed by the union of spikes bearing *two* rows of spikelets, he has it "disrupt" into a central spike bearing eight rows and a number of lateral spikes each bearing *four* rows (**28**, *pl. 39, f. 13*). Incidentally it may be said that the "disrupted" ear figured is not *abnormal* at all but a normal tassel of a sucker.

Collins (**9**, p. 526) advances another theory which probably offers the best explanation of the origin of both of the organs in question. He suggests that the male inflorescence might have been developed from a loose panicle by the shortening of some of the branches until pairs of spikelets were left on a central spike and a few lateral branches; the ear could easily have been developed from this by the loss of the side branches. He abandons this theory for want of sufficient evidence in the form of intermediate steps, but Gernert's Branch Corn (FIGS. 14–19) supplies the needed evidence and strengthens a very consistent theory.

Hybrid origin of maize.—A new variety of corn known as *Zea canina* was reported from Mexico about 1890, and Bailey (**1**) and Harshberger (**17**) concluded that it was the long-sought wild ancestor of the species, the latter making it the basis of his monograph on corn. But correspondence with Mexicans who knew the plant showed that *Zea canina* could be produced at will by hybridizing teosinte and ordinary maize. Accordingly, previous conclusions had to be revised, and along with Harshberger's revision (**18**) came the suggestion of three possible explanations of the botanical nature of maize: (1) that maize is a distinct species; (2) that maize originated as a hybrid between teosinte and some unknown grass; and (3) that maize is the result of a cross between teosinte and some variety of teosinte which had been changed by cultivation. He favors the last-named possibility, and in his latest expression on the subject (**21**, pp. 398–399) this is the only theory given.

His conclusions were reached as a result of hybridization experiments with maize and teosinte, in which a graded series of intermediates between the ear of the one and the female spike of the other were produced. A series of this kind always suggests evolution, but this one does not possess the advantage of having maize at one end and its two hypothetical ancestors at the other. Moreover, the status of the hybridization problem at the time at which this theory was proposed (1896) and the evolutionary influences attributed to cultivation, especially to irrigation, do not show up so well alongside the genetics of this later day.

Collins's theory (**9**) is similar to the second possibility suggested by Harshberger; that is, he thinks that maize originated in a cross between teosinte and some unknown grass similar to pod corn and belonging to the Andropogoneae. With respect to a large number of characteristics, ordinary maize is shown to be intermediate between the primitive pod corn and the highly specialized teosinte; and this is considered evidence that *Zea* is a hybrid between the two extremes.

Although this theory is the most elaborate and the most widely accepted of all the attempts that have been made to explain the origin of maize, yet it falls short of its aim in some respects. Granting the accuracy of the observations upon which it is based, we may still question the value of the facts as constructive evidence leading to the conclusion. Is it safe to assume on this basis alone that an intermediate of this kind is necessarily a hybrid between the two extremes? And is a hybrid usually intermediate in character between its parents? But many of the supposed facts upon which this theory is based will not stand the light of a close examination; and the actual conditions are capable of a more simple and more direct explanation in another way.

The theory depends upon some hypothetical pure variety of pod corn, which can be approached in reality only by inbreeding some one of the many available genetic complexes commonly known as pod corn. But inbreeding for purity implies intelligent selection among the pure lines reached or approached; and this places a burden of responsibility upon him who makes such selection the basis of a theory of this kind. Collins has in mind, however, some strain of pod corn the like of which he considers one of the ancestors of maize; and, in describing its simple, primitive nature, he makes some statements which are not in accord with the morphological facts that I have already set forth. The extreme type of pod corn is described (9, p. 527) as having no ear, the absence of branches being a primitive characteristic. Disregarding the difficulty occasioned by the fact that these earless plants are incapable of self-propagation, we may cite the fact that they have buds in the axils of their leaves, indicating the suppression of ears. If a plant that never had any ears is primitive, one that has vestiges of ears that it has lost must be highly specialized. He says (p. 528): "In the branched forms of pod corn staminate flowers have never been observed on any of the branches." Contrary to this is the fact that sucker branches of pod corn often bear mixed or staminate inflorescences, these having often been mistaken, no doubt, for earless plants, especially when more than one plant is grown in a hill; and in several cases ears of pod corn have been found bearing well-developed stamens. Applying the specialization test to the ears, he says (p. 528): "In pod corn branches have never been observed in the axils of prophylla;" but I have often seen such branches, especially when the main ear had been injured and buds are to be found in the axils of the husks of all kinds of corn. From the foregoing citations it may be seen that Collins does not necessarily hold to any one variety of pod corn for his evidence, switching from earless to branched types as he finds structures to fit his hypothesis; and, even with this latitude of choice, he fails to find sufficient evidence that pod corn is wholly primitive. It is readily granted by anyone that the tunicate character and the tendency toward hermaphroditism are primitive characters, but otherwise the plant is modern, as the fasciated silk, the husks of the ear, and the many degenerate organs go to show. The earless plants are the most highly specialized of all, as indicated by the vestigial ear-buds in the axils of their leaves.

Similar inconsistencies occur in the description of teosinte, which is held to be highly specialized; the mention of a single example will be sufficient. In support of a detailed argument that the extreme differentiation between the male and female inflorescences of teosinte points toward specialization higher than that in maize, he says (p. 524) that female flowers have never been observed in the male inflorescence of *Euchlaena*. I have already described mixed inflorescences of this plant; but the importance of this point is diminished by the fact that in this entire group of plants we are dealing with flowers which are structurally bisexual.

Readily granting that monoecism is a less fixed characteristic and that the separation of male and female flowers is not so sharp in maize as in teosinte, yet I do not believe that pod corn has been shown to be sufficiently different from ordinary corn to merit the prominent position that it holds in this theory.

In a recent report on this theory (11) the intolerance of self-pollination in maize is given as another evidence of its hybrid nature, it being almost if not quite unique among the grasses in this respect. But possibly another explanation for this may be found in its having a very small number of monoecious inflorescences and, because of protandry or protogyny, a limited chance for self-pollination under normal conditions, in which respect it is also unique among the grasses. All the other members of the Maydeae, teosinte, for example, produce a large number of inflorescences and have a flowering period much longer than that of maize, the chances for self-pollination being correspondingly better. *Tripsacum* can be excluded from this consideration because it depends mostly upon vegetative propagation for increase in number of individuals. In those grasses which have perfect flowers self-pollination is the rule. Tolerance of self-pollination may thus be interpreted as a matter of adjustment to the conditions which have prevailed during the development of the plant in question.

Traumatic evolution.—Maize was one of the principal plants considered by Blaringhem (**3**, **4**, **5**) in arriving at his theory of mutation by traumatic influences, and his conclusion as to its evolution may best be stated in his own words (**6**, p. 228): "L'étude des variations observées à la suite de mutilations permet de reconstituer l'évolution du genre *Zea*, et d'établir que l'ancêtre sauvage du Maïs cultivé est l'espèce *Euchlaena mexicana*. Le genre *Zea* est une forme monstreuse du genre *Euchlaena* née et propagée par les soins de l'homme." The chief interest in his work in this connection lies not so much in his contribution to our knowledge of the evolution of the plant as in the peculiar methods employed and the peculiar interpretation of results.

By mutilating plants in various ways he causes them to send up sprouts whose terminal inflorescences bear both male and female flowers. Seeds from these sprouts provide the starting points for numerous new varieties characterized by such peculiarities as suckers with mixed inflorescences, ears with perfect flowers, branched ears, tubular leaf sheaths, etc. Many of these breed true and are given the rank of elementary species, a number of new varietal names being contributed to the already overburdened list associated with the variations of this monotypic genus. Throughout the discussion, the sucker bearing a female or mixed inflorescence is considered an abnormality; but if this is the correct interpretation for the suckers of the whole genus, it constitutes a case where the exception is quite as common as the rule. In his description of the spikelets of the normal plant (**6**, p. 21) he states that neither the male nor the female flower contains organs of the opposite sex; and this fallacy becomes the basis for his assumption (**5**, p. 1253) that the acquisition of perfect flowers by some of his new varieties constitutes a *progressive* step. No change that he has produced in the plant involves any characteristic that is actually new, and, as Gernert suggests (**14**, p. 6), most of the results may be explained on a basis in no way connected with the original mutilation. As the theory stands, we can justly ask that the experiments be repeated successfully with more than one variety of maize, and the results interpreted on the basis of a more sound understanding of the morphology of the plant throughout its normal range of variation, before we consider this a substantiated explanation of the past history and present tendencies of the plant.

Montgomery's theory.—Along with his explanation of the ear of corn as the homologue of the central spike of the tassel (**24**), Montgomery proposes a theory of evolution, which, while not worked out in full detail, is probably the most consistent solution of the problem yet offered. He considers maize a distinct genus coördinate with teosinte, both having developed from a common teosinte-like ancestor.

A THEORY BASED UPON MORPHOLOGY

Exact knowledge of the past conditions being out of the question, the ancestry of the maize plant and the steps taken in its evolution can only be built up in theory from a study of the modern plant and its near relatives; and some attempts previously made in this direction have already been discussed. Any theory that is to receive serious consideration must be based upon, and consistent with, recognized facts; and, of two or more explanations of the same thing, the simplest and most direct is to be preferred. Several kinds of evidence are available for use in the study of maize; but morphology, the basic constructive factor of most of our theories of evolution, has never been utilized to the full extent. To be sure, the gross structure of this group of plants has several times been considered, but a morphological study that does not go to the bottom of the question is likely to mislead the investigator. The study of abnormal structures is always instructive, but it is more significant to find in the normal plant a morphological basis for its abnormalities. Other considerations, such as may be occasioned by experiments in hybridization and selection for a few generations, constitute instructive checks on other methods; but they must not be over-emphasized as constructive material, and they are never any better than the morphology upon which they are based.

Ancestry of maize.—It is neither necessary nor desirable, I believe, to look for the ancestor of maize and its near relatives in any plant now living; its evolution along different lines to the present forms would imply its own probable disappearance. There are found in different members of the Andropogoneae, however, all the characteristics necessary for a theoretical progenitor of maize and its American relatives. In the evolution of these plants from their common ancestor, many steps were probably taken, no suggestion of which has passed down to modern times. It is almost certain that the Asiatic species of the Maydeae arose from this same stock, and many lines of descent may have led to other forms now long extinct. Geology and archeology are of little value to us in solving these problems, since the oldest remains of these plants found in the rocks or in human habitations are practically modern.

Theoretically the ancestor of these plants was an herbaceous perennial, whose tall, jointed, leafy stems sprang from a rhizome. A branch was borne at practically every node of the aërial stem, each being somewhat shorter than the main stem and having about as many nodes as the latter above the point of branching. Branches upon branches occurred to the third and fourth or higher orders. The main stem and each branch was terminated by a loose, ovoid or pointed, monopodially branched panicle. In this panicle the spikelets were probably borne in pairs, one sessile and one pedicelled, in many irregular peduncled clusters on the main axis and its branches. Each spikelet had two perfect flowers; the pistil had two feathery stigmas. From this plant the three genera here considered, and probably the other genera of the Maydeae and some of the Andropogoneae as well, have been evolved by the *suppression of parts*, whose rudiments are, in most instances, still to be found in the modern plants.

The cause of this suppression and the mechanism of its accomplishment are unsolved problems, but the phenomenon is not peculiar to this group of plants alone. It is known that monoecism among the angiosperms has been reached independently in many groups as a result of the suppression of one set of organs in each flower; and the suppression of whole inflorescences and of vegetative parts is also common. Whether this suppression is due to environment, or to inherent tendencies, or to a selection by the environment among the results of inherent tendencies, is unknown; but the comparative structure of *Zea*, *Euchlaena*, and *Tripsacum* indicates that, in their development from a common ancestor, certain tendencies have found expression in different ways in the different genera; and this expression has often come in the nature of a response to external conditions. In other words, we assume that these three genera are closely related, not because the characteristics which they have were present in a common ancestor, but because they have been evolved from an ancestor which had tendencies to suppress pistils in some flowers and stamens in others, whole flowers in some cases, and in some cases vegetative organs. Unless this assumption is made, we cannot base any close relationship between *Euchlaena* and *Tripsacum* upon monoecism, for the separation of the sexes in these two genera has been accomplished in different ways.

The first division of the progeny of this ancestral form set off a group in which the upper spikelet of each pair had lost its pistils, this giving rise to a number of genera of the Andropogoneae. On the other hand, in some of the plants whose inflorescences had retained their perfect flowers, the peduncles bearing groups of spikelets grew shorter (FIGS. 15–19) until the spikelets were arranged as in the tassels of maize or teosinte (FIGS. 3, 4, 5, 21). Pairs or larger groups of spikelets could have been left in this way. The plants in which the central spike of the inflorescence survived this process became the ancestors of *Zea;* while those in which this spike was lost gave rise to *Euchlaena* and *Tripsacum.* In the separation of these two genera, two lines of evolution were followed, depending upon the manner in which monoecism came about.

Origin of Euchlaena.—In the line tending toward *Euchlaena*, the uppermost inflorescences—those terminating the main branches—lost their female elements and assumed the form of the present teosinte tassel (FIG. 20), while the lower inflorescences lost their male elements; between these two extremes were formed some mixed spikes, the upper portions being staminate and the lower pistillate. In the pistillate spikes, or portions of spikes, the pedicelled spikelet and the lower flower of the sessile one became aborted (FIGS. 27, 28). Each branch bearing a female inflorescence shortened enough that the inflorescence was covered by the sheath of the leaf just below it; at the same time, all but one (or rarely more) of the spikes of this inflorescence disappeared, and the two stigmas of each pistil, lying side by side and elongating to keep their tips exposed beyond the enveloping leaf sheath, united, except at their exposed tips, to form the silk. The brittle rachis came with the hardening of the outer glume of the spikelet and the walls of the alveolus in which the spikelet was imbedded. The leaf whose sheath enclosed the female spike has since then almost lost its lamina (FIG. 25). By a continued shortening of the internodes, the sheaths of lower and larger leaves were later caused to envelop clusters of these simple female spikes and their husks (FIG. 26). There is nothing to indicate when *Euchlaena* became an annual, but this habit is probably correlated with a reduced supply of moisture.

Origin of Tripsacum.—In those individuals tending toward *Tripsacum*, monoecism came about as a result of the loss of female elements from the upper part and male elements from the lower part of each spike of the inflorescence (FIG. 32). The point of division between the male and female portions of a spike was higher in the inflorescences of the branches than in that of the main stem. In the male portion, the pedicellate spikelet became almost sessile; the female portion became essentially as in teosinte. There was no appreciable shortening of any internodes, and the inflorescence was not covered by a leaf sheath; consequently there was no reduction in the number of its branches, and the two stigmas have persisted (FIG. 31). This plant usually grows in rich, wet soil, and it has remained perennial; its ability to produce viable seeds is restricted.

Origin of Zea.—In the evolution of *Zea* from its progenitor, the inflorescence terminating the main stem lost its female elements and approached its present form (FIG. 2). Those terminating some of the primary branches near the middle of the main stem lost their male elements, and these branches began to shorten their internodes. As this shortening continued, the secondary branches were reduced to buds; and, as the leaf sheaths began to enclose the terminal inflorescence of the branch, this inflorescence lost its lateral branches, only the central spike remaining. Up to this time the mature fruits were covered by the palets and glumes, but, as a response to the covering of husks, these bracts became shorter, leaving the mature fruits naked except for the husks of the ear. The leaves whose sheaths formed the husks, tended to lose their laminae and ligules (FIG. 7); these remain, however, in some varieties (FIG. 6). The two stigmas united, as in teosinte, to form the silk. At some time in the development of the ear, the lower flower of each female spikelet lost its function, but when and why this occurred is not clear at present. Probably all the primary branches of the stem, except those low enough to take root, went through this process, and most of them became still further reduced; at present, one to five or six usually remain as ears, and the rest have been reduced to buds in the axils of the leaves of the main stem. Those primary branches low enough to take root (FIG. 1) did so and have met with the varied fate characteristic of the suckers of the plant. Some are like the main stalk and others like ears, depending probably upon their relative independence; but the great majority share the characteristics of both (FIGS. 11–13).

Meaning of variations in maize.—In the light of this theoretical history of the species we are able to interpret many of the ordinary variations of maize. The podded ear is a reversion to the condition of the ear unprotected by husks, and very probably not a primitive form that has come down to us unchanged. Grains in the tassel mark a resumed function of the pistils in the male flowers, and they are usually characterized by the fasciated silk, showing that their flowers have not reverted in all characteristics. Gernert's Branch Corn (**15**) is a reversion to the primitive paniculate inflorescence by a plant which is modern in other respects. Emerson's dwarf variety (**13**) and one of Blaringhem's new varieties (**5**), both of which have perfect flowers in the ear, are, in so far as the perfect flowers are concerned, analogous to the varieties with perfect flowers in the tassel. Two-flowered female spikelets, such as those regularly found in Country Gentleman sweet corn (**25**, p. 135) and a few other varieties, are reversions to the primitive two-flowered condition. We should not expect any one plant to show reversion in all respects; characteristics probably behave as units in reversion as much as in heredity.

Some freaks, such as ears divided at the tip (**17**, p. 81; **14**, p. 37) and fasciated kernels (**27**), are probably best interpreted as anomalies of ontogeny, giving no more clue to the past than is afforded by Siamese twins or lilies with two-parted flowers. Indeed, an ancestral form that would be consistent with all the teratological ears that have been used as evidence would be an impossibility. It is a fact worth mentioning, also, that many of the teratological conditions that do not fit into the foregoing theory as reversions are not inherited, while those in accord with this theory often form the starting points of new varieties tending to breed true.

It is not deemed advisable here to attempt to trace the probable origin of all the more or less fixed varieties of corn that have come into existence after the generic characteristics were reached; but no constant characteristic is known in any variety, which is inconsistent with the general theory here outlined. The development of the annual habit was similar to that of teosinte, and no further explanation is offered. The restricted period of flowering has a morphological cause in the reduced number of inflorescences.

CONCLUSION

It is granted that the foregoing theory involves a measure of speculation, but that is to be expected of any theory; it is as conservative as any that have been advanced to explain the origin of maize, and much more so than some of them. It is believed to be a logical deduction from the best and most recent evidences available, and in it are embodied parts of some of its predecessors. No point in it is known to be out of harmony with a rational interpretation of any established fact of structure, history, or genetic behavior concerning the plants with which it deals.

How much of this evolution of maize was due to natural agencies, and how much to the influence of primitive agriculture, we have no means of knowing; but, from the botanical point of view, the changes wrought by four hundred years of civilization

FIG. 36. A corn plant very highly specialized by scientific breeding. The suckers have all been lost, and the entire energy of the plant is directed toward the production of a single large ear.

are insignificant as compared with those preceding the advent of the white man. The varieties of corn which Columbus first saw in the West Indies in the fifteenth century were probably in no essential way different from those now grown on many Indian reservations (FIG. 1); and the highest attainment of corn breeding, as represented by the dent varieties of the Mississippi valley today (FIGS. 7, 36), is merely one of a combination of these varieties, with a few more organs dropped, a little more concentrated fructification, and a little greater vegetative vigor.

SUMMARY

Vestigial organs being considered, *Zea*, *Euchlaena*, and *Tripsacum* are identical in structural plan. The present aspect of each is due to the suppression of some parts which were present in a primitive ancestor having perfect flowers borne in one type of inflorescence.

The ear of maize is the homologue of the central spike of the tassel. There is no morphological evidence to support the view that either of these organs originated in the fusion of more simple parts; and there is in no one of the genera here considered any organ the like of which could have united to form either the ear or the central spike of the tassel.

The prevailing theory that maize is a species of hybrid origin has little to suggest it when maize and its near relatives are thoroughly understood, and it is not in harmony with the most significant facts of morphology. It seems much more probable that *Zea*, *Euchlaena*, and *Tripsacum* have descended independently from a common ancestral form now extinct.

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The relationship between the number of sporophylls and the numbers of stamens and pistils—a criticism

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In a paper entitled, "The interrelationship of the number of stamens and pistils in the flowers of *Ficaria*," Harris* has attempted, by statistical methods, to throw some light on the biological factors which determine the sex of an organism. The relative numbers of pistils and stamens present are assumed to indicate which sex is more influenced as the total number of sporophylls increases. Without a knowledge of the number of functional spores that are produced the ratio of the two kinds of sporophylls can hardly be considered as a fundamental measure of the sex of a flower. Nevertheless the quantitative relations between stamens and pistils, if handled so as to be of biological and not purely statistical significance, may suggest more precisely the factors that influence the development of the two sexes.

Harris correlates the deviations of the total number of sporophylls and those of the pistils and stamens from their "probable values." He means by this the average frequency of pistils and stamens to be expected according to the total number of sporophylls. He does this rather than correlate directly with the numbers of pistils and stamens in order to eliminate, as he believes, the spurious correlation which would exist in the latter case. He finds the correlation between the number of sporophylls and the deviation of the pistils from their "probable number" to be of equal magnitude to that of the stamens, but positive, while that of the stamens is negative. From this he concludes that as the number of sporophylls increases, the pistils increase relatively more rapidly than the stamens.

It can be shown that this result necessarily follows from the fact that there are more stamens than pistils while their varia-

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* Biol. Bull. **34**: 7–17. 1918.

bilities are almost equal, and consequently has only mathematical and not biological significance.

According to Harris's formula, if $(n + s)$ represents the mean number of sporophylls with their deviations and, let us say, p the percentage of pistils and z_p their deviations from their "probable number" the pistils would be represented by the formula $(n + s)p + z_p$, and the stamens by the formula $(n + s)(1 - p) - z_s$, where z_s is the deviation of the stamens from their "probable number" and $z_s = z_p$. The sum of the pistils and stamens must, of course, equal $(n + s)$, the total number of sporophylls. He then correlates the variables s and z, assuming that z is not contained in s.

We may analyze Harris's formula for pistils to determine which values are known and which are unknown. If n represents the average total number of sporophylls, n_p that of pistils, n_s that of stamens then $n = n_p + n_s$. $n_p + x$ are the pistils with their deviations, $n_s + y$ the stamens with their deviations. The deviation of the total number of sporophylls from their mean, s, equals $x + y$; so that Harris's value for sporophylls $(n + s) = n_p + n_s + x + y$. Since p represents the percentage of pistils, it is equal to $n_p/(n_p + n_s)$, and Harris's value for pistils, given above, becomes

$$(n + x + y)\frac{n_p}{n_p + n_s} + z_p$$

z_p is the only unknown value. We may find its value from the following equation:

$$(n + x + y)\frac{n_p}{n_p + n_s} + z_p = n_p + x,$$

the number of pistils plus their deviation. Solving this

$$z_p = \frac{n_s x - n_p y}{n_p + n_s},$$

$$s = x + y.$$

Therefore, correlating s, the total number of sporophylls, with z_p, the deviation of the pistils from their "probable value,"

$$z_p s = \frac{n_s x - n_p y}{n_p + n_s}(x + y)$$

and averaging

$$[z_p s] = \frac{n_s\sigma_x^2 - n_p\sigma_y^2 + (n_s - n_p)r\sigma_x\sigma_y}{n_p + n_s}.$$

According to Harris's result $[z_p s]$ is always positive. The formula shows that this must be the case when

$$n_s\sigma_x^2 - n_p\sigma_y^2 + (n_s - n_p)r\sigma_x\sigma_y > 0$$

or when

$$n_s(\sigma_x^2 + r\sigma_x\sigma_y) > n_p(\sigma_y^2 + r\sigma_x\sigma_y).$$

If σ_x and σ_y are equal this can happen only when $n_s > n_p$, or in other words when the stamens are more numerous than the pistils.

From the original data from which Harris has drawn the material for this study (see Harris for references) it is evident that the standard deviations for pistils and stamens are nearly equal and that the stamens are more numerous than the pistils. For the average values for Europe given by Pearson the mean number of pistils is 19.432 with a standard deviation of ± 4.8508; the mean number for stamens 26.498 with a standard deviation of ± 4.2562. The coefficient of correlation is + 0.5584. Substituting these values we find the results obtained by Harris necessarily follow from the existing numerical relations.

From this consideration it seems evident that the results obtained by Harris do not add anything to the observations on the numbers of pistils and stamens and their variabilities. Just so the higher coefficients of variation given by Harris in Table I of his paper result from the fact that the same value (standard deviation) is divided in the case of the pistils by a lower value (mean for pistils) than in the case of the stamens (mean for stamens).

It might be said that the total number of sporophylls and the per cent of stamens and pistils vary independently, in which case the expression $(n + s)(p + v)$ would represent the number of pistils. Disregarding the value sv, since it is small in comparison to the other values, the expression becomes $p(n + s) + nv$ and the same relations will hold as in the case discussed above.

New York Botanical Garden

INDEX TO AMERICAN BOTANICAL LITERATURE

1918

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Appleman, C. O. Respiration and catalase activity in sweet corn. Am. Jour. Bot. **5**: 207–209. *f. 1.* 16 My 1918.

Arthur, J. C. New species of Uredineae—X. Bull. Torrey Club **45**: 141–156. 1 My 1918.

New species are described in *Uromyces* (2), *Puccinia* (8), *Aecidium* (10), and *Uredo* (3).

Arthur, J. C. Uredinales of Costa Rica based on collections by E. W. D. Holway. Mycologia **10**: 111–154. My 1918.

New species are described in *Ravenelia* (1), *Uromyces* (3), *Puccinia* (13), *Aecidium* (3), and *Uredo* (2).

Arthur, J. C. Uredinales of the Andes, based on collections by Dr. and Mrs. Rose. Bot. Gaz. **65**: 460–474. 15 My 1918.

Includes the new genus *Cleptomyces* and new species in *Sphenosporea* (1), *Puccinia* (4), and *Aecidium* (1).

Ashe, W. W. Notes on southern woody plants. Torreya **17**: 71–74. 8 My 1918.

Vaccinium Margarettae sp. nov. is described.

Atkinson, G. F. Some new species of *Inocybe*. Am. Jour. Bot. **5**: 210–218. 16 My 1918.

Twenty-four new species are described.

Blake, S. F. Note on the proper name for the sassafras. Rhodora **20**: 98, 99. 1 My 1918.

Britton, E. G. "The catkin-hypnum, with long hoses." Bryologist **21**: 32. 30 Ap 1918.

Britton, E. G. Mosses from Florida collected by Severin Rapp. Bryologist **21**: 27, 28. 30 Ap 1918.

Britton, N. L. John Adolph Shafer. Jour. N. Y. Bot. Gard. **19**: 97–99. My 1918.

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Brandes, E. W. Anthracnose of lettuce caused by *Marssonina panattoniana*. Jour. Agr. Research **13**: 261–280. *pl. C, 20* + *f. 1–4*. 29 Ap 1918.

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Cowgill, H. B. Studies in inheritance in sugar cane. Jour. Dept. Agr. Porto Rico **2**: 33–41. Ja 1918.

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Includes *Mimusops huberi* sp. nov.

Duggar, B. M., & Bonns, W. W. The effect of Bordeaux mixture on the rate of transpiration. Ann. Missouri Bot. Gard. **5**: 153–174. Ap 1918.

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Fairman, C. E. Notes on new species of fungi from various localities—II. Mycologia **10**: 164–167. My 1918.

Includes new species in *Phoma* (1), *Phomopsis* (1), *Sphaeropsis* (2), *Camarosporium* (1), *Rhabdospora* (1), *Microdiplodia* (1), *Hendersonia* (1), *Dictyochora* (1), *Platystomum* (1).

Fernald, M. L. *Rosa blanda* and its allies of northern Maine and adjacent Canada. Rhodora **20**: 90–96. 1 My 1918.

Rosa johannensis and *R. Williamsii*, spp. nov., are described.

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Includes new species in *Cercospora* (1), *Coryneum* (1), *Cryptospora* (1), *Cryptosporium* (1), *Dendrodochium* (1), *Diplodia* (2), *Eutypella* (1), *Gloeosporium* (1), *Leptosphaeria* (1), *Massarinula* (1), *Microdiplodia* (1), *Phoma* (1), *Ramularia* (1), *Septoria* (3), *Sphaeropsis* (3).

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Löfgren, A. Novas contribuições para as Cactaceas brasileiras sobre os generos *Zygocactus* a *Schlumbergera.* Arch. Jard. Bot. Rio de Janeiro **2**: 19–32. *pl. 3–6.* 1918.

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New species are described in *Puccinia* (3), *Septoria* (1), *Cercospora* (1), and *Helmintosporium* (1).

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

SEPTEMBER, 1918

Wound periderm in certain cacti

MARY WOTHERSPOON COUTANT

(WITH PLATE 9 AND THREE TEXT FIGURES)

NORMAL TISSUE

The two cacti upon which the work of this paper is based are *Opuntia versicolor* Engelmann and *O. discata* Griffiths. These are jointed, branching forms, characteristic of the flora in the vicinity of Tucson, Arizona. Morphologically they differ in that the joints of the *O. versicolor* are composed of fluted cylinders, while those of the *O. discata* are more or less disc-shaped. Necessarily, a cross section of the former presents the appearance of a circle with an undulating margin, while one of the latter is more of an elongated ellipse. Anatomically considered, they are identical in all essentials. There is (1) a distinct pith in the center, bounded (2) by a ring of bundles equidistant from the exterior; outward from the bundles (3) a ring of cortical tissue, which extends to the (4) hypoderm, outside of which is the (5) epidermis. Subepidermally, in plants several years old, normal periderm occasionally, but not typically, forms in isolated areas.

Schleiden (3), in his early work on the cacti, describes fairly accurately several forms, which, however, do not include either *O. versicolor* or *O. discata*.

A further discussion of the tissues in their normal condition is prerequisite to a complete understanding of their behavior as a result of wounding.

[The BULLETIN for August (**45**: 309–352) was issued September 9, 1918.]

The pith is composed of thin-walled, isodiametric cells, loosely packed together, and with consequent large intercellular spaces. The cells themselves contain, aside from the usual protoplasmic contents, a considerable quantity of stored starch, and small crystals of calcium oxalate. These crystals are found in large quantities in practically all of the tissues of both opuntias, sometimes causing, parallel with their own growth, an hypertrophy of the cells containing them. In a concentrated solution of hydrochloric acid, the calcium oxalate of a medium-sized crystal does not dissolve for over half an hour. Lauterbach (**2**) describes these crystals as being star-shaped clusters composed of monoclinic prisms, which have a short principal axis, and states that they make up 85 per cent. of the weight of the ash.

The bundles vary somewhat in their structure with the age of the plant and their position in the stem. Essentially, they are of the open collateral type, with hadrome and leptome on the same radius, separated by a cambial layer. The hadrome, much greater in extent than the leptome, consists of annular and spiral ducts, occasional parenchyma cells, and, in many cases, large interspersed masses of stereome tissue. The ducts and stereome cells are lignified, as shown by testing with phloroglucin and hydrochloric acid, and in cross section the latter greatly resemble the median optical view of the lignified-walled cells, to be described later in the formation of the periderm. The cells of the cambial region, as seen in cross section, present the typical brick-shaped appearance, and form, at the most, a layer not more than three or four cells deep. The leptome is composed of the characteristic sieve tubes and their accompanying companion cells, interspersed with parenchyma tissue. In cross section the peripheral portion of the leptome mass appears dome-shaped, and is capped by a mass of collenchymatic cells which resemble those of the hypoderm, referred to later on. The walls of these cells often become more or less mucilaginous, an occurrence similar to that found by Lauterbach (**2**, p. 262) in *Pereskia*, also one of the Cactaceae. The subcortical cells in the bundle region appear isodiametric, like those of the pith. However, there is a gradual merging of these cells with those in the outer cortical region, which are distinctly cylindrical and arranged end on end, with their long axes at right angles to the periphery. The outer five or six rows are normally rich in chloroplasts, and practically all of the cortical tissues contain a plentiful supply of stored starch. In seedlings a single-layered epidermis covers the distinctly parenchymatic cortical cells. However, as the plant matures, the outer cortex gives rise to a clearly differentiated tissue, the hypoderm, socalled by Solereder in his Systematic Anatomy of the Dicotyledons (**4**). The cells of the hypoderm are, in both opuntias here studied, from five to seven layers in depth, and decidedly collenchymatous in character. Schleiden (**3**, p. 348) describes this condition as arising through loss of water, from cells originally mucilaginous. PLATE 9, FIG. 1 will serve to give an idea of the thick cellulose walls, traversed by pit canals which radiate out from the comparatively small lumina, indicating protoplasmic continuity between the cell contents. The outer layer, which lies just underneath the epidermis, is characteristically so filled with oxalate crystals as to almost obliterate the walls. Occasional crystals are found in the other cells. This tissue has been described for different species of *Opuntia* by Lauterbach (**2**, pp. 259–264), as well as by the two authors mentioned above.

The epidermis is a single layer of cells in thickness and covered thickly with cutin, as shown by staining with Sudan III and heating. The stomatal openings extend through the hypodermal tissue down to the cortical cells. The guard cells are somewhat sunken, and the whole cavity is lined with cutin continuous with that on the outside. This fact was brought out by Mohl (see Solereder, **4**, p. 408) in his work on the cacti.

The normal periderm, mentioned in the introduction as forming in plants several years old, arises superficially, and gives the appearance of circular markings on the surface. When examined in a transverse section of the stem, it is seen to be composed of alternating zones of thin- and thick-walled tissue, each zone being itself several layers of cells in thickness (PLATE 9, FIG. 6). The thin-walled cells appear brick-shaped, and superficially greatly resemble meristematic tissue, except that their walls are highly suberized. The thick-walled cells are, on the contrary, lignified, reacting with phloroglucin and hydrochloric acid as did the stereome mentioned in discussing the structure of the bundles.

A single layer of this lignified tissue is never deeper than three cells, arranged one on top of another; the outer tangential and the radial walls are thicker than the inner tangential ones, and in consequence the peripheral portions of the lumina are dome-shaped, as is so common in thickened cutinized tissue of the epidermis. In very thin sections stained with Bismarck brown, distinct striations can be seen in the walls, coarser near the lumen, and becoming finer toward the exterior; while running at right angles to these striations are numerous fine pores. PLATE 9, FIG. 5, gives an optical transverse view of this tissue. The middle lamellae are shown, but the striations and pits above referred to are not indicated. In describing the origin of this particular tissue, Schleiden (3, p. 352) says that there arises a thick, yellow-brown, granular, slimy mass, in which eventually cells are formed. At present such an hypothesis is not to be accepted. However, although omitting any reference to lignification, he brings out clearly the fact that in the mature periderm there are alternating zones of suberized thin- and thick-walled tissue.

EFFECT OF WOUNDING ON NORMAL TISSUE

Having studied the normal tissues, with especial reference to the periderm, the next problem was to find out what reactions would follow as a result of injury. Wounds were brought about by making longitudinal slits down the plants with a razor, usually cutting deeper than the bundle ring, but never beyond the center of the pith. A contraction of the cells near the cut surface resulted, thereby opening up the wound, and exposing the tissue to the air. After the elapse of definite periods this material was placed in alcohol. Some stems were wounded with glass, in order to avoid a possible stimulus which might result from the acids of the tissues acting on the steel of the razor, and the resultant formation of soluble iron salts. In running a parallel series, however, there was found to be no difference in the rate of wound reaction between the two, so the use of the razor was adhered to.

All of the material used came originally from Tucson, Arizona. In the spring of 1913, cuttings were sent from Tucson, which were immediately wounded and killed, but gave unsatisfatory results. Plants from Tucson were wounded while growing in the Barnard

College greenhouse, but, although giving fairly good results, they were by no means as dependable as those obtained from material wounded and killed directly in its natural habitat in Tucson. Material of this character, collected by Dr. H. M. Richards in 1911 and by Dr. D. T. MacDougal in 1914, serves as the basis for the observations which follow.

Practically all of the studies have been made from transverse sections through the stems, where, owing to the above mentioned opening of the wound, the two exposed surfaces form a "V." Hand sections stained with Bismarck brown served to show clearly all cell walls, and the unstained portions were easily tested for cutin, cellulose, lignin, etc. Although most of the figures were made from such hand sections, those cut with a microtome were used for reference.

The only visible change during the first day after wounding is the partial loss of starch in a region running parallel with the exposed surface of the wound, but not bordering directly upon it. By the second day, that region is entirely starchless, and the reaction with iodine of the starch in the cells on the wound surface does not give the normal purplish blue, but more of a reddish color, suggesting the presence of a greater proportion of erythrodextrin.

In three-day-old wounds, some of the oxalate crystals in the most exposed cells have increased in size. The starchless area in the upper part of the "V" has become divided into two practically equal parts, by the foreshadowing of a meristematic layer running parallel to the surface of the wound. The cells in the outer region, that is, between this future meristem and the cut surface, are somewhat discolored. The cells comprising this prospective wound-phellogen are one layer in depth, and although no divisions have as yet taken place, there seems to be an adjustment of the containing cytoplasm to form a flat plate, continuous from one cell to another, and parallel to the wound surface. PLATE 9, FIG. 2, will give an idea of how this appears in section.

A wound four days old shows the meristematic or phellogen layer more clearly, especially near the periphery, where the cells seem about to divide. Near the base of the cut, particularly if the wound is deep and the circulation of air slight, it is undeveloped, possibly due to lack of available oxygen or perhaps to the lessening of the transpiration. See TEXT FIG. 1. The latter is suggested by a fact mentioned by Küster (1, p. 187), that a preliminary condition for the production of wound-cork is that at least a small degree of transpiration must be possible for the exposed tissue. Here, as pointed out, the cells on the cut surface near the periphery must have at least a normal amount of transpiration, while those deep in the cut can have much less.

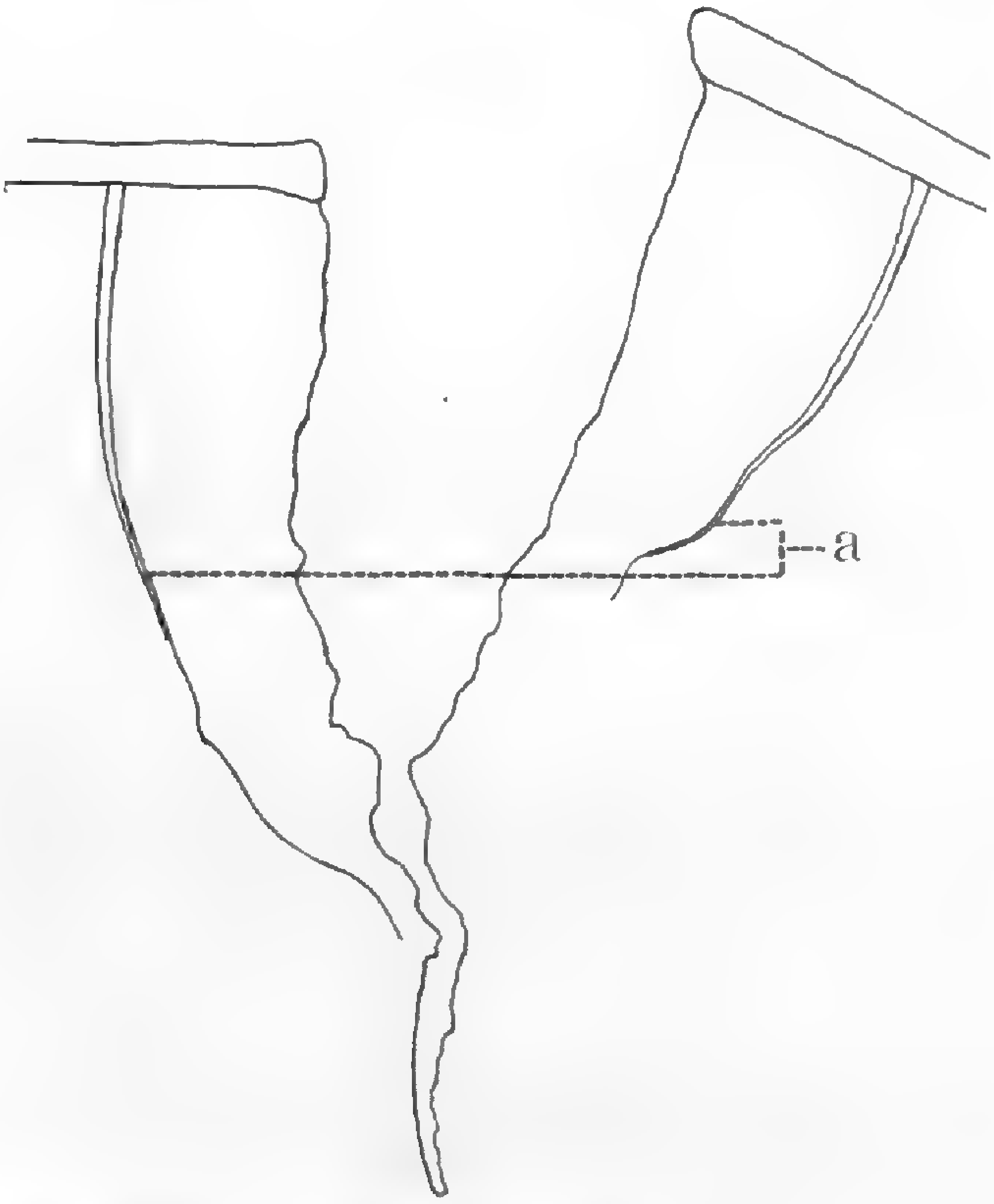

FIG. 1. Cross section of a four-day-old wound of an *Opuntia discata* plant, showing the characteristic V-shaped cut and the formation of the wound-phellogen only in the outer parts of the wound, × 28. *a*, phellogen layer.

Another change from the three-day-old wound is that the walls of the discolored cells nearest to and outside of the developing phellogen, have become lignified.

A study of a five-day-old wound can best be made by referring to TEXT FIG. 2. The phellogen is clearly distinguishable and has produced, except near the periphery, what may be spoken of as a distinct phellem. This phellem is about three cells deep, and the walls are highly suberized. The lignified cells just outside

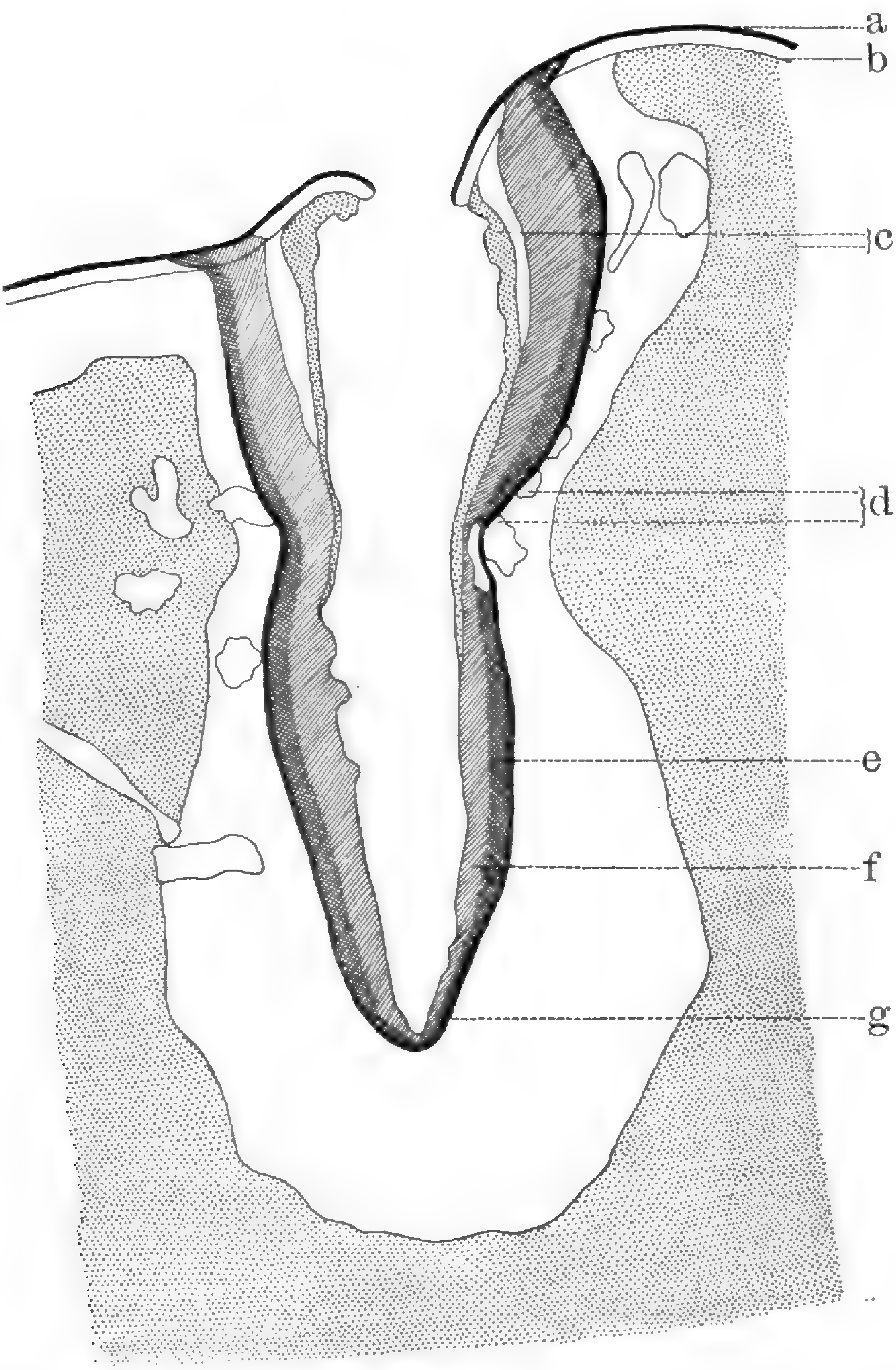

FIG. 2. Diagrammatic cross section through a five-day-old wound of an *Opuntia versicolor* plant, × 24; the open white areas consist of normal cellulose-walled cells; starch is found only in regions indicated. *a*, epidermal cells, with heavily cutinized outer walls; *b*, hypodermal tissue; *c*, cellulose-walled cells, containing stored starch; *d*, vascular bundles; *e*, cells, the walls of which have become discolored and lignified; *f*, cells, the walls of which have become discolored; *g*, suberized, thin-walled cells, produced through action of the first wound-meristem.

of them also give the suberin test, leaving, however, the large number of discolored cells unlignified, or giving the lignin test and no other. This phenomenon of cell walls giving the tests for both suberin and lignin Küster (1, p. 165) finds in the callus tissue of poplar cuttings. He says he does not doubt that the same substance, or a similar one, is the cause of these reactions. However, this statement is perhaps open to question. There seems no reason why both suberin and lignin might not be present together.

In wounds six and seven days old the phellogen has produced on the outside more suberized-walled phellem cells and on the inside what may be called a distinct phelloderm, the walls of which are pure cellulose (PLATE 9, FIG. 3). For the sake of convenience these tissues will be spoken of as phellem, phellogen and phelloderm, with the realization that, although analogous to the normal periderm of plants, they are not necessarily homologous. Although the phellem extends up through the hypoderm, few cells have been produced there. At this stage, still more of the cells in the discolored tissue have become lignified.

A wound ten days old shows several marked advances. The periderm is in all about eighteen cells deep. However, the phellogen, instead of producing only suberized phellem tissue, has given rise to a few thick-walled lignified cells, five or six in a cross section, appearing on one side, about half way down the "V." These cells were previously described in discussing the normal periderm. A further lignification of the discolored tissue is apparent. Another change is in the distribution of the stored starch. With the formation of waterproofing cells covering the wound, the normal activities of the tissues seem to be resumed, and small grains of storage starch appear in the phelloderm cells, and in the cortical cells below the phelloderm. These grains are, however, very few and very scattered.

The next wound studied in detail was twenty-four days old. Considering the various zones of tissues which extend from the wounded surface into the interior of the plant, we have (1) on the outside, the cells, in no way discolored, which retain the original stored starch they contained at the time of wounding. Some enclose oxalate crystals which have increased considerably in size.

Within is (2) the layer of discolored cells whose protoplasmic contents appears to have degenerated and the walls of which are

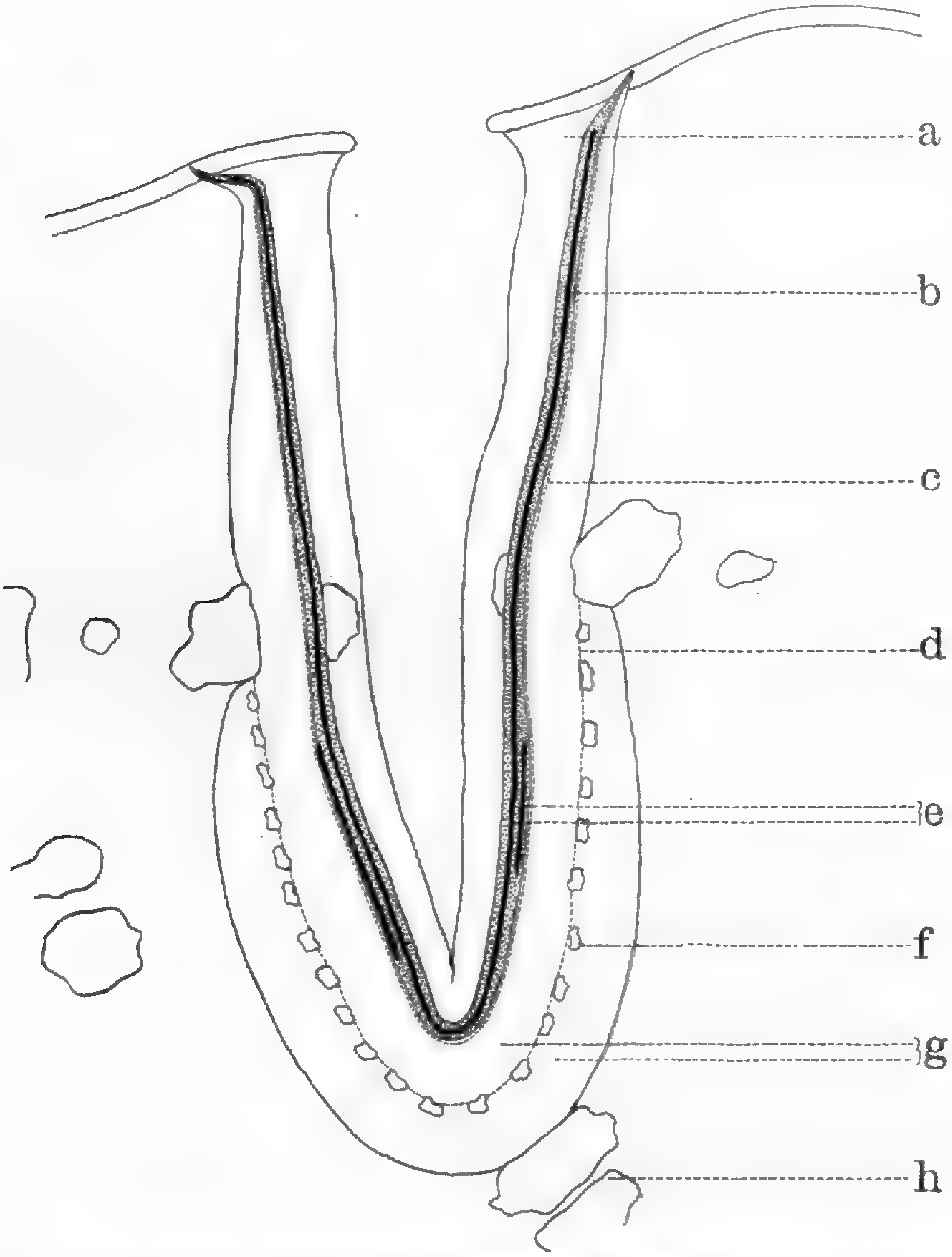

FIG. 3. Diagrammatic cross section through a thirty-one-day-old wound of an *Opuntia versicolor* plant, × 24. *a*, old tissue, bordering upon wound surface; very outermost cells are unchanged, others are discolored and their walls lignified; *b*, lignified thick-walled cells, produced by first wound-meristem; *c*, first wound-meristem; *d*, second wound-meristem; *e*, suberized thin-walled cells, produced by first wound-meristem; *f*, young vascular bundles produced by second wound-meristem; *g*, "phelloderm" tissue, produced by first and second wound-meristems, the cells being cellulose-walled, and containing small amounts of stored starch and oxalate crystals; *h*, old vascular bundles.

almost completely lignified. Bordering upon them is (3) the suberized phellem tissue, averaging four or five cells deep, below which are (4) the thick-walled lignin cells, usually two, but occasionally three deep. Inside is (5) more suberized tissue, which arises directly from (6) the phellogen. The phelloderm (7) below this, averages from ten to twelve cells deep, but is considerably thicker near the base of the "V," where the appearance of some of the cells seems to indicate the formation of a second meristem. The walls of the cells in this region are of cellulose, and the contents include small, probably newly formed oxalate crystals, and a considerable quantity of stored starch. The cortical cells (8) underneath the phelloderm have now practically regained their normal starch content.

TEXT FIG. 3 will aid in the study of a thirty-one-day-old wound. The periderm is more developed, and now includes in certain areas two more alternating layers of thick- and thin-walled tissue. However, the big advance made here comes in the further development of the second layer of meristematic tissue forming within the old periderm, parallel to the exposed surface. The function of this meristem seems to be to produce new vascular bundles.

These bundles develop first near the innermost portion of the wound, where the meristem was first seen to form. Küster (1, p. 164), in his discussion on the histology of callus, mentions the formation of tracheids, especially in the inner layer. By the union of many of these tracheids, he says, primitive vascular bundles, and a wood-like tissue are produced. However, here in the cacti, we have not just scattered rudiments of bundles, but distinct masses arranged in a definite position.

Eventually the first wound-meristem extends peripherally into the hypodermal tissue, but not until it is elsewhere very well developed. Another point to be noticed is that where the bundles were cut through, or where they are merely in a line with the wound phellogen, their prosenchymatic as well as their parenchymatic cells seem capable of reverting to a meristematic condition. Whether the stereome and hadrome tissues are able to revert is possibly questionable, but in these wounds it does not look as if the meristematic cells adjoining them had arisen from parenchyma cells some distance away.

DISCUSSION AND CONCLUSIONS

The series of changes which take place after injury, as described in the different ages of the wounds, really gives in itself a summary of what reactions took place.

The disappearance of starch in certain cells of the cacti prior to normal cork formation, is noted by Soraurer (**5**, p. 428), so it is not surprising to find it here, prior to the development of wound periderm, which, as can be seen, greatly resembles that produced normally.

This latter fact was noted by Schleiden (**3**, p. 353) who states that the best analogy to the natural cork building process is seen in the effect of wounding, and that this can be observed nowhere so easily as among the cacti. He does not, however, go greatly into detail, but describes the "drying up" of the cells on the surface of the wound, due to the "evaporation of their liquid contents" and says that this layer of "dried out" cells forms a protection to the cells underneath, out of which is formed the cork. He also states that the wound formation does not take place exclusively in cells exposed to air, but in behalf of this, gives no convincing proof.

Küster (**1**, p. 186) in his work on the histology of wound-cork, says that the walls are always thin, and often folded, and that differentiation of any kind whatsoever is entirely absent. This, of course, is not the case in these cacti. The formation of the thick-walled lignin cells is in itself enough to disprove the fact.

The essential new facts brought out by this paper are (1) the lignification of the old outer cortical cells, (2) the production of both thin- and thick-walled cells by the activity of the wound phellogen, and (3) the formation of the second interior meristematic layer, forming the new vascular bundles, parallel to the wound surface.

I wish to thank both Dr. D. T. MacDougal, of the Carnegie Desert Laboratory at Tucson, and Dr. H. M. Richards, of Barnard College, for their kindness in providing me with material, and to express my sincerest appreciation to Dr. Richards for the aid he has given me in my work.

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COLUMBIA UNIVERSITY

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Explanation of plate 9

All figures are Zeiss camera lucida drawings from hand sections, which, with the exception of that shown in FIG. 5, were taken transversely through the stem. In some cases, as noted, the sections were stained to bring out the structures more clearly.

FIG. 1. Section through the hypoderm and epidermis of stem of an *Opuntia versicolor* plant, stained with Bismark brown, × 730. *a*, epidermis; *b*, outer layer of hypodermal cells, filled with calcium oxalate crystals; *c*, stomatal opening, leading down through hypodermal cells to cortical tissue; *d*, hypodermal cells; *e*, cortical tissue.

FIG. 2. Section taken near the periphery of a three-day-old wound in an *Opuntia versicolor* plant, × 245. *a*, cells bordering on wound surface which have retained their starch content; *b*, outermost portion of starchless layer, which has become somewhat discolored; *c*, cells which will later divide, and so form the first wound-meristem; *d*, inner portion of starchless layer.

FIG. 3. Section from near the periphery of a seven-day-old wound in an *Opuntia versicolor* plant, × 390, *a*, starchless cells, with lignified walls; *b*, starchless cells, the walls of which give test for both lignin and suberin; *c*, suberized-walled cells, which have arisen through the activity of the first wound-meristem; *d*, first wound-meristem; *e*, "phelloderm" tissue, produced by first wound-meristem; *f*, starchless cortical cells.

FIG. 4. Section through a twenty-four-day-old wound of an *Opuntia versicolor* plant, stained with Bismark brown, × 475. *a*, starchless cells, with lignified walls; *b*, outermost mass of suberized walled cells, produced through activity of first wound-meristem; *c*, lignified-walled cells, produced by first wound-meristem; *d*, inner mass of suberized-walled cells, produced through activity of first wound-meristem; *e*, first wound-meristem; *f*, "phelloderm" cells, produced by first wound-meristem.

FIG. 5. Transverse optical section of lignified-walled cells, produced through activity of first wound-meristem, stained with phloroglucin and hydrochloric acid, × 390, *a*, cell lumen; *b*, middle lamella.

FIG. 6. Portion of wound-periderm produced in an *Opuntia versicolor* plant, injured thirty-one days; all tissues shown have arisen from first wound meristem; stained with Bismark brown; × 475. *a*, outer mass of suberized thin-walled cells; *b*, outer mass of lignified thick-walled cells; *c*, middle mass of suberized thin-walled cells; *d*, inner mass of lignified thin-walled cells; *e*, inner mass of suberized thin-walled cells, arising from first wound-meristem (not shown).

The ferns and flowering plants of Nantucket—XIX

Eugene P. Bicknell

SUPPLEMENTARY NOTES

Ophioglossum vulgatum L. Abundant in a meadow near the Polpis schoolhouse, June, 1909, and in a Madequet meadow, July, 1912. New stations of only a few plants are in Squam and Shawkemo, in the shade of thickets, and by a pool on the Nantucket golf links.

Osmunda spectabilis Willd. Of luxuriant growth among wet thickets in Squam.

Osmunda Claytoniana L. When mentioning Clayton's Fern in Part I of this series no other evidence of its occurrence on Nantucket could be added to Mrs. Owen's record of a single specimen long ago found by Mr. Dame. Later exploration has discovered it in the present-day flora of the island. A single tuft in a meadow near the Creeks, observed first in 1908, was still there in 1912, when, also, a thriving colony was met with in a thicket in Squam. One tuft seen on Tuckernuck, June 17, 1911.

Asplenium Filix-foemina (L.) Bernh. Common locally, especially in Squam. The largest examples, in a Quaise thicket, were over three feet in length and fourteen inches in maximum width.

Two different kinds of lady ferns grow near together at Watt's Run, one green throughout, and having small fronds with close set, merely pinnate divisions, the other, characterized especially by a red-purple rachis, having broader fronds with less crowded pinnae and more deeply cut pinnules. This red-stalked plant, which I have long thought to be a distinct species, is common enough among the forms combined under this fern, but I have not seen it elsewhere on Nantucket.

It has recently been shown by Dr. F. K. Butlers (Taxonomic and geographic studies in North American ferns. Rhodora **19**: 179–216. *pl. 123*. S 1917) that, "in the eastern parts of North

America there are two species of the lady fern group which appear to be amply distinct from each other and from the true *Athyrium Filix-femina* [of Europe]. These are *A. asplenoides* (Michx.) Desv. and *A. angustum* (Willd.) Presl." In accordance with the indications of this paper the common Nantucket plant should bear the name *Athyrium angustum*. The large form that I have mentioned answers to var. *elatius* (Link) Butters, and the red-stalked form to var. *rubellum* (Gilbert) Butters. *Athyrium asplenioides* seems not to have been found on Nantucket, although it is cited by Mr. Butters from Sandwich, Massachusetts, and from Block Island.

Dennstaedtia punctilobula (Michx.) Moore. Abundant in dryish open places in parts of Trot's Swamp.

Equisetum arvense L. Proves to be well distributed, and is abundant in many localities.

Lycopodium obscurum L. Additional stations are Taupawshas swamp and south of the Fair Grounds, well-fruited at both places.

Lycopodium complanatum L. The Nantucket plant is the var. *flabelliforme* Fernald. Localities on the eastern side of the island are in Squam, where it fruits abundantly, near Sachacha Pond, Pout Ponds, Shawkemo.

Lycopodium tristachyum Pursh. In great abundance in the pine barrens towards the South Pasture, where it fruits prolifically, the peduncles sometimes bearing seven spikes.

Pinus rigida Mill. Observed on the north side of Tuckernuck Island, June 17, 1911, a few scattered trees, none of them over five feet high.

Larix decidua Mill. In 1911 the tallest trees were estimated to be perhaps twenty feet in height.

Juniperus virginiana L. The tallest red cedars are found scattered through the oak woods in Coskaty, and probably exceed twenty feet. Among the extensive growth of red cedars on Coatue bright green and blue glaucous forms are everywhere grouped together in agreeable contrast. On July 13, 1912, both were well fruited, the blue form being the more prolific.

Typha angustifolia L. Under this name are two rather distinct appearing cat-tails that seem to call for critical study. One is the abundant species of our coastwise marshes, the other a scarcer and much more slender and narrower-leaved plant perhaps exclusively of fresh water bogs. A comparison of living plants, in July, 1912, showed a very obvious difference in their general coloring, the narrower-leaved plant quite wanting the bluish tinge of leaf and stem so characteristic of the other; the leaves were also more attenuate, and considerably longer at the time the plants were beginning to bloom, and the very slender spikes were separated by an unusually wide interval. Less obvious differences were the more striate stem of the smaller plant and the absence from its cortex of the numerous pale puncticulae that, under a lens, appeared distinctly in the contrasted form. On July 1 the slender plant was just in flower, the broader-leaved form somewhat more advanced. *Typha latifolia* was not seen in flower until July 10.

Sparganium eurycarpum Engelm. Much earlier flowering than the other island species; fruiting heads are of full size sometimes as early as the third week in June. *S. americanum* had no mature staminate flowers up to July 12, 1912.

Potamogeton Oakesianus Robbins. Flowering and fruiting abundantly in June.

Potamogeton pulcher Tuckerm. Flowering abundantly, sometimes before the end of May. As early as June 5, 1911, it was blooming freely and bore well-formed fruit, while yet the leaves were far from maturity, even the uppermost retaining their early tenderness and pinkish-brown color.

Potamogeton pectinatus L. In full flower and with immature fruit as early as June 10, 1908.

Ruppia maritima L. Professors Fernald and Wiegand, in their paper, "The genus *Ruppia* in eastern North America" (Rhodora **16**: 119–127. *pl. 110.* 1914), have referred the Nantucket plant to var. *longipes* Hagström, citing and figuring a specimen collected in Sachacha Pond by Professor F. S. Collins. Specimens of this form collected in Sachacha Pond, June 12, 1911, were in full flower. It is quite possible that plants observed in a ditch on

Swain's Neck, only just in flower September 17, 1907, were of a different form.

Zanichellia palustris L. Fresh water ditches in Shawaukemmo Spring meadow; abundant in a salt creek on Little Neck, where it was flowering and fruiting freely June 22, 1910. At both stations the plants appeared to be perfectly typical of var. *pedunculata* J. Gay, the peduncles becoming 1–3 mm. long and bearing stipitate nutlets; these were denticulate, and margined along the dorsal ridge by a narrow semi-transparent membranous expansion.

Naias flexilis (Willd.) Rostk. & Schmidt. A second station is Hummock Pond where it was collected by Miss Gardner, September 12, 1915.

Naias guadalupensis (Spreng.) Morong. In Hummock Pond, the third Nantucket pond in which it is now known to occur.

Triglochin maritima L. In flower as early as May 30, 1909; some plants still in bloom July 10, 1912.

Alisma subcordatum Raf. Pool north of the town, 1908; pool not far from the original station, 1912.

Sagittaria Engelmanniana J. G. Sm. In early flower July 10, 1912.

Sagittaria latifolia Willd. A large form occurs at No-Bottom Pond having the leaf blades and their basal lobes narrowly elongated and tapering, sometimes becoming over 20 cm. in length while only 10 mm. wide at the base.

Panicum linearifolium Scribn. True *P. linearifolium* has not been collected on Nantucket. The grass somewhat intermediate between it and *P. depauperatum*, previously referred, with reservations, to *P. linearifolium*, has been determined by Professor Hitchcock to be the variety of *P. depauperatum* mentioned by Hitchcock and Chase in North American species of *Panicum* (Contr. U. S. Nat. Herb. **15**. 1910), p. 152.

Panicum Owenae Bicknell. A fully developed mature tuft, collected July 1, 1912, well attests the distinctness of this grass from *P. Addisonii* Nash, to which less perfect examples were referred by Hitchcock and Chase (North American species of

Panicum, p. 243). It has now been collected at four stations scattered within a distance of little more than a mile north and west of the town. At each station only a single tuft was found, or a few together, growing in association with *P. depauperatum* and *P. meridionale*. In many of its characters *P. Owenae* is somewhat intermediate between these abundant Nantucket grasses and, although they belong to rather distinct groups in their genus, the possibility seems to appear that *P. Owenae* may be a hybrid between them. *P. Owenae* has been figured in Britton and Brown's Illustrated Flora from a specimen collected June 20, 1908.

Panicum Bicknellii Nash. Collected a second time on Nantucket, June 17, 1911, on the downs east of Long Pond.

Panicum dichotomum L. Additional localities are in Siasconset and Squam and near Sachacha Pond.

Panicum tennesseense Ashe. This proves to be rather a common species on Nantucket.

Chaetochloa versicolor Bicknell. A restudy of this grass has not enabled me to view it as being the same as *C. imberbis perennis* (Hall) Scrib. (*C. occidentalis* Nash) to which it has been referred. Nor does its obviously closer relationship to true *C. imberbis* establish identity with that species. Although it is said to intergrade with *C. imberbis*, I have yet to see specimens of mature plants that cannot readily be separated.

Stipa avenacea L. Quite unexpectedly this grass has proved to be a characteristic species of Nantucket occurring, however, mainly on the eastern side of the island where it is well distributed and locally abundant. It is found in scrub oak barrens along the railroad and towards Siasconset and Sankaty Head, and in Wauwinet, Pocomo and Quaise; it is also common on the Smooth Hummocks on the western side of the island, and was observed on Tuckernuck. It is locally common on Chappaquiddick Island. Inflorescence appearing June 9, 1909; just in flower June 15, 1911, June 24, 1910.

Alopecurus geniculatus L. Stations distant from the town are Quidnet and Millbrook swamp.

Aira caryophyllea L. In full flower June 5, 1910, the larger plants 7 cm. high, but many not over 1 cm. and bearing only a terminal spikelet. These diminutive plants were massed so thickly over damp sandy tracts as to have the appearance of beds of flowering moss.

Poa pratensis L. A variety that grows in sandy soil, often in pure sand, is low and pale glaucous green, with firm culms and contracted purple panicles, the leaves often slightly pubescent on the upper surface and on the sheaths. In such forms the middle and marginal veins of the palea were found to be more bearded than in the ordinary pasture form.

Panicularia grandis (S. Wats.) Nash. *P. americana* (Torr.) MacM. Of luxuriant growth about Millbrook swamp and along ditches west of the town.

Panicularia acutiflora (Torr.) Kuntze. Millbrook swamp; head of Hummock Pond; Polpis; Quidnet.

Panicularia pallida (Torr.) Kuntze. A reduced form, abundant in Rotten Pumpkin Pond, June 11, 1911, seemed to answer quite exactly to descriptions of var. *Fernaldii* Hitchc., but were regarded by Professor Hitchcock, to whom specimens were submitted, as being scarcely typical. In a recent paper on the "Status of *Glyceria Fernaldii*" (Rhodora **19**: 75–76. 1917) Dr. Harold St. John has placed this grass in specific rank under the generic name *Glyceria*, marking it off sharply from *P. pallida* by certain characters hitherto unnoticed, among which very small anthers and reflexed lower branches of the panicle seem especially noteworthy. By the test of these characters the Nantucket plant is definitely excluded from *G. Fernaldii*, its anthers, even in the dried state measuring as much as 1–1.5 mm. long, and all the panicle branches remaining flexuously ascending or erect. In other respects, however, such as narrow leaves and small few-flowered spikelets its agreement with *G. Fernaldii* seems to be quite perfect.

On Long Island the problem is even more confused. Some Long Island specimens appear to have all the characters of *G. Fernaldii* except reflexed panicle branches; other equally small-anthered forms are as broad leaved as typical *P. pallida;* in yet others the size of the anthers is half way between the two extremes. It sometimes occurs that summer rains following a drought will revive a growth of *P. pallida* in drying pond holes where it had earlier flowered as an aquatic, not infrequently bringing it to a second flowering period, and it is to be noted that this interruption of its course of growth has a repressive influence, sometimes very obvious, both on the plant as a whole and in its parts. Nevertheless between *P. pallida* and authentic *G. Fernaldii* there is a certain difference of aspect not readily definable and this, together with the differing distribution of each as worked out by Dr. St. John, may well point to something in their diversity more fundamental than a mere response to casual changes in the conditions that immediately affect growth.

Puccinellia distans (L.) Parl. At the only station for this grass known to me on Nantucket, where it is in abundance, well-developed plants possess all the characters of typical *P. distans* as defined by Fernald (Rhodora **18**: 12–13. 1916), while reduced examples, these the more numerous, correspond perfectly to the description of var. *tenuis* (Uechtritz) Fernald; intermediate forms grow with the extremes.

Festuca octoflora Walt. Not uncommon, and rather widely distributed: near the Cliff; Island View farm; Tom Never's Swamp; Madequet.

Festuca myuros L. Widely scattered and growing in close abundance at many places.

Festuca capillata Lam. Common and well distributed, even far out on the plains and commons.

Festuca ovina L. Abundant and widespread in dry sandy soils.

Bromus tectorum L. Up to 1908 this grass had become established only sparingly, although growing freely on the low dunes near the bathing beach and observed at stations as far east as Polpis and Pocomo and west towards Madequet. In succeeding years it was found to be spreading freely and fast becoming common.

Bromus hordeaceus L. The prevailing grass in many lots and fields.

Bromus secalinus L. Observed only at two stations in the town and in waste ground near Surfside.

Hordeum jubatum L. Reported by Mrs. Flynn as having been found by her as early as 1895. Collected at Siasconset, September 14, 1915, by Miss Gardner.

Hordeum vulgare L. Awned and awnless forms are frequent in old fields.

Eleocharis tricostata Torr. Almanac Pond remains the only known station on Nantucket for this spike rush. It was in early flower there June 11, 1912.

Scirpus validus Vahl. Less infrequent than at first appeared. Additional stations are: head of hummock Pond; Squam Pond; South Shore ponds; Coatue.

Carex hirta L. A second station is in a damp lot back of the Springfield House, where it was well established June 11, 1911.

Carex stricta Lam. Additional localities are near Long Pond and in a bog on Little Neck.

Carex virescens Muhl. At Beechwood, in woodland shade, occurs a taller form, dark green, with much reddened sheaths and narrow spikes, liable to be mistaken for *C. costellata* Britton. This is not an uncommon form in shaded woodland, and furnishes examples, such as I referred to in Part III of this series, that correspond accurately with Schkuhr's original illustration of this species.

Carex leptalea Wahl. Additional localities are Shawankemmo meadow, Sachacha Pond, Little Neck bog.

Carex muricata L. Found as far from the town as beyond the water works, at Tristram Coffin's monument around the base of the shaft, south of the Thorn lot and east of Island Home.

Carex incomperta Bicknell. A second station is a boggy place near Monomoy, about one and one half miles from the type locality—June 28, 1912.

Carex Howei Mackenzie, Bull. Torrey Club 37: 245. 1910. Mr. Mackenzie has thus renamed this distinct sedge, the name *C. delicatula*, given to it in Part III of this series, having been preoccupied by its employment earlier the same year by C. B. Clarke in the Kew Bulletin.

Arisaema pusillum (Peck) Nash. On Nantucket extremes of this plant are at marked contrast. At Watt's Run and in Trot's Swamp the smallest and most delicate form, with narrow black-purple spathes and slender linear spadix, may be seen growing near by much larger examples having broader, striped, or even wholly green spathes and with the spadix sometimes slightly clavate. In some plants the spathe is fluted or ribbed on the inner as well as the outer side. Observed in flower from June 1 to July 4.

Lemna minor L. Sachacha Pond; Shawkemo; Capaum Pond.

Lemna trisulca L. Choking the ditches in meadows north of the town, and in great masses floating and submerged in No-Bottom Pond.

Tradescantia virginiana L. Scattered through a sandy lot on the north side of the town; also a large tuft in a grassy opening in pine woods south of the Fair grounds, June, 1910.

Juncus balticus Willd. At several localities in Shawkemo growing in abundance along the borders of fresh water bogs near the shore as well as in brackish soil.

Lilium philadelphicum L. Leaves commonly very narrow and often somewhat scattered, suggesting an approach to *L. umbellatum* Pursh; but the capsules, although often attenuate at base, are very variable in size and form and are mostly obovoid or obovoid-oblong.

Vagnera stellata (L.) Morong. Additional localities are Trot's swamp, where it is locally common, and Thorn lot, Shawkemo. Small plants growing on the open plains near the South Shore have the later leaves perfectly glabrous beneath.

Polygonatum biflorum (Walt.) Ell. *Salomonia biflora* Farwell. To be regarded as not uncommon rather than scarce or local, but not met with on the western side of the island.

Medeola virginiana L. Restricted to the same parts of the island as the preceding and mainly to the same thickets, in some of which, especially in Shawkemo, it is a frequent plant.

Smilax herbacea L. Not infrequent, extending from the localities previously reported into Pocomo.

Hypoxis hirsuta (L.) Coville. A second station is near Long Pond where a solitary flowering plant was found June 1, 1909.

Gymnadeniopsis clavellata (Michx.) Rydb. A second station, for this orchid is "'near the Cliff, 1888,' Miss Mary Foster Coffin and Leroy Schumacher," *F. G. Floyd.*

Blephariglottis ciliaris (L.) Rydb. "'Not far from the first station, about twenty-five plants, 1897,' Lorin L. Dame," *F. G. Floyd.*

Liparis Loeselii (L.) Richard. "'Near the Cliff, one plant, 1888, and Monomoy, about a dozen plants, 1891,' Miss Mary Foster Coffin," *F. G. Floyd.*

Salix tristis Ait. On the north side of the island observed only near Capaum Pond, a single patch.

Salix petiolaris Sm. A second locality is Trot's Swamp, 1910.

SALIX BEBBIANA × CINEREA? A willow collected in Tom Never's swamp, June 3, 1908, growing with other willows, including the tree of *Salix cinerea* that is established there, and also *Salix Bebbiana*, quite unmistakably, I think, shows in combination leaf and branch characters of both these species as well as other evidences of being a hybrid.

Another ambiguous willow collected near Gibbs' Pond, September 19, 1899, is strongly suggestive of a cross between *Salix eriocephala* and *S. Smithiana*, both in the shape of the leaves and their dense velvety pubescence.

Myrica Gale L. A second station is by a tidal pond near Abraham's Point where a thick cluster six feet across and three feet in height was observed June 7, 1911, no specimens being taken. In specimens collected at the Capaum Pond station, September 12, 1907, the leaves are either wholly glabrous beneath or with some obscure pubescence on the midrib near the base. But specimens in the herbarium of Miss Gardner collected at the same station, August 21, 1915, are more or less evidently pubescent on the lower surface. I do not know, therefore, whether an exact determination of the Nantucket plant would place it with the typical form of the species or with var. *subglabra* (Chevalier) Fernald (Rhodora **16**: 167. 1914).

Myrica carolinensis Mill. At Coskaty twelve to fourteen feet high, the stoutest trunk thirteen inches in circumference; a somewhat lower shrub near Abraham's Point was fourteen inches in girth of trunk.

Hicoria alba (L.) Britton. A wide-spreading tree in a Shawkemo thicket, in 1909, was about twelve feet in height and thirty-one inches around the trunk; the lower branches descended to the ground and in their widest reach overspread a space paced at forty feet.

Hicoria glabra (Mill.) Britton. The stump of a tree in Shawkemo, recently felled in 1901, measured thirty-seven inches in circumference.

Hicoria microcarpa (Nutt.) Britton. Not far from the tree at Wauwinet previously reported is a group of three trees discovered June 10, 1911, the largest of which, about fifteen feet in height, had a maximum trunk circumference of twenty-six inches and a spread of branches close to the ground of not less than thirty-five feet.

Carpinus caroliniana Walt. "'Rare and shrublike, 1901,' Lorin L. Dame," *F. G. Floyd.*

Betula populifolia Marsh. The largest trees seen grew among pines near the Wauwinet road and, in 1911, were estimated to be eighteen feet in height.

Fagus grandifolia Ehrh. Undoubtedly the largest of our forest trees growing on Nantucket today are beeches. The tallest are in Beechwood and must be fully thirty-five feet in height. The stoutest trunks seen there were, one fifty inches, another forty-four inches in girth near the base. A much stouter tree in Squam, difficult of access through its encompassment of dense thickets, although not over twenty feet in height, measured seventy-three inches in circumference one foot above the base.

Quercus coccinea Muench. Native trees occur at Coskaty, the largest twenty-five to thirty feet in height, by estimate, the stoutest trunk forty-one inches around one foot above the base.

Quercus velutina Lam. The stoutest black oak seen on Nantucket, in Squam, measured forty-two inches in maximum girth. But much stouter trees grow on Tuckernuck where trunks were measured forty-seven and fifty inches and one sixty-eight inches in circumference about one foot above the ground, decreasing to forty-five inches a span higher up.

Quercus stellata Wang. New stations are Acquidness Point, a close group of five trees, the largest eight feet high (1911) and near Wigwam Ponds, four scattered trees from four to seven feet high (1912).

Quercus pagodaefolia (Elliot) Ashe. On June 9, 1911, the oak tree discussed in Part IV under this name was found to be dead, but a second and perfectly healthy tree of about the same height, and twenty-five inches in girth of trunk near the base, was discovered not far off in the same thicket. Some old acorn cups found beneath the tree are saucer-shaped to hemispheric, some of then contracted to a short scaly base, 1.5–3 cm. wide, the slightly tomentulose scales closely imbricated to a firm margin, the individual scales contracted to a lanceolate obtuse termination. A few partly decayed nuts were ovoid-globose, the exposed portion apparently about one half their length.

Quercus ilicifolia Wang. Two forms of the bear oak differing markedly in leaf pattern are common on Nantucket. In characteristic form the leaf of this oak has short lobes of more or less triangular general outline. In the variant the lobes of the leaves are narrower and more tapering, becoming lanceolate or even somewhat falcate, the sinuses cut much nearer to the midrib and the terminal lobe often elongated after the manner of *Q. falcata* Michx. Some leaves indeed are strikingly similar to those of that species. The two forms of leaf present extremes of divergence that are very noteworthy and suggest an interesting subject for critical study.

Quercus rufescens (Rehder) sp. nov.

Quercus prinoides var. *rufescens* Rehder, Rhodora **9**: 60. 1907.

This scrub oak proves to maintain so notable a constancy in its characters and is so readily recognizable that, as a result of field observations both on Nantucket and on Long Island I have come to accept it as essentially distinct from *Q. prinoides;* nor have I yet encountered any trees so nearly intermediate between the two as to have the appearance of being hybrids.

It may be noted that the anthers of *Q. rufescens* are perceptibly smaller on relatively shorter filaments than those of *Q. prinoides,* that is to say this proved to be true in numerous cases when I was enabled to make satisfactory comparison in the field.

QUERCUS ALBA × RUFESCENS? An oak about five feet high of somewhat straggling form, observed near the Wigwam Ponds, July 6, 1912, conveyed a strong impression of being a hybrid between *Q. alba* and *Q. rufescens.* The pubescence of the leaves and branchlets is much as in *Q. rufescens,* while the size of the leaves, some of them 14 × 8 cm., and their deep lobing seem to point rather clearly to *Q. alba* as one of its parents.

QUERCUS ILICIFOLIA × VELUTINA Rehder. A thriving oak, a hybrid, there seems little reason to doubt, grows in the dense thicket on the western side of Dyleave Swamp. It was about twelve feet in height and nineteen inches in girth low on the trunk June 26, 1910. In its foliage it is very distinct from any other Nantucket oak that I have seen, and the forms of its leaves and their pubescence suggest, rather convincingly, I think, a mixed origin from the two oaks above indicated as probable parents. Such a hybrid was described and figured by Mr. Rehder (Rhodora 3: 137. *pl. 24.* 1901). The leaves of the Nantucket tree show remarkable variation in form, and have no close similarity to those figured by Mr. Rehder, but the pattern characters by which they differ appear to be such as might well result from a crossing of *Q. velutina* with the form of *Q. ilicifolia* having narrow deeply cut leaf lobes rather than with the more usual short-lobed form. They are, however, considerably larger than those which Mr. Rehder has described, the largest being 17 × 14 cm. When young the lower surface is whitened with a close tomentulose pubescence, although in less degree than those of *Q. ilicifolia,* but this is impermanent, the leaves becoming quite green beneath in age. The cups of some old acorns found beneath the tree were turbinate, their scales tomentulose to partly glabrate; nuts conic ovoid or oblong, 10–14 mm. long, tomentulose and strigose towards the apex.

QUERCUS COCCINEA × VELUTINA? Ambiguous trees at Coskaty growing with *Q. coccinea* and *Q. velutina* are difficult to understand except as hybrids of those species.

Quercus palustris Muench. Besides the introduced pin oaks still persisting in the Thorn lot, a few scattered trees, the largest eight to ten feet in height, were observed among the Miacomet pines in 1909, and a single tree among pines south of the fair grounds in 1910. The latter had the appearance of being adventive.

Quercus bicolor Willd. Some small trees persist in the Thorn lot among the other introduced oaks previously reported as growing there.

Humulus Lupulus L. Localities far from cultivated ground where the hop has every appearance of being indigenous are Trot's swamp; west side of Long Pond; Swamp in Madequet, where there is much of it.

Cannabis sativa L. Prospect Hill, herbarium of Miss Gardner; Pleasant Street, Mrs. Flynn.

Rumex crispus L. Plants with the grain short and rounded seem to be less common than those with attenuate and acute grain (*Rumex elongatus* Guss.); the character, however, seems to be inconstant and even varies much in the same plant.

Rumex persicarioides L. Dr. Harold St. John, who has revised our former understanding of this species (Rhodora **17**: 73–83. *pl. 113, f. 34.* 1915), considers that the Nantucket plant should stand as *Rumex maritimus* var. *fueginus* (Phil.) Dusén.

Polygonum maritimum L. Professor Fernald has convincingly shown that our plant is distinct from the European *P. maritimum* and should bear the name *Polygonum glaucum* Nutt. (Rhodora **15**: 68–73. 1913).

Persicaria pensylvanica (L.) Small. Two varieties of this common plant have recently been recognized by Professor Fernald (Rhodora **19**: 70–73. 1917). The prevailing Nantucket form, described in Part V of this series, is *Polygonum pensylvanicum* var. *nesophilum* Fernald. The closely related var. *laevigatum* Fernald also occurs on Nantucket as well as the more distinct type form of the species, which is scarce.

Agrostemma Githago L. Occasional in fields and waste places.

Dianthus Armeria L. In abundance by the railroad near the town; on the Cliff; near the waterworks.

Alsine graminea (L.) Britton. Old cartway over the commons east of the town, June 14, 1911; north of the town, June, 1912.

Castalia odorata (Ait.) Woodville & Wood. In Wigwam Pond, July 7, 1912, some leaves were as large as twelve and one half inches long and wide.

Liriodendron Tulipifera L. Mr. Floyd has sent me a note that young tulip trees were found by Mr. Dame in 1901 "growing freely in the Thornlot." Had any of these trees long survived it would seem that other collectors would have since observed them.

Coptis trifolia (L.) Salisb. Bloomingdale Swamp, June 17, 1914, collected by Mrs. G. A. Spear; specimen examined by me in Miss Gardner's herbarium. It is a matter of much satisfaction that the gold thread is thus definitely established as a Nantucket plant. It had been admitted in its place in this catalogue because included in Mrs. Owen's list, and also reported to me as having been found in the Thorn lot, but it has since appeared that both of these records are open to serious doubt. In a letter to Mr. Floyd under date of August 21, 1911, Mrs. Owen wrote, "I find no authority for *Coptis* on Nantucket," adding that she could not understand how the name got into the original Godfrey list. "When I was compiling my 'Flora of Nantucket,'" she stated further, "I probably used that printed list and took without question what I found there." The Thorn lot report I feel sure should be regarded as an error involved in some way with the trifoliolate-leaved *Rubus hispidus*, an abundant plant in that locality.

Actaea rubra (Ait.) Willd. In dense thickets eastward from the locality previously reported as far as Beechwood. Much scarlet fruit June 26, 1912.

Ranunculus repens L. Abundant all over the island, mainly in low grounds.

Thalictrum polygamum Muhl. Previously admitted because of Mrs. Owen's record on the authority of Mr. Dame. The discovery that *Thalictrum dasycarpum* Fisch. & Lall. occurs on Nantucket now makes necessary a substantiation of this record.

Sassafras Sassafras (L.) Karst. Trees as high as twelve to fifteen feet were seen in Shawkemo and Quaise, and in Squam one not less than eighteen feet, its trunk twenty-three and one quarter inches in circumference one foot above the ground.

Radicula palustris (L.) Moench. Waste ground north of the town, June 9, 1911, a group of plants just in flower; bog near Oldest House, August 18, 1915, herb. Grace Brown Gardner.

Erysimum cheiranthoides L. Recently collected by Miss Gardner on the Cliff road, a second station for Nantucket.

Conringia orientalis (L.) Dumort. Yard on North Water Street, June 17, 1911, one well-fruited plant; waste ground at Surfside, July 9, 1912, several fruiting plants and one just in bloom.

Reseda lutea L. A few plants in a field near Island Home, just in flower June 14, 1911; Fay farm, Squam, July 11, 1912, in flower and fruit. The original station in Polpis mentioned by Mrs. Owen was visited by Mr. Floyd in 1895; some plants were still growing there "although subjected to occasional mowing."

Drosera rotundifolia L. Racemes of buds but no open flowers, July 6, 1912. On Martha's Vineyard belated flowers of this sundew, as of the next, persist into September.

Drosera intermedia Hayne. *D. longifolia* L. in part. First flowers July 9, 1912.

Drosera filiformis Raf. Not yet in flower July 2, 1912.

Rosa cinnamomea L. Here and there by fieldsides and fence borders in the suburbs.

Amelanchier nantucketensis Bicknell. Further observation of this shadbush, later in the summer than I had previously studied it, show that the fruit ripens early in July, when it is red or purple in color, later becoming deep purple blue. By the middle of the month the shrubs, sometimes even those of the smallest size, may be seen thickly ornamented with the glaucous fruit in all stages of maturity and varying in color from white through pink and red to purple all in the same cluster, producing a variegated and very pleasing color effect.

It has been suggested by Professor Wiegand in a paper entitled, "The genus *Amelanchier* in eastern North America" (Rhodora **14**: 117–161. *pl. 95, 96.* 1912) that this Nantucket shrub is a hybrid between *A. oblongifolia* and a proposed new species, named by him *A. stolonifera.* This theory, I think, scarcely takes sufficiently into account that *A. nantucketensis* is one of Nantucket's characteristic shrubs, more numerous indeed, and more generally distributed than the other shadbushes of the island, and also bearing fruit more abundantly and with greater regularity season by season. In Professor Wiegand's description of his *A. stolonifera* there seems to be little to differentiate it from *A. nantucketensis* beyond larger petals, a variable character, I find, in *A. nantucketensis*, and densely woolly summit of the ovary. In *A. nantucketensis* the exposed surface of the ovary is, as I have described it, nearly or quite glabrous; this is its condition at maturity, in its earlier stages it is clothed with a white woolly pubescence. Its close relationship to Professor Wiegand's new species is also to be inferred from its having been attributed to Nantucket on the basis of Miss Day's collection, No. 95, June, 1900, a sheet of which in the herbarium of the New York Botanical Garden formed part of the material used in formulating my description of *A. nantucketensis.* This specimen is the counterpart of numerous specimens of my own collecting, and was not cited only for the reason that the species was so abundant on Nantucket that no need appeared of any citation of specimens other than the type and co-type.

Crataegus chrysocarpa Ashe. A group of four shrubs, June 29, 1912, about two miles west of the original station.

Prunus maritima Wang. I do not know that the yellow or amber fruited form of the beach plum has ever been found on Nantucket. I was told that it occurred on Tuckernuck and it is locally abundant on Chappaquiddick Island and in other parts of Martha's Vineyard. It is not generally disseminated and is evidently scarce elsewhere than in the localities where it abounds. I have myself seen little of it except as gathered by the islanders who, in collecting it, are accustomed to keep it separate from the purple form for use, I was told, in making a light-colored jelly. On September 16, 1913, a group of plum gatherers returning across Chappaquiddick Island were laden with baskets of these plums, as many filled with the amber fruit as with the purple. I have likewise seen large sacks of the amber plums at Edgartown which, it was said, had been brought in from Chilmark. No constant difference in size or form between the yellow and purple fruit could be discovered, but on Chappaquiddick I observed a particular bush of the yellow-fruited form on which the plums were of unusually large size and ovoid rather than globose. The yellow fruit is somewhat translucent, and varies in color from amber to light yellow and pale orange.

Laburnum vulgare Gris. Several well-grown trees of the laburnum are scattered in partly open ground among the pines near Miacomet Pond, where they were in full bloom June 11, 1911.

Erodium cicutarium (L.) L'Hér. "A well-established colony of about twenty plants in a field near the Thorn lot," in flower and fruit, September 15, 1915; specimens in the herbarium of Miss Grace Brown Gardner. Not reported as growing in Nantucket since 1851.

Linum striatum Walt. Collected by Miss Gardner at Hummock Pond, September 12, 1915, the second known station on Nantucket.

Cicuta bulbifera L. Collected by Miss Gardner, September, 1915, at the original station discovered in 1899 by Mrs. Flynn.

Arctostaphylos Uva-ursi (L.) Spreng. Mr. Floyd writes me that he has occasionally observed on the commons a form with crimson flowers, and that Mrs. Owen had told him that this crimson-flowered bearberry had been familiar to her for many years.

AMSINCKIA ARENARIA Suksd. A recent paper by Dr. J. Francis Macbride (A Revision of the North American Species of *Amsinckia*, Contr. Gray Herb. 49. 1917) makes clear that the plant reported in Part XIV of this series as *A. intermedia* F. & M. is not that species. Specimens have been submitted to Dr.

Macbride who considers them referable, perhaps not without some uncertainty, to *A. arenaria* Suksd. of the northwest.

Thymus Serpyllum L. Law nor Sankaty Bluff, August 28, 1915, Miss Gardner.

Setiscapella subulata (L.) Barnhart. Peat bog between Polpis and Quidnet, 1915, Miss Gardner.

Houstonia caerulea L. Miss Alice O. Albertson has sent me an interesting specimen of this species collected on the Nantucket golf course, May 13, 1916. It is matted and subspreading, the stems and long peduncles relatively stout, and the flowers large, spreading 1.5 cm. in the pressed plant; the calyx lobes are oblong to obovate-oblong and more or less foliaceous, becoming 1.5 mm. or more wide, with somewhat spreading tips, and equalling the short and broad tube of the corolla in the single specimen seen.

Viburnum venosum Britton. The largest example seen, Rattlesnake bank, June 8, 1911, was of the stature of a small tree, the trunk eleven inches in girth near the base.

Lactuca virosa L. Collected by Miss Gardner in the town, August 24, 1915, a second station on Nantucket for this intruding weed, and too probably an indication that it is becoming established there.

ADDENDUM

Under *Sabbatia campanulata* in Part XIV of this series read, on page 32, *S. stellaris* for *S. campanulata*.

The following two plants, new to Nantucket, have recently come to light in a collection of specimens kindly sent to me by Mrs. Flynn:

*HELIANTHUS PETIOLARIS Nutt. Old field near Windmill, August 5, 1911, collected by Mrs. Nellie F. Flynn.

*KOELLIA INCANA (L.) Kuntze. Collected by Miss Mina K. Goddard, August 17, 1895. Locality not mentioned. The species is an interesting addition to the native flora of Nantucket. Mrs. Flynn, who has recently made inquiries in regard to this specimen, writes me that Miss Goddard believes it was probably found at Wauwinet where, as disclosed by her records, she collected plants on the very date that appeared on the specimen label.

INDEX TO AMERICAN BOTANICAL LITERATURE

1902-1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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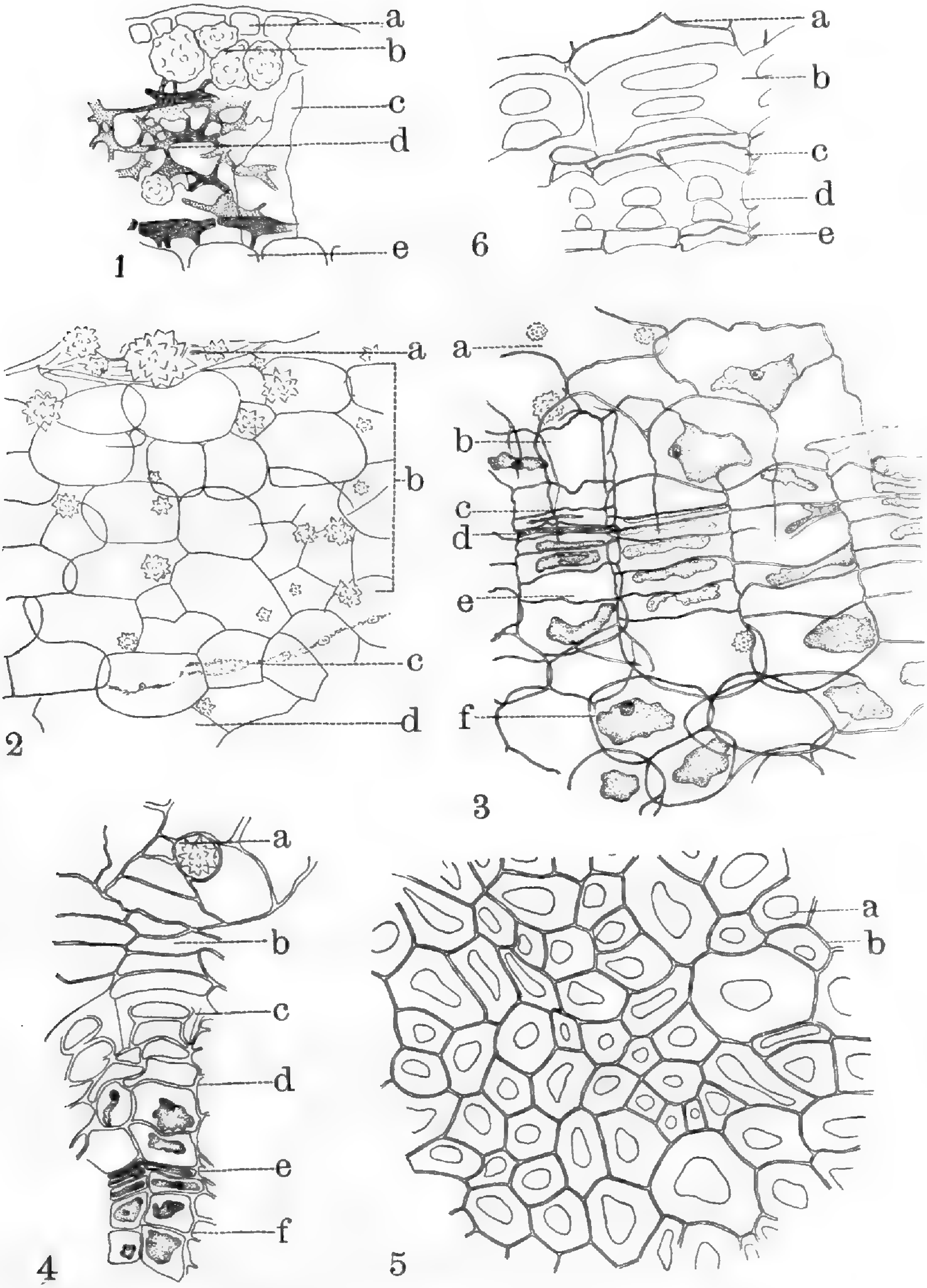

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Regeneration in Phegopteris polypodioides*

Elizabeth Wuist Brown

(WITH THREE TEXT FIGURES)

Introduction

The fact that plants are able to reproduce lost parts was known long before it was discovered that animals possessed this same power. It was natural that the first experimental investigation on regeneration in plants should have been carried on with the higher plants as it was a common practise to propagate many plants by means of cuttings. However, the study of regeneration has since been extended to include not only the lower groups of plants, such as the algae, fungi, liverworts, mosses and ferns, but also many groups of animals. This has resulted in the accumulation of a large amount of evidence regarding the possibilities of regeneration by most groups of organisms.

Experimental evidence has also indicated that the regenerative power of some plants is much greater in earlier than later life, while in others this power is lost completely in later life.

Goebel (**2**, pp. 196–203), experimenting with ferns, found that the primary leaves of the young sporophytes of some ferns, either while attached to the sporophyte or cut off and placed under moist conditions, were able to regenerate new fern plants or prothallia or intermediate forms between leaves and prothallia. Here the regenerative power seemed confined to the primary

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* Contribution from the Osborn Botanical Laboratory.

[The Bulletin for September (**45**: 353–390. *pl.* 9) was issued September 20, 1918.]

leaves of the young sporophytes, as in no case did regeneration take place with leaves of the older plants. It was thought of interest to see if the primary leaves of the young sporophytes of *Phegopteris polypodioides* Fée could regenerate in the manner indicated by Goebel, as apogamy had occurred so frequently in cultures of this fern.

EXPERIMENTAL

Spores of *Phegopteris polypodioides* were obtained from Brooklin, Maine, through the kindness of Dr. A. H. Graves. Cultures were started in the early part of October. The spores were sown on Prantl's and Knop's full nutrient solutions and modifications of these solutions. After the spores were sown the cultures were placed before an east window. In an effort to induce apogamy the prothallia were not transferred to fresh nutrient solutions from time to time, but were allowed to develop upon the same nutrient solutions upon which the spores had been sown. As a result growth and development of the prothallia was slower and fewer sporophytes formed, the majority of which were apogamous.* The primary leaves of both normal and apogamous young sporophytes were used in the regeneration experiments.

March 14, 1917, primary leaves 5–7 mm. in length were cut from the young sporophytes and placed on sand in watch glasses. In some cases the petiole of the leaf was inserted in the sand to a depth of 1–2 mm., placing the blade of the leaf in an upright position. In other cases the leaf was laid on the sand; while in still others various parts of the blades were covered with the sand. The sand in some of the watch glasses was moistened with Knop's and Prantl's full nutrient solutions, while in the others it was moistened with distilled water. All the cultures were placed in large plates and covered with bell jars. The sand was never allowed to dry and water was kept standing in the plates. In this way the air under the bell jar was always moist.

No experiments were tried to see if the leaves would regenerate while attached to the young sporophytes and no such cases were observed among either the solution or soil cultures, although frequently the leaves of this and other species of ferns, especially in

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*Wuist, Elizabeth Dorothy. Apogamy in *Phegopteris polypodioides* Fée, *Osmunda cinnamomea* L., and *O. Claytoniana* L. Bot. Gaz. **64**: 435. 1917.

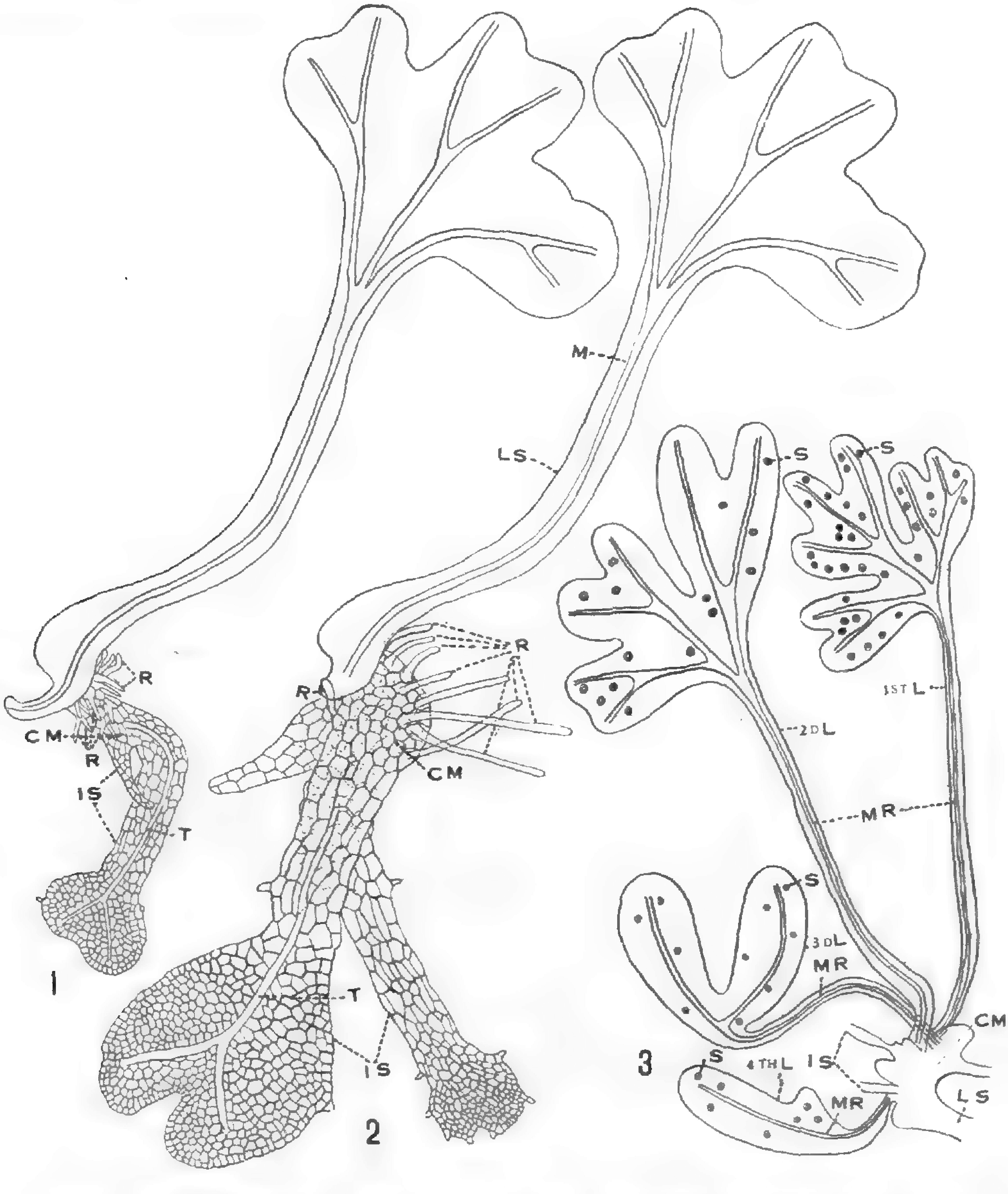
the soil cultures became appressed to the soil as a result of accidents in watering.

Only one case of regeneration was obtained, although a large number of leaves were experimented with. Regeneration began in about six weeks after the leaf had been removed from the sporophyte and laid on sand moistened with Knop's full nutrient solution. One side of the petiole, near its base, was destroyed by decay, and a short distance above this point on the opposite side of the petiole a slight swelling occurred, from which a cellular mass developed. At first it was slightly elongated, FIG. 1, afterwards it became much thickened and broadened, FIG. 2, and finally assumed the shape shown in FIG. 3. From this cellular mass there developed two intermediate structures between leaves and prothallia, then rhizoids and four normal leaves. Neither a true root nor a stem "Anlage" was formed.

The first of the intermediate structures resembled a very much elongated prothallium, one cell in thickness, with an expanded heart-shaped apex. Tracheids arranged in rows resembling a true midrib extended up through the portion of the structure corresponding to the petiole into the expanded or blade-like part. Here the rows of tracheids branched dichotomously one branch going to each lobe (FIGS. 1 and 2). The margins of both the elongated and expanded regions were for the most part smooth, with the exception of two papillae, one of which developed on the elongated and one on the expanded part.

The second intermediate structure which developed from the cellular mass was even more thalloid in form and structure than the first one. Both the elongated and broadened portions like those of the first were only one cell in thickness. The expanded portion differed somewhat in appearance as it was not so distinctly heart-shaped and its margin bore many more papillae. There were no indications of tracheids present in either of the portions representing petiole or blade.

Growth was rapid and apparently normal in both of these intermediate structures, but the second one never attained the size of the first. Neither was long-lived, death occurring soon after the normal leaves began to develop. The rhizoids resembled in every way those of a normal fern gametophyte. They formed from the cells of both the upper and lower surfaces of the cellular mass, although the majority came from the upper surface cells. Their



Figs. 1–3. Stages in the regeneration of the young leaf of a sporophyte of *Phegopteris polypodioides* Fée, x 550. *R*, rhizoids; *LS*, leaf of sporophyte; *CM*, cellular mass; *IS*, intermediate structure; *MR*, midrib; *T*, tracheids; *S*, stomata; *1st L*, first leaf; *2d L*, second leaf; *3d L*, third leaf; *4th L*, fourth leaf.

development began at about the same time as that of the intermediate structures.

After a number of rhizoids had been formed from the surface cells of the mass, normal leaves began to develop. The first and second of the four leaves appeared almost simultaneously and their growth was very rapid. They resembled, in all respects, the leaves of a normal young sporophyte of this species of fern (FIG. 3); although the blade of the second leaf was somewhat simpler in form, having only two main divisions, each of which was lobed, instead of three main lobed divisions. However, such irregularities are to be noted in leaves of normal young sporophytes of this and other species of ferns. These two leaves attained a height of 6 mm. The third leaf, which was much slower in growth and development reached a height of only 4 mm. and was much simpler in form. The blade consisted of only two lobes, which were entire. The fourth leaf showed still greater simplicity in form and reached a height of only 3 mm. The blade was almost entire, with a slight lobe on the one side. The blades of these latter leaves, like those of the first and second ones, bore stomata.

DISCUSSION AND CONCLUSION

The various theories which account for regeneration, as advanced by the many writers on the subject, consider the following influences: (1) external influences to which the plant is subjected; (2) tendencies inherent in the plant body.

The factors considered as the possible controlling or influencing ones may be placed in the following classes: (1) nutrition disturbances; (2) wound stimuli; (3) changes in the water content; (4) the accumulation, at certain places, of definite formation substances; (5) the presence of dormant or latent rudiments; (6) correlation; (7) age and maturity of the parts; (8) form disturbance; (9) growth tension; (10) interruption of the functions of respiration, transpiration or photosynthesis; (11) isolation from the influence of the whole; (12) presence of enzymes which are responsible for the formation of the part regenerated.

The fact that regeneration was never observed in attached leaves of *Phegopteris polypodioides* and did occur in a leaf which had been separated from the plant would seem to indicate that the separation from the repressing influence of the plant body played an important part, as believed by Loeb (4, p. 153); although the fact that cases have occurred in other species of ferns when the leaves were still attached would not seem to refute this theory. Experimental evidence has shown that many species of ferns, either in the younger or older stages of their gametophytic or sporophytic life history and especially in the younger stages, does not always react in the same way to the same environmental conditions; but each has a sort of individualism which enables it to react in the way best fitted for its particular needs. It seems very probable that in this particular case regeneration is closely connected with nutrition for the reason that the severed leaf was not able to regenerate immediately another sporophyte, but could produce a cellular mass which appeared to be a reversion to a prothallus-like structure. This structure after rhizoids developed gave rise, in an apogamous manner, first to structures intermediate between leaves and prothallia; then, as the number of rhizoids increased, enlarging the absorptive surface, which in turn increased the amount of nourishment, true leaves were produced. The first of these were the ordinary type of young sporophytic leaf but later ones were much more primitive in character, due doubtless to the lowered vitality of the prothallus-like structure. This coincides with Goebel's (1, vol. 2, p. 42) views. He considers a reversion to a juvenile form as being the result of unfavorable conditions to which the plant is subjected. It is also in keeping with the results obtained by Miss Kupfer (3, p. 229) in her experiments, which indicated that at the time of cutting under normal conditions reserve food was present in sufficient quantities to initiate the first stages of regeneration. If this food was absent and its formation prevented regeneration was prohibited.

Such an explanation as this does not lose sight of the importance of the other factors so strongly emphasized by various workers, for all these factors doubtless play an important part in nutrition.

Experimental data in this particular case are not extensive enough to permit drawing conclusions as to which of the above factors or groups of factors acting separately or together, was the determining one. However, since an intimate relation exists between growth and regeneration and since growth is dependent upon nutrition, it would seem as if some phase of nutrition must be an important factor in regeneration, if not the most important factor.

SUMMARY

1. Regeneration took place near the base of the petiole of a detached leaf of a young sporophyte of *Phegopteris polypodioides*, placed upon sand moistened with Knop's solution in moist air.

2. A cellular mass, resembling a prothallium, was formed, from which rhizoids, intermediate structures between leaves and prothallia, and true leaves developed.

3. At first true leaves resembling those of normal young sporophytes were formed; then leaves of a much simpler type developed.

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Taxonomy and distribution of Adenostegia

ROXANA STINCHFIELD FERRIS

(WITH PLATES 10–12)

The genus *Adenostegia* was first described by Bentham* with the description of one species, *A. rigida*. Ten years later the same author published in De Candolle's Prodromus† four Nuttallian species, substituting Nuttall's manuscript name, *Cordylanthus*. This change was made on the ground that the meaning of the word *Cordylanthus* (*cordule*, club; *anthos*, flower) was more characteristic of the new species than was *Adenostegia* (*aden*, gland; *stege*, covering). The proper generic name, according to present-day rules of nomenclature, was revived by Greene in 1891,‡ and later accepted by Kuntze § and Wettstein. ||

The affinities of *Adenostegia* are with *Castilleia* and *Orthocarpus*, and in Wettstein's generic arrangement of the Scrophulariaceae it is placed between them. The most noticeable likeness to *Castilleia* is shown in the section *Anisocheila* in the elongated upper lip of the corolla. A much more marked connection is found between the section *Chloropyron* and *Orthocarpus*, for here there are points of resemblance not only in the distinctly three-saccate flower but in the spike-like inflorescence as well.

The sections *Euadenostegia* and *Chloropyron* of *Adenostegia* exhibit the conspicuous degree of variability that is characteristic of many of the Scrophulariaceae. In *Euadenostegia* there are, besides the fixed species, two plastic groups, *rigida* and *pilosa*, in which the range of intraspecific variation creates difficulties in defining the species. The species of the *rigida* group are characterized by their hispid or hirsute pubescence and their tri-

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* In Lindley, J. A natural system of botany. Ed. 2. 445. 1836.

† Prodr. Syst. Nat. 10: 597, 598. 1846.

‡ Some neglected priorities in generic nomenclature. Pittonia 2: 180–181. 1891.

§ Rev. Gen. Plant. 2: 456, 457. 1891.

|| In Engler & Prantl, Nat. Pflanzenfam. 4^{3b}: 98. 1891.

partite, callous bracts. The species of the *pilosa* group have a puberulent or pilose pubescence and their bracts are typically linear, though they are parted in *A. viscida* and *A. Hanseni.*

The genus is confined to western America and is characteristic of California and the Great Basin. Of the twenty-one species, there are but five that are not recorded from California and nine are known only from that state. According to the present records the range of the genus extends from Washington and southwestern Montana to Sonora, Chihuahua, and northern Lower California.

The members of the genus are found principally in open, exposed places in the Upper and Lower Sonoran and the Arid Transition Zones. Certain of the species may at times be met with in the Humid Transition Zone, but they occur only on exposed slopes that are truly "islands" of Upper Sonoran. All the species of the section *Chloropyron,* which is in part coastal, are found in salt marshes and on alkaline soils. This unusual habitat may account for the fact that this group appears not to conform to the ordinary zonal lines.

In preparing this paper I have had the opportunity of examining the material in the herbaria of the following institutions: the National Herbarium, the University of California and Stanford University.

I wish to express appreciation of the kindness shown me at the University of California during my work in that herbarium and to the National Herbarium for the loan of material. I also wish to thank Dr. L. R. Abrams for his advice and assistance and Dr. B. L. Robinson, of the Gray Herbarium, for fragments and photographs of types.

ADENOSTEGIA Benth.

Adenostegia Benth. in Lindley, Nat. Syst. ed. 2. 445. 1836.

Cordylanthus Nutt.; Bentham in De Candolle, Prodr. **10**: 597. 1846.

Chloropyron Behr, Proc. Calif. Acad. **1**: 61. 1855.

Rigid, summer-blooming annuals with divaricate or paniculate branches and yellow roots. Leaves alternate, entire, parted or dissected, those subtending the branches much longer than the others, deciduous with age; flowers in spikes, heads, or scattered along the branches; floral bracts entire, dissected, or parted;

calyx one- to two-leaved, lower leaf, when present, saccate at the base, upper leaf erect, winged at the base except in the section *Chloropyron;* corolla cylindrical, bilabiate, the lips nearly equal except in *A. laxiflora;* upper lip enclosing stamens and pistil, lower lip obscurely three-crenulate or entire, more or less saccate; stamens two or four, in unequal pairs, the anthers one- or two-celled, the lower cell, when perfect, subtending the upper, filaments generally hairy; capsule flattened, lanceolate or slightly rounded; seed irregular, more or less reticulate.

Key to sections

Lower lip of the corolla one-half the length of the upper lip.	I. ANISOCHEILA.
Lower lip of corolla equalling upper lip.	
Tube of the corolla one fifth the length of the throat.	II. PRINGLEA.
Tube of corolla more than one fifth the length of the throat.	
Calyx diphyllous.	III. EUADENOSTEGIA.
Calyx monophyllous.	
Calyx-leaf equalling corolla.	
Inflorescence capitate.	IV. KINGIA.
Inflorescence spicate.	VI. CHLOROPYRON.
Calyx leaf one half the length of the corolla.	V. DICRANOSTEGIA.

Section I. ANISOCHEILA

Cordylanthus § *Adenostegia* (in part) Gray, Proc. Am. Acad. **7**: 381. 1868; Wats. Bot. King's Exped. 459.

Cordylanthus § *Anisocheila* Gray, Syn. Fl. $\mathbf{2}^1$: 303. 1886.

Adenostegia § *Anisocheila* Wettstein in Engler & Prantl, Nat. Pflanzenfam. $\mathbf{4}^{3b}$: 98. 1891.

Flowers scattered along the stems; calyx diphyllous, upper lip of corolla twice as long as lower; anthers one-celled or with vestige of second cell.

1. ADENOSTEGIA LAXIFLORA (Gray) Greene

Cordylanthus laxiflorus Gray, Bot. Mex. Bound. **2**: 120. 1859; Gray, Proc. Am. Acad. **7**: 383; Wats. Bot. King's Exped. 232, 460; Gray, Syn. Fl. $\mathbf{2}^1$: 303.

Adenostegia laxiflora Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Wettstein in Engler & Prantl, Nat. Pflanzenfam. $\mathbf{4}^{3b}$: 98.

Paniculately branching annual, 3–4 dm. high, pubescent throughout with soft, glandular hairs; leaves 8–13 mm. long, one- to three-parted; flowers many, solitary or in groups of two to four; floral bract one half the length of calyx, deeply three-parted into linear divisions rounded at the apex; upper calyx-leaf 11–16 mm. long, six- or seven-nerved, winged at the base, lanceolate or bidentate, pubescence sparse; lower calyx-leaf 10–15 mm. long, four-nerved, wider than the upper, rounded at the apex; corolla 16–18 mm. long, glabrous, the lower lip saccate; filaments glabrous; capsule 7–8 mm. long, slightly rounded; seeds reticulate. [PLATE 10, FIG. 1; PLATE 11, FIG. 1.]

TYPE LOCALITY: "Rocky hills, Sonora, Mexico, *Thurber*."

DISTRIBUTION: Hills and ravines in Arizona and northern Sonora.

SPECIMENS EXAMINED:—ARIZONA: "Point of Mountain," *Rothrock 721;* Pine Creek near Pine, *MacDougal 693;* hills, Beaver Creek, *Purpus 8298*.

Section II. PRINGLEA

Flowers in heads; calyx diphyllous; tube of corolla short and dilated; stamens four, perfect, the filaments villous.

2. ADENOSTEGIA PRINGLEI (Gray) Greene

Cordylanthus Pringlei Gray, Proc. Am. Acad. **19**: 94. 1883; Gray, Syn. Fl. **2**^{1}: 453; Jepson, Fl. W. Mid. Calif. ed. 2. 387.

Adenostegia Pringlei Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Jepson, Erythea **7**: 112; Jepson, Fl. W. Mid. Calif. 416.

Slender, glabrous annual, 4–6 dm. high; leaves 5–9 mm. long, linear-filiform, early deciduous, the lower sparsely pubescent, the upper glabrous; heads many, compact, three- to five-flowered; floral bracts 5–7 mm. long, glabrous, with five to seven equal lobes; calyx-leaves 9–11 mm. long, nearly equal, upper part covered with large, tack-like glands; corolla 8–9 mm. long, lips densely hairy; capsule rounded. [PLATE 10, FIG. 2; PLATE 11, FIG. 2.]

TYPE LOCALITY: "California, on dry hills in Lake Co., August, 1882, Pringle."

DISTRIBUTION: Exposed slopes in the mountains of Lake and Napa Counties, California; Upper Sonoran Zone.

SPECIMENS EXAMINED:—CALIFORNIA: Lake County, August, 1882, *Pringle;* Snow Mountain, Lake County, August 25, 1892, *Katharine Brandegee;* Cobb Mountain, Lake County, 1910, *Katharine Brandegee;* near Bartlett Springs, Lake County, August, 1916, *A. Stinchfield.*

Section III. EUADENOSTEGIA

Cordylanthus § *Adenostegia* (in part) Gray, Proc. Am. Acad. **7**: 381. 1868; Wats. Bot. King's Exped. 459; Gray, Bot. Calif. **1**: 580; Gray, Syn. Fl. **2**^{1}: 303.

Adenostegia § *Euadenostegia* Wettstein in Engler & Prantl, Nat. Pflanzenfam. **4**^{3b}: 98. 1891.

Flowers scattered along the branches or in heads; calyx diphyllous; corolla lips equal; anthers one- or two-celled, filaments villous.

Key to species of § Euadenostegia

- Stamens two . . . . 3. *A. capitata.*
- Stamens four.
  - Anthers one-celled . . . . 9. *A. Nevinii.*
  - Anthers two-celled.
    - Bracts entire or with the callous tips notched.
      - Herbage densely cinereous pilose . . . . 4. *A. pilosa.*
      - Herbage puberulent with few pilose hairs . . . 5. *A. tenuis.*
    - Bracts distinctly parted.
      - Bracts three-parted.
        - Flowers scattered along the branches; herbage pilose.
          - Tips of bracts enlarged or calloused.
            - Flowers 14 mm. or less long; middle lobe of bract exceeding lateral lobes . . . . 6. *A. viscida.*
            - Flowers 16 mm. or more long; lobes of bracts nearly equal . . . . 7. *A. Hanseni.*
          - Tips of bracts not enlarged or calloused . . . . 8. *A. parviflora.*
        - Flowers in heads; herbage hispid or hirsute.
          - Bracts parted nearly to base; pubescence long hirsute . . . . 10. *A. filifolia.*
          - Bracts parted only to middle.
            - Lower calyx-leaf about 1 mm. longer than the upper.
              - Pubescence sparsely hispid . . . 11. *A. rigida.*
              - Pubescence copious hirsute . . . 11*a*. *A. rigida brevibracteata.*
            - Lower calyx-leaf at least 2 mm. longer than the upper . . . . 12. *A. littoralis.*
      - Bracts five- to seven-parted.
        - Corolla 15–17 mm. long . . . . 13. *A. ramosa.*
        - Corolla 22–30 mm. long . . . . 14. *A. Wrightii.*

3. ADENOSTEGIA CAPITATA (Nutt.) Greene

Cordylanthus capitatus Nutt.; Bentham in De Candolle, Prodr. **10**: 597. 1846; Gray, Proc. Am. Acad. **7**: 382; Wats. Bot. King's Exped. 231, 459; Gray, Bot. Calif. **1**: 580; Gray, Syn. Fl. **2**^{1}: 304.

Adenostegia capitata Greene, Pittonia **2**: 180. 1891; Kuntze, Rev. Gen. **2**: 457; Howell, Fl. N. W. Am. 537; Piper, Contr. U. S. Nat. Herb. **11**: 518; Rydberg, Bull. Torrey Club **40**: 484. 1913.

Adenostegia ciliosa Rydb. Bull. Torrey Club **34**: 35. 1907.

Cordylanthus bicolor A. Nels. Bot. Gaz. **54**: 416. 1912.

Paniculately branching annual, 4–6 dm. high, short-pilose throughout with glandular hairs; leaves many, 2–5 cm. long, linear or three-parted; heads two- to five-flowered; flowers spreading, giving an open appearance to the head; floral bracts 8–10 mm. long, three-parted, the divisions linear-lanceolate, spreading, the middle division twice as long as the lateral divisions; calyx-leaves purplish, the upper 8–9 mm. long, thin, two-nerved, two-toothed, the teeth 2–3 mm. long, the lower 10–13 mm. long, five-nerved, broad at the apex and curved outward; corolla 10–12 mm. long, covered with reflexed hairs, the tube longer than the throat, purple, tipped with yellow; stamens two, the anthers one-celled with vestiges of a second cell, the filaments nearly glabrous, with a U-shaped curve near the anther; capsule 5–6 mm. long, slender, pointed; seeds few, reticulate. [PLATE 10, FIG. 3.]

Co-types of *Cordylanthus bicolor* examined by the author are not distinct from *A. capitata.* Specimens of *A. ciliosa* have not been examined, but Rydberg (Bull. Torrey Club **40**: 484. 1913) states that his species is identical with Nelson's.

TYPE LOCALITY: "In Novâ Californiâ (Nuttall!)."

DISTRIBUTION: Mountain ranges of Washington and Idaho to Lassen County, California; Arid Transition Zone.

SPECIMENS EXAMINED:—WASHINGTON: Yakima Region, 1882, *Brandegee;* Falcon Valley, *Suksdorff 201.* IDAHO: Redfish Lake, *Evermann 408;* Blaine County, *Nelson & MacBride 1239;* Pinehurst, Boise County, *Macbride 1671.* OREGON: Powder River, *Cusick 1784;* same locality, *Piper 2482;* Hepburn Ridge, Wallowa County, *Sheldon 8643;* same locality, *Howell.* CALIFORNIA: hills near Lassen Creek, *Mrs. Austin 146.* NEVADA: Coleman Valley, *Coville & Leiberg 95;* Clover Mountains, *Watson 816;* Gold Creek, Elko County, *Kennedy 4282.*

4. ADENOSTEGIA PILOSA (Gray) Greene

Cordylanthus pilosus Gray, Proc. Am. Acad. **7**: 382. 1868; Wats. Bot. King's Exped. 459; Gray, Bot. Calif. **1**: 581; Gray, Syn. Fl. **2**^{1}: 304; Jepson, Fl. W. Mid. Calif. ed. 2. 387.

Adenostegia pilosa Greene, Pittonia **2**: 180. 1891; Kuntze, Rev. Gen. **2**: 456; Jepson, Fl. W. Mid. Calif. 416.

Stout, paniculately branching annual, 6–12 dm. high; stems somewhat reddish, glandular with rather short, pilose hairs; leaves 10–20 mm. long, truncate and often callous-emarginate at apex; flowers scattered along the branches; floral bracts linear, 15–25 mm. long, cinereous-pilose, the callous tip dilated, sometimes three-notched, three-nerved; upper calyx-leaf 20–22 mm. long, shallowly bidentate, three-nerved, pubescence sparse, the lower calyx-leaf 19–21 mm. long, broadly lanceolate, with pubescence as on the bracts; corolla 15–18 mm. long, the tube shorter than the throat, greenish white with reddish-purple markings at base of throat and on lower lip; stamens four, perfect, the filaments villous; capsule not sharply pointed; seeds few, slightly reticulate. [PLATE 10, FIG. 4.]

TYPE LOCALITY: "Dry soil near San Jose."

DISTRIBUTION: Interior valleys and foothills of California, from Trinity and Mendocino Counties southward to Santa Clara County; Upper Sonoran Zone. The specimens from the higher elevations in Lake and Mendocino Counties are less pilose but do not differ structurally from the typical form.

SPECIMENS EXAMINED:—CALIFORNIA: Eureka — Red Bluff Road, Trinity County, *Abrams 6158;* between Harris and Alder Point, Trinity County, *Abrams 5964;* near summit of Mt. Sanhedrin, Lake County, *Heller 5997;* Cobb Mountain, Lake County, August 13, 1910, *Katharine Brandegee,* near Bartlett Springs, Lake County, August, 1911, *A. Stinchfield;* Princeton, Colusa County, October, 1905, *Chandler;* St. Helena Sanitarium, Napa County, *Abrams 5752;* foothills, Yolo County, *Stinchfield 345;* Petrified Forest, Sonoma County, *Bioletti & Michener 1731a;* Weldon Cañon, Vaca Mountains, Salona County, September 13, 1891, *Jepson*; near San Jose, Santa Clara County, *Brewer;* foothills west of Los Gatos, Santa Clara County, *Heller 7532;* same locality, *Eastwood*; Palo Alto, *Baker 1714;* Stevens Creek Road, Santa Clara County, *Stinchfield 247;* near Stanford University, *Stinchfield 255;* Raymond Ranch, Santa Cruz Mountains, August 14, 1911, *Blasdale*;

near Saratoga, *Pendleton 270;* near Colley's Landing, Palo Alto, September 29, 1906, *Abrams.*

5. ADENOSTEGIA TENUIS (Gray) Greene

Cordylanthus tenuis Gray, Proc. Am. Acad. **7**: 383. 1868; Wats. Bot. King's Exped. 232, 460; Gray, Bot. Calif. **1**: 581; Gray, Syn. Fl. **2**^{1}: 304; Hall, Yosemite Flora 229.

Cordylanthus pilosus var. *Bolanderi* Gray, Proc. Am. Acad. **7**: 382. 1868; Gray, Bot. Calif. **1**: 581; Gray, Syn. Fl. **2**^{1}: 304.

Adenostegia tenuis Greene, Pittonia **2**: 180. 1891; Kuntze, Rev. Gen. **2**: 456; Wettstein in Engler & Prantl, Nat. Planzenfam. **4**^{3b}: 98.

Adenostegia pilosa var. *Bolanderi* Greene, Pittonia **2**: 180. 1891.

Adenostegia Bolanderi Kuntze, Rev. Gen. **2**: 456. 1891.

Slender, paniculately branching annual, 2–6 dm. high; stems puberulent with short, scattered, glandular, pilose hairs, sometimes glabrous; leaves 1–3 cm. long linear, occasionally with callous tips; flowers scattered along the branches; floral bracts 12–20 mm. long, puberulent, ciliate with glandular, pilose hairs, linear-lanceolate, entirely herbaceous or with callous tips; calyx-leaves with pubescence as on bracts, the upper 15–18 mm. long, three-nerved, lanceolate, sometimes bidentate, the lower 14–18 mm. long, five-nerved, broadly lanceolate; corolla 12–15 mm. long, the tube about equalling the throat, inconspicuously hairy; capsule 8 mm. long; seeds few, somewhat reticulated. [PLATE 10, FIG. 5.]

The glabrous or puberulent type of *A. tenuis* is found in the Lake Tahoe region and in western Nevada, while the form described as *A. pilosa* var. *Bolanderi* is characteristic of the mountain ranges north of this region. This last-named form was described by Gray as being more nearly related to *A. pilosa*, but an examination of co-type material shows that the bracts are not notched as they are in *A. pilosa* and that in the pubescence it is like *A. tenuis* except for the presence of scattered, pilose hairs.

The specimens from Lake County are like the Nevada form, while those from the Kings River region more closely resemble *A. pilosa*.

TYPE LOCALITY: "Dry sandy soil near Lake Tahoe, Nevada, Brewer, Dr. C. L. Anderson."

DISTRIBUTION: Exposed slopes in Lake County in the Coast

Range and in the Sierra Nevada Mountains from Lassen County to Fresno County, California, and in western Nevada; Transition and Canadian Zones.

SPECIMENS EXAMINED:—CALIFORNIA: Mt. Hannah, Lake County, *Tracy 3247;* Susanville Summit, Lassen County, July 2, 1897, *Jones;* Grizzly Hill, Plumas County, *Leiberg 5207;* Clio, Plumas County, *Eggleston 6240;* Sierra Valley Hot Springs, Sierra County, August, 1909, *Dudley;* Soda Springs, Nevada County, *Jones 2589;* Susie Lake Trail, Eldorado County, *McGregor 125;* Lake Tahoe, Eldorado County, *Leiberg 5327;* Agricultrual Station, Amador County, *Hansen 697;* between Big Trees and Gardner's, Calaveras County, August, 1906, *Dudley;* near Mariposa Big Trees, Mariposa County, *Abrams 5397;* same locality, August 11, 1895, *Congdon;* Mariposa Big Tree Grove, *Bolander 4993* (cotype of *A. pilosa* var. *Bolanderi*); Yosemite National Park, Glacier Point, *Hall 9202;* Tamarack Flat, *Abrams 5474;* near foot of Yosemite Falls, *Abrams 5466;* trail between Illillouette and Glacier Point, *Abrams 5430;* Converse Basin, Fresno County, October, 1900, *Dudley;* Kings River Region, Fresno County, August, 1904, *Dudley;* west of Bearskin Meadow, August, 1904, *Dudley;* same locality, *Hall & Chandler 179.* NEVADA: near Lake Tahoe, *Brewer 2150;* Clear Lake Cañon, Ormsby County, *Baker 1408;* mountains west of Bowers, Washoe County, *Heller 10663;* Galena Creek, Washoe County, *Heller 10671;* Lake Tahoe, Washoe County, *Kennedy 1458.*

6. ADENOSTEGIA VISCIDA Howell

Adenostegia viscida Howell, Fl. N. W. Am. 537. 1903.

Paniculately branching annual, 2–4 dm. high; short pilose throughout with viscid-glandular hairs; leaves 18–25 mm. long, linear-lanceolate, occasionally three-parted; flowers scattered along the branches, solitary or in groups of three or four; bracts 10–14 mm. long, slender, three-parted, enlarged and slightly calloused at the apex; calyx-leaves 15–16 mm. long, the upper the longer, four-nerved, the lower five-nerved; corolla 12–14 mm. long; stamens four, perfect, the filaments villous; capsule 6–7 mm. long. [PLATE 10, FIG. 6.]

A. viscida in Shasta and Plumas Counties is inconspicuously glandular-pilose as compared with the typical form and approaches *A. tenuis*, to which this species is very closely related.

TYPE LOCALITY: "On dry slopes, eastern base of the Coast Mountains, near Waldo, Southern Oregon."

DISTRIBUTION: Siskiyou Mountains, Oregon, south to Plumas County, California.

SPECIMENS EXAMINED:—OREGON: Illinois River in the Siskiyou Mountains, *Cusick 2937;* same locality, July, 1887, *Howell;* near Fort Klamath, *Leiberg 636;* Klamath County, *Mrs. Austin & Bruce 1773;* Rogue River, *Brackenridge 1192;* Upper Metolins River, Crook County, *Coville & Applegate 700;* Wimer, Jackson County, *Hammond 318.* CALIFORNIA: Mt. Eddy, Siskiyou County, *Heller 11744;* Weed, *Heller 11723;* Burney Falls, Shasta County, August, 1899, *Dudley;* Bear Valley Mountains, Shasta County, June and August, 1893, *Baker;* Big Meadows, Plumas County, *Mrs. Bruce 411;* Lassen Buttes, Plumas County, *Brown 637;* Grizzly Hill, Plumas County, *Leiberg 5107.*

7. **Adenostegia Hanseni** sp. nov.

Stout, paniculately branching annual, 5–12 dm. high; stem reddish, glandular throughout with long, cinereous, pilose hairs which are often 4–5 mm. long; leaves 12–30 mm. long, truncate and often calloused at the apex; flowers scattered along the branches; floral bracts 15–30 mm. long, 3-nerved, 3-parted, the divisions 4–7 mm. long, nearly equal, enlarged and callous-emarginate at apex; calyx leaves 15–22 mm. long, the upper lanceolate, the lower rounded; corolla 16–18 mm. long, the tube nearly equalling the throat; stamens 4, perfect, the filaments villous; capsule 7–8 mm. long. [PLATE 10, FIG. 7; PLATE 11, FIG. 3.]

This species closely resembles *A. pilosa* in habit, but is readily distinguishable by the tripartite bract and the long, pilose hairs.

TYPE LOCALITY: Agricultural Station, Amador County, California; alt. 2,000 ft., September, 1893, *Hansen 138.* TYPE, No. 21142 of the Dudley Herbarium.

DISTRIBUTION: Foothills of the Sierra Nevada from Shasta County to Tuolumne County, California; Upper Sonoran Zone.

SPECIMENS EXAMINED:—CALIFORNIA: north of Redding, Shasta County, *Heller 12501;* between Bellavista and Ingot, Shasta County, July, 1914, *McMurphy;* four miles east of Placerville, Tehama County, *Heller 12551;* east of Oroville, Butte County, *Heller 11569;* Agricultural Station, Amador County, alt. 2,000 ft., *Hansen 138;* near Ione, Amador County, *Braunton 121;* Wards Ferry, alt. 1,500 ft., Tuolumne County, *Abrams 4717;* French Flat, near Rawhide, Tuolumne County, *Stinchfield 64;* plains of the Sacramento, *Pickering 1348.*

8. **Adenostegia parviflora** sp. nov.

Divaricately branching annual, 3 dm. high, puberulent and minutely viscid-pilose throughout; leaves 10–15 mm. long; flowers many, scattered along the branches; floral bracts 5–6 mm. long, three-parted into linear divisions with rounded, herbaceous tips; calyx leaves 11–13 mm. long, the lower slightly exceeding the upper; corolla 10–11 mm. long, tube nearly equalling throat; stamens 4, perfect, the filaments villous; capsule lanceolate. [PLATE 10, FIG. 8; PLATE 11, FIG. 4.]

TYPE LOCALITY: Grand Canyon of the Colorado River, near the San Francisco Mountains, Arizona, *Knowlton 270.* TYPE, No. 48859 of the U. S. National Herbarium.

9. ADENOSTEGIA NEVINII (Gray) Greene

Cordylanthus Nevinii Gray, Proc. Am. Acad. **17**: 229. 1882; Gray, Syn. Fl. **2**^{1}: 454.

Adenostegia Nevinii Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Hall, Univ. Calif. Pub. Bot. **1**: 114.

Slender, paniculately branching annual, 3–4 dm. high; hirsute when young, puberulent in age; lower leaves dense, 20–25 mm. long, three-parted into linear divisions, the upper leaves scarcely 10 mm. long, linear, rarely parted, covered with a short, cinereous pubescence; flowers in axillary clusters of two to four; floral bracts scarcely one half the length of the calyx, short pubescent, three-parted into linear divisions with emarginate, glandular tips; calyx leaves hispidulous throughout and with soft ciliate edges, the upper 12–13 mm. long, 6-nerved, winged at the base, the lower equalling the upper, 5–6-nerved, broadly lanceolate; corolla 11–12 mm. long, glandular, the tube less than one half the length of the throat; stamens 4, the anthers 1-celled, the filaments villous; capsule not sharply pointed. [PLATE 10, FIG. 9.]

TYPE LOCALITY: "California, in the San Bernardino Mountains, at about 5000 feet, *Rev. J. C. Nevin,* 1880; *S. B. & W. F. Parish,* 1881."

DISTRIBUTION: Mountain ranges of Southern California, from

Mt. Pinos to the Cuyamaca Mountains, San Diego County; Arid Transition Zone.

SPECIMENS EXAMINED:—CALIFORNIA: Upper San Antonio Cañon, Los Angeles County, *Johnston 1662;* Swartout Cañon, San Gabriel Mountains, San Bernardino County, September, 1904, *G. R. Hall;* Bear Valley, San Bernardino County, *Abrams 2079;* same locality, *Davidson,* 1894; same locality, June 29, 1897, *Chandler;* San Bernardino Mountains, *Parish Brothers 992;* San Jacinto Mountains, Riverside County, *Hall 2619;* Lockwood Valley, Ventura County, *Hall 6644;* Cuyamaca, San Diego County, 1884, *Orcutt;* same locality, October 15, 1894, *Brandegee.*

10. ADENOSTEGIA FILIFOLIA (Nutt.) Abrams

Cordylanthus filifolius Nutt.; Bentham in De Candolle, Prodr. **10**: 597. 1846; Wats. Bot. King's Exped. 459 (in part); Gray, Bot. Calif. **1**: 581 (in part); Gray, Syn. Fl. **2**^{1}: 303 (in part).

Adenostegia rigida Greene, Pittonia **2**: 180 (in part). 1891; Hall, Univ. Calif. Pub. Bot. **1**: 114.

Adenostegia filifolia Abrams, Fl. Los Angeles 372. 1904.

Cordylanthus rigidus var. *filifolius* McBride, Contrib. Gray Herb. N. S. **49**: 58. 1917.

Slender, paniculately branching annual, 3–5 dm. high, the stems hirsute, the lower part puberulent; leaves linear or three-parted, puberulent with scattered, hirsute hairs; mature floral heads compact, flat topped, five- to eight-flowered; floral bracts 12–16 mm. long, deeply three-parted into linear divisions of one fourth the length of the bract, densely covered with long, spreading, hirsute hairs, tips of the divisions enlarged, calloused, emarginate, with a large gland in the emargination; calyx-leaves 13–16 mm. long, short-hirsute, the upper 4–5-nerved, rounded at apex; corolla 12–15 mm. long, the tube shorter than the throat; stamens four, the anthers two-celled; capsule not sharply pointed; seeds slightly reticulate. [PLATE 10, FIG. 10.]

TYPE LOCALITY: "Ad San Diego (Nuttall!)."

DISTRIBUTION: Dry ridges and open places from Ventura County in California to the northern part of Lower California; Upper and Lower Sonoran Zones.

SPECIMENS EXAMINED:—CALIFORNIA: San Felipe, Los Angeles County, *Hayes 582;* Glendora, Los Angeles County, 1892, *Miss Palmer;* Ramona, Los Angeles County, July, 1903, *Brandegee;*

Hobart, Los Angeles County, *Braunton 513;* Newhall, October 14, 1882, *Pringle;* Victorville, San Bernardino County, *Parish 10523;* Lytle Creek Cañon, San Bernardino County, *Abrams 2745;* same locality, *Hall 1423;* San Jacinto Mountains, Riverside County, *Hall 2621;* San Diego, San Diego County, August, 1916, *McMurphy;* same locality, September, 1903, *Brandegee;* same locality, August, 1906, *Katharine Brandegee;* same locality, July, 1895, *Stokes;* Point Loma, San Diego County, *Hall 8325;* Viejas Grade to Descanso, San Diego County, July, 1906, *Katharine Brandegee;* between La Mesa and Jamul, San Diego County, *Abrams 5006;* Del Mar, San Diego County, August 5, 1906, *Katharine Brandegee;* Witch Creek, San Diego County, *Anderson 248;* Tecate River, San Diego County, *Shoenfeldt 3741;* same locality, *Mearns 3797;* Laguna Mountains, Imperial County, *McGregor 97;* Southwestern Colorado Desert, Imperial County, June, 1889, *Orcutt.*

11. ADENOSTEGIA RIGIDA Benth.

Adenostegia rigida Benth. in Lindley, Nat. Syst. ed. 2. 445. 1836; Bentham in De Candolle, Prodr. **10**: 537; Greene, Pittonia **2**: 180 (in part); Wettstein in Engler & Prantl, Nat. Pflanzenfam. 4^{3b}: 98; Jepson, Fl. W. Mid. Calif. 416.

Cordylanthus filifolius Gray, Bot. Mex. Bound. **2**: 120. 1859; Gray, Proc. Am. Acad. **7**: 382. Not Nuttall.

Cordylanthus rigidus Jepson, Fl. W. Mid. Calif. ed. 2. 387. 1911.

Diffusely branching annual, 3–6 dm. high; stems often reddish, puberulent with scattered, hirsute hairs, glabrous with age; leaves 12–15 mm. long, linear-filiform, occasionally three-parted, canescent-puberulent; mature heads compact, six- to twelve- rarely fifteen-flowered; floral bracts 12–20 mm. long, sparsely hispid, the ciliate margins interspersed with soft hairs, three-parted into linear divisions, the apex calloused, enlarged and truncate or slightly emarginate, the veins prominent; calyx-leaves 18–21 mm. long, sparsely hispid, five-nerved, the lower broad, 1 mm. longer than the upper; corolla 16–19 mm. long, the tube equalling or slightly shorter than the throat; stamens four, the anthers two-celled; capsule not sharply pointed; seeds slightly reticulate. [PLATE 10, FIG. 11.]

TYPE LOCALITY: "Herba Novo-californica." The exact type locality of this species is doubtful, but of various specimens sent to the Kew Herbarium by Dr. Abrams in 1903, one from Nacimiento River, Monterey County, was said to agree most closely with Douglas's specimen. It is known that Douglas visited San Antonio Mission and collected in the Santa Lucia Mountains. So we may safely assume that the type locality of this species is in that region.

DISTRIBUTION: Exposed slopes in the inner Coast Ranges of California from the Santa Cruz Mountains to the Santa Lucia Mountains; Upper Sonoran Zone.

SPECIMENS EXAMINED:—CALIFORNIA: Crystal Springs, Santa Cruz Peninsula, 1896, *Eastwood;* Permanente Creek, July, 1903, *Dudley;* Castle Rock Ridge, October, 1906, *Abrams;* near Congress Springs, *Stinchfield 248;* near Saratoga, *Pendleton 234;* near Wrights, *Dudley*, 1894; California Redwood Park, *Stinchfield 253;* same locality, *Abrams 6384;* Glenwood Station, August, 1900, *Davis;* head of Aptos Creek, *Abrams 3028;* Santa Lucia Mountains, *Condit 8;* same locality, *Vasey 483;* same locality, May–July, 1892, *Vortriede;* Jolon, July 30, *Brandegee;* Tassajara Hot Springs, July 18, 1908, *Cox.*

11a. ADENOSTEGIA RIGIDA BREVIBRACTEATA (Gray) Greene

Cordylanthus filifolius var. *brevibracteatus* Gray, Bot. Calif. **1**: 622. 1876; Gray, Syn. Fl. **2**^{1}: 304.

Adenostegia rigida var. *brevibracteata* Greene, Pittonia **2**: 180. 1891; Coville, Contr. U. S. Nat. Herb. **4**: 173.

Habit as in typical *A. rigida;* bracts with distinctly calloused, emarginate tips, often dark colored, with prominent veins; bracts and calyx-leaves copiously hirsute-ciliate. [PLATE 10, FIG. 12.]

The short bracts upon which Gray based the name are characteristic of the specimens from Fresno and Kern Counties. These specimens, however, have the hirsute-ciliate pubescence of all the Sierran forms. A form growing at Santa Barbara and near Visalia, Tulare County, has less conspicuously calloused bracts, but seems to grade into typical *brevibracteata.*

I have examined the following three collections from the Kaweah region: meadows near Monarch Lake, *Dudley 1230;* Bearskin Meadow, King's River region, August, 1904, *Dudley;* Grant Forest Reservation, August, 1910, *Katharine Brandegee.* These undoubtedly belong to the *A. rigida* group but cannot be correctly identified because of insufficient material. The form represented in these collections differs from *A. rigida brevibracteata* in being glabrous throughout, except for the slightly ciliated bracts, and in the shape and herbaceous character of the bracts.

TYPE LOCALITY: "Near Soda Spring on Kern River, at 8,500 feet, *Rothrock*, in Wheeler's Exped., 1875."

DISTRIBUTION: Mariposa County to Tulare County, California, and also on the eastern side of the Mt. Hamilton Range; Upper Sonoran Zone. This variety is characteristic of the Digger Pine Belt and ranges from Mariposa County along the foothills of the Sierra Nevada to Tehachapi Pass, while a slightly different form occurs in Santa Barbara and Tulare Counties.

SPECIMENS EXAMINED:—CALIFORNIA: Western slope of Pecheco Pass, Santa Clara County, *Abrams 5285;* Mormon Bar, Mariposa County, 1883, *Congdon;* Wawona, Mariposa County, October, 1895, *Ward;* Yosemite National Park, *Bolander 5012;* Marble Fork of Kaweah River, Tulare County, August, 1905, *Katharine Brandegee;* Soda Springs of Kern River, Tulare County, *Hall & Babcock 5572;* Visalia, Tulare County, October, 1881, *Congdon;* North Fork of Kern River, Kern County, *Coville & Funston 1602;* Poso Creek, Kern County, August, 1853, *Heerman;* Tehachapi, Kern County, August, 1894, *Eastwood;* Santa Barbara, Santa Barbara County, *Elmer 3741;* La Cumbre Trail, Santa Inez Mountains, Santa Barbara County, *Abrams 4302;* road to Monteci, Santa Barbara County, *Eastwood 199;* Mountain Drive, Santa Barbara, *Abrams 4113*.

12. **Adenostegia littoralis** sp. nov.

Diffusely branching annual, 3–6 dm. high; stems puberulent, without hirsute hairs; leaves 13–15 mm. long, entire; flower-heads compact, five- to ten-flowered; floral bracts 14–22 mm. long, three-parted, the divisions slender, pubescence soft-puberulent with an occasional hispidulous hair, tips truncate or with a tack-like enlargement of the veins, not distinctly calloused; lower calyx-leaf at least 2 mm. longer than the upper, pubescence as on the bracts; corolla 16–19 mm. long, the tube equalling or slightly shorter than the throat; stamens four, the anthers two-celled. [PLATE 10, FIG. 13; PLATE 12, FIG. 1.]

This species was recognized as a form distinct from *A. rigida* by Heller (Muhlenbergia **2**: 251), but no name was applied to it.

It differs most noticeably from *A. rigida* in the divisions of the bracts, which are narrow instead of broad, in the pubescence and in the long lower calyx-leaf.

TYPE LOCALITY: Carmel, Monterey County, California, open pine woods, August 17, 1909, *Abrams 4254*. TYPE, No. 21173 of the Dudley Herbarium.

DISTRIBUTION: Sand dunes and open woods of the Monterey Peninsula, California; Transition Zone.

SPECIMENS EXAMINED: — CALIFORNIA: Carmel, Monterey County, *Abrams 4254;* near Del Monte, Monterey County, *Heller 8247;* Del Monte, *Elmer 4080.*

13. ADENOSTEGIA RAMOSA (Nutt.) Greene

Cordylanthus ramosus Nutt.; Bentham in De Candolle, Prodr. **10**: 597. 1846; Wats. Bot. King's Exped. 232, 459; Gray, Bot. Calif. **1**: 580; Gray, Syn. Fl. $\mathbf{2}^1$: 303; Coulter & Nelson, Man. Bot. Rocky Mts. 462.

Adenostegia ramosa Greene, Pittonia **2**: 180. 1891; Kuntze, Rev. Gen. **2**: 456; Howell, Fl. N. W. Am. **1**: 537.

Paniculately much branched annual, 2–3 dm. high, cinereous puberulent throughout; leaves 15–20 mm. long, linear-filiform, one- to three-parted, flowers sometimes solitary, mostly in three- to five-flowered heads; floral bracts often scantily hirsute-ciliate, parted into five to seven linear divisions; upper calyx-leaf 18–22 mm. long, broadly lanceolate or inconspicuously bidentate, five-nerved, lower calyx-leaf 17–20 mm. long, lanceolate or two-lobed, pubescence like that of bract; corolla 15–17 mm. long, the tube longer than the throat; stamens four, the anthers perfect, the filaments villous; capsule 10–11 mm. long, slender; seeds many, small, reticulate. [PLATE 10, FIG. 14.]

TYPE LOCALITY: "In mont. Scopulosis (Nuttall! Tolmie!)."

DISTRIBUTION: Southwestern Montana to southwestern Colorado and westward to Oregon and Lassen County, California; Arid Transition Zone.

SPECIMENS EXAMINED: — OREGON: Grizzly Butte, Crook County, *Leiberg 848;* Lake County, *Mrs. Austin 1772;* Warner Range, Lake County, *Coville & Leiberg 55;* White Horse Mountains, Lake County, *Griffiths & Morris 449;* eastern Oregon, *Cusick 1750, 1197.* CALIFORNIA: Plumas Junction, Lassen

County, *Eggleston 6205;* Goose Lake Valley, Lassen County, *Mrs. Austin 245.* NEVADA: Kings Cañon, Ormsby County, *Baker 1499;* Quinn River Crossing, Humboldt County, *Griffiths & Morris 139;* Tuscarora, Elko County, *Heller 9182;* same locality, *Kennedy 606;* Blaine, Elco County, *Heller 11115;* Humboldt Wells, Elco County, *Heller 9182;* hills around Austin, Lander County, *Kennedy 4038;* Toyabe Range, Lander County, *Kennedy 4093;* Wells, Lander County, August, 1882, *Jones.* IDAHO: Pocatello, Snake Plains, *Palmer 408;* near big Camas Prairie, *Henderson 3160;* Dry Creek, Snake Plains, *Palmer 336;* Houston, *Henderson 3799;* Flint Creek, Owyhee County, *MacBride 496;* Blackfoot, Snake Plains, *Palmer 292;* Minidoka, Lincoln County, *Nelson & MacBride 1313.* UTAH: Parley's Park, Summit County, *Smith 1887;* Echo Cañon, *Watson 817.* MONTANA: Grasshopper Valley, southwest Montana, *Watson 323.* WYOMING: Fossil Station, August 10, 1885, *Letterman;* Dubois, *Nelson 711;* Evanston, July 10, 1897, *Williams;* river bottoms, Carbon County, *Tweedy 3409;* Cokeville, *Cary 704;* Crook Creek, Fremont County, *Goodding 528;* Fort Bridger, July 29, 1873, *Porter;* Slater, Colorado-Wyoming line, Carbon County, *Goodding 1727.* COLORADO: Mancos, July, 1890, *Miss Eastwood.*

14. ADENOSTEGIA WRIGHTII (Gray) Greene

Cordylanthus Wrightii Gray, Bot. Mex. Bound. **2**: 120. 1859; Gray, Proc. Am. Acad. **7**: 382; Wats. Bot. King's Exped. 459; Gray, Syn. Fl. **2**^{1}: 453; Coulter, Contr. U. S. Nat. Herb. **2**: 316; Coulter & Nelson, Man. Bot. Rocky Mts. 462.

Adenostegia Wrightii Greene, Pittonia **2**: 180. 1891; Kuntze, Rev. Gen. **2**: 457; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 590.

Paniculately branching annual, 3–5 dm. high; inconspicuously puberulent or in age glabrous; leaves linear-filiform, often dissected; heads five- to ten-flowered, spreading; floral bracts 18–20 mm. long, glabrous, deeply divided into dissected, filiform divisions; upper calyx-leaf 23–28 mm. long, five-nerved, shallowly bidentate, lower calyx-leaf 24–30 mm. long, three- to four-nerved, tip lanceolate or two- to four-toothed, the teeth 1–4 mm. long; corolla 22–30 mm. long, the tube longer than the throat; stamens four, the anthers two-celled, the filaments villous; capsule 11–12 mm. long; seeds reticulate. [PLATE 10, FIG. 15.]

A form with scattered flowers, corresponding to an herbarium specimen named by Gray for Dr. Matthews, occurs within the range of *A. Wrightii.* As it appears to differ from *A. Wrightii* only in having the flowers in smaller clusters it is not here considered distinct.

TYPE LOCALITY: "Prairies from 6–30 miles east of El Paso, western Texas; Wright (450). Sand Hills, Chihuahua; Thurber."

DISTRIBUTION: Utah and southern Colorado to Arizona and south to Chihuahua, Mexico.

SPECIMENS EXAMINED:—UTAH: Willow Creek, southeastern Utah, *Miss Eastwood 98;* La Salle Mountains, *Purpus 7020.* COLORADO: Mesa Verde, southwestern Colorado, August, 1892, *Miss Eastwood.* ARIZONA: Chiricahua Mountains, *Blumer 1744;* White Mountains, *Griffiths 5379;* Oracle, August 28, 1903, *Jones;* Black River, *Rothrock 795;* Strawberry Valley, *Toumey 360;* Keans Cañon, 1897, *Hough;* Navajo to Hawthorne, *Griffiths 5801;* San Francisco Mountains, *Knowlton 210;* Cosmino, *Jones 4026;* Flagstaff, *Leiberg 5780.* NEW MEXICO: Navajo Indian Reservation, in Tunitcha Mountains, *Standley 7841;* Cedar Hill, San Juan County, *Standley 7953;* Fort Wingate, *Matthews 1883;* San Lorenzo, July 26, 1896, *Wooton;* Mogollon Mountains, *Rushby 319;* Farmington, San Juan County, *Standley 7121;* Bear Mountain, Grant County, *Metcalf 695.* MEXICO: Chihuahua, *Pringle 780.*

Section IV. KINGIA

Cordylanthus § *Hemistegia* (in part) Wats. Bot. King's Exped. 460. 1871; Gray, Syn. Fl. **2**^{1}: 304.

Flowers in heads, calyx monophyllous; corolla as in *Euadenostegia;* stamens four, perfect.

15. ADENOSTEGIA KINGII (Wats.) Greene

Cordylanthus Kingii Wats. Bot. King's Exped. 233, 460. *pl. 22, f. 3–6.* 1871; Gray, Bot. Calif. **1**: 581; Gray, Syn. Fl. **2**^{1}: 304; Parry, Am. Nat. **9**: 346; Coulter & Nelson, Man. Bot. Rocky Mts. 462.

Adenostegia Kingii Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Wettstein in Engler & Prantl, Nat. Pflanzenfam. **4**^{3b}: 98; Rydberg, Fl. Colo. 318.

Paniculately branching annual, 1–3 dm. high, glandular puberulent throughout, sometimes short-villous; leaves 20–30 mm. long, three-parted into linear divisions; heads few-flowered, the flowers spreading, giving an open appearance to the head; floral bracts 15–18 mm. long, three-nerved, irregularly dissected into five to seven linear divisions; calyx-leaf 22 mm. long, five-nerved, the teeth at the apex 1–2 mm. long; corolla 21–22 mm. long, the tube glabrous, somewhat longer than the throat, the latter covered with soft, reflexed hairs; filaments hairy; capsule pointed. [PLATE 10, FIG. 16.]

TYPE LOCALITY: "Rare; found only on a limestone ridge near Roberts Station in Monitor Valley, Nevada; 6,000 feet altitude; July."

DISTRIBUTION: White Pine County, Nevada; Emery, Garfield and Iron Counties, Utah.

SPECIMENS EXAMINED:—UTAH: two miles south of Ferron, *Jones 5454;* Sink Valley, June 20, 1890, *Jones;* Panguitch Lake, *Jones 6015;* head of Sevier River, *Jones 6032;* southern Utah, 1875, *Siler.*

16. **Adenostegia Helleri** sp. nov.

Paniculately branching annual, 2–4 dm. high; glandular-villous throughout with short, spreading hairs; leaves 6–15 mm. long, one-, sometimes three-, nerved; heads many, terminating the branchlets, one- to four-flowered; floral bracts 8–12 mm. long, five- to eight-parted; calyx-leaf lanceolate or shallowly two-toothed, four-nerved, winged at base; corolla 1–2 mm. longer than the calyx, throat soft-pubescent, equaling or slightly exceeding the tube; filaments nearly glabrous; capsule sharply pointed. [PLATE 10, FIG. 17; PLATE 12, FIG. 2.]

This species has been confused with *A. Kingii* but it differs in habit and in the bracts which in *A. Helleri* are smaller and regularly instead of irregularly divided.

TYPE LOCALITY: Hills north of Reno, Nevada, September 20, 1910, *Heller 10238.* TYPE, No. 2122 of the Dudley Herbarium.

DISTRIBUTION: Western Nevada, in the vicinity of Reno.

SPECIMENS EXAMINED:—NEVADA: Reno, *Brown 1564;* hills north of Reno, *Heller 10238.*

Section V. DICRANOSTEGIA

Cordylanthus § *Dicranostegia* Gray, Proc. Am. Acad. **19**: 95. 1883; Gray, Syn. Fl. **2**^{1}: 454.

Adenostegia § *Dicranostegia* Wettstein in Engler & Prantl, Nat. Pflanzenfam. **4**^{3b}: 98. 1891.

Inflorescence spicate; calyx monophyllous; calyx-leaf deeply divided into two parts.

17. ADENOSTEGIA ORCUTTIANA (Gray) Greene

Cordylanthus Orcuttianus Gray, Proc. Am. Acad. **19**: 95. 1883; Gray, Syn. Fl. **2**^{1}: 454.

Adenostegia Orcuttiana Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Wettstein in Engler & Prantl, Nat. Pflanzenfam. **4**^{3b}: 98.

Divaricately branched, often decumbent, annual, 15–35 cm. high; stems stout, densely hirsute, sparsely so with age; leaves 25–30 mm. long, one-nerved, densely hirsute, sparsely so with age; leaves 25–30 mm. long, one-nerved, hispidulous, irregularly dissected into linear divisions; spike 2–6 cm. long; floral bracts 20–25 mm. long, setose-ciliate, three-nerved, tip broadly rounded; calyx-leaf 6 mm. long, thin, two-nerved, deeply or completely divided into acuminate divisions, the margins with soft pubescence interspersed with hirsute hairs; corolla about equalling the bracts, tube longer than the throat, curved outward, throat soft-pubescent; stamens four, the anthers small, one-celled with vestiges of a second cell, the upper anther sterile, the lower fertile, filaments glabrous. [PLATE 10, FIG. 18; PLATE 12, FIG. 3.]

TYPE LOCALITY: "Lower California, about 70 miles below the U. S. boundary, *H. C. Orcutt* and son."

DISTRIBUTION: Northwestern part of Lower California, from the international boundary to Ensenada.

SPECIMENS EXAMINED:—LOWER CALIFORNIA: Tia Juana, June 30, 1884, *Orcutt & Son;* same locality, July, 1896, *Stokes;* Mexican Boundary, *Mearns 3927;* Las Huevitas, 1893, *Brandegee;* Ensenada, October 5, 1892, *Brandegee;* San Pedro Martir, *Robinson 45* (probably San Pedro Martir Island, not San Pedro Martir Mountains).

Section VI. CHLOROPYRON

Chloropyron Behr, Proc. Calif. Acad. I. **1**: 61. 1855; Heller, Muhlenbergia **3**: 133.

Cordylanthus § *Hemistegia* Gray, Proc. Am. Acad. **7**: 383. 1868; Wats. Bot. King's Exped. 460 (in part); Gray, Syn. Fl. **2**^{1}: 304.

Flowers in spikes; calyx monophyllous; corolla slightly saccate, pink with purplish tip; stamens two or four, the upper, when present, imperfect, the lower with dilated filaments.

Key to species of § Chloropyron.

Stamens two.
  Bracts densely villous-hirsute .... 18. *A. mollis.*
  Bracts sparsely hirsute .... 19. *A. palmata.*

Stamens four.
  Herbage canescent, bracts lanceolate .... 20. *A. canescens.*
  Herbage glaucous, bracts generally three-toothed .... 21. *A. maritima.*

18. ADENOSTEGIA MOLLIS (Gray) Greene

Cordylanthus mollis Gray, Proc. Am. Acad. **7**: 384. 1868; Wats. Bot. King's Exped. 460; Gray, Bot. Calif. **1**: 582; Gray, Syn. Fl. $\mathbf{2}^1$: 304; Jepson, Fl. W. Mid. Calif. ed. 2. 287.

Adenostegia mollis Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Wettstein in Engler & Prantl, Nat. Pflanzenfam. $\mathbf{4}^{3b}$: 98; Jepson, Fl. W. Mid. Calif. 417.

Chloropyron molle Heller, Muhlenbergia **3**: 133. 1907.

Simple or divaricately branching annual, 3–4 dm. high with sparsely hirsute stems; leaves 5–7 mm. long, the lower entire, the upper incised, pubescence dense villous-hirsute; spike 3–10 cm. long, dense, and drooping; floral bracts 18–22 mm. long, villous-hirsute with long, spreading hairs, shallowly five- to eight-parted into finger-like divisions, the middle division exceeding the others, three-nerved; calyx-leaf 17–18 mm. long, four- or five-nerved, with two, sometimes three, erect teeth, completely hidden by the wide floral bract, lower part nearly glabrous, upper villous-hirsute; corolla 15–16 mm. long, the tube longer than the throat; stamens two, the upper pair lacking; capsule 7–9 mm. long, rounded; seeds 2–5 mm. long, deeply reticulate. [PLATE 10, FIG. 19.]

TYPE LOCALITY: "Mare Island, Bay of San Francisco, Charles Wright, in N. Pacif. Expl. Expedition, November, 1855."

DISTRIBUTION: A very local species, found only along the northern side of San Francisco Bay from Suisun to San Rafael.

SPECIMENS EXAMINED:—CALIFORNIA: Vallejo, July, 1883, *Congdon;* salt marshes near San Rafael and Petaluma, *Davy 4063;* Suisun Marshes near Suisun, *Heller 7551;* Suisun Marshes, 1892, *Jepson;* Mare Island, 1855, *Wright* (co-type).

19. **Adenostegia palmata** sp. nov.

Low annual, 1–2 dm. high, branching divaricately from the base, sparsely hirsute throughout with short hairs; leaves 8–18 mm. long, mostly incised, the lower sometimes entire; spike 5–10 cm. long, dense, erect; floral bracts 12–18 mm. long, deeply parted into five to eight finger-like divisions, the middle division exceeding the others, three- to five-nerved, often reddish; calyx-leaf 11–15 mm. long, entire or bidentate; corolla 12–16 mm. long, conspicuous, tube longer than throat; stamens two, the upper pair lacking. [PLATE 10, FIG. 20; PLATE 12, FIG. 4.]

TYPE LOCALITY: In alkaline soil, overflowed lands at Tule near College City, Colusa County, California, June 17, 1916, *Stinchfield 284*. TYPE, No. 70613 of the Dudley Herbarium.

This species differs most conspicuously from *A. mollis* in its sparse pubescence and its deeply parted, palmate bracts.

20. ADENOSTEGIA MARITIMA (Nutt.) Greene

Cordylanthus maritimus Nutt.; Bentham in De Candolle, Prodr. **10**: 598. 1846; Gray, Proc. Am. Acad. **7**: 383; Wats. Bot. King's Exped. 460; Gray, Bot. Calif. **1**: 581; Gray, Syn. Fl. **2**^{1}: 304; Jepson, Fl. W. Mid. Calif. ed. 2. 387.

Chloropyron palustre Behr, Proc. Calif. Acad. **1**: 61. 1855.

Adenostegia maritima Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Wettstein in Engler & Prantl, Nat. Pflanzenfam. **4**^{3b}: 98; Jepson, Fl. W. Mid. Calif. 417; Abrams, Fl. Los Angeles 372.

Chloropyron maritima Heller, Muhlenbergia **3**: 133. 1907.

Decumbent annual, 2–3 dm. high, branching diffusely from the base or above, erect when young; stems puberulent, sometimes sparsely pubescent; floral bract 2–3 cm. long, pubescence varying from short-hairy to short-villous, 1-nerved, broadly lanceolate or shallowly three-toothed, the lateral teeth the smaller; calyx-leaf 12–15 mm. long, toothed at apex, the teeth scarcely 1 mm. long, covering as on bract; corolla 10–18 mm. long, covered with soft, short pubescence; stamens four, the upper pair with second cell imperfect or absent, the filaments glabrous; seeds 1–2 mm. long, deeply reticulate. [PLATE 10, FIG. 21.]

This variable species has two intergrading forms. Around San Francisco Bay and to the northward the plant is, in general, twice as large as the Southern California form. Both of these forms, however, vary in the pubescence of the spike from nearly glabrous to short-villous in their respective localities. The floral bracts are either lanceolate or toothed, generally the latter. In its extreme variations the San Francisco Bay form approaches *A. mollis.* The species is very closely related to *A. canescens,* but the lanceolate bracts, the soft villous pubescence and the scantily hairy filaments of the latter furnish a basis for their separation.

TYPE LOCALITY: "Ad San Diego Californiae (Nuttall!)."

DISTRIBUTION: Salt marshes along the Pacific Coast from Humboldt Bay in California to San Quintan, Lower California.

SPECIMENS EXAMINED:—CALIFORNIA: Hookton, Humboldt Bay, Humboldt County, *Tracy 3697;* Samoa, Humboldt Bay, *Tracy 1257;* San Rafael, Marin County, *Bolander 2403;* Tiburon Peninsula, Marin County, *Heller 5722;* near San Francisco, *Vasey 1875;* Shell Mound, Oakland, Alameda County, July, 1880, *Rattan;* Belmont, San Mateo County, *Davy 4063;* Cooley's Landing, Palo Alto, September 14, 1901, *Dudley;* Ravenswood, Palo Alto, *Philips & Stinchfield 269;* Palo Alto, *Baker 3557;* same locality, 1901, *Congdon;* same locality, *Elmer 3423;* Alviso, Santa Clara County, July 18, *Dudley;* Milpitas, Santa Clara County, June, 1905, *Smith;* Playa del Rey, Los Angeles County, *Abrams 1714;* San Pedro, Los Angeles County, *Grant 3124;* Coronado Sand Spit, San Diego County, *Chandler 4003;* South San Diego, October 3, 1903, *Brandegee;* mouth of the Tia Juana River, *Mearns 3914;* Mexican Boundary Monument 258, *Mearns 3931.* LOWER CALIFORNIA: San Quintan, May, 1899, *Brandegee.*

21. ADENOSTEGIA CANESCENS (Gray) Greene

Cordylanthus canescens Gray, Proc. Am. Acad. **7**: 383. 1868; Wats. Bot. King's Exped. 233, 460; Gray, Bot. Calif. **1** 581; Gray, Syn. Fl. **2**^{1}: 304.

Cordylanthus Parryi Wats. in Parry, Am. Nat. **9**: 346. 1875.

Cordylanthus canescens var. *Parryi* Gray, Syn. Fl. **2**^{1}: 304. 1886.

Adenostegia canescens Greene, Pittonia **2**: 181. 1891; Kuntze, Rev. Gen. **2**: 457; Rydberg, Bull. Torrey Club **40**: 484.

Adenostegia Parryi Greene, Pittonia **2**: 181. 1891.

Chloropyron canescens Heller, Muhlenbergia **3**: 134. 1907.

Chloropyron Parryi Heller, Muhlenbergia **3**: 134. 1907.

Divaricately and sometimes corymbosely branching annual, 2–4 dm. high, more or less canescent throughout with spreading, villous hairs; leaves 10–20 mm. long, lanceolate, prominently one-nerved, rarely three-nerved; spike erect, 2–4 cm. long; floral bracts 20–25 mm. long, more canescent than the leaves, lanceolate, often purplish at the tip; calyx-leaf 1–3 mm. shorter than the bract, two- or three-toothed at apex, the teeth erect or spreading with age; corolla tube equaling or slightly shorter than the throat; stamens four, the upper pair with second cell imperfect or absent, the filaments with scattered hairs, occasionally glabrous; capsule rounded; seeds reticulate. [PLATE 10, FIG. 22.]

Examination of a fragment and a photograph of the type of *Cordylanthus Parryi* shows that this is an immature specimen of *A. canescens.*

TYPE LOCALITY: "Near Carson City, Nevada, Dr. C. L. Anderson."

DISTRIBUTION: Saline lakes and springs in the Great Basin from eastern California and Oregon to Utah.

SPECIMENS EXAMINED:—OREGON: Goose Lake Valley, Lakeview, *Cusick 2767;* Denio, August, 1901, *Griffiths & Morris.* CALIFORNIA: Lake Lessons, Modoc County, *Mrs. Manning 328;* Honey Lake Valley, Lassen County, *Davy 3390;* Alkaline Meadows, San Bernardino County, 1888, *Parish.* NEVADA: Steamboat Springs, *Heller 10367;* same locality, *Kennedy 1488, 1499;* Eagle Valley, *Baker 1265;* Black Rock Desert, *Griffiths & Hunter 535;* Glendale, *Kennedy 1953;* near Carson City, *Anderson 201.* UTAH: Smelter Beach, Tooele County, 1891, *Smith;* Garfield Beach, Salt Lake, *Rydberg 6897;* Salt Lake City, *Jones 1403;* Ogden Hot Springs, August 16, 1893, *Ries.*

Explanation of plates 10–12

PLATE 10

1. *Adenostegia laxiflora* (Gray) Greene; bract from specimen from Beaver Creek, Arizona, × 4.

2. *Adenostegia Pringlei* (Gray) Greene; bract from specimen from near Bartlett Springs, California, × 2.

3. *Adenostegia capitata* (Nutt.) Greene; bract from specimen from Gold Creek, Elko County, Nevada, × 1½.

4. *Adenostegia pilosa* (Gray) Greene; bract from topotype specimen, × 1½.

5. *Adenostegia tenuis* (Gray) Greene; bract from co-type specimen from near Lake Tahoe, Nevada, × 1½.

6. *Adenostegia viscida* Howell; bract from specimen from Siskiyou Mountains, Oregon, × 2.

7. *Adenostegia Hanseni* Ferris; bract from the type, × 1½.

8. *Adenostegia parviflora* Ferris; bract from the type, × 3½.

9. *Adenostegia Nevinii* (Gray) Greene; bract from specimen from Bear Valley, San Bernardino County, California, × 4.

10. *Adenostegia filifolia* (Nutt.) Abrams; bract from specimen from San Diego, California, × 1½.

11. *Adenostegia rigida* Benth.; bract from specimen from the Santa Lucia Mountains, California, × 4½.

12. *Adenostegia rigida brevibracteata* (Gray) Greene; bract from co-type specimen, × 3½.

13. *Adenostegia littoralis* Ferris; bract from type, × 1½.

14. *Adenostegia ramosa* (Nutt.) Greene; bract from specimen from Grizzly Butte, Crook County, Oregon, × 1½.

15. *Adenostegia Wrightii* (Gray) Greene; bract from specimen from Chiracahua Mountains, Arizona, × 1½.

16. *Adenostegia Kingii* (Wats.) Greene; bract from specimen from near Ferron, Utah, × 1½.

17. *Adenostegia Helleri* Ferris; bract from type, × 1½.

18. *Adenostegia Orcuttiana* (Gray) Greene; bract from specimen from Tia Juana, Lower California, × 1½.

19. *Adenostegia mollis* (Gray) Greene; bract from specimen from Suisun Marshes, Solano County, California, × 1½.

20. *Adenostegia palmata* Ferris; bract from type, × 1½.

21. *Adenostegia maritima* (Nutt.) Greene; bract from specimen from Palo Alto, California, × 1½.

22. *Adenostegia canescens* (Gray) Greene; bract from specimen from Smelter Beach, Tooele County, Utah, × 1½.

PLATE 11

1. *Adenostegia laxiflora* (Gray) Greene; Beaver Creek, Arizona.

2. *Adenostegia Pringlei* (Gray) Greene; co-type specimen from Lake County, California.

3. *Adenostegia Hanseni* Ferris; type.

4. *Adenostegia parviflora* Ferris; type.

PLATE 12

1. *Adenostegia littoralis* Ferris; type.

2. *Adenostegia Helleri* Ferris; type.

3. *Adenostegia Orcuttiana* (Gray) Greene; Tia Juana, Lower California, *Stokes*.

4. *Adenostegia palmata* Ferris; type.

INDEX TO AMERICAN BOTANICAL LITERATURE

1916–1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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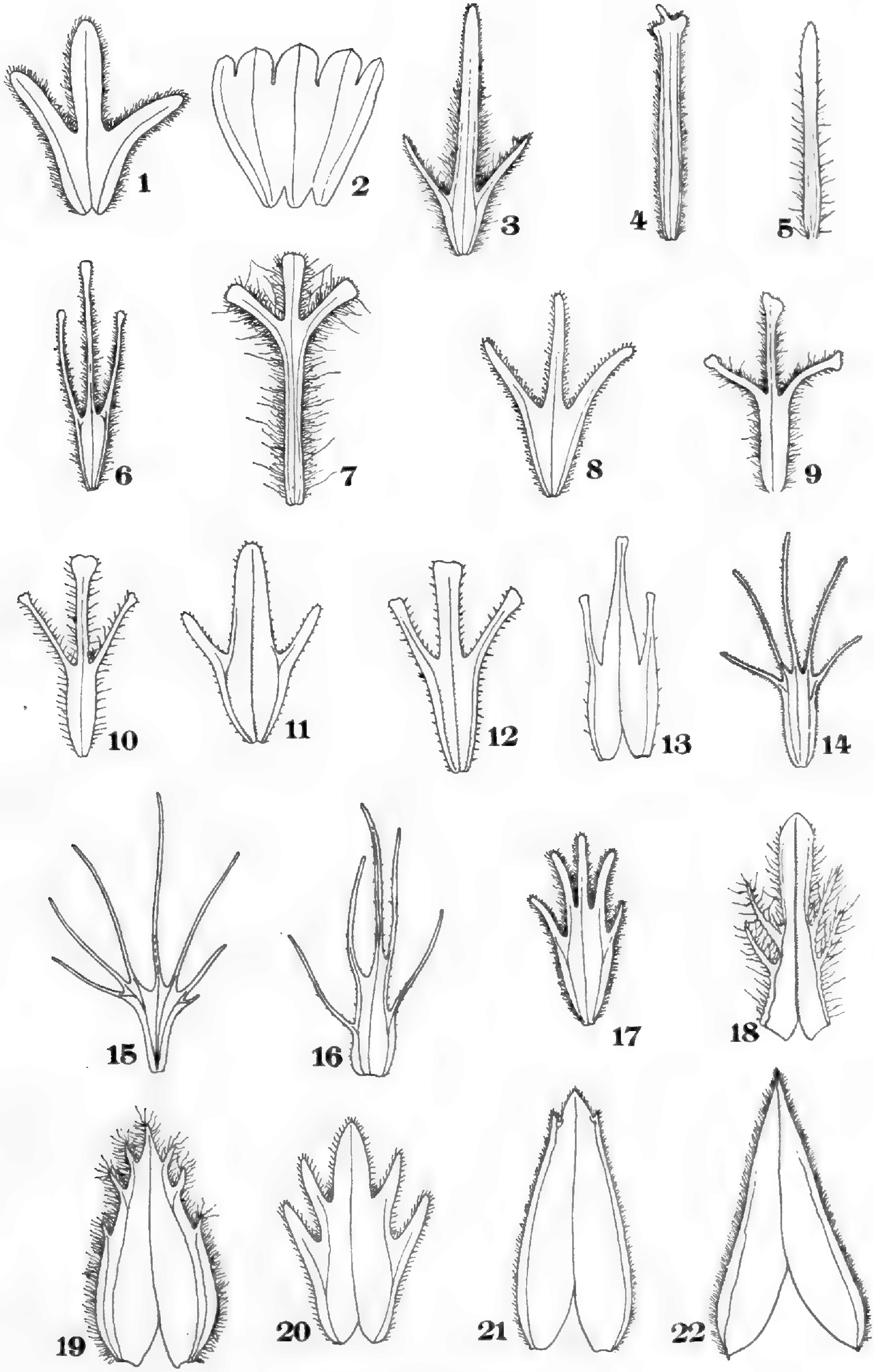

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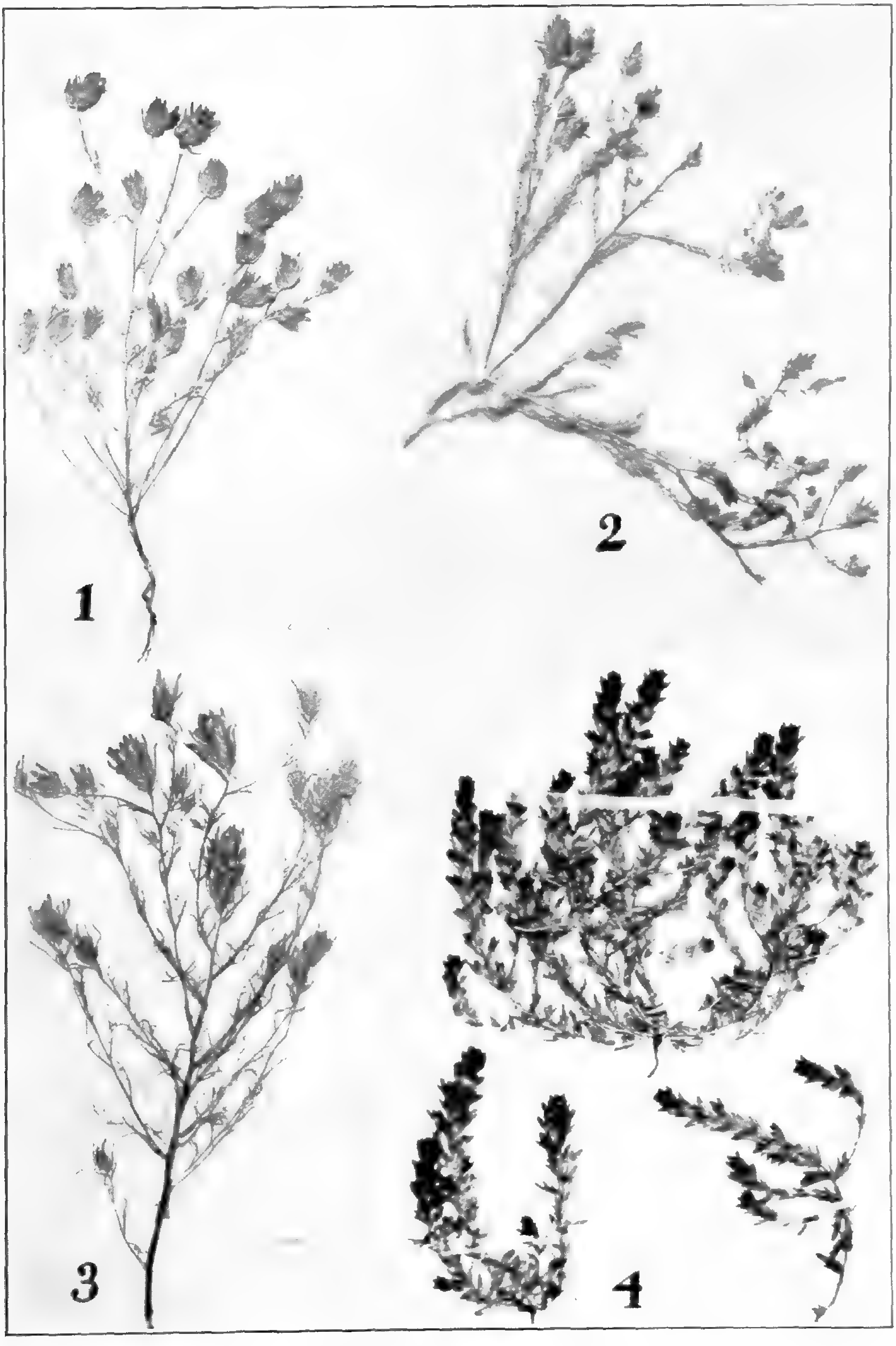

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Revision of the North American species of Encalypta

DOROTHY COKER

(WITH PLATES, 13 AND 14)

The family Encalyptaceae, of which there is only one genus, *Encalypta*, is closely related to the Pottiaceae, because of the twisted and crisped habit of its leaves when dry, the small, thick-walled, very papillose cells of the upper portion of the leaves, and the large hyaline cells at the base. The costa also is strong and often excurrent. The genus is noted for the great diversity in the structure of its peristome, ranging from double, with several remarkable variations, to single or absent.

Hedwig (**4**, p. 88), in 1782, based the genus *Leersia* on two species, *Bryum pulvinatum* and *B. extinctorium*, referring the latter to its Linnean synonym (see p. 103 in the descriptions of figures 19 and 24). Of these two species *Bryum pulvinatum*, which is a *Grimmia*, precedes *B. extinctorium;* and since *Grimmia*, according to Ehrhart (**6**, p. 176), antedates *Leersia* by one year, the name *Leersia* has been discarded. Hence, the adoption of the name *Encalypta* Schreb., 1791 (**9**, p. 759), instead of *Leersia* Hedw., 1782, is due to the fact that *Leersia*, which in reality antedates *Encalypta*, was originally used by Hedwig to include *Grimmia*. Subsequently Hedwig, in 1801 (**12**, pp. 60–63), accepted the name *Encalypta* in place of *Leersia*.

Following the older authors, Lesquereux and James (**32**, pp. 180–184) placed *Encalypta* under the Orthotrichaceae, and Schim-

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per (**28**, pp. 307–340) with the Grimmiaceae; Lindberg (**30**, p. 26) and Braithwaite (**33**, pp. 279–287) adopted *Leersia* for *Encalypta*, referring it, as a subfamily, to the Tortulaceae, because of the leaf-characteristics. Limpricht (**32**, pp. 102–123) and Dixon (**40**, pp. 227–231) agree in recognizing the Encalyptaceae as distinct from the Pottiaceae, but Dixon places it under the subgroup Aplolepideae and Limpricht uses the terms Haplolepideae and Diplolepideae only in the specific descriptions. Loeske (**48**, p. 100) rejects Lindberg's usage of *Leersia* under the Tortulaceae and also the placing by Brotherus (**44**, pp. 436–439) of the Encalypteae as a subfamily of the Pottiaceae, and agrees with Fleischer (**46**, p. xiii), who places them under a new group, the Heterolepideae, because the peristome varies from the Haplolepideae to the Diplolepideae, stating that they should be treated as a separate family.

In 1904 Paris Index (**45**, pp. 119–126) listed 30 species, of which 18 were recorded for North America. According to Brotherus, in 1902 (**44**, pp. 436–439), there were 35 species, of which 21 were recorded for the whole of America, 14 being endemic and 18 occurring north of Mexico. We* have reduced this number to 8 by careful comparison of original and authentic specimens and by studying the types whenever possible, having seen type specimens of *E. longipes*, *E. Macounii*, and *E. Selwyni* from the Austin and Mitten Herbaria, and authentic material of *E. alaskana*, *E. leiocarpa*, *E. subspathulata*, *E. cucullata*, *E. subbrevicolla*, and *E. labradorica* from the Macoun collections. The accompanying lists and synonymy show the changes that have been made. Only one species remains doubtful, *E. lacera* Ren. & Card. (**38**, p. 91); it was described in a footnote to their check list of North American mosses from specimens collected in Oregon by L. F. Henderson, and no specimens have been obtainable.

Chronological list of the North American species of Encalypta†

1753. *E. extinctoria* (L.) Sw. Disp. Musc. Suec. 24. 1799.
1782. *E. laciniata* (Hedw.) Lindb. Acta Soc. Sci. Fenn. **10**: 267. 1872.
1788. *E. contorta* (Wulf.) Lindb. Oefv. K. Vet. Akad. Foerh. **20**: 396. 1863.

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* The responsibility for these reductions rests largely with Mrs. Britton.

† Adapted from Brotherus (**44**) and Paris Index (**45**).

1805. *E. alpina* Smith; Sowerby, Engl. Bot. *pl. 1419.* 1805.

1811. *E. rhabdocarpa* Schwaegr. Suppl. **1**: 56. *pl. 16.* 1811.

1827. *E. apophysata* Nees & Hornsch. Bryol. Germ. **2**: 49. *pl. 15, f. 5.* 1827.

1832. *E. procera* Bruch, Abh. Akad. Münch. **1**: 283. *pl. 11.* 1832.

1849. *E. mexicana* C. Müll. Syn. **1**: 516. 1849.

1865. *E. longipes* Mitt. Jour. Linn. Soc. **8**: 29. *pl. 5.* 1865.

1877. *E. Macouni* Aust. Bot. Gaz. **2**: 97. 1877.

1877. *E. Selwyni* Aust. Bot. Gaz. **2**: 109. 1877.

1889. *E. leiocarpa* Kindb. Bull. Torrey Club **17**: 275. 1889.

1892. *E. subspathulata* C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 93. 1892.

1892. *E. leiomitra* (Kindb.) Kindb.; Macoun, Cat. Can. Pl. 6: 94. 1892.

1892. *E. cucullata* C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 96. 1892.

1892. *E. alaskana* Kindb.; Macoun, Cat. Can. Pl. 6: 269. 1892.

1892. *E. lacera* Ren. & Card. Rev. Bryol. **19**: 91. 1892.

1897. *E. subbrevicolla* Kindb. Eur. & N. Am. Bryin. **2**: 295. 1897.

1897. *E. labradorica* Kindb. Eur. & N. Am. Bryin. **2**: 295. 1897.

Arrangement of the North American species of Encalypta[*]

§ 1. PYROMITRIUM (Wallr.) Kindb.

1. *E. alpina* Smith (*E. commutata* Nees & Hornsch.).

§ 2. XANTHOPUS Kindb.

2. *E. ciliata* (Hedw.) Hoffm. = *E. laciniata* (Hedw.) Lindb.
3. *E. Macounii* Aust. = *E. apophysata* Nees & Hornsch.
4. *E. alaskana* Kindb. = *E. laciniata.*

§ 3. RHABDOTHECA Kindb.

5. *E. vulgaris* (Hedw.) Hoffm. = *E. extinctoria* (L.) Sw.
6. *E. rhabdocarpa* Schwaegr. (including *E. leiomitra* Kindb.).
7. *E. lacera* Ren. & Card. = *E. rhabdocarpa?*
8. *E. subspathulata* C. Müll. & Kindb. = *E. rhabdocarpa.*
9. *E. mexicana* C. Müll. = *E. laciniata.*

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[*] Adapted from Kindberg (**42**, pp. 292–297) and Brotherus (**44**, pp. 436–439).

§ 4. DIPLOLEPIS Kindb.

10. *E. longipes* Mitt. = *E. procera.*
11. *E. leiocarpa* Kindb. = *E. apophysata.*
12. *E. subbrevicolla* Kindb. = *E. brevicolla* Bruch.
13. *E. labradorica* Kindb. = *E. extinctoria.*

§ 5. STREPTOTHECA Kindb.

14. *E. contorta* (Wulf.) Lindb. (*E. streptocarpa* Hedw.).
15. *E. cucullata* C. Müll. & Kindb. = *E. procera* + *E. extinctoria.*
16. *E. procera* Bruch.
17. *E. Selwyni* Aust. = *E. procera.*

ENCALYPTA Schreb. Genera **2**: 759. 1791

Leersia Hedw. Fundam. **2**: 88, in part. 1782

Plants growing in dense compact cushions or mixed with other cespitose mosses; stems usually low and crowded, seldom more than 4 cm. high; branches usually simple and sub-apical, erect, the leaves uniformly spaced; leaves usually curled and twisted when dry, spreading above when moist, from an erect clasping oblong base, seldom more than 6 mm. long by 1.5 mm. broad; costa stout, either ending below the apex or excurrent into a subulate or mucronate point, cross-section of costa usually papillose above on both faces, with a large dorsal band of stereid cells and several upper layers of large ducts in 3–4 rows, the upper epidermal cells with thick walls and smaller papillae; cells of the upper part of the leaf-blade deeper than wide with clusters of prominent, minute papillae, those of the lower part of blade larger, oblong and usually without papillae, except in one species (*E. apophysata*) which has them on the short end walls; margins entire, flat or slightly recurved, rarely undulate. Perichaetial leaves generally smaller, more acuminate and often subulate.

Monoicous, or in one exception (*E. contorta*) dioicous; sometimes sterile and frequently propagating by elongated septate brood-bodies; the antheridia in small lateral axillary buds; archegonia terminal, vaginule enlarged, cylindric and often ochreate; seta usually elongate, smooth except in *E. streptocarpa*, seldom more than 1–2 cm., rarely 3 cm., long (*E. longipes*), usually twisted; calyptra large, 0.5–1 cm., completely covering the capsule to the base, cylindric and glossy, smooth or papillose at apex, sometimes slightly papillose over the entire surface, ragged or fringed at base; lid (operculum) large, never equalling the urn (theca), longrostrate; peristome originating at or below the mouth; simple (haplolepideous) or compound (diplolepideous), sometimes lacking; preperistome sometimes present; annulus simple or compound; teeth varying in length, usually papillose or striate, entire or split along the median line, rarely more or less united and attached to the endostome by a hyaline membrane, sometimes nodose or with short intermediate cilia; walls of the urn (theca) either smooth or striate, striae sometimes visible only after sporosis, sometimes spirally twisted or deeply grooved; neck (column) short, stomatose, or the stomata scattered along the wall; spores smooth or rough, usually maturing in spring or summer, variable in size.

Type species, *Bryum extinctorium* L.

The genus divides itself naturally into two groups or sections: § 1. *Haplolepideae*, with the peristome single or absent, and § 2. *Diplolepideae*, with the peristome double and variable.

In § 1 are included 4 species that are found in Europe and North America: *E. alpina*, *E. extinctoria*, *E. laciniata*, and *E. rhabdocarpa*, the last two approaching the *Diplolepideae* by having a preperistome.

In § 2 are included 4 species, also common to Europe and North America: *E. apophysata*, *E. brevicolla*, *E. procera*, and *E. contorta;* of these *E. contorta* has not yet been found fruiting on this continent.

Key to species

§ 1. HAPLOLEPIDEAE. Peristome simple or lacking; teeth, when present, short, lanceolate; capsule not twisted.
  Capsule striate, or becoming so when old.
    Calyptra lacerate at base, nearly smooth at apex.
      Peristome only occasionally found. Walls of cells at base of leaves thickened. 1. *E. extinctoria.*
      Peristome usually present, often with preperistome. Walls of cells at base of leaves not thickened. 2. *E. rhabdocarpa.*
  Capsule smooth.
    Calyptra lacerate at base but not fringed. Peristome never present, spores papillose. 3. *E. alpina.*
    Calyptra with a persistent or fugacious fringe of larger cells. Peristome usually present, deeply inserted. 4. *E. laciniata.*

§ 2. DIPLOLEPIDEAE. Peristome double, teeth usually long and slender; endostome more or less adherent to the teeth.
  Capsule smooth, calyptra fringed or lacerate.
    Teeth perforate or split along median line. Basal cells of leaves with short walls papillose. 5. *E. apophysata.*

Teeth more or less united in pairs, unequal in length. Basal cells of leaves not papillose.	6. *E. brevicolla.*
Capsule striate and spirally twisted, calyptra lacerate.	
Monoicous, seta smooth, spores 15–25 μ; leaves slightly toothed at base.	7. *E. procera.*
Dioicous, seta slightly papillose, spores 8–12 μ, leaves entire.	8. *E. contorta.*

§ 1. **Haplolepideae**

1. ENCALYPTA EXTINCTORIA (L.) Sw. Disp. Musc. Suec. 24. 1799

Bryum extinctorium L. Sp. Pl. 1116. 1753.

Leersia extinctoria Hedw. Fundam. **2**: 88. 1782.

Leersia marginata Hedw. Fundam. **2**: 103. 1782.

Leersia vulgaris Hedw. Descr. **1**: 46. 1787.

Encalypta vulgaris Hoffm. Deuts. Fl. **2**: 27. 1796.

Encalypta cucullata C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 96, in part. 1892.

Encalypta extinctoria subsp. *tenella* Kindb.; Röll, Hedwigia **35**: 65. 1896.

Plants small, about 0.5–1 cm. high; leaves up to 4 mm. long, 1 mm. wide; apical blade lingulate, apex cucullate contracted to an abrupt point; costa ending below the apex, smooth on both faces except slightly toothed at tip on back; margins plane, erose above; papillose cells 12–14μ long; cells of hyaline base oblong, up to 55μ long by 15μ wide, walls brown, slightly thickened at ends, with 7–8 rows of long narrow cells at margin; perichaetial leaves shorter and blunt at apex, usually carinate when moist. Monoicous; vaginule about 1.5 mm. long; seta 5–8 mm., red brown, not twisted; calyptra entire or ragged at base, slightly papillose at apex; lid about 1.5 mm. long; capsule 2–3 mm. long by 1 mm. wide, cylindric, smooth when young, ribbed when old; annulus simple, narrow; mouth marked by an irregular, broken row of 1–2 quadrate, small, thickened cells; urn with the stomata sparsely scattered over the entire surface; neck short, red, without stomata; peristome, when present, of simple fugacious teeth; spores rough with large rounded papillae, 24–32μ, maturing in early spring.

TYPE LOCALITY: European.

DISTRIBUTION: On rocks and earth in the Rocky Mountains, from British Columbia to Colorado, and South Dakota; western states from Nevada to California. Also Eurasia and Australasia, according to Paris Index (**45**).

ILLUSTRATIONS: Dill. Hist. Musc. *pl. 45. f.* 8. 1741 (as *Bryum*); Hedw. Descr. **1**: *pl. 18.* 1787 (as *Leersia*); Bryol. Eur. *pl. 199.* 1838 (as *E. vulgaris*).

EXSICCATAE: Macoun, Can. Musci *491* (as *E. cucullata*); Holz. Musci Acro. Bor. Am. *214*. 1906.

1a. ENCALYPTA EXTINCTORIA APICULATA Wahl. Fl. Lapp. 344. 1812

Costa usually excurrent into a short hair-point; capsule when mature striate and somewhat ribbed.

DISTRIBUTION: Colorado, Montana, and Assiniboia. Also Europe.

1b. ENCALYPTA EXTINCTORIA MUTICA Brid. Musc. Recent. Suppl. 4: 28. 1819

Costa disappearing far below the blunt apex; mature capsule ribbed.

DISTRIBUTION: Colorado to British Columbia. Also Europe.

2. ENCALYPTA RHABDOCARPA Schwaegr. Suppl. 1: 56. 1811

Leersia rhabdocarpa Lindb. Musci Scand. 26. 1879.
Encalypta rhabdocarpa var. *leiomitra* Kindb. Ottawa Nat. 4: 61. 1890.
Encalypta subspathulata C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 93. 1892.
Encalypta leiomitra Kindb.; Macoun, Cat. Can. Pl. 6: 94. 1892.

Plants 1.5–2 cm. high; leaves 3–4 mm. by 0.66–1 mm. wide, lingulate, flat and spreading when moist; costa extending beyond the suddenly contracted apex of leaf into a long mucronate hair-point or ending below the apex, papillose on back below the middle and on the upper surface above the middle of the leaf; margin plane; papillose cells, hexagonal, diameter 15–20μ; cells of hyaline base, irregular, not papillose, 24–48μ long by 24μ wide; walls orange, not thickened, with a distinct marginal border of 6–8 rows of cells, 60μ long by 6–10μ wide; perichaetial leaves smaller and tapering to a hair-point. Monoicous; seta 6–8 mm., orange, not twisted; calyptra entire or ragged at base, papillose at apex and sometimes to about the middle; lid about 2 mm.; capsule 2–3 mm. long by 1 mm. wide, cylindric, striate, each ridge of about 5–6 rows of cells; annulus simple; rim of the mouth marked by 2–3 rows of small brown quadrate cells; stomata numerous, scattered throughout the entire surface of the urn; neck short, red, deeply wrinkled with large loose cells; peristome usually present, single, of 16 red, finely striate, papillose teeth, with 4–5 segments, and occasionally with a narrow lateral preperistome covering 1–2 segments at base of the teeth; spores 40–50μ in diameter, very rough with large granular warts, ripe in late spring.

According to Limpricht (**39**, p. 115. *f. 245, 246*) there is great variation in the peristomes of this species. However, we have not found any peristome to correspond with his *f. 246* in American specimens.

TYPE LOCALITY: European.

DISTRIBUTION: Arctic America, Greenland, Labrador to Quebec and northern New York, Rocky Mountains from Montana to New Mexico, Pacific Coast ranges from Washington to California. Also Europe and Asia.

ILLUSTRATIONS: Schwaegr. Suppl. **1**: *pl. 16.* 1811; Bryol. Eur. *pl. 205.* 1838.

EXSICCATAE: Drummond, Musci Am. *50, 51* in part; also *52.* 1828. Sull. & Lesq. Musci Bor. Am. *112.* 1856; ed. 2. *166.* 1865; Macoun, Can. Musci *131, 421* (as *E. subspathulata*).

E. leiomitra differs from *E. rhabdocarpa* only in that the apex of the calyptra is nearly smooth.

E. subspathulata is undoubtedly *E. rhabdocarpa*, but all of the older capsules are badly infected by fungi and filled with hyphae.

2a. ENCALYPTA RHABDOCARPA PILIFERA (Funck) Nees & Hornsch. Bryol. Germ. **2**: 41. 1827

Encalypta pilifera Funck, in Sturm, Deuts. Fl. 17: *pl. 5.* 1819.
Leersia extinctoria var. *pilifera* Lindb. Musc. Scand. 20. 1879.

Leaves somewhat broader and more ovate; costa excurrent into a long toothed hair; peristome perfect.

DISTRIBUTION: Fraser River Valley, Canada. Also Europe.

ILLUSTRATION: Sturm, Deuts. Fl. 17: *pl. 5.*

2b. ENCALYPTA RHABDOCARPA MICROSTOMA Breidler; Limpr. Laubm. **2**: 115. 1895

Capsule narrowing to a small mouth. Lid small, extended into a long point; peristome perfect or rudimentary. A parallel form to *E. laciniata microstoma.*

DISTRIBUTION: Alpine regions of the Rocky Mountains. Also Europe.

3. ENCALYPTA ALPINA Smith; Sowerby, Engl. Bot. *pl. 1419.* 1 F 1805

Encalypta affinis Hedw. f. Weber & Mohr's Beitr. **1**: 121. Mr 1805.

Encalypta commutata Nees & Hornsch. Bryol. Germ. **2**: 46. 1827.
Leersia alpina Lindb. Musci Scand. 20. 1879.

Plants 4–6 cm. high; leaves 3–4 mm. by 1 mm. subspatulate, carinate; apex cucullate when moist; costa excurrent into a long hair-point or ending below the apex, smooth except for a few teeth just below the apex of leaf; margin plane; upper cells hexagonal, 12μ–16μ, not densely papillose; cells of hyaline base 32μ–48μ long by 16μ wide, walls not thickened, becoming narrower and longer toward the margin; perichaetial leaves smaller and tapering to a long hair point. Monoicous; vaginule about 1 mm. long; seta 7–9 mm. long, orange, seldom twisted; calyptra laciniate at base, very slightly papillose at apex; lid 1.5 mm. long; annulus of 2–3 rows of cells; capsule 2–3 mm. long by 0.75 mm. wide, cylindric, smooth when young, appearing striate when old; mouth marked by 1–2 rows of small red-brown quadrate cells often irregularly broken; neck short, wrinkled, stomatose; peristome none; spores 25μ–35μ, warty, often flattened and irregular, ripe in late summer.

TYPE LOCALITY: European.

DISTRIBUTION: Alpine regions of the Rocky Mountains from Colorado to Washington; Alaska and Greenland. Also Europe and Asia.

ILLUSTRATIONS: Sowerby, Engl. Bot. *pl. 1419.* 1805; Weber & Mohr's Beitr. **1**: *pl. 4.* 1805; Schwaegr. Suppl. **1**: *pl. 16.* 1811 (as *E. affinis*); Bryol. Eur. *pl. 198.* 1838.

EXSICCATAE: Drummond, Musci Am. *49.* 1828 (as *E. affinis*).

4. ENCALYPTA LACINIATA (Hedw.) Lindb. Acta Soc. Sc. Fenn. 10: 267. 1872

Bryum extinctorium var. β. L. Sp. Pl. 1116. 1753 (see Dillen, **1**, p. 349; also Druce & Vines, **47**, p. 210).
Leersia laciniata Hedw. Fundam. **2**: 103. *pl. 5, f. 24a.* 1782.
Leersia ciliata Hedw. Descr. **1**: 49. 1787.
Encalypta ciliata Hoffm. Deuts. Fl. **2**: 27. 1796.
Encalypta mexicana C. Müll. Syn. **1**: 516. 1849.
Encalypta alaskana Kindb.; Macoun, Cat. Can. Pl. 6: 269. 1892.

Plants growing on wet limestone rocks; about 1–3 cm. high; leaves carinate when moist, up to 5 mm. long, to about 1.3 mm. wide; apical blade elliptic or lingulate, suddenly contracted to a short mucronate point; costa thick, tapering into the short finely serrulate tip or ending below the apex, slightly toothed on the back; margins revolute below the middle, above entire or erose with truncate, minutely papillose cells up to 13–24μ in diameter; cells of the hyaline base not papillose, oblong, up to 60μ long by 13–21μ wide, becoming narrower toward the margin, the basal cells with brown walls; perichætial leaves slightly smaller. Monoicous; seta yellow to brown, 5–10 mm. high; calyptra broadening at base into a deep regular fringe of larger cells, smooth or slightly roughened at apex; lid beaked, up to 2 mm. long; annulus present, of one row of cuneate cells; capsule 3–5 mm. long by 1 mm. wide, cylindric, smooth; mouth narrow bordered by 3–5 rows of smaller thickened cells; urn with numerous large stomata from the middle to the neck; peristome deeply inserted, single; teeth lanceolate with 5–7 joints, which are longitudinally papillose inside and occasionally with a darker colored preperistome partially covering the basal segments; spores up to 37μ in diameter, with radiating stellate lines, maturing in summer.

TYPE LOCALITY: European.

DISTRIBUTION: Alpine and mountain regions; Eastern States from Maine to northern New York; North Central States from Michigan to Wisconsin, Minnesota; Rocky Mountains from Montana to New Mexico; west coast from Washington to California; British America from Ontario to British Columbia. Also Europe, Asia, Africa and Australia.

ILLUSTRATIONS: Dill. Hist. Musc. *pl. 45. f. 9.* 1741; Hedw, Descr. 1. *pl. 19.* 1787; Bryol. Eur. *pl. 200.* 1838.

EXSICCATAE: Drummond. Musci Am. *50.* 1828; Sull. & Lesq. Musci Bor. Am. *111.* 1856; ed. 2. *165.* 1865; Austin, Musci Ap. *174.* 1870; Macoun, Can. Musci *132* (as *E. ciliata*), and *133* (as *E. Macounii*); Allen, Mosses of Cascade Mts. Wash. *45*; Holz. Musci Acro. Bor. Am. *213.* 1906; Pringle, Plantae Mexicanae *10547* (as *E. mexicana*).

4*a*. **Encalypta laciniata microstoma** (Schimp.) comb. nov.

Encalypta ciliata var. *microstoma* Schimp. Coroll. Bryol. Eur. 38. 1855.

Seta only 3–6 mm. high; calyptra with brown fringe; capsule narrowing to a small mouth. Neck somewhat longer and running down into the seta; peristome smaller, irregular, often lacking; spores very finely papillose, less transparent, and the radiating lines less distinct; ripe in August.

DISTRIBUTION: Northern New York and in the alpine regions of the Rocky Mountains. Also Europe and Asia.

Diplolepideae

5. ENCALYPTA APOPHYSATA Nees & Hornsch. Bryol. Germ. **2**: 49. 1827

Encalypta Macounii Aust. Bot. Gaz. **2**: 97. 1877.

Encalypta leiocarpa Kindb. Bull. Torrey Club **17**: 273. 1890.

Plants 1.5–2 cm. high; leaves 3–4 mm. long by 1 mm. wide, carinate, lingulate; costa ending in the blunt apex or rarely excurrent into a short mucronate point, densely papillose on both surfaces with coarse spinose teeth on dorsal apex; margins revolute above; cells of upper blade 8–10μ, irregular, those of the hyaline base 50–60μ long by 8–10μ wide with the end walls thickened, with papillose projections; perichaetial leaves slightly broader. Monoicous. Seta 10–12 mm. long, smooth; calyptra 6–7 mm. long by 1 mm. wide, very scabrous at apex, papillose over the entire surface, basal fringe sometimes fugacious, cells of fringe narrow; lid about 2 mm. high; capsule 2–3 mm. long by 0.5 mm. wide, not striate, neck apophysate when dry or when wet long and tapering; annulus of 2–3 rows of cells, more or less persistent; mouth bordered by 3–4 rows of small thick-walled hexagonal cells; peristome obscurely double; teeth slender, very papillose, perforate, rarely bifid, inner peristome white, papillose, adhering closely and almost invisibly to the outer; spores 18–24μ, finely papillose, maturing in summer.

TYPE LOCALITY: European.

DISTRIBUTION: Rocky Mountains of British Columbia to Montana; and (according to Paris Index) Scoresby Straits, Arctic America. Also Europe and Asia.

ILLUSTRATIONS: Bryol. Eur. *pl. 201*. 1838; Limpricht, Laubm. **2**: *f. 247*. 1891.

EXSICCATAE: None. Drummond, Musci Am. *50*, is *E. laciniata;* so are many of the specimens cited in Macoun's Catalogue (**37**) for *E. Macounii.* The American specimens of this species seem to have the leaves more often blunt than is usual in the European ones, though Limpricht (**39**) describes them as *obtuse* or *short-pointed.* The type specimens of *E. Macounii* in Austin's herbarium are immature and no spores were formed, but in all other characters they agree with *E. apophysata.* The description of *E. leiocarpa* is erroneous in two important characters, for the calyptra is fringed and the peristome is double.

6. ENCALYPTA BREVICOLLA (B. S. G.) Bruch; C. Müll. Syn. 1: 519. 1849

Encalypta longicolla var. *brevicolla* B. S. G. Bryol. Eur. (4:) Encalypta 12. 1838.

Encalypta labradorica Kindb. Eur. & N. Am. Bryin. **2**: 295. 1897.

Encalypta subbrevicolla Kindb. Eur. & N. Am. Bryin **2**: 295. 1897.

Plants 1–1.5 cm. high; leaves 4–5 mm. long by 1 mm. wide, subacuminate, carinate; costa excurrent into long colorless hair-point, sometimes toothed at the base of awn, papillose on both surfaces; margins plane; upper cells of blade 12–16µ in diameter, irregular; those at the hyaline base 40–48µ long by about 16µ wide, becoming narrower and colorless at the smooth margins; walls orange-colored, slightly thickened at ends; perichaetial leaves slightly shorter and broader. Monoicous; seta 1 cm. long, smooth, red; calyptra 5 mm. long by 1 mm. wide, very scabrous at the apex, papillose over the entire surface, lacerate at base; lid 2–2.25 mm. high, with a red border; capsule about 3 mm. long by 1 mm. wide, not striate; neck short, stomatose, with large basal cells; annulus none; mouth bordered by 4–5 rows of small, thick-walled, quadrate cells; peristome double, deeply inserted; teeth .8 mm. high, irregularly broken and branched, usually united in pairs at base and perforate above, papillose; inner peristome similar and attached to the outer, median segments longer than the lateral ones; spores 28–32µ, very rough.

TYPE LOCALITY: European.

DISTRIBUTION: Labrador and, according to Paris Index, the eastern coast of Greenland. Also Europe.

ILLUSTRATIONS: Bryol. Eur. *pl. 202, β.* 1838.

EXSICCATAE: None.

7. ENCALYPTA PROCERA Bruch, Abh. Akad. Münch. 1: 283. 1832

Encalypta longipes Mitt. Jour. Linn. Soc. **8**: 29. 1865.

Encalypta Selwyni Aust. Bot. Gaz. **2**: 109. 1877.

Leersia procera Lindb. Musci Scand. 20. 1879.

Leersia Selwyni E. G. Britton, Bull. Torrey Club **18**: 50. 1891.

Encalypta cucullata C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 96, in part. 1892.

Plants 2–4 cm. high; leaves more or less spreading when dry, 5–6 mm. long by 1 mm. wide; apical blade subspathulate, apex blunt; costa ending below apex, papillose on upper surface, scabrous on back; margin revolute above; upper cells 12–16µ in diameter, round; those of the hyaline base, 48–60µ long by 12–16µ wide;

walls deep orange, thickened at ends, basal margin slightly serrate; with 3–4 rows of narrow cells, walls colorless and ends unthickened; perichaetial leaves acuminate, tapering, with the costa percurrent into a long hair-point. Monoicous; seta about 1.5–2 cm., smooth, purple shading to orange above; calyptra 6–7 mm. long by 1.5 mm. wide, papillose at apex, very slightly so over the entire surface, lacerate at base but without differentiation of cells; lid 2 mm., marked by ragged broken cells at base; capsule 3–4 mm. long by 0.4 mm. wide, cylindric, slightly striate when young, marked when old by 8 striae, spirally twisted once or twice around the capsule; annulus large, compound; mouth bordered by 2 rows of small thick-walled quadrate cells; neck short, stomatose; peristome double, teeth about 0.5 mm. long, narrow, red, smooth or papillose, basal segments of teeth united and perforated; endostome papillose, orange, as long as the teeth, attached to a papillose basal membrane, the segments alternating with short cilia; spores 15–25μ, smooth, granular inside.

TYPE LOCALITY: European.

DISTRIBUTION: On earth in crevices of rocks and on banks; Ontario to British Columbia and Alaska; the Rocky Mountains of Idaho and Montana; Greenland. Also northern Europe and Asia.

ILLUSTRATIONS: Abh. Akad. Münch. **1**: *pl. 2.* 1832; Bryol. Eur. *pl. 205.* 1838; Mitt. Jour. Linn. Soc. **8**: *pl. 5.* 1865 (as *E. longipes*).

EXSICCATAE: Drummond, Musci Am. *48.* 1828 (as *E. streptocarpa*); Macoun, Can. Musci *134* (as *E. Selwyni*), 474 (as *E. longipes*), *491* in part (as *E. cucullata*), and *565* (as *E. procera*).

8. ENCALYPTA CONTORTA (Wulf.) Lindb. Oefv. Sv. Vet.-Akad. Förh. **20**: 396. 1863

Bryum contortum Wulf.; Jacq. Coll. **2**: 236. 1788.

Encalypta streptocarpa Hedw. Sp. Musc. 62. 1801.

Leersia contorta Lindb. Musci Scand. 19. 1879.

Plants 2–4 cm. high; leaves spreading when dry, 5–6 mm. long by 1.5 mm. wide; apical blade lingulate, carinate; apex tapering to the blunt point; costa ending below the apex, very papillose on both surfaces, scabrous on back at basal portion; margins plane; upper cells 12–16μ in diameter, round, those of the hyaline base, 40–48μ long by 16μ wide, not papillose; walls deep orange, slightly thickened at angles, basal margins bordered by 2–3 rows of long narrow cells; perichaetial leaves 2–3 mm., more acuminate. Dioicous. Seta about 1.5–2 cm. long, slightly papillose, purple; calyptra 8–10 mm. long by 1 mm. wide, brown, lacerate at base, very rough at apex, entire surface slightly papillose; lid 1.5 mm. long; capsule 4–5 mm. by 2–3 mm. wide, larger at base, deeply grooved with 8 striae, which are spirally twisted 2–3 times around the capsule; annulus large, compound, persistent; mouth bordered by 2–3 rows of small thick-walled quadrate cells; neck short, stomatose, red; peristome double; teeth long, narrow, orange-colored, very papillose; endostome with 32 paler papillose segments, one half the length of teeth, united at base by a thin papillose membrane; spores 8–12μ, smooth, irregular, ripe in early summer.

TYPE LOCALITY: European.

DISTRIBUTION: On limestone rock, sand and earth in temperate and alpine regions of Canada and Ontario to the Rocky Mountains; Eastern States from Vermont to Virginia; Central States from Ohio to Minnesota; Colorado and California, according to Paris Index. Also Europe and Asia. Fruit plentiful in Europe but not yet found in North America.

ILLUSTRATIONS: Hedw. Sp. Musc. *pl. 10.* 1801 (as *Encalypta streptocarpa*); Bryol. Eur. *pl. 204.* 1838.

EXSICCATAE: Sull. Musci Allegh. *152.* 1845; Aust. Musci App. *175.* 1870; Macoun, Can. Musci *135;* Holz. Musci Acro. Bor. Am. *141.* 1904.

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Description of plates 13 and 14

PLATE 13

A. ENCALYPTA EXTINCTORIA (L.) Sw. 1. Plant, natural size. 2. Single plant, enlarged. 3. Various forms of leaves. 4. Base of leaf showing hyaline cells with border. 5. Apex of leaf showing smaller papillose cells. 6. Capsule enlarged. 7. Calyptra with rough apex. 8. Rough spores.

B. ENCALYPTA RHABDOCARPA Schwaegr. 1. Plants, about natural size. 2. Forms of leaves. 3. Smooth basal cells. 4. Apical papillose cells. 5. Ribbed capsule. 6. Calyptra with rough apex. 7. Peristome showing basal preperistome. 8. Rough spores.

C. ENCALYPTA ALPINA Smith. 1. Plants, natural size. 2. Forms of leaves. 3. Basal cells. 4. Apex with subulate awn. 5. Capsule. 6. Calyptra. 7. Portion of capsule walls showing ragged rim of mouth and one stoma. 8. Rough spores.

D. ENCALYPTA LACINIATA (Hedw.) Lindb. 1. Plants, about natural size. 2. Leaves. 3. Basal cells and border. 4. Apex with mucronate point. 5. Capsule. 6. Fringed calyptra. 7. Basal portion enlarged. 8. Rough peristome, and rim of capsule. 9. Smooth, stellate spores.

PLATE 14

A. ENCALYPTA APOPHYSATA Nees & Hornsch. 1. Plants, natural size. 2. Leaves. 3. Basal cells, with papillose transverse walls. 4. Apical cells. 5. Capsule. 6. Papillose calyptra. 7. Base of same, fringed. 8. Double peristome, the inner more or less attached to the outer. 9. Rough spores.

B. ENCALYPTA BREVICOLLA Bruch. 1. Plants. 2. Leaves. 3. Cells of base. 4. Cells of apex. 5. Capsule. 6. Papillose calyptra. 7. Double papillose peristome, the inner more or less branched. 8. Rough spore.

C. ENCALYPTA PROCERA Bruch. 1. Plant. 2. Stem and perichaetial leaves. 3. Smooth basal cells. 4. Papillose apical cells. 5. Twisted capsule. 6. Papillose ragged calyptra. 7. Double peristome, the inner perforate at base. 8. Fragment of annulus. 9. Smooth spores.

D. ENCALYPTA CONTORTA (Wulf.) Lindb. 1. Plants. 2. Leaf. 3. Basal cells. 4. Apical cells. 5. Twisted capsule. 6. Papillose and ragged calyptra. 7. Double peristome more or less united with intermediate cilia. 8. Smooth spores.

Philippine Basidiomycetes—III

PAUL W. GRAFF*

(WITH PLATE 15)

A large number of basidiomycetous fungi have been added from time to time to those known from the Philippine Islands and, as opportunity has offered, numerous tropical species described by different botanists have been checked. The result is that, with the extension of our knowledge, many ranges have been extended, and not a few supposedly distinct species have proven to be identical. The confusion of names has, to a considerable extent, been due to a failure to compare authentically named specimens from the larger museums and herbaria and to a slight and possibly unconscious tendency to limit species distribution with geographic boundaries. A brief review of the synonymy in the following pages, in company with a comparison of named specimens, will show the value of a comparative study of species from various localities, and the need for a continuation of such studies. Extensive studies should also be made of material from Japan, Formosa, China, the Malay States, Borneo, Java, Celebes, New Guinea and Australia. This would bring to light many interesting facts regarding little-known species. Likewise, a comparative study of material from these localities with fungi collected in other more distant and less related tropical countries would probably broaden many views regarding the localization of fungal distribution. For example, *Auricularia mesenterica* (Dicks.) Fr. is also of common occurrence in the American tropics and southern Europe; *Corticium caeruleum* (Schrad.) Fr. is found in North America, southern Europe and northern Africa; and *Pleurotus flabellatus* Berk. & Br. has been collected in tropical America, Ceylon, and South Africa, as well as in the Philippines.

The material in the following list of fungi was collected on the islands of Luzon, Mindoro, Polillo, Leyte, Negros, Culion, and

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Mindanao. All of the collections cited are preserved in the herbarium of the Bureau of Science, Manila. The preceding parts of this series have been published in the Philippine Journal of Science (**8**: Bot. 299–307. 1913; **9**: Bot. 235–254. 1914).

USTILAGINEAE

USTILAGO Persoon

USTILAGO ANDROPOGONIS-ACICULATI Petch, Ann. Roy. Bot. Gard. Perad. **4**: 303. 1909.

LUZON: Manila, May, 1910, *Merrill 7070*, on *Andropogon aciculatus* Retz.

Originally described from material collected on the same host at Peradeniya, Ceylon.

USTILAGO EMODENSIS Berk. Jour. Bot. & Kew Gard. Misc. **3**: 202. 1851.

LUZON: Subprovince of Benguet, December, 1906, *Mearns*, on *Polygonum chinense* L.

Described from material in Hooker's Sikkim-Himalayan collection from Tonglo, at an elevation of 3,300 m. The species is closely related to *U. Candollei*.

USTILAGO KOORDERSIANA Bref. Unters. Mykol. **12**: 132. *pl. 8, f. 5, 6.* 1895.

NEGROS: Cabacalan, March, 1910, *Merrill 6766*, on *Polygonum barbatum* L.

Originally described on the same host from Java.

USTILAGO PANICI MILIACEI (Pers.) Wint.; Rabenhorst, Krypt.-Fl. **1**^{1}: 89. 1884.

Uredo (*Ustilago*) *segetum* var. *Panici miliacei* Pers. Syn. Fung. 224. 1801.

Uredo carbo var. *Panici miliacei* DC. Fl. Franç. **6**: 76. 1815.

Caeoma destruens Schlecht. Fl. Berol. **2**: 130. 1824.

Uredo destruens Duby, Bot. Gall. ed. 2. **2**: 901. 1830.

Erysibe Panicorum Wallr. Fl. Crypt. Germ. **2**: 216. 1833.

Ustilago carbo var. *destruens* Tul. Ann. Sci. Nat. Bot. III. **7**: 81. 1847.

Tilletia destruens Lév. Ann. Sci. Nat. Bot. III. **8**: 372. 1848.

Ustilago destruens Schlecht.; Rabenhorst, Herb. Myc. Nov. *400*.

MINDANAO: District of Cotobato, Cotobato, May 8, 1904, *E. B. Copeland, Bur. Sci. 1349*, on *Panicum* sp.

Previously reported from North and South America and southern Europe. Probably of very general distribution.

USTILAGO TONKINENSIS (P. Henn.) Sacc. Syll. Fung. **11**: 232. 1895.

Uredo tonkinensis P. Henn. Hedwigia **34**: 11. 1895.

LUZON: Province of Rizal, Caloocan, November 20, 1909, *C. B. Robinson, Bur. Sci. 9554*, on *Ischaemum aristatum* var. *gibbum*.

Collected previously in the vicinity of Hanöi, French Indo-China, parasitic on *Andropogon* sp.

CINTRACTIA Cornu

CINTRACTIA LEUCODERMA (Berk.) P. Henn. Hedwigia **34**: 335. 1895.

Ustilago leucoderma Berk. Ann. Mag. Nat. Hist. II. **9**: 200. 1852.

Cintractia Krugiana Magn. Bot. Jahrb. **17**: 490. 1893.

Cintractia affinis Peck, N. Y. State Mus. Bull. **67**: 28. 1903.

MINDANAO: District of Davao, Lake Lanao, Camp Keithley, September, 1907, *Mary S. Clemens*, on *Rynchospora glauca* Vahl; District of Zamboanga, November–December, 1911, *Merrill 8322*, on *Rynchospora aurea* Vahl.

Reported from the southern portion of the United States, the West Indies, Mexico, Brazil, and Borneo.

USTILAGINOIDEA Brefeld

USTILAGINOIDEA VIRENS (Cooke) Tak. Bot. Mag. Tokyo **10**: 19. 1896.

Ustilago virens Cooke, Grevillea **7**: 15. 1878.

Ustilaginoidea Oryzae Bref. Unters. Mykol. **12**: 194. 1895.

Tilletia Oryzae Pat. Bull. Soc. Myc. Fr. **13**: 124. 1897.

LUZON: vicinity of Manila, *P. W. Graff;* Province of Laguna, Santa Rosa, December, 1912, *P. W. Graff*, on *Oryza sativa* L.

This fungus is a common parasite on rice and is found in most of the rice-growing districts of India, Japan, the Philippines, and Malaya.

PUCCINEAE

HAMASPORA Koernicke

HAMASPORA ACUTISSIMA Syd. Monogr. Ured. **3**: 80. 1912.

LUZON: Province of Benguet, Pauai, June, 1909, *R. C. McGregor, Bur. Sci. 8510a*, at an altitude of about 2,100 m.; Province of Tayabas, Mount Banjao, March, 1907, *F. W. Foxworthy, Bur. Sci. 2399a*. NEGROS: Canlaon Volcano, April, 1910, *Merrill 222a*. The host plant of the three collections is *Rubus Rolfei* Vidal.

The species has also been reported on *Rubus moluccanus* L., collected in Java and Australia.

PUCCINIA Persoon

PUCCINIA HYPTIDIS (M. A. Curt.) Tracy & Earle, Bull. Miss. Agr. Exp. Sta. 34: 86. 1895.

Uredo Hyptidis M. A. Curt. Amer. Jour. Sci. **2**: 6. 1820.

Uredo Ciberti Speg. Anal. Soc. Cien. Arg. **9**: 15. 1880.

Puccinia Ciberti Speg. Anal. Mus. Nat. Buenos Aires II. **6**: 220. 1899.

Aecidium Hyptidis P. Henn. Hedwigia **34**: 337. 1895.

Aecidium tucumanense Speg. Anal. Mus. Nat. Buenos Aires III. **9**: 35. 1908.

MINDANAO: District of Davao, Davao, March 21, 1904, *Copeland 595*, on *Hyptis spicigera* Lam. (*Uredo* stage).

Previously collected in the southern portion of the United States and the tropical and temperate portions of South America.

PHRAGMIDIUM Link

PHRAGMIDIUM SUBCORTICIUM (Schrank) Wint.; Rabenhorst, Krypt.-Fl. **1**^{1}: 228. 1881.

Lycoperdon subcorticium Schrank, Bot. Tasch. Hoppe 68. 1793.

Uredo miniata var. *Eglanteriae* Pers. Syn. Fung. 216. 1801.

Uredo elevata Schum. Enum. Pl. Sael. **2**: 229. 1803.

Aecidium Rosae Röhling, Deuts. Fl. ed. 2. **3**: 122. 1813.

Uredo Eglanteriae H. Mart. Fl. Mosq. ed. 2. 230. 1817.

Caeoma miniatum Schlecht. Fl. Berol. **2**: 120. 1824.

Caeoma Rosae var. *miniatum* Link; Willd. Sp. Pl. **6**^{2}: 30. 1825.

Erysibe miniata var. *Rosarum* Wallr. Fl. Crypt. Germ. **2**: 200. 1833.

Coleosporium miniatum Bon. Gatt. Coniom. 60, in part. 1860.

Phragmidium Rosarum f. *R. pimpinellifoliae* Rabenh. Fungi Eur. *1671* (hyponym). 1873.

Phragmidium Rosae pimpinellifoliae Diet. Hedwigia **44**: 339. 1905.

Caeoma exitiosum Syd. Ured. 1700 (hyponym). 1913.

LUZON: Subprovince of Benguet, Baguio, June 10, 1913, *J. C. Wagner, Bur. Sci. 21002.*

This species is of wide distribution, having been reported from North America, Europe, Africa and Australia. It is probable that the fungus was introduced into the Philippines with either European or American cultivated rose stock.

AURICULAREAE

AURICULARIA Bulliard

AURICULARIA LOBATA Sommerf.; Fries, Elench. Fung. **2**: 34. 1828.

LUZON: Province of Rizal, Antipolo, October, 1912, *M. Ramos, Bur. Sci. S76.*

Previously collected on the River Niger, Africa.

AURICULARIA MESENTERICA (Dicks.) Fr. Epicr. Myc. 555. 1838.

Helvella mesenterica Dicks. Plant. Crypt. **1**: 20. 1785.

Auricularia tremelloides Bull. Hist. Champ. Fr. 278. *pl. 290.* 1791–1798.

Auricularia violacea Bull. Hist. Champ. Fr. 278. 1791–1798

Thelephora mesenterica Pers. Syn. Fung. 571. 1808.

Thelephora purpurea Pers. Syn. Fung. 571. 1808.

Auricularia corrugata Sowerb. Engl. Fungi *pl. 290.* 1797–1815.

Auricularia ornata Pers.; Gaudichaud, Bot. Voy. Uranie 177. *pl. 2, f. 4.* 1826.

Phlebia mesenterica Fr. Elench. Fung. **1**: 154. 1828.

Oncomyces mesentericus Klotz. Linnaea **7**: 195. 1832.

LUZON: Province of Rizal, January 16, 1906, *F. W. Foxworthy, Bur. Sci. 121;* same locality, February, 1911, *M. Ramos, Bur. Sci*

12552. MINDANAO: District of Davao, Davao, April, 1904, *Copeland "F."*

Of common occurrence in the American and European tropics.

AURICULARIA RUGOSISSIMA (Lév.) Bres. Hedwigia **53**: 78. 1912.

Phlebia rugosissima Lév. Ann. Sci. Nat. Bot. III. **2**: 214. 1844.

Phlebia reflexa Berk. Jour. Bot. & Kew Gard. Misc. **3**: 16. 1851.

MINDORO: Mount Halcon, November, 1905, *Merrill 6118.* NEGROS: Gimagaan River, January, 1904, *Copeland 25.*

Previously collected in the West Indies and northern India.

HIRNEOLA Fries

HIRNEOLA AFFINIS (Jungh.) Bres. Annal. Myc. **8**: 587. 1910.

Merulius affinis Jungh. Fl. Crypt. Java 76. 1838.

Laschia velutina Lév. Ann. Sci. Nat. Bot. III. **2**: 217. 1844.

LUZON: Province of Laguna, Mount Maquiling, February, 1912, *P. W. Graff, Bur. Sci. 15934.*

Originally described from material collected in Java. This fungus has also been reported from Japan.

HIRNEOLA AMPLA (Pers.) Fr. Fungi Nat. 26. 1848.

Auricularia ampla Pers.; Gaudichaud, Bot. Voy. Uranie 77. 1826.

Exidia nobilis Lév. Ann. Sci. Nat. Bot. III. **2**: 218. 1844.

Exidia ampla Lév. Ann. Sci. Nat. Bot. III. **5**: 159. 1846.

Hirneola nobilis Fr. Fungi Nat. 26. 1848.

LUZON: vicinity of Manila, February, 1904, *Copeland 41*, on *Gliricidia maculata* H.B.K. NEGROS: Gimagaan River, January, 1904, *Copeland 30*, on *Dipterocarpus* sp.

Reported previously from Japan and Natal.

HIRNEOLA AURICULA-JUDAE (Fr.) Berk. Outl. Brit. Fung. 289. 1860; Fr. Hym. Eur. 695. 1874.

Tremella auricula L. Sp. Pl. 1157. 1753.

Merulius auricula Roth, Tent. Flor. Germ. **1**: 535. 1788.

Peziza auricula L. Syst. Veg. ed. 13. 1018. 1789.

Tremella auriformis Hoffm. Veg. Crypt. **2**: 31. *pl. 6, f. 4.* 1790.

Tremella caragana Pers. Syn. Met. Fung. 625. 1808.

Auricularia sambucina Mart. Fl. Crypt. Erlang. 459. 1817.

Exidia auricula-judae Fr. Syst. Myc. **2**: 221. 1822.

Auricularia auricula Underw. Mem. Torrey Club **12**: 15. 1902.

LUZON: Province of Rizal, Bosoboso, July, 1906, *M. Ramos, Bur. Sci. 1185*, on *Gliricidia maculata.*

Reported from southern Europe, Guiana, Japan, and the East Indies.

HIRNEOLA TENUIS (Lév.) Fr. Fungi Nat. 27. 1848.

Exidia tenuis Lév. Ann. Sci. Nat. Bot. III. **2**: 219. 1844.

LUZON: Province of Isabela, Cordon, May 8, 1909, *M. Ramos, Bur. Sci. 8135.*

Previously collected in Natal, Borneo and Brazil.

THELEPHOREAE

CORTICIUM Persoon

CORTICIUM CAERULEUM (Schrad.) Fr. Epicr. Myc. 562. 1838.

Thelephora caerulea Schrad. Spicil. Fl. Germ. 187. 1794.

Thelephora fimbriata Roth, Catal. Bot. **2**. *pl. 9, f. 2.* 1800.

Auricularia phosphorea Sowerb. Engl. Fungi *pl. 350.* 1797–1815.

Thelephora indigo Schwein. Schr. Nat. Ges. Leipzig **1**: 107. 1822.

Merisma fimbriata Schwein. Schr. Nat. Ges. Leipzig **1**: 110. 1822.

Thelephora atro-caerulea Trog, Flora **15**: 560. 1832.

MINDORO: Mount Halcon, November, 1906, *Merrill 5545*, on decaying tree branches, host plant undetermined.

Previously collected in North America, southern Europe and northern Africa.

HYMENOCHAETE Léveillé

HYMENOCHAETE ADUSTA (Lév.) Bres. Hedwigia **51**: 323. 1912.

Stereum adustum Lév. Ann. Sci. Nat. Bot. III. **2**: 213. 1844.

Thelephora adusta Lév.; Gaudichaud, Bot. Voy. Bonite 192. *pl. 139, f. 2.* 1846.

MINDANAO: District of Davao, Mount Apo, May, 1909, *Elmer 10607.*

Originally described from material collected in the vicinity of Manila by Gaudichaud-Beaupré, on the occasion of the visit of the French vessel "Bonite" to that port, and deposited in the herbarium of the Museum of Paris.

HYMENOCHAETE CACAO Berk. Jour. Linn. Soc. Bot. **10**: 333. 1869.

Stereum cacao Berk. Jour. Bot. & Kew Gard. Misc. **6**: 169. 1854.

LUZON: Subprovince of Ifugao, Payauan, January 26, 1913, *R. C. McGregor, Bur. Sci. 20038;* Province of Nueva Ecija, Cabanatuan, September, 1908, *R. C. McGregor, Bur. Sci. 5250;* Province of Bataan, November, 1909, *H. M. Curran, For. Bur. 19209.* MINDANAO: District of Davao, March, 1904, *Copeland 495, 523;* District of Zamboanga, Zamboanga, January, 1908, *Whitford & Hutchinson, For. Bur. 9269, 9296.*

This species is of very general tropical distribution.

HYMENOCHAETE NIGRICANS (Lév.) Pat. Bull. Soc. Myc. France **23**: 75. 1907.

Thelephora nigricans Lév. Ann. Sci. Nat. Bot. III. **2**: 212. 1844.

Stereum nigricans Sacc. Syll. Fung. **6**: 561. 1888.

NEGROS: Province of Negros Oriental, Dumaguete, April, 1908, *Elmer 9851.*

Previously reported from Cochin China.

HYMENOCHAETE RHEICOLOR (Mont.) Lév. Ann. Sci. Nat. Bot. III. **5**: 211. 1846.

Stereum rheicolor Mont. Ann. Sci. Nat. Bot. II. **17**: 23. 1842.

LUZON: Province of Laguna, Mount Maquiling, February, 1912, *P. W. Graff, Bur. Sci. 15948.*

Collected previously in the East Indies and French Guiana.

HYMENOCHAETE TENUISSIMA Berk. Jour. Linn. Soc. Bot. **10**: 333. 1869.

Stereum tenuissimum Berk. Jour. Bot. **6**: 510. 1847.

LUZON: Province of Tayabas, Lucban, May, 1907, *Elmer 7548.*

Previously reported from the island of Ceylon.

STEREUM Persoon

STEREUM BELLUM Kunze, Flora **13**: 370. 1830.

MINDANAO: District of Davao, Todaya, April 26, 1904, *Copeland 1294,* on a decaying log.

Previously collected in the Madeira Islands.

STEREUM CONCOLOR Berk. Hook. Flor. Tasm. 259. 1860. Not *Stereum concolor* (Jungh) Sacc., 1888.

LUZON: Province of Tayabas, Lucban, May, 1907, *Elmer 8166*, on dead and decaying branches.

Described from material collected in Tasmania.

STEREUM CRENATUM Lév. Ann. Sci. Nat. Bot. III. **2**: 210. 1844.

MINDANAO: District of Zamboanga, San Ramon, May, 1904, *Copeland 763*, on a root clump of living *Cocos nucifera* L.

Previously collected in the island of Java.

STEREUM INVOLUTUM Klotz. Linnaea **7**: 499. 1832.

NEGROS: Province of Negros Occidental, Mount Canlaon, September, 1909, *H. M. Curran, For. Bur. 13738*. MINDANAO: District of Davao, Davao, April, 1904, *Copeland 1294*.

Previously collected in Mauritius.

STEREUM LUGUBRE Cooke, Grevillea **12**: 85. 1884.

LUZON: Province of Rizal, Bosoboso, July, 1906, *M. Ramos, Bur. Sci. 1203*. LEYTE: Dagami Panda, September 5, 1913, *Wenzel 3*.

Collected previously in New Zealand.

STEREUM OSTREA (Bl. & Nees) Fr. Epicr. Myc. 547. 1838.

Thelephora ostrea Bl. & Nees, Fung. Java 13. *pl. 2, f. 1.* 1826.

LUZON: Province of Benguet, Pauai, June, 1909, *R. C. McGregor, Bur. Sci. 8709*, at an altitude of 2,100 m.

Found in Malacca and Java, and probably distributed throughout Malaya in general.

STEREUM OSTREA var. CONCOLOR (Jungh.) Bres. Hedwigiä **53**: 76. 1912.

Thelephora concolor Jungh. Fung. Java 38. 1826.

Thelephora lobata Kunze, Linnaea **5**: 527. 1830.

Stereum lobatum Fr. Epicr. Myc. 547. 1838.

Stereum perlatum Berk. Lond. Jour. Bot. **1**: 153. 1842.

Stereum concolor Sacc. Syll. Fung. **6**: 561. 1888. Not *Stereum concolor* Berk., 1860.

LUZON: Province of Rizal, Bosoboso, July, 1906, *M. Ramos, Bur. Sci 1210;* Palawan, Mount Pulgar, May, 1911, *Elmer 13057*. MINDANAO: District of Davao, Mount Apo, May, 1909, *Elmer 10556*.

This appears to be a case where the variety is much more widely known than the species. It is certainly much the commoner in the Philippines. While the species, so far as is at present known, seems to be quite rare in the Islands, the variety is one of the most common of this group of plants. The three collections enumerated above indicate range rather than prevalence. Berkeley's species, *Stereum perlatum,* was originally described from Philippine material.

Reported from the West Indies, Guiana, Brazil, Cochin China, Sumatra, and generally throughout the East Indies.

STEREUM PRINCEPS (Jungh.) Lév. Ann. Sci. Nat. Bot. III. **2**: 210. 1844.

Thelephora princeps Jungh. Fl. Crypt. Java 39. 1838.

Stereum scytale Berk. Jour. Bot. & Kew Gard. Misc. **6**: 170. 1854.

Stereum contrarium Berk. Jour. Linn. Soc. Bot. **16**: 52. 1878.

POLILLO: October–November, 1909, *R. C. McGregor, Bur. Sci. 10547*. MINDANAO: District of Davao, Mount Apo, June, 1909, *Elmer 11006*.

Collected previously in Cuba, Brazil, Japan, Java, and northern India.

STEREUM SPECTABILE Klotz.; Meyen, Nov. Act. Acad. Nat. Cur. **19**: Suppl. 1. 238. *pl. 5, f. 2.* 1843.

Stereum radiato-fissum Berk. & Br. Trans. Linn. Soc. II. **2**: 63. *pl. 14, f. 8–11.* 1883.

Stereum luzoniense Ricker, Philip. Jour. Sci. **1**: Suppl. 283. 1906.

LUZON: Province of Bataan, summit of Mount Mariveles, on prostrate logs, October, 1903, *Merrill 3531* (type of *Stereum luzoniense*); Province of Laguna, Calauan, December 7, 1910, *R. C. McGregor, Bur. Sci. 12520*.

Ricker's species must be combined with *Stereum spectabile,* as a synonym, the two proving, on a careful comparison of the type material of *Stereum luzoniense* with authentically named specimens of the former, to be identical.

Besides being found in the Philippines, this species has been reported from Australia and Mauritius.

CLADODERRIS Persoon

CLADODERRIS ELEGANS (Jungh.) Fr. Fung. Nat. 21. 1848.

Cymatoderma elegans Jungh. Ann. Sci. Nat. Bot. II. **16**: 320. 1841.

LUZON: Province of Rizal, Bosoboso, July, 1906, *M. Ramos, Bur. Sci. 1189*. MINDANAO: Subprovince of Butuan, March–July, 1911, *Weber 1283*.

This species shows a considerable tendency toward a transition into *Cladoderris infundibuliformis*. So far, however, not enough comparative material has been obtained to enable one to state definitely whether this is a general condition or that the few specimens showing the similarity are exceptional.

Collected previously in South Africa and the East Indies.

CLADODERRIS INFUNDIBULIFORMIS (Klotz.) Fr. Fung. Nat. 21. 1848.

Actinostroma infundibuliformis Klotz.; Meyen, Nov. Act. Acad. Nat. Cur. **19**: Suppl. 1. 237. 1843.

Cladoderris Blumei Lév. Ann. Sci. Nat. Bot. III. **2**: 213. 1844.

Cladoderris Decandolleana Lév. Ann. Sci. Nat. Bot. III. **2**: 214. 1844.

LUZON: Province of Rizal, Bosoboso, July, 1906, *M. Ramos, Bur. Sci. 1184*.

Cladoderris Blumei Lév., described from Javan material in Blume's herbarium and Philippine material in Delessert's herbarium, should unquestionably be placed as a synonym of *C. infundibuliformis*.

Collected previously by Meyen, between 1830 and 1832, in the vicinity of Manila. The fungus has been also collected in Java, South Africa, and Brazil.

HYMENOLICHENES

CORA Fries

CORA GYROLOPHIA Fr. Epicr. Myc. 556. 1838.

Gyrolophium aeruginosum Kunze; Krombh. Consp. Fung. *pl. 5, f. 16*. 1821.

LEYTE: Dagami Panda, September 8, 1913, *Wenzel 5*, growing in the moist forest at an altitude of 60 m., on tree ferns.

Previously collected in Mauritius.

CORA PAVONIA (Web. & Mohr) Fr. Epicr. Myc. 556. 1838.

Thelephora pavonia Web. & Mohr, Beitr. Naturk. **1**: 326. 1805.

LUZON: Province of Benguet, vicinity of Baguio, May, 1911, *C. B. Robinson, Bur. Sci. 14107*.

Collected previously in the West Indies and other parts of the American tropics.

CLAVARIEAE

LACHNOCLADIUM Léveillé

LACHNOCLADIUM FLAGELLIFORME (Berk.) Cooke, Austr. Fungi 179. 1892.

Clavaria flagelliformis Berk.; Hooker, Fl. New Zeal. 186. 1855.

MINDANAO: District of Davao, Mount Apo, May, 1909, *Elmer 11301*.

Described from material collected in New Zealand. As yet reported only from these Pacific regions.

LACHNOCLADIUM USAMBARENSE P. Henn. Bot. Jahrb. **29**: 44. 1904.

MINDORO: Bulalacao, August–September, 1906, *Bermejos, Bur. Sci. 1553*.

Previously known only from East Africa.

PHYSALACRIA Peck

PHYSALACRIA ORINOCENSIS Pat. Bull. Soc. Myc. Fr. **1**: 41. *pl. 13, f. 2.* 1884.

LUZON: vicinity of Manila, October, 1912, *Merrill*, on decaying bamboo stalks.

This interesting little species of "Bubble Cap" has also been collected by the writer in Manila, where it was growing in profusion on bamboo joints which were being used for flower pots. Being used for seedling plants and cuttings, these pots were kept constantly moist and in a shady place so that they formed an ideal substratum for a fungal growth.

Collected previously in tropical America.

HYDNEAE

IRPEX Fries

IRPEX FLAVUS Klotz. Linnaea **8**: 488. 1833.

Polyporus flavus Jungh. Flor. Crypt. Java 46. 1838.

NEGROS: Gimagaan River, January, 1904, *Copeland 26*, on decaying wood.

Coriolopsis melleoflavus Murr. (Bull. Torrey Club **35**: 393. 1908) is not a synonym for this species as stated by Bresadola (Hedwigia **53**: 75. 1912) but belongs rather among the numerous synonyms of *Polystictus cervino-gilvus* (Jungh.) Fr. For this arrangement see Graff (Philip. Jour. Sci. **9**: Bot. 239. 1914).

Collected in North America, Java, and the East Indies. When further known the species will, in all probability, be found to grow in the American tropics as well.

POLYPOREAE

POLYPORUS (Micheli) Fries

POLYPORUS ADUSTUS (Willd.) Fr. Syst. Myc. **1**: 363. 1821.

Boletus adustus Willd. Fl. Berol. Prod. 392. 1787.

Polyporus carpineus Sowerb. Engl. Fungi *pl. 231*. 1799.

Polyporus crispus Fr. Obs. Myc. **1**: 127. 1815.

Polyporus pallescens Fr. Syst. Myc. **1**: 369. 1821.

Boletus isabellinus Schw. Schr. Nat. Ges. Leipzig **1**: 96. 1822.

Polyporus subcinereus Berk. Ann. Mag. Nat. Hist. II. **3**: 391. 1839.

Polyporus Halesiae Berk. & Curt. Ann. Mag. Nat. Hist. II. **12**: 434. 1853.

Polyporus Lindheimeri Berk. & Curt. Grevillea **1**: 50. 1872.

Bjerkandera adusta Karst. Medd. Soc. F. et Fl. Fenn. **5**: 38. 1879.

Myriadoporus adustus Peck, Bull. Torrey Club **11**: 27. 1884.

Polyporus Burtii Peck, Bull. Torrey Club **24**: 146. 1897.

MINDANAO: District of Davao, Mount Apo, April 20, 1904, *Copeland 1075;* Lake Lanao, Camp Keithley, July, 1907, *Mary S. Clemens.*

A fungus of very general distribution.

POLYPORUS ATYPUS Lév. Ann. Sci. Nat. Bot. III. **2**: 184. 1844.

Trametes aurora Ces. Myc. Borneo 5. 1879.

Coriolus atypus Pat. Tax. Hymén. 94. 1900.

Polystictus atypus Bres. & Syd. Philip. Jour. Sci. **9**: Bot. 348. 1914.

MINDORO: Puerto Galera, June, 1912, *P. W. Graff, Bur. Sci. S30*, growing on dead branches.

Previously collected in Java and Borneo.

POLYPORUS BENGUETENSIS (Murr.) Graff, Philip. Jour. Sci. **9**: Bot. 236. 1914. [PLATE 15, FIG. 1].

Coltricia benguetensis Murr. Bull. Torrey Club **35**: 391. 1908.

Polystictus benguetensis Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 321. 1912.

LUZON: Province of Benguet, Baguio, October–November, 1905, *Merrill 5003* (type of *Coltricia benguetensis* Murr.); same locality, March, 1904, *Elmer 6047*—both collections from prostrate logs of *Pinus insularis* Endl.

Upper surface and pore layer of the same shade of brown and quite distinct in color from the flesh of the pileus which is a shining golden yellow-brown when broken. The characteristics are so distinct that its place in the genus *Polyporus* cannot be questioned.

As yet, only collected in the Philippines.

POLYPORUS LUZONENSIS (Murr.) Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 266. 1912.

Spongipellis luzonensis Murr. Bull. Torrey Club **34**: 473. 1907.

LUZON: Province of Bataan, Mount Mariveles, November, 1904, *Elmer 6944*, on dead wood.

Described from Philippine material and, so far, not reported from elsewhere.

FOMES Fries

FOMES ALBOMARGINATUS (Lév.) Sacc. Syll. Fung. **6**: 185. 1888.

Polyporus albomarginatus Lév. Ann. Sci. Nat. Bot. III. **2**: 191. 1844.

Polyporus kermes Berk. & Br. Jour. Linn. Soc. Bot. **14**: 49. 1875.

Polyporus laeticolor Berk. Jour. Linn. Soc. Bot. **16**: 46. 1878.

Fomes pyrrhocreas Cooke, Grevillea **14**: 11. 1885.

Polyporus ochrocroceus P. Henn. Monsunia **1**: 145. 1899.

Pyropolyporus albomarginatus Murr. Bull. Torrey Club **34**: 478. 1907.

MINDANAO: District of Davao, Mount Apo, April 20, 1904, *Copeland 1077*, growing on a fallen log in the forest.

Collected previously in Ceylon, Java, and New Guinea.

FOMES FULLAGERI Berk. Jour. Linn. Soc. Bot. **16**: 54. 1878.

NEGROS: Province of Negros Occidental, Farar, October 8, 1909, *H. M. Curran, For. Bur. 17476*, growing on living *Shorea* sp.

According to the collector's note, the fungus sporophore was growing from a wound, and the fungus had caused a rotting of the heartwood of the tree. The rot is not accompanied by any staining of the wood. It is possible that this fungus may be found to be one of the important timber destroyers of the Philippine Islands.

This fungus has been previously collected in Australia.

FOMES MELANOPORUS (Mont.) Sacc. Syll. Fung. **6**: 196. 1888.

Polyporus melanoporus Mont.; Ramon de la Sagra. Hist. Phys. Polit. Nat. Cuba **9**: 422. 1841.

Polyporus cinereo-fuscus Curt. Trans. Linn. Soc. II. **1**: 124. *pl. 19, f. 1.* 1876.

Fomes melanoporoides Ces. Myc. Borneo 6. 1879.

Fomes cornu-bovis Cooke, Grevillea **13**: 2. 1884.

Nigrofomes melanoporus Murr. Bull. Torrey Club **31**: 425. 1904.

LUZON: Province of Bataan, Mount Mariveles, November, 1904, *Elmer 6959*.

Reported from Cuba, Borneo, Malacca and India.

FOMES MERRILLII (Murr.) Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 287. 1912.

Pyropolyporus Merrillii Murr. Bull. Torrey Club **34**: 479. 1907.

CULION: December, 1902, *Merrill 3575*, on decaying tree trunks near the seashore.

As yet reported only from the Philippines.

FOMES ROSEUS (Alb. & Schw.) Cooke, Grevillea **14**: 21. 1885.

Boletus roseus Alb. & Schw. Consp. Fung. 251. 1805.

Polyporus roseus Fr. Syst. Myc. **1**: 372. 1821.

Polyporus carneus Nees, Nov. Act. Acad. Nat. Cur. **13**: 14. *pl. 3*. 1827.

Polyporus rufo-pallidus Trog, Flora **15**: 556. 1832.

Fomitopsis rosea Karst. Rev. Myc. **3**: 18. 1881.

Fomes carneus Cooke, Grevillea **14**: 21. 1885.

LUZON: Province of Laguna, Mount Maquiling, April, 1913, *P. W. Graff, Bur. Sci. 21042*, on a prostrate log near the trail at an altitude of 150 m.

Previously collected in North, Central and South America, Europe, Australia and Java. In the Americas its habitat is confined to the tropical and warmer temperate portions. In all probability Africa will be added to this list in the course of time and the species will be found to be of universally tropical distribution.

POLYSTICTUS Fries

POLYSTICTUS ABIETINUS (Dicks.) Fr. Syst. Myc. **1**: 370. 1821.

Boletus abietinus Dicks. Plant. Crypt. Brit. **3**: 21. *pl. 9, f. 9*. 1793.

Polyporus incarnatus Schum. Enum. Plant. Saell. **2**: 391. 1803.

Sistotrema violaceum Pers. Syn. Fung. 551. 1808.

Polyporus dolosus Pers. Myc. Eur. **2**: 77. 1828.

Coriolus abietinus Quél. Enchir. Fung. 175. 1886.

LUZON: Bontoc Subprovince, February–March, 1911, *Vanoverbergh 1117*, on the bark of *Pinus insularis* Endl.

Found in northern North America, Cuba and Europe.

POLYSTICTUS PERPUSILLUS (Murr.) Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 319. 1912.

Coriolus perpusillus Murr. Bull. Torrey Club **35**: 396. 1908.

MINDANAO: District of Davao, Lake Lanao, Camp Keithley. July, 1907, *Mary S. Clemens*.

Reported only from the Philippines.

POLYSTICTUS RUBRITINCTUS (Murr.) Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 320. 1912.

Coriolus rubritinctus Murr. Bull. Torrey Club **35**: 396. 1908.

MINDORO: Mount Halcon, November, 1906, *Merrill 6117*.

As yet collected only in the Philippines.

POLYSTICTUS TABACINUS Mont.; Gay, Hist. Fisica Pol. Chili **7**: 361. *pl. 7, f. 6.* 1845.

Polyporus tabacinus Mont. Ann. Sci. Nat. Bot. II. **3**: 349. 1835.

Polyporus spadiceus Jungh. Flor. Crypt. Java 54. *pl. 30.* 1838. Not *P. spadiceus* Berk.

Polystictus microcyclus Zipp.; Léveillé, Ann. Sci. Nat. Bot. III. **2**: 188. 1844.

Polystictus spadiceus Fr. Nov. Symb. Myc. 1851.

Polystictus xerampelinus Kalchbr. Grevillea **4**: 72. 1876.

Cycloporellus microcyclus Murr. Bull. Torrey Club **34**: 468. 1907.

Polystictus substygius Bres. Hedwigia **53**: 66. 1912.

Cyclomyces spadiceus Pat. Philip. Jour. Sci. **10**: Bot. 95. 1915.

Cyclomyces tabacinus Pat. Philip. Jour. Sci. **10**: Bot. 95. 1915.

LUZON: Province of Laguna, Mount Maquiling, February, 1912, *P.W. Graff, Bur. Sci. 15956, 15981.*

Originally described from material collected in Juan Fernandez, later from material collected in Chili, New Zealand and Java.

POLYSTICTUS TABACINUS var. **barbatus** (Murr.) comb. nov. [PLATE 15, FIG. 2.]

Cycloporellus barbatus Murr. Bull. Torrey Club **35**: 397. 1908.

Polystictus barbatus Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 321. 1912.

Polystictus spadiceus var. *barbatus* Graff, Philip. Jour. Sci. **9**: Bot. 242. 1914.

LUZON: Province of Zambales, November–December, 1907, *H. M. Curran & M. L. Merrit, For. Bur. 8208* (type of *Cycloporellus barbatus* Murr.).

As yet this variety has only been collected in the Philippine Islands.

POLYSTICTUS TABACINUS var. **substygius** (Berk. & Br.) comb. nov.

Fomes substygius Berk. & Br.; Cooke, Praec. Polyp. *522.*

Fomes spadiceus var. *halconensia* Bres. Hedwigia **53**: 59. 1912.

LUZON: Province of Rizal, February, 1911, *M. Ramos, Bur. Sci. 13467;* Mindoro, Mount Halcon, November, 1906, *Merrill 6114* (var. type).

There are two varieties of *Polystictus tabacinus*, which represent two different sorts of development and variation from the type. The first variety, *barbatus*, does not vary in pilear texture but in the fact that the upper surface is covered with a long tomentum, and has a somewhat darker shade of color. This tomentum varies in length from short, at the outer margin, to about 3 mm., near the place of attachment of the fungus.

In the case of the second variety, *substygius*, the variation is one of which insufficient notice has been taken; namely, a tendency toward the assumption of a perennial development in an occasional species, which is typically annual, when growing under the warm conditions of a tropical climate. This second variety has developed in this manner. The context of the plant develops much thicker and harder than normally. The upper surface loses its characteristic velvety tomentum, becoming hard and smooth. Otherwise than this the plant retains its usual characters. To one unfamiliar with the variations through which this plant may pass the natural tendency would be to place it in the genus *Fomes*. While pore layers have been occasionally observed in this variety they are the exception rather than the rule.

Fomes spadiceus (Berk.) Cooke is not this species, but a quite distinct plant.

Reported from Samoa, the Philippines, Malacca, and the East Indies.

TRAMETES Fries

TRAMETES ELMERI (Murr.) Graff, Philip. Jour. Sci. **9**: Bot. 243. 1914.

Tyromyces Elmeri Murr. Bull. Torrey Club **34**: 475. 1907.

Polyporus Elmeri Sacc. & Trott.; Saccardo, Syll. Fung. **21**: 279. 1912.

LUZON: Province of Bataan, Mount Mariveles, November, 1904, *Elmer 6954*, on dead wood.

The generic characters of this fungus are those of *Trametes* rather than *Polyporus*. Saccardo evidently made the change on general principles rather than after a critical study of the species.

As yet collected only in the Philippines.

TRAMETES INSULARIS Murr. Bull. Torrey Club **35**: 405. 1908.

LUZON: Province of Benguet, Baguio, April, 1909, *R. C. McGregor, Bur. Sci. 8311*, on *Pinus insularis* Endl.

The limited distribution of pines makes this fungus very local in the Islands. As this is but the second collection which has been made to date, this form must be rare even in the pine regions.

Not reported outside the Philippine Islands.

UNIVERSITY OF MONTANA,
MISSOULA, MONTANA

Explanation of plate 15

FIG. 1. *Polyporus benguetensis* (Murr.) Graff. Specimen from the herbarium of the Bureau of Science, Manila, *Merrill 5003*, co-type material of *Coltricia benguetensis* Murr.

FIG. 2. *Polystictus tabacinus* var. *barbatus* (Murr.) Graff. Specimen from the herbarium of the Bureau of Science, Manila, *Curran & Merritt, For. Bur. 8208* co-type of *Cycloporellus barbatus* Murr.

INDEX TO AMERICAN BOTANICAL LITERATURE

1914–1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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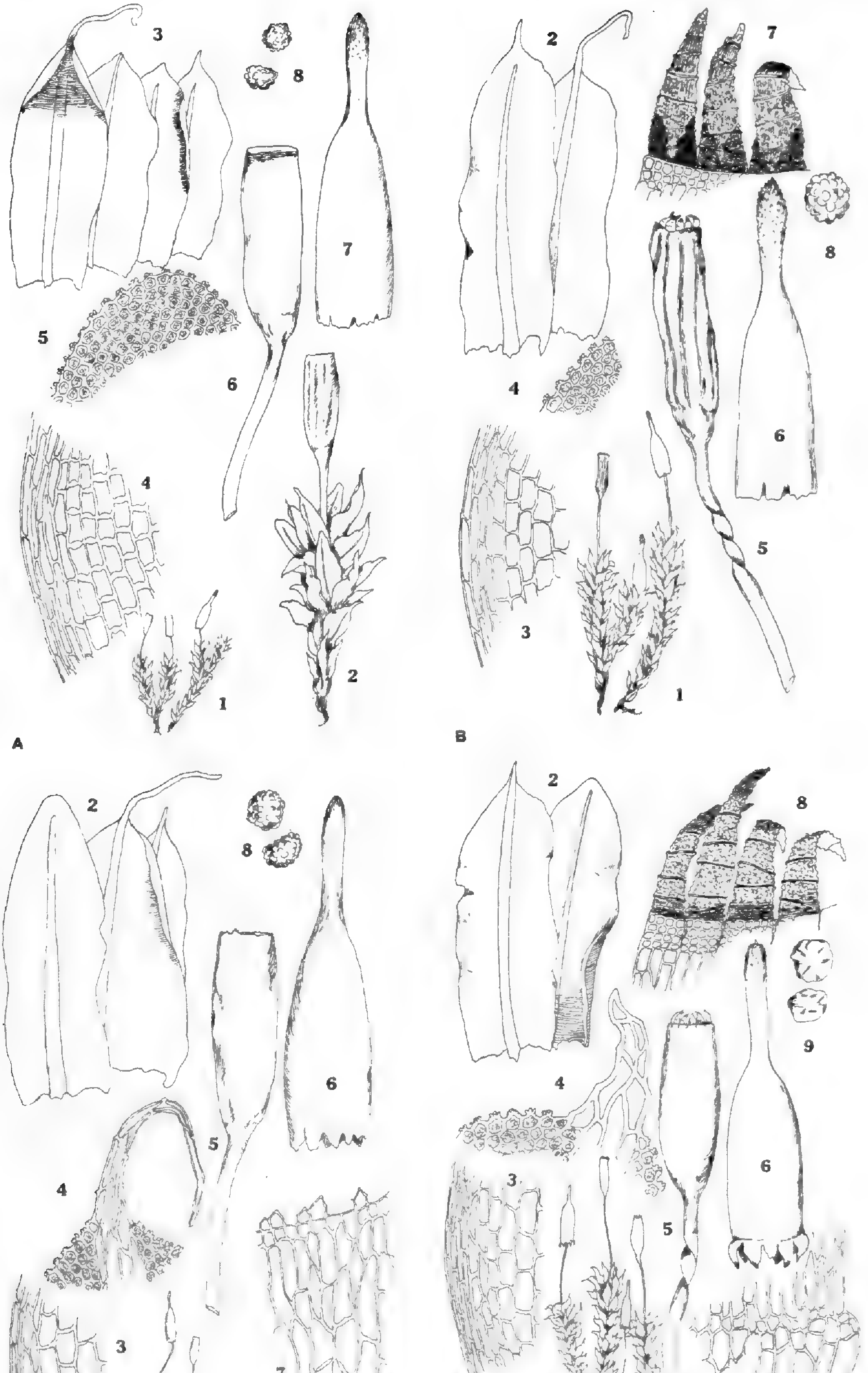
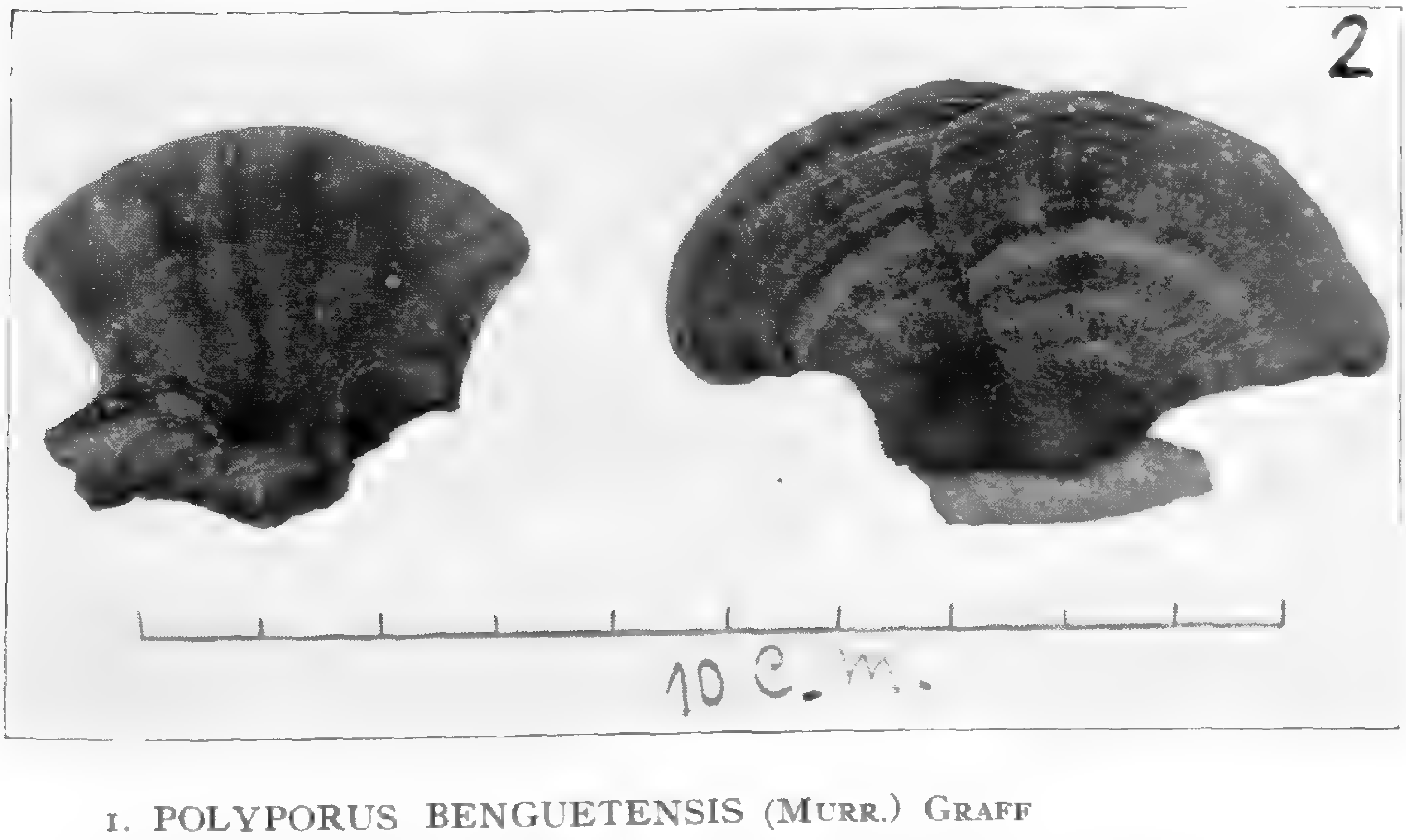


A. ENCALYPTA EXTINCTORIA (L.) SW.
B. ENCALYPTA RHABDOCARPA SCHWAEGR.
C. ENCALYPTA ALPINA SMITH
D. ENCALYPTA LACINIATA (HEDW.) LINDB.

A. ENCALYPTA APOPHYSATA Nees & Hornsch.
B. ENCALYPTA BREVICOLLA Bruch
C. ENCALYPTA PROCERA Bruch
D. ENCALYPTA CONTORTA (Wulf.) Lindb.



1. POLYPORUS BENGUETENSIS (MURR.) GRAFF
2. POLYSTICTUS TABACINUS VAR. BARBATUS (MURR.) GRAFF

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

DECEMBER, 1918

Notes on plants of the southern United States—IV

FRANCIS W. PENNELL

THE GENUS CROTONOPSIS

In 1803 Michaux published in his "Flora Boreali-Americana" a new genus of plants to which, from its evident likeness to *Croton*, he gave the name of *Crotonopsis*. The genus has been maintained continuously from that time, although twice have attempts been made to rechristen it. In 1826 Sprengel, without comment, proposed to substitute *Friesia*, and twelve years later Rafinesque, remarking that "the name previously given was absurd and incorrect," announced his *Leptemon*. According to current rules of nomenclature *Crotonopsis* must be held.

Michaux collected *Crotonopsis* twice, and, in the plate which accompanies the description of his species *C. linearis*, he fortunately figured both the specimens obtained. The drawing to the left hand shows a low plant with lanceolate or elliptic-lanceolate leaves and with fruits few and axillary, that to the right is of a side-branch of a taller plant with narrower longer leaves and with conspicuously elongated spikes. Two localities are cited in the text, Long-bay, Carolina, and the Illinois region. From evidence to be presented it is clear that two species are illustrated, and, from the form of its leaves, that to the right is the one entitled to the name *C. linearis*. Fortunately it is also that from the locality first cited. True *C. linearis* Michx. is a plant restricted to the Coastal Plain of the southeastern states.

[The BULLETIN for November (**45**: 433–476, *pl. 13–15*) was issued November 15, 1918.]

In 1805, but two years later, Willdenow added a second species, *Crotonopsis elliptica*. His plant is stated to differ from the linear-leaved *C. linearis* Michx. in its leaves being elliptic, rounded to each end, and in its spikes being shorter. Evidently *C. elliptica* is our oldest name for the widely-ranging northern and inland species. As this plant extends to the Gulf coast, incidentally overlapping the range of *C. linearis*, the type-region, "Carolina," is well within its normal range.

The later history of the genus may be briefly sketched. Pursh in 1814 combined both species, though as varieties, in one, his *C. argentea*. Nearly to the close of the past century the genus was uniformly considered monotypic. But in 1895 Nash, from a single collection from Florida, added a second species, *C. spinosa*. As a matter of fact he was actually recharacterizing Michaux's *C. linearis*, laying primary emphasis upon newly discovered features of the fruit.

Spikes short, of but one or two fruits. Staminate flowers less than 1 mm. in diameter; filaments shorter than the sepals, and but little longer than the anthers. Fruit ovoid, with an evident median vein on each side; scale-like hairs on fruit with broad brown disk, umbonate to tuberculate-raised, even occasionally into a short spine, and with its margin of relatively uniform closely appressed white rays. Leaves lanceolate to ovate-lanceolate, 1.5–3 cm. long; stellate hairs on upper surface with long rays which overlap those of adjoining hairs. Plant usually 1–5 dm. tall. 1. *C. elliptica.*

Spikes longer, slender, of three to six fruits. Staminate flowers more than 1 mm. in diameter; filaments longer than the sepals, and much longer than the anthers. Fruit ellipsoid, without evident vein on the side; scale-like hairs on fruit with minute disk, which is usually raised into a decided tubercle or spine, and with long irregular stellate not closely appressed slightly brownish rays. Leaves lanceolate-linear, 2–4 cm. long; stellate hairs on upper surface with short rays which do not overlap those of adjoining hairs. Plant usually 4–8 dm. tall. 2. *C. linearis.*

1. CROTONOPSIS ELLIPTICA Willd.

Crotonopsis elliptica Willd. Sp. Pl. **4**: 380. 1805. "Habitat in Carolina."

Crotonopsis argentea elliptica Pursh, Fl. Am. Sept. **1**: 206. 1814.

Dry sandy soil, Connecticut to northern Florida, west to eastern Kansas and central Texas; northward in or near the Coastal Plain, southward mostly inland, on granitic rocks of the Piedmont and southern Appalachian regions. Numerous specimens seen. The most southwestern studied are from sandy post-oak woods, Sheridan, Colorado County, Texas, my number *5533*, and are unique in that the plants were uniformly 7–8 dm. tall, and the fruit relatively large and somewhat brownish instead of being nearly black.

2. CROTONOPSIS LINEARIS Michx.

Crotonopsis linearis Michx. Fl. Bor. Am. **2**: 186. *pl. 46* p.p. 1803. "*Hab.* in maritimis Carolinae, juxta *Long-Bay*, et in regione Illinoensi." Two plants figured. One is a plant with lanceolate-linear leaves and slender spikes, the other with lanceolate to ovate-lanceolate leaves and flowers one to two together. As Illinois specimen certainly the latter, and as the former is known in the maritime region of Carolina, and is the plant to which the name *linearis* better applies, this is selected as the type.

Crotonopsis argentea Pursh, Fl. Am. Sept. **1**: 206. 1814. Consists of two varieties; name is here applied to first.

Crotonopsis argentea linearis Pursh, *l. c.*

Friesia argentea Spreng. Syst. **3**: 850. 1826. Without citation of Pursh.

Leptemon lineare Raf. Sylva Tellur. 67. 1838.

Crotonopsis spinosa Nash, Bull. Torrey Club **22**: 157. 1895. "Collected by Mr. W. T. Swingle [*1397a*] at Dunellon [Florida], July 24 [1894]." Type seen in the herbarium of Columbia University at the New York Botanical Garden.

Dry sandy soil, in the Coastal Plain, South Carolina to central Florida and eastern Texas, extending inland near the Mississippi River to southern Illinois and southeastern Missouri, and in Texas to Dallas.

SOUTH CAROLINA. Beaufort: Bluffton, *Mellichamp* (M). Charleston: Mt. Pleasant, *L. R. Gibbes* (Y).

GEORGIA. Lowndes: Olympia, *R. M. Harper 1593* (M, U, Y). Mitchell: *R. M. Harper 1168* (M, U, Y).

FLORIDA. Baker: Macclenay, *L. H. Lighthipe 586* (Y). Brevard: Melbourne, *Curtiss 5715* (M, U, Y). Escambia: Pensacola, *J. M. Macfarlane* (P). Hillsboro: Tampa, *A. P. Garber* (U). Jefferson: *Hitchcock* (M). Lake: Eustis, *Nash 1971* (M, U, Y). Leon: Tallahassee, *N. K. Berg* (Y). Marion: Dunnellon, *Swingle 1397a* (U, Y). Orange: *A. Fredholm 5389* (Y). Pinellas: Ozona, *F. L. Lewton* (Y). St. John: St. Augustine, *M. C. Reynolds* (P). Sumter: Wildwood, *H. J. Webber* (M). Suwanee: Live Oak, *Curtiss 6897* (M, U, Y).

MISSISSIPPI. Oktibbeha: Starkville, *S. M. Tracy* (M).

ILLINOIS. Mason: "sandy barrens," *E. Hall* (M).

MISSOURI. Dunklin: Campbell, *Bush* (M). Stoddard: *Bush 124* (Y).

TEXAS. Dallas: Dallas, *Reverchon 869* (M, Y), *3177* (M), *4366* (M, U). Waller: Hempstead, *E. Hall 575* p.p. (M, U, Y).

MISCELLANEOUS RECORDS

HYPERICUM OPACUM T. & G.

Collected in flower August 15, 1912, in moist long-leaf pineland, Ozone Park, St. Tammany Parish, Louisiana, my number *4216*.

LECHEA LEGGETTII Britton & Hollick

Collected in fruit August 14, 1912, in dry open long-leaf pineland, Abita Springs, St. Tammany Parish, Louisiana, my number *4162*. Wide-spread through the southeastern states, reaching Florida and Louisiana.

RHEXIA LUTEA Walt.

Collected in fruit August 14, 1912, in moist long-leaf pineland, Abita Springs, Louisiana, my number *4198*.

RHEXIA NASHII Small

Collected in flower August 16, 1912, moist sandy soil near Mandeville, St. Tammany Parish, Louisiana, my number *4239*. Through the long-leaf pineland of the Coastal Plain, North Carolina to Florida and Louisiana. When seen living, readily distinguished from *R. mariana* L. by its flowers, the petals of which are much larger, 18–25 mm. long, and deep purple-pink.

Rhexia interior Pennell, nom. nov.

Rhexia latifolia Bush, Rhodora **13**: 167. 1911. Not *Rhexia latifolia* Aubl. Pl. Gui. **1**: 336. 1775. Aublet's plant is not retained in the genus *Rhexia* as today understood, a fact which under the Vienna Code permits the repetition of the same specific name.

Collected in fruit September 8, 1913, moist shady soil, west of Sapulpa, Creek County, Oklahoma, my number *5389*.

The following key to the species of *Rhexia* is offered:

Anthers relatively short, oblong, straight, not spurred at base.

Petals yellow. Leaves lanceolate. 1. *R. tulea* Walt.

Petals pink-purple. Leaves ovate.

Hypanthium glabrous. Upper surface of the leaves hirsute. 2. *R. petiolata* Walt.

Hypanthium glandular-hirsute. Upper surface of the leaves glabrous. 3. *R. serrulata* Nutt.

Anthers longer, linear, curved, spurred at the base.

Anther-sacs very slightly spurred. Petals less than 10 mm. long, white. 4. *R. parviflora* Chapm.

Anther-sacs evidently spurred. Petals more than 10 mm. long, pale pink (or white in *R. lanceolata*) to pink-purple.

Leaves membranous, green; lateral nerves not close to the margin; upper surface of some or all leaves hirsute. Hypanthium glandular-hirsute to glabrous.

Apex of hypanthium not lanose. Calyx-lobes less than one-third length of hypanthium.

Stem obscurely if at all winged, internodes conspicuously hirsute. Leaves narrowed at base. Neck of hypanthium equaling or but slightly shorter than the body.

Petals pale-pink to white, 10–15 mm. long. Buds with sepal tips mostly spreading-recurved.

Leaves elliptic-ovate to lanceolate, all evidently three-veined, mostly over 2 cm. long, the lower with a more or less petiolar base.

Leaves elliptic-ovate, on evident petioles 3–4 mm. long. Petals about 10 mm. long. 5. *R. delicatula* Small.

Leaves lanceolate to elliptic-lanceolate, on ill-defined petioles. Petals 12–15 mm. long. 6. *R. mariana* L.

Leaves narrowly-lanceolate to linear, only the main stem-leaves if any three-veined, mostly less than 2 cm. long, sessile. Petals 10–12 mm. long. 7. *R. lanceolata* Walt.

Petals deep purple-pink. Buds with sepal-tips mostly ascending-appressed.

Petals 18–25 mm. long. Hypanthium 10–14 mm. long, its neck equaling the body. Stem obscurely angled.

Leaves linear, sparsely hirsute, lateral nerves obscure. 8. *R. cubensis* Griseb.

Leaves lanceolate, conspicuously hirsute, lateral nerves prominent. 9. *R. Nashii* Small.

Petals 10–14 mm. long. Hypanthium 7–8 mm. long, its neck slightly shorter than the body. Stem relatively sharply angled. 10. *R. interior* Pennell.

Stem conspicuously wing-angled, the internodes sparsely hirsute to glabrous. Leaves rounded at base, the upper clasping. Neck of hypanthium much shorter than the body. Petals deep purple-pink.

Internodes of stem sparsely hirsute. Leaves ovate. Hypanthium hirsute. 11. *R. virginica* L.

Internodes of stem glabrous. Leaves ovate-lanceolate. Hypanthium sparsely glandular-pubescent to glabrous. 12. *R. stricta* Pursh.

Apex of hypanthium lanose with glandless yellow hairs. Calyx-lobes more than one-half length of hypanthium. 13. *R. aristosa* Britton.

Leaves firm, glaucescent, lateral nerves following closely the margin of the blade; upper surface glabrous. Hypanthium densely glandular-pubescent. 14. *R. Alifanus* Walt.

RAIMANNIA DRUMMONDII (Hook.) Rose

Collected in flower October 12, 1912; beachs and, Sullivan Island, Charleston County, South Carolina, my number *4857*. Extensively spreading from Texas along the coastal dunes of the southeastern states.

MYRIOPHYLLUM PROSERPINACOIDES Gill.

Pool in long-leaf pine-land, Mandeville, St. Tammany Parish, Lousiana, my number *4205*. Established also in ditches at Houma, Terre Bonne Parish. Naturalized from Chile.

The strand flora of the Hawaiian Archipelago—II. Ecological relations

VAUGHAN MACCAUGHEY

TEMPERATURE

The Hawaiian littoral zone is characterized by relatively warm and uniform thermal conditions throughout the year. Sudden fluctuations are exceedingly rare and are never of great magnitude. The lowest recorded littoral temperature is 47° F., the highest is 98° F.; the mean of all littoral temperatures is 74° F. The mean monthly temperature at Honolulu, which may be taken as a representative coastal station, varies from about 70.5° F. to 76.8° F., in January and July respectively.

The following table, arranged from data of the Hawaiian Section, U. S. Weather Bureau, will show the temperature conditions (for 1915) of a number of littoral stations on the various islands. Data are not available from more strictly littoral stations—i. e., at the actual beach line itself. This is a problem that awaits future field investigation.

Station		Elevation in feet	Temperature		
			Mean	Max.	Min.
KAUAI:	Mana	30	73.9°	93°	51°
	Kealia	15	73.1	88	47
OAHU	Kahuku	25	76.6	88	60
	Honolulu	111	75.0	87	58
	U. S. Mag. Sta.	45	75.5	92	50
	Waianae	6	76.2	93	52
	Waialua Mill	30	74.3	93	52
MOLOKAI:	Kalawao	70	75.2	90	57
MAUI:	Kaanapali	12	72.8	91	55
	Hana	145	75.6	89	58
HAWAII:	Mahukona	11	75.5	98	58
	Niulii	200	73.5	87	58
	Pepeekeo	100	73.3	86	57
	Hilo	100	72.6	87	54
	Kapoho	110	72.8	89	58

Olsson-Seffer ('10) presents data to show that on tropical and subtropical coasts the variations in the temperature of sea-water are mainly due to changes in the direction of the winds and currents. Close to the shore, or where the water is shallow, the temperature of the water is higher when the surface is calm, but low when the sea is rough. This is the natural consequence of the solar radiation in the former case, and of the mixing by the waves of the surface water with the cooler water from below when the sea is disturbed.

The annual thermal ranges of the oceanic waters of four representative regions will make a significant contrast with the conditions prevailing in Hawaiian waters: Sydney Harbor, Australia, 55.8°–72.4° F.; San Francisco Bay, California, 42°–69° F.; Woods Hole, Massachusetts, below freezing–70° F.; Plymouth, England, 44.1°–58.9° F.

The great oceanic current from the northeast, which travels down the Pacific Coast and out past Hawaii, as part of the Equatorial Drift, has so profound an effect upon the Hawaiian climate in general and the littoral zone in particular, that it merits special consideration here. Dr. Sereno O. Bishop, who made Hawaii his home for many years, writes ('04) of this current, as follows:

> That remarkable stream of cold water, which flows in a vast stream southerly, skirting southeast Alaska, Vancouver's Island, the Pacific States of Washington, Oregon, and California, and finally passes out westward to Hawaii, beyond which group it becomes merged into the great equatorial current running westward.
>
> This stream is of very low temperature, of immense volume, and of great velocity. It is unique in its powerful effects upon the climates of the coasts along which it flows. . . . Finally turning westward like the trade winds under the impulse of the earth's rotation, this mighty stream broadens out into the open ocean, gradually gaining warmth.

Dall ('04) states:

> As it moves down the coast it loses its heat and produces the rain and fogs of the Oregonian region, cooling off so that when it reaches the latitude of the Golden Gate it has only the temperature of 54° or thereabouts, and is colder than the normal sea-water for that latitude. It continues southward as a cold current, as described by Dr. Bishop. After traversing 2,200 miles it reaches the Hawaiian Islands, still at the low temperature of 70° in late summer, and of below 60° in late winter. This imparts to that favored group a uniformly subtropical climate such as is unknown to any other land in the same latitude.

Cowles, in describing the strand of the Lake Michigan dune region ('99, p. 107), states that on the beach, due to the "absence of vegetation and the general exposure . . . the temperature is higher in summer and lower in winter than in most localities. This great divergence between the temperature extremes is still further increased by the low specific heat of sand." This is also true of the Hawaiian sand strands. There is a greater temperature range on the beach itself than in the protected zone lying immediately behind the beach. However, the temperature range of the littoral is insignificant when contrasted with that of the mountains that ascend directly from the lowlands, and in many places directly from the littoral. The diurnal range in temperature increases as one ascends the mountain slopes, and this range reaches its maximum on the high summits of Kea and Loa (nearly 14,000 ft.). Guppy ('03–'06) found the mean daily range of temperature on the summit of Loa, August, 1897, to be 30.6° F.; the lowest reading was 15°, the highest 61.2°.

Although sand has low specific heat, the upper dry layer becomes excessively hot under a cloudless sky. Cockayne ('11) records surface temperatures of 120°–127° F. on the New Zealand strand; these figures are even higher than the generalization made by Guppy in the table given below. It should be noted, however, that the wet underlayers of sand absorb heat much more slowly. At the depth of a few inches below the surface the sand is always moist, so that the roots of sand-strand plants descend very quickly into relatively cool soil.

Guppy ('03–'06) makes the following generalizations concerning beach temperatures, the data applying to ordinary beaches under an unclouded sky, in the hot season, during the early afternoon:

		Surface—half-inch deep	Four inches deep
Temperate	about 50°–55° lat.	100°–105° F.	77° F.
Subtropical	" 30 –35 "	105 –110	80
Tropical	" 10 –20 "	110 –120	85

Olsson-Seffer ('09, pp. 88, 89) gives an extensive series of strand temperatures secured by him in various parts of the world.

With reference to temperature, Hawaiian strand regions may be classified as follows:

I. Warmer strands—leeward, facing SE., S., or SW.

1. Typical leeward beaches: e. g., Mana, Barber's Point, leeward Molokai, Lahaina, and Kawaihae.
2. Slope approaches plane perpendicular to incident sunlight: flat beaches, like those of Midway, Laysan, leeward Kauai and Puna.

3. Not subjected to shadows: as for 2.
4. Heat reflected by neighboring objects: e. g., Mana dune strand, Koko Head tufa cliff coast, Mokapu.
5. Composed of dark materials which absorb and retain heat: lava beaches of Hawaii, Maui, and parts of Oahu and Kauai.
6. Texture unfavorable for rapid evaporation of moisture: mud beaches and tufa cliff beaches, e. g., Pearl Harbor Inlet and Mokapu.
7. Arid or semiarid: not receiving the cooling effects of rain, waterfalls, etc., e. g., southwestern coasts of Maui and Hawaii.

II. Cooler strands—windward, facing NE., N., or NW.

8. All of the windward beaches.
9. Slope more or less precipitous: high beaches, e. g., Hamakua coast, windward East Molokai, Napali and Nihoa.

ILLUMINATION

The brilliant illumination of the Hawaiian strand is one of its most distinctive ecological features. The intense light of open beaches as contrasted with other regions, has been commented upon by ecologists in various parts of the world, but nowhere is this better exemplified than in the Hawaiian Islands. On the low islands the sky is cloudless, except during the infrequent rains. On the high islands the clouds heap over the mountainous interior, leaving the peripheral strand zone almost continuously exposed. The total insolation, in diurnal or in annual terms, is therefore exceedingly high. The Hawaiian coast, with its excessive insolation, may be contrasted, for example, with the gray, foggy coast of Washington and Oregon. On the coral and tufa beaches the intensity of the direct illumination is greatly increased by reflection. The glare on a coral beach, during the middle part of the day, as almost as intolerable to the eyes as that from a snow-field.

There are few data as to the direct and indirect effects of excessive insolation, save as an integral part of the xerophyte-producing complex. In general, light retards growth, and too great an intensity of light causes cessation of the growth of an organ. Pfeffer ('03, p. 87) states:

> The internodes become shorter and the plant more condensed as the intensity of the light increases, while the leaves attain their maximal size at a certain medium intensity of illumination. This latter is owing to the fact that moderate light stimulates the growth of the leaves, whereas intense light retards it.

Jost ('07, p. 125) makes the following statements:

> We are not accurately acquainted with the precise way in which assimilation is dependent upon the intensity of light. All researches agree on one point, viz., that assimilation of carbon is approximately proportional in amount to the intensity of light; it is questionable, however, whether this is the rule with higher intensities . . . it may be easily imagined that a further increase in assimilation, following on increase in light, is impossible owing to the deficiency in carbon-dioxide. Carbon-dioxide may be present in sufficient quantity under ordinary circumstances to employ all the energy of sunlight, but when light is artificially increased the usual amount of carbon dioxide would constitute a sub-optimum.

Schimper ('03, p. 58) states as a result of excess light;

> Terrestrial plants . . . frequently suffer from a considerable disintegration of their chlorophyll. The vegetation of very sunny spots is never pure green, but always exhibits an admixture of yellow and brown tints due to the products of decomposition of chlorophyll . . . intense tropical light may even completely bleach the foliage.

Many of the Hawaiian beach plants are grayish or yellowish green. This is characteristic, not only of Hawaii, but also of other strands. As Cockayne ('11) suggests:

> The yellow colour of certain dune plants belonging to different unrelated families is doubtless correlated with excess of light, and seems to me a possible example of heredity of an acquired character.

The author cannot share the latter view, as beach plants which have happened to grow in the shade develop normal green pigment, instead of the bleached beach pigment. Such species as *Santalum Freycenetianum* var. *littorale*, *Lepidium owaihense*, *Euphorbia cordata*, *Batis maritima*, *Argyreia tiliaefolia*, and *Cressa cretica* furnish excellent examples of this pronounced difference between the sun leaves and shade leaves of littoral plants.

A further comparison may be made which will illustrate the intensity of the strand illumination. In the rain-forest and summit-bog zones, and in the deep ravines of the lower and middle forests, the ordinary illumination on cloudy days—and these are regions of almost continuous cloudiness—necessitates a photographic exposure of say three minutes, whereas the same subject, distance, and aperture on the strand would require but one seventy-fifth of a second. The difference in illumination indicated by these figures is thus about 13,500, that is, the beach illumination is approximately 13,500 times as great as that of the cloudy rain-forest. Of course, these figures do not include all of the light-factors involved, but they are sufficient to indicate the great differences in the illumination of regions not far removed from one another.

Precipitation

All precipitation on the Hawaiian littoral occurs in the form of rain, dew, and rarely hail; snow is unknown. The strand is characteristically xerophytic or semi-xerophytic, as contrasted with the mesophytic lowland areas, and the montane rain-forests. The following data from representative stations of the U. S. Weather Bureau, 1915, will show these differences, the amount of rainfall being given in inches:

Island	Littoral station	Mesophytic station	Hygrophytic station
Kauai	16.98	38.02	75.52
Oahu	18.99	42.29	114.22
Maui (1914)	20.91	42.70	397.26
Hawaii	8.41	39.10	159.60

A few littoral stations are mesophytic or hygrophytic, but this is a relatively unusual condition—e. g., Na Pali coast of Kauai, north coast of East Molokai, and Hamakua coast of Hawaii.

The relationship between the annual precipitation on the strand and the character of the vegetation is very close. The paucity of the Hawaiian arborescent strand flora is undoubtedly due in part to the xerophytic character of the littoral. In those few strand regions which do possess sufficient rainfall, the forest extends down to the beachline. The Puna, Hilo, and Hamakua regions, illustrate this condition. Schimper ('03, p. 407) makes the generalization:

> Open littoral formations occur throughout the tropics, and in districts with a small rainfall they are almost the only ones. The close woodland above high-tide mark and the mangrove growing within reach of the tide are luxuriantly developed only in districts with abundant rain; and as the atmospheric precipitations decrease they become lower in stature, less close, and poorer in species.

In the case of the Hawaiian littoral vegetation, much emphasis must be laid upon the exterminating and limiting agencies which have been introduced into the islands within historic times. The ravages of wild live-stock, such as cattle, goats, sheep, and swine; the clearing of the lowlands for agricultural and other purposes; the building of roads; the large quantities of firewood which were drawn from the nearest and most easily available sources; the introduction of a great variety of pernicious foreign weeds—all of these factors have contributed largely to the depletion of the lowland and littoral floras, and have given them an aspect of meagerness that they probably did not possess in their primitive state. Man and his domestic animals have been much more potent limiting factors than has been precipitation.

WIND ACTION

The wind is a powerful agency in its direct mechanical effects upon beach vegetation. Many strand plants have forms that are more or less protective, i. e., prostrate, creeping, rosette, or hemispherical aerial bodies. Plants of upright habit are permanently deflected and shaped by the wind; the windward branches are stunted and warped, and growth takes place chiefly on the leeward side of the plant. Seaside plants of *Acacia farnensiana*, *Prosopis juliflora*, *Santalum Freycinetianum* var. *littorale*, *Calophyllum inophyllum*, and *Kadua littorale* commonly illustrate this condition. These wind-beaten plants are invariably dwarfed.

The mechanical effect of the wind is greatly augmented on those coasts upon which it is able to pick up quantities of beach sand. At storm times, in such regions, the wind becomes a veritable sand-blast. The evidences of this sand-blast action, upon the trunks of both living and dead trees, and upon the local topography itself, are familiar to all who have travelled along a windy coast. The fantastic sculpturing of the seaward slopes of tufa in the Koko Head region, and at Mokapu Peninsula, admirably illustrate this sand-blast work. The herbaceous vegetation on these slopes is either prostrate or rosette, e. g., *Sesuvium Portulacastrum*, *Argyreia tiliaefolia*, *Boerhaavia diffusa;* or tough and wiry, e. g., *Sporobolus virginicus*, *Fimbristylis pycnocephala*.

On the Hawaiian littoral the wind is not as important an ecologic agent as in such a region as the Lake Michigan sand dunes. Here, according to Cowles ('99, p. 108), it "is the chief destroyer of plant societies," acting in two ways—either by undermining plant individuals and groups, or by burying them with dune sand. Neither of these processes is particularly conspicuous along Hawaiian coasts; the vegetation is not sufficiently luxuriant to emphasize the former, nor are the dunes of sufficient size or mobility to give much importance to the latter. Here and there, however, both of these processes may be witnessed.

On the whole, the Hawaiian beach winds are retarding rather than destructive agencies. The Hawaiian strands may be divided into the following classes, based upon the relative exposure to wind action:

1. *Shores exposed to prevailing winds.*—The windward strands are much more exposed than are those along the leeward sides of the islands. Excellent contrasts are: the Hamakua and South Kona shores of Hawaii; the northeast and southwest shores of Haleakala; the north and south coasts of East Molokai; the Koolau and Waianae shores of Oahu; the Kilauea and Kekaha shores of Kauai.

2. *High or promontory-like shores.*—These are more exposed than are low flat shores. Good examples are: Hamakua, Hawaii; Hana and Kaanapali, Maui; the great pali of Molokai; Makapuu and Kaena, Oahu; Napali, Kauai; and the cliffs of Nihoa.

3. *Shores devoid of surface irregularities or vegetation sufficient to break the force of the wind.*—Low, flat shores, not protected by mountains behind them nor covered with forest, are exposed to the full force of the wind. In this class belong the coral atolls, and such shores as Kahuku and Mokapu, Oahu, the western extremity of Molokai, the Maui isthmus, and the extreme south point of Hawaii.

TRANSPIRATION

This is unquestionably the most important single physiological factor in determining the character of the Hawaiian strand flora. Only those plants which possess comparatively low transpiratory rates are able to permanently establish themselves upon the strand. Those species which invade the strand from the interior, and are characteristically mesophytic, undergo marked structural changes when they appear as members of the strand association.

The importance of the evaporation factor, particularly in the early stages of an association, is admirably emphasized by Transeau ('08, p. 230), who states:

> The greatest decrease in the demands for transpiration on the part of seedlings takes place during the first stages. This greatly aids in accounting for the well-known fact that the development toward a closed association proceeds with such increasing rapidity when once a few plants gain a foothold. Attention has been frequently called to the importance of pioneers as shade-producers, while their effectiveness in reducing transpiration has been underestimated.

On the Hawaiian beaches a combination of factors—warmth, brilliant insolation, and exposure to powerful and rarely intermittent winds—tend to augment transpiration, and make of it an influence of great potency in retarding certain plants and completely inhibiting many others.

HAWAIIAN TIDES AS RELATED TO THE LITTORAL

On all oceanic coasts and embayments the tides exert an influence of greater or less power in determining the seaward limits of the land vegetation, and the landward extensions of the marine flora. In regions where the tidal range is great the effect upon the shore-line vegetation is proportionately augmented; in regions where the range is slight, its influence is small or negligible. The Hawaiian Archipelago comes under the latter class.

The greatest tidal contrasts in the Hawaiian Islands are due to coastal topography, i. e., sea-cliffs contrasted with mud-flats that lie only a few inches above low tide. At the foot of the sea-cliffs which rise directly from the water is a tidal (and wave-splash) zone of two or three feet. This zone is conspicuously marked by the coralline algae, which form a reddish-purple or lavender band. If conditions for land-plants are favorable, they may occur only a few feet above this zone, within reach of the salt spray, and from a distance appear to rise from the sea itself. Plant-clad cliffs of this character also occur in many of the South Pacific islands.

The mud-flats, however, present broad, rocky, mud-covered platforms, a few rods to a half-mile in width, almost free from seawater at low tide, but covered at high tide with six to twenty-four inches of water. The land vegetation is restricted to the shoreward limits of these flats. The absence of the land-building halophytes—*Rhizophora*, *Bruguiera*, *Ceriops*, *Kandelia*, etc.—makes invasion very slow.

The mean range of the Hawaiian tides is very slight, that at Honolulu being 1.3 feet, and that at Hilo, 1.8 ft. These ranges are typical for all the islands, and contrast forcibly with the large ranges of many other littorals. For example at Apia, Samoa, the average rise is 3 ft. per tide; the tides in Sydney Harbor rise 6–7 ft.; Johnson and York ('15, p. 131) in their comprehensive ecological study of the tide-levels at Cold Spring Harbor, New York, found a mean tidal range of 7.63 ft., with a variation of from 4.2 ft. to 10.8 ft.

The following data from the U. S. Coast and Geodetic Survey Tide Tables show the tidal range through a single typical month, January, at Honolulu, in feet:

Date	Moon	1	2	3	4
3	New; farthest south	2.2	0.1	0.6	−0.2
4	Perigee	2.3	0.1	0.6	−0.1
9	Equator	0.5	1.4	0.0	1.0
10	First quarter	0.7	1.2	0.0	1.2
16	Farthest south	2.1	0.2	0.6	−0.1
18	Full moon; apogee	2.1	0.2	0.6	−0.1
24	Equator	0.4	1.3	0.0	1.1
26	Third quarter	0.7	0.9	0.0	1.5
30	Farthest south	2.1	0.2	0.7	−0.2

Contrasting sharply with the poorly defined tidal zones of the Hawaiian littoral are those regions with large tidal fluctuations. For example, Ganong ('06, p. 85) in his studies of the Miscou Island littoral, in the extreme northeast corner of New Brunswick, on the Gulf of St. Lawrence, found three well defined beach zones:

First—"a broad sloping inter-tidal beach of pure sand without vegetation." This corresponds to the mud-flats along the southern shores of Oahu.

Second—a "narrow band between ordinary and extreme high tides." This zone was practically barren of vegetation. This zone is negligible in Hawaii.

Third—a "broad shelf, . . . reached only by the very highest tides." This is an "upper beach," and is characterized by scattered drift-wood and dry, ever-shifting sand. Some of the typical plants of this zone are *Salsola Kali*, *Cakile edulenta*, *Atriplex patula hastata*, and *Ammophila arenaria*. Ganong states "that this vegetation is distinctly adjusted to the physical conditions, for it is of great paucity, of small and slow growth, annually renewed, closely ground-appressed, and strongly xerophytic."

Brownlie ('02) makes much of the irregularity of the tidal intervals in the Pacific, and states that at Honolulu the intervals of time from one high water to the next vary from ten and three-quarters to thirteen and three-quarters hours. A range so wide apart shows great irregularity compared with the absolute regularity of the movements of the moon. Although this tidal phenomenon is of great significance from the standpoint of tide studies themselves, it is not a factor of any special importance in the littoral ecology of land-plants.

Although the Hawaiian marine flora is closely limited by tidal intervals, these intervals are of little significance in determining the zonation of land-plants, as compared with the importance of other ecological factors. This contrasts with the findings of Johnson and York ('15, p. 149), at Cold Spring Harbor, who state:

> A careful study of the vertical distribution of the littoral plants about this harbor shows that this depends primarily and very definitely on the relative time of their submergence and emergence with the rise and fall of the tide. Moreover, the vertical range of littoral species is strictly, sometimes very narrowly limited. There are no species here, except two or three algae, that are distributed "between tidemarks" (*i. e.*, from low water up to high water), as is so often reported. The nearest approach to this range found for any seed plant is that of *Spartina glabra*.

It must be noted that the above statement uses the term littoral in a relatively narrow sense, as does their further statement that the vertical range of a littoral plant is exactly proportional to the range of the tide. This does not apply to the customary usage of the term littoral, which includes all vegetation along the coasts or strands, the ranges of which are more or less closely maritime.

NATURE OF THE SUBSTRATUM

The character of the littoral substratum obviously plays an important rôle in determining the nature and distribution of the littoral flora. Warming ('09, p. 223) groups halophytic plants into four classes, according to the nature of the substratum upon which they reach their optimum development: lithophilous, psammophilous, pelophilous, and helophilous. This will serve as a convenient basis for classifying the Hawaiian strand, with the reservation that not all strand plants are halophytes. The Hawaiian types to be considered may he referred to the lithophilous and psammophilous classes, as follows:

A. Lithophilous

1. Sheet or flow lava.
2. Vertical rock shores or sea cliffs.
3. Littoral creviced rocks.
4. Lava boulder and pebble beaches.
5. Tufa beaches.
6. Coral limestone strands.

B. Psammophilous

7. Coral sand.
8. Root molds.

1. *Sheet or flow lava.*—This type of strand is of first importance in the Hawaiian group, both quantitatively and from the standpoint of ecologic history. There are more miles of lava beach than of any other type, or of all the other types combined. The relatively large areas and recent formation of Maui and Hawaii have caused this to be the dominant type. Historically it is first to appear, and it eventually gives way to strands of other types. The lava flows may be either relatively recent and uneroded, like many on the island of Hawaii, or they may be of extreme antiquity and deeply carved, like those of the Na Pali coast of Kauai, or Kaena and Makapuu, on Oahu. The beach itself, in either case, is formed of exposed lava beds, very rocky, with practically no sand or soil, and distinctly uncongenial to plant life. Lava sheet beaches occur on all the larger islands, but are best exhibited on the shores of Hawaii and East Maui. Every gradation may be found from very low, flat lava strands, only a few feet above sea-level, to bare sea precipices 600–700 feet in height.

From the historic standpoint the lava beach is of twofold significance. If of recent flow material—e. g., the Hawaii flows of 1840, '59, '68, '87—it indicates the extinction of the vegetation which occupied the old strand, and the exposure of a new littoral surface to plant invasion. On the other hand, in the early geological history of the islands the Hawaiian strand was wholly of sheet lava, and today remnants of this primitive beach condition exist here and there along the coasts. Thus there is great diversity in the ages of the various shores, and in the amount of plant invasion, both from within and from without, to which they have been exposed.

2. *Vertical rock shores or sea cliffs.*—These are composed either of sheet lava or laminated tufa. They are produced by sea action and fracture. Some of the stupendous sea-cliffs of Hawaii, Molokai, and Kauai, may have been produced by volcanic or seismic activity. The sea-cliffs either rise sheer from the water, or have a narrow strand at the base; this depends upon the depth of the off-shore water and both conditions are of frequent occurrence. None of the sea-cliffs, no matter how precipitious or apparently uncongenial for plant life, are wholly devoid of vegetation. Here and there on the surface of the cliff are crevices, ledges, and little pockets where plants establish themselves.

On the arid precipices—e. g., Koko Head, Makapuu, Mokapu and Kaena—occur such plants as *Euphorbia cordata, Lepidium owaihense, Schiedea globosa, Kadua littoralis, Tetramolopium* spp., *Lipochaeta integrifolia, Gossypium tomentosum, Sida* spp., *Jacquemontia sandwicensis, Boerhaavia diffusa, Cassia Gaudichaudii* and *Capparis sandwichiana.*

On the humid sea-cliffs—e. g., Waipio, Nahiku and East Molokai—are such forms as *Campylotheca molokaiensis, Schiedea Lydgatei, Lysimachia spathulata, Metrosideros polymorpha, Tribulus cistoides* and *Nama sandwicensis.*

3. *Littoral creviced rocks.*—Along the lava flow and tufa-cliff coasts, and to a lesser degree along the uplifted coral limestone shores, the rock crevices are the special habitats of many strand plants. The crevices are of two kinds: those due to the lamination of the rock, that is of the sheets or layers of lava or tufa; and those due to the vertical faulting of these layers. The former condition produces horizontal crevices, which on the sea-cliffs often front on ledges of greater or less magnitude. The vertical checking and faulting produces numberless irregular crevices upon the surface of the exposed strata, and in these crannies soil, seeds, and spores are lodged. Many of the crevices are less than an inch in

width, and the plants grow on top of the crevice, merely rooting in it. Others are several inches wide, and the smaller plants, such as *Lipochaeta succulenta*, *Lepidium owaihense*, and *Cressa cretica*, grow down within the crevice, only the upper parts of the branches showing above the rock. In the very large fissures,—one to three feet wide, the entire plant body may be concealed within the fissure.

4. *Lava boulder and pebble beaches.*—Wherever the shore line lava-sheets are subjected to the action of the sea, they are gradually broken into massive boulders, which in turn are slowly ground into pebbles. These metamorphoses are abundantly illustrated along the windward coasts of Hawaii, Maui, and Molokai, and in such places as Kaena, Oahu, and Kilauea, Kauai.

The boulders are usually 2–3 ft. in diameter, more or less oblate, smooth, black, very hard, heavy, and resonant. A beach composed of these ponderous rocks is very impressive, particularly during storm time, when the sea mills them with irresistible power. In various places, especially on the coasts of Kauai and Oahu, the lava boulders are consolidated in a calcareous matrix, formed of re-deposited coral lime.

The seaward portion of a boulder beach is barren of terrestrial vegetation, as is to be expected, but the upper or landward portion, which is not disturbed by ordinary wave action, is the habitat of such forms as *Sesuvium Portulacastrum*, *Ipomaea glaberrima*, *I. insularis*, *Euphorbia cordata*, *Tetramolopium* sp., *Kadua littoralis*, and *Wikstroemia Uva-ursi*.

The pebble beaches are relatively uncommon on Kauai and Oahu, but are more common on Maui and Hawaii. The pebbles, at the upper margin of the beach, are intermingled with soil, and the line of demarcation between beach and lowland is not distinct.

5. *Tufa beaches.*—Tufa craters occur here and there throughout the islands, from sea-level up to the highest mountain summits. In a few instances tufa cones stand so close to the shore line that the sea has cut beach platforms in their slopes. In these cases the strand is made of the solid wave-cut tufa rock. Leahi, Koko Head, Koko Crater, Manana, and Mokapu, illustrate this condition. The tufa is soft and easily sculptured by the waves; it usually does not form boulders or pebbles, but fractures easily and

disintegrates into mud. The main part of the tufa platform is wave-swept and barren of vegetation; the upper portion is the habitat of such forms as *Nama sandwicense, Sicyos hispidus, Jacquemontia sandwicensis, Tribulus cistoides, Cenchrus calyculatus, Waltheria americana.*

Tufaceous sand or mud is brownish or yellowish green in color, much finer in texture than the coral sand, and much more retentive of moisture. It often contains large quantities of olivine; this imparts the greenish hue. Some common plants of the muddy beaches are: *Batis maritima, Polypogon littoralis, Thespesia populnea, Ruppia maritima, Cyperus laevigatus, Chenopodium album.*

A number of small islets, such as Moku Manu, Manana and Molokini, are made up largely or wholly of tufaceous deposits, and represent the eroded remains of former tufa cones.

6. *Coral limestone strands.*—Within recent geological times there has been a slight uplift at various points in the Archipelago, which has resulted in elevating above sea-level broad shelves of coral limestone. Such areas are especially abundant on the island of Oahu, and portions of the shore around Pearl Harbor, Kaneohe Bay, Waianae, Kahuku, and Barber's Point are formed of the exposed coral limestone. These shores are often undercut by the surf, and are sculptured from above by the action of rain-water. The limestone along the beach may be actually wave-washed, or may be more or less buried beneath coral sand. Further back from the shore it is usually covered with a layer of soil.

7. *Coral sand.*—Beaches of pure coral sand are abundant on the islands of Oahu and Kauai, and also occur on the islands of Maui and Molokai. On the coral atolls to the leeward the coral strand is, of course, dominant. The sand is washed ashore from the coral reefs, and sometimes accumulates in sufficient quantities to form dunes. Mana, Kauai, Makaha and Heleloa, Oahu, and West Molokai, are representative dune regions. Fine stretches of coral beach may be found at Waikiki, Makapuu, Waimanalo, Mokapu, Kanuku, Waianae, and Ewa.

The Hawaiian coral strands correspond to the xerophytic beaches of Cowles ('99, p. 112), who recognizes two classes of beaches: hydrophytic and xerophytic, defining the latter as essentially a product of wave action and comprising the zone which is or has been worked over by the waves. Hence the beach may be defined as the zone between the water level and the topographic form produced by other agents. This definition is closely applicable to the Hawaiian coral sand beaches, which are uniformly xerophytic in their characteristics. Olsson-Seffer ('10) has stated that the competition for food is more intense, the water supply less, the light stronger, the temperature higher, the transpiration greater, the foothold more uncertain and difficult, the conditions for plant life generally more adverse, than on any other soil.

Shaler ('94) has made some significant generalizations concerning sandy beaches. He points out that dunes and beaches of coral sand never march far inland, as do quartz sand dunes, for the reason that the limestone grains speedily become consolidated into a tolerably firm set rock. It is characteristic of coral beaches that the materials of which they are composed, unlike those of ordinary shores, are readily taken into solution, and in that state may be borne away by the currents to any distance. Notwithstanding the constant robbery of their materials, which is effected by the solving process, the coral beaches often widen with great rapidity. Shaler emphasizes that one of the most noticeable features which is exhibited by beach sands is their extraordinary endurance of the beating of the waves. He compares the rapid abrasion of rocks and boulders to the very insignificant abrasion of sand particles. Though subjected for ages to the beating of the waves, with perhaps a hundred times as much energy applied to the surface of which it forms a part as would suffice to reduce a granite boulder containing a cubic foot of material to a granular or powdery state, the beach sand remains unworn. This endurance is due to the capillary water. So long as the beach is full of water the particles do not touch each other. Thus the blow of the waves is used up in compressing the interstitial water and is converted into heat without wearing the mineral matter in an appreciable degree.

Sandy beaches have a relatively slight water capacity, as the percolation is very rapid. The capillarity is not as pronounced as in soils of finer texture, and the evaporation from a sandy surface is quite rapid. All of these conditions tend to greatly reduce the available water supply of a beach, even though the latter be exposed to normal precipitation. In other words, the physical characteristics of the sandy beach, as has already been suggested, tend strongly toward xerophytism. Olsson-Seffer ('10) shows that it is the volume of water which a soil is capable of placing at the disposal of the plant, which is the limiting factor in the production of its vegetative covering and the controlling condition in the distribution of this vegetation. Percolation in sand is so rapid that were it not for the counteracting influence of surface tension very little water would be retained by sand. Permeability increases as the sand particles increase in size. Internal dew formation in the sand is the direct cause of a portion of the permanent moisture of the strand or dune. It is also to be noted, in this connection, that extreme changes in the salinity of the soil water, due to flooding by fresh water, are detrimental to the strand flora.

The two important constituents of the soil water of the sandy beach are lime and salt. On coral beaches the percentage of lime is very high. It is dissolved out by the rain-water, and ultimately forms consolidated limestone. The soluble salt content is coastal and is not of as great ecologic importance as was formerly supposed. An excellent statement is given by Olsson-Seffer ('10). Sandy soil yields its water to plants more freely than do other soils, and below the superficial layer of dry sand there is always a surprising amount of water. Fuller ('12) found this to be more than double the wilting coefficient of dune soil.

Owing to the frequent inundations by waves and subsequent rapid changes in evaporation, the soil temperatures of the lower sand beach are more variable than on any other formations of the sandy strand. On account of the low specific heat of sand, the surface layers are rapidly heated in the daytime and quickly cooled at night. Thus there is considerable fluctuation of diurnal temperatures.

The list of plants enumerated by Schauinsland ('99) as occuring on the Laysan atoll may be taken as representative of the coral strand flora of the leeward isles. This list includes:

Lepidium owaihense
*Capparis sandwichiana**
Portulaca oleracea
Tribulus cistoides
Sicyos hispidus
Sicyos microcarpus
Sesuvium Portulacastrum
Lipochaeta integrifolia
Scaevola Lobelia
Solanum laysanense
Ipomoea Pes-caprae
Ipomoea insularis
Nama sandwicensis
Heliotropium curassavicum
Phyllostegia variabilis
Boerhaavia diffusa
Achyranthus splendens
Euxolus viridis
Chenopodium sandwicheum
Santalum Freycinetianum
Cyperus laevigatus
Cyperus pennatus
Cenchrus calyculatus
Sporobolus virginicus
Eragrostis hawaiiensis
Lepturus repens
Pritchardia Gaudichaudii

8. *Root-Molds.*—An interesting formation along the Hawaiian littoral, that has also been recorded from other parts of the world (see Dolley, '89, pp. 131, 132; and Darwin, '60), is the root-mold. This is well developed on sandy shores with persistent winds, where there has been considerable vegetation. The west end of Molokai, the Maui isthmus, Makapuu and Kaena on Oahu, and the Mana region of Kauai all possess notable root-mold formations. The molds are produced by the cementing together of the sand particles which lie near the ramifying roots of beach plants; the cementing process is undoubtedly due to specific root excretions, as well as to the percolating rain-water which follows the courses of the larger roots. In the course of time the vegetation dies, the winds sweep away the loose sand from around the more solid molds, and the latter are eventually exposed. They appear either as isolated cylinders, rising here and there above the sand, or as irregular masses of branching tubes. They rise to a height of three to twenty inches above the present level of the sand, and in color are white or yellowish brown.

The lumen varies from a fraction of an inch to nearly a foot and is rarely open; it is more or less completely filled with limestone. The smaller sizes are the most common, as the majority

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* This abundant indigenous pseudolittoral was inadvertently omitted from the list on p. 276. It is a straggling shrub, inhabiting arid rocky lowlands and beaches; a favorite habitat, for example, is a rocky talus slope near the sea.

of beach plants are slender-rooted. Upon close examination the wall is found to be composed of sand, coral particles, and other minutiae compactly cemented together. In cross section the wall shows a very much hardened inner layer forming a distinct zone. The outer layer is relatively soft and easily crumbled.

These molds are the fossils of the root-ramifications of a previous plant formation. Molds identical in mode of formation with those of the coral strands are also plentiful in the tufa slopes, and attain much larger sizes than the sand molds. Punchbowl, Round Top, Diamond Head, and Koko Head are typical regions where these molds occur in abundance and in all stages of development.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1913–1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

Adams, J. F. *Keithia* on *Chamaecyparis thyoides.* Torreya **18**: 157–160. *f. 1, 2.* 7 S 1918.

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