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# BULLETIN

OF THE

# TORREY BOTANICAL CLUB

VOL. 41

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EDITOR

ALEXANDER WILLIAM EVANS

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NORMAN TAYLOR

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1914

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## CONTENTS

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BRITTON, NATHANIEL LORD. Studies of West Indian Plants—V	1
GRIGGS, ROBERT F. Observations on the behavior of some species at the edges of their ranges	25
ROBINSON, WINIFRED J. A taxonomic study of the Pteridophyta of the Hawaiian Islands—IV (plates 1, 2)	51
BICKNELL, EUGENE P. The ferns and flowering plants of Nantucket—XII	71
RYDBERG, P. A. Phytogeographical notes on the Rocky Mountain region—II. Origin of the alpine flora	89
MILLER, FRED A. The propagation of medicinal plants	105
FISHER, G. CLYDE. Seed development in the genus <i>Peperomia</i> (plates 3-6) [To be concluded.]	137
DODGE, B. O. The morphological relationships of the Florideae and the Ascomycetes	157
HARPER, ROLAND M. The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession	209
FISHER, G. CLYDE. Seed development in the genus <i>Peperomia</i> (plates 3-6) [Concluded.]	221
HARRIS, J. ARTHUR. On the relationship between the number of ovules formed and the number of seeds developing in <i>Cercis</i>	243
KUNKEL, LOUIS OTTO. Physical and chemical factors influencing the toxicity of inorganic salts to <i>Monilia sitophila</i> (Mont.) Sacc.	265
BERRY, EDWARD WILBER. Contributions to the Mesozoic flora of the Atlantic coastal plain, X.—Maryland	295
BAILEY, VERNON. The wild cotton plant ( <i>Thurberia thespesioides</i> ) in Arizona	301
SLOSSON, MARGARET. Notes on two North American ferns (plate 7)	307
RYDBERG, P. A. Notes on Rosaceae—VII	319
ATWELL, RUTH S. The appearance of polar bodies in the spermatogenous tissue of <i>Ricciocarpus natans</i> (L.) Corda. (plate 8)	333
TURESSON, GÖTE. Slope exposure as a factor in the distribution of <i>Pseudotsuga taxifolia</i> in arid parts of Washington	337
VESTAL, ARTHUR G. A black-soil prairie station in northeastern Illinois	351
BOWMAN, HOWARD H. M. Mechanical tissue development in certain North American vines	365
HOWE, R. HEBER, JR. The nomenclature of the genus <i>Usnea</i> (plates 9-14)	373
GRIGGS, ROBERT F. Observations on the edge of the forest in the Kodiak region of Alaska	381
BENEDICT, RALPH C. A revision of the genus <i>Vittaria</i> J. E. Smith—I. The species of the subgenus <i>Radiovittaria</i> (plates 15-20)	391
BICKNELL, EUGENE P. The ferns and flowering plants of Nantucket—XIII	411
ALLARD, H. A. A review of investigations of the mosaic disease of tobacco, together with a bibliography of the more important contributions	435



RYDBERG, P. A. Phytogeographical notes on the Rocky Mountain region	
—III. Formations in the alpine zone	- - - - - 459
RYDBERG, PER AXEL. Notes on Rosaceae—VIII	- - - - - 483
STANDLEY, PAUL C. New or notable species of <i>Amaranthus</i>	- - - - - 505
GLEASON, HENRY ALLEN, and MCFARLAND, FRANK THEODORE. The introduced vegetation in the vicinity of Douglas Lake, Michigan	- - - - - 511
HARRIS, J. ARTHUR. Further observations on the relationship between the number of ovules formed and the number of seeds developing in <i>Cercis</i>	- - - - - 533
HARPER, ROLAND M. A superficial study of the pine-barren vegetation of Mississippi	- - - - - 551
EVANS, ALEXANDER W. Report on the Hepaticae of Alaska (plate 21)	- 577
BLACK, CAROLINE A. Branched cells in the prothallium of <i>Onoclea sensibilis</i> L. (plates 22, 23)	- - - - - 617
FARWELL, OLIVER A. The correct name for the hemlock spruce	- - - - - 621
—————	
INDEX TO AMERICAN BOTANICAL LITERATURE	- - - - - 61,
	131, 203, 257, 311, 347, 387, 429, 475, 523, 569, 631
—————	
INDEX TO VOLUME 41	- - - - - 641

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### Errata

- Page 90, line 9, for monotypic read monotopic.  
 Page 90, line 15, for polytypic read polytopic.  
 Page 116, line 11 from bottom, for *gloxinioides* read *gloxiniæflora*.  
 Page 226, line 17 from bottom, for cells read cell.  
 Page 237, line 10, for 2 read 2<sup>1</sup>.  
 Page 463, line 18, for *Dasiphora* read *Dasiophora*.  
 Page 470, line 10, for *Lloydea* read *Lloydia*.



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Observations on the behavior of some species at the edges of their ranges.	ROBERT F. GRIGGS	25
A taxonomic study of the Pteridophyta of the Hawaiian Islands—IV. (Plates 1 and 2).	WINIFRED J. ROBINSON	51
INDEX TO AMERICAN BOTANICAL LITERATURE . . . . .		61

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THE NEW ERA PRINTING COMPANY

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JANUARY, 1914

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Studies of West Indian plants—V

NATHANIEL LORD BRITTON

23. ADDITIONAL SEDGES FROM JAMAICA\*

CYPERUS COMOSUS Poir. in Lam. Encycl. 5: 185. 1817  
Shettlewood, Hanover (*Harris 11647*).

DISTRIBUTION: Cuba; continental tropical America.

SCIRPUS CUBENSIS Kunth, Enum. 2: 172. 1837

River Head, near Ewarton (*Underwood 1860*).

DISTRIBUTION: Southern United States; Cuba; Hispaniola;  
Trinidad; continental tropical America; tropical Africa.

RYNCHOSPORA CYMOSA (Michx.) Ell. Bot. S. C. and Ga. 1: 58.  
1816

Savannah, Upper Clarendon (*Harris 11103*).

DISTRIBUTION: Southeastern United States; Cuba; Hispaniola;  
Porto Rico; Martinique; South America.

***Rynchospora jamaicensis* sp. nov.**

Rootstocks short; culms clustered, slender, 6–8 dm. long, reclining. Leaves 2–3 mm. wide, rather stiff, the lower 2–5 cm. long, the middle ones 12–15 cm. long, those subtending the clusters of spikelets 6–10 cm. long; sheaths of all the leaves densely short-pubescent; spikelets loosely paniced in several distant axillary clusters and in a terminal one, short-pedicelled, the axis of the inflorescence loosely pubescent; spikelets narrowly conic, 4–5 mm.

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\* See Bull. Dept. Agric. Jam. 5: Suppl. 1. 1907. Bull. Torrey Club 35: 568, 569. 1909.

[The BULLETIN for December (40: 653–712. pl. 25, 26) was issued 8 Ja 1914.]



long, maturing 2 achenes; lower empty scales broadly ovate, the others lanceolate, acuminate; bristles none; achenes obovate-orbicular, 1 mm. long, pale brown, shining, finely cancellate; tubercle triangular-lanceolate, acuminate, flat, about one-third longer than the achene, its base nearly truncate.

Rocky banks in the Blue Mountains of Jamaica; *type*, from Hardware Gap, *N. L. Britton 3322*, collected Sept. 9, 1908. Related to *R. elongata* (Boeckl.) Clarke, and to *R. polyphylla* Vahl, but at once distinguished from them by its pubescent sheaths.

## 24. THE GENUS PITHECOLOBIUM IN CUBA

### A. Pods curved or coiled, dehiscent, the valves twisting after separating.

1. Seeds with a fleshy aril; stipules spinescent; pinnae 1 or 2 pairs; leaflets 2-4 pairs.

Leaflets 1-6 cm. long (species perhaps confluent).

Leaflets spinulose-mucronate.

1. *P. circinale*.

Leaflets obtuse or mucronulate.

Leaflets chartaceous; petioles of the lower leaves, at least, longer than the petiolules.

2. *P. Unguis-cati*.

Leaflets coriaceous; petioles shorter than the petiolules or as long.

Petioles and petiolules stout; leaflets large, 2.5-6 cm. long.

3. *P. guadalupense*.

Petioles and petiolules slender; leaflets small, 1-3 cm. long.

4. *P. bahamense*.

Leaflets only 3-7 mm. long.

5. *P. Hystrix*.

2. Seeds without a fleshy aril; stipules not spinescent; pinnae 2 pairs or more; leaflets 3 pairs or more.

1. Leaflets obovate to oval, large, 1.5-6 cm. long, 3-6 pairs to each pinna.

Calyx subtruncate at base; seeds oblong, about twice as long as wide.

6. *P. savannarum*.

Calyx narrowed at base; seeds suborbicular to obovate.

Pinnae 3 or 4 pairs; leaflets 4-6 pairs; calyx narrowly campanulate, thin.

7. *P. discolor*.

Pinnae 1 or 2 pairs; leaflets 2-4 pairs; calyx broadly campanulate, coriaceous.

Calyx truncate, its teeth minute, mucronulate.

8. *P. truncatum*.

Calyx teeth large, broadly ovate.

Calyx short-campanulate; stamen-tube short; leaflets broadly obovate.

9. *P. obovale*.

Calyx long-campanulate; stamen-tube 5-6 mm. long; leaflets oblong to obovate.

10. *P. pinetorum*.



2. Leaflets linear to oblong, small, 5-16 mm. long,  
6-many pairs to each pinnule.  
Leaflets 2-3 mm. long, oblong, coriaceous. 11. *P. nipense*.  
Leaflets 5-16 mm. long, thin, dull.  
Leaflets obliquely oblong, narrowed at base. 12. *P. asplenifolium*.  
Leaflets linear, linear-lanceolate or oblong,  
obtuse, rounded or subcordate at the base.  
Leaflets oblong, 5-7 mm. long. 13. *P. trinitense*.  
Leaflets linear.  
Pinnae 2 pairs; leaflets acute, strongly  
veined; pod compressed. 14. *P. guantanamense*.  
Pinnae 3-11 pairs; leaflets obtuse, not  
strongly veined; pod swollen. 15. *P. arboreum*.

**B. Pods straight, or curved, indehiscent, or dehiscent, the valves not twisting.**

Unarmed trees.

- Pod straight or a little curved, compressed, turgid,  
fleshy; leaflets oblong to obovate, large. 16. *P. Saman*.  
Pod straight, thin, very flat, chartaceous; leaflets  
linear, small, very numerous. 17. *P. Berterianum*.  
Trees or shrubs, armed with spinescent stipules (*P. tortum*  
sometimes unarmed).  
Pod coriaceous, tardily dehiscent; stamens 2 cm. long  
or less, the tube short; leaflets many; spines straight. 18. *P. tortum*.  
Pod chartaceous, thin and flat, dehiscent; stamens 5-6  
cm. long, the tube much exerted; leaflets few;  
spines curved. 19. *P. prehensile*.

**I. PITHECOLOBIUM CIRCINALE (L.) Benth. Lond. Journ. Bot.  
3: 201. 1844**

*Mimosa circinalis* L. Sp. Pl. 517. 1753.

Thickets in dry districts at low elevations, southern Oriente;  
Hispaniola.

Bentham's record of this species for the Bahamas appears  
to refer to *P. mucronatum* Britton, which has quite different  
leaves. The Oriente plant differs from the typical one of His-  
paniola in having smaller, thicker leaflets, less cuneate at the  
base, and is either glabrous or densely pubescent.

**2. PITHECOLOBIUM UNGUIS-CATI (L.) Mart. Hort. Monac. 188.  
1829**

*Mimosa Unguis-cati* L. Sp. Pl. 517. 1753.

Cayo Sabinal, Camagüey (*Shafer* 1063); recorded by Richard  
as in various parts of the island, but is apparently rare. West  
Indies (except Bermuda); northern South America.



3. *PITHECOLOBIUM GUADALUPENSE* Chapm. Fl. S. U. S. 116.  
1860

Cays of Camagüey; Bahamas; Florida Keys.

4. *PITHECOLOBIUM BAHAMENSE* Northrop, Mem. Torrey Club  
12: 38. 1909

Cays of Camagüey; Bahamas.

5. *PITHECOLOBIUM HYSTRIX* (A. Rich.) Benth. in Hook. Icon. Pl.  
*pl.* 1168. 1876

*Inga Hystrix* A. Rich. Ess. Fl. Cub. 1: 471. 1845.

*Pithecolobium calliandrifolium* C. Wright; Griseb. Cat. Pl. Cub.  
83. 1866.

Coastal thickets and hillsides: Camagüey, Santa Clara,  
Havana, Pinar del Rio; Bahamas.

6. *Pithecolobium savannarum* sp. nov.

A tree up to 7 m. high, with smooth bark, the foliage finely and densely puberulent when young, glabrous or sparingly puberulent when old. Leaves 1.5–2 dm. long, the rather stout petioles 1–2.5 cm. long, the glands somewhat elevated; pinnae about 4 pairs, the petiolules slender, 2 cm. long or less; leaflets 4–6 pairs, obliquely obovate, 1.5–3 cm. long, chartaceous, loosely reticulate-veined, deep green and somewhat shining above, pale and dull beneath, obtuse or retuse at the apex, acute at the base; peduncles axillary, slender, striate, glabrous, 7–9 cm. long; flowers short-racemose, white; pedicels slender, glabrous, 3–6 mm. long; calyx 3–4 mm. long, subtruncate at the base, campanulate, its teeth acute, ovate, often somewhat unequal; corolla funnelform, appressed-pubescent, 8 mm. long, its lobes ovate-oblong; stamens 15 mm. long, united about one-third their length; ovary and young pod densely pubescent; old pods 8–10 cm. long, the valves doubly coiled after dehiscence, moniliform, 4–6 mm. wide across the seed cavities, 2 mm. wide between them; seed cavities oblong, 8–10 mm. long.

Along a water course on barren savannas southeast of Holguin, Oriente, April 7, 1909 (*Shafer 1194*).

7. *Pithecolobium discolor* sp. nov.

A shrub 3 m. high, or a small tree up to 7 m. high, the young twigs and leaves densely puberulent, the old leaves glabrous or



somewhat puberulent, 1-2 dm. long, the stout petioles 2 cm. long or less, the glands on the rachis between the pinnae orbicular, small. Pinnae 3 or 4 pairs; leaflets 4-6 pairs, obovate, chartaceous, 1.5-2.5 cm. long, dark green above, pale beneath, loosely reticulate-veined, obtuse or retuse at the apex, obliquely narrowed at the base; peduncles axillary, puberulent above, 5-11 cm. long; flowers short-racemose; pedicels puberulent, 4-6 mm. long; calyx narrowly campanulate, 4-5 mm. long, narrowed to the base, puberulent, its teeth ovate, 1 mm. long; corolla 7-8 mm. long, campanulate-funnelform, pubescent, its lobes oblong-ovate, ciliate; stamens 1.5-2 cm. long, the filaments united about one-fourth their length; pod coiled, 6-8 cm. long, 8-10 mm. wide, more or less constricted between the seeds; seeds blue and white, shining, orbicular, 4 mm. broad, the funicle slender.

Provinces of Havana, Pinar del Rio and Camagüey. Type from Batabano, April 10, 1903 (*Shafer 161*); apparently the same species at Old Kerr's Point, Abaco, Bahamas (*Brace 2017*).

#### 8. *Pithecolobium truncatum* sp. nov.

A tree up to 12 m. high, the bark rough, the young twigs and leaves brownish-puberulent, the old foliage glabrous. Leaves 15 cm. long or less; petiole stout, 1-2 cm. long; glands oblong-orbicular; pinnae 1 or 2 pairs; leaflets 3 or 4 pairs (on leaves of shoots 1 or 2 pairs), obovate, coriaceous, 1.5-4 cm. long (those of shoots larger and suborbicular), obtuse at the apex, narrowed at the base, pinnately veined; peduncles axillary, 4-9 cm. long; flowers short-racemose; pedicels stout, puberulent, about 2 mm. long; calyx broadly campanulate, puberulent, coriaceous, 3 mm. long, the limb truncate, the teeth minute, mucronate; corolla finely pubescent, its tube 5-6 mm. long, its lobes 3 mm. long, lanceolate, acute; stamens about 2.5 cm. long, the filaments united about one-fourth their length; pod curved to a nearly complete circle, 6 or 7 cm. long, 8-10 mm. wide, scarcely or not at all constricted between the seeds; seeds blue and white, somewhat compressed, obovate, shining, 4 or 5 mm. long.

Southern Oriente. Type from gravelly hills, El Cobre, west of Santiago, March 23, 1912 (*Britton, Cowell & Shafer 12874*).

9. *PITHECOLOBIUM OBOVALE* (A. Rich.) C. Wright; Sauvalle,  
*Anales Acad. Habana* 5: 407. 1868  
*Inga obovalis* A. Rich. *Ess. Fl. Cub.* 1: 472. 1845.  
*Calliandra revoluta* Griseb. *Cat. Pl. Cub.* 83. 1866.



Leaflets mostly broadly obovate; stamen tube very short; pod flat, curved in a partly complete circle.

Hillsides and river banks. Pinar del Rio and Isle of Pines.

10. *Pithecolobium pinetorum* sp. nov.

A tree up to 10 m. high, the young twigs and leaves puberulent, the old foliage nearly or quite glabrous. Leaves 2 dm. long or less; petioles stout, 1.5–3 cm. long; glands oblong, somewhat elevated; pinnae 1 or 2 pairs; leaflets 3 or 4 pairs, coriaceous, oblong or obovate-oblong, pinnately and loosely reticulate-veined, rounded at the apex, narrowed or obtuse at the base, 3–6 cm. long; peduncles axillary, 3–6 cm. long; calyx coriaceous, campanulate, 5 mm. long, its teeth broadly obovate, rounded, somewhat unequal; corolla pubescent, its tube about 6 mm. long, its lobes 3 mm. long, ovate-lanceolate, acute; stamens 2–2.5 cm. long, united about one-fourth their length; pod curved into a nearly complete circle, about 7 cm. long, 12 mm. wide, flat, not constricted between the seeds; seeds blue and white, shining, orbicular-obovate, 5–6 mm. long.

Mountain pinelands of northern Oriente. Type from southeast of Paso Estancia, May 1–2, 1909 (*Shafer 1725*); fruit and seeds described from *Shafer 3096*, collected in pinelands of Sierra Nipe.

11. *Pithecolobium nipense* sp. nov.

A shrub or a tree up to 10 m. high, the young twigs, petioles and rachises permanently short-pubescent. Leaves 4–6 cm. long; petioles 6 mm. long or less; glands circular, elevated; pinnae 3 or 4 pairs; leaflets 10–16 pairs, oblong, coriaceous, approximate, 2–3 mm. long, 1.5 mm. wide, slightly inequilateral, obtuse at the apex, rounded or subtruncate at base, glabrous, dark green and lustrous above, pale and dull green beneath with the midvein prominent, glabrous or with a few scattered hairs; flowers unknown; pod curved into a partly complete circle, 6–10 cm. long, 7–8 mm. wide, compressed, glabrous, short-stipitate, not constricted between the seeds, or occasionally constricted; seeds blue, shining, oblong-obovate to obovate-orbicular, 6 mm. long.

Mountains of northern Oriente. Type from near Woodfred, Sierra Nipe, 450–550 m. altitude, Dec. 20, 1909 (*Shafer 3220*).

12. *PITHECOLOBIUM ASPLENIFOLIUM* Griseb. Cat. Pl. Cub. 83.

1866

Western Cuba. Known only from the type collection of *C. Wright 2403*.



13. *Pithecolobium trinitense* sp. nov.

A tree up to 10 m. high; young twigs, petioles and rachises densely brown-puberulent. Leaves 10–15 cm. long; glands circular, 1 mm. in diameter; petioles 1.5 cm. long or less; pinnae 6–8 pairs, approximate; leaflets 12–16 pairs on each pinna, oblong, chartaceous, slightly inequilateral, 5–7 mm. long, 3 mm. wide or less, rounded at the apex, obliquely obtuse at the base, glabrous or nearly so and dark green above, pale, and pubescent beneath, at least on the veins, the midvein prominent; peduncles densely puberulent when young, glabrous when old; young flower-heads densely puberulent; flowers unknown, apparently capitate; pod curved into a nearly complete circle, about 6 cm. long and 7 mm. wide, somewhat constricted between the seeds; seeds blue, shining, orbicular-obovoid, somewhat compressed, 5 mm. long.

Hillside, El Porvenir to Aguacate, Trinidad Mountains, Santa Clara, at 700–900 m. altitude, March 10, 1910 (*Britton & Wilson 5346, type*).

14. *Pithecolobium* (?) *guantanamense* sp. nov.

A tree, 10 m. high with flexuous twigs, the foliage sparingly villous-pubescent. Leaves 6–8 cm. long, petioles slender, 1 cm. long or less; glands scutellate, 0.5 mm. in diameter; pinnae 2 pairs; leaflets 20 pairs or fewer, linear, chartaceous, 5–7 mm. long, 1–1.5 mm. wide, inequilateral, pale green but somewhat darker above than beneath, acute at the apex, obliquely obtuse at the base, the few veins prominent beneath; flowers unknown; pod compressed, glabrous, chartaceous, dehiscent, doubly coiled, 6–8 cm. long, 7–8 mm. broad over the seeds, constricted between them, the coils about 2 cm. broad; immature seeds suborbicular, somewhat flattened, 4 mm. in greatest diameter.

Bank of a water course, United States Naval Station, Guantánamo Bay, Oriente, March, 1909 (*Britton 2051*).

15. *PITHECOLOBIUM ARBOREUM* (L.) Urban, *Symb. Ant.* 2: 259. 1900

*Mimosa arborea* L. *Sp. Pl.* 519. 1753.

*Pithecolobium filicifolium* Benth. in *Hook. Lond. Journ. Bot.* 3: 205. 1844.

? *Mimosa filicifolia* Lam. *Encycl.* 1: 13. 1783.

Hillsides, river-banks and woodlands at lower and middle elevations, ascending, in Oriente, to at least 330 m.; all provinces



and Isle of Pines; Hispaniola; Porto Rico; Jamaica; Mexico and Central America.

16. PITHECOLOBIUM SAMAN (Jacq.) Benth. Lond. Journ. Bot. 3:  
216. 1844

*Mimosa Saman* Jacq. Fragm. 15. 1809.

*Calliandra Saman* Griseb. Fl. Br. W. I. 225. 1860.

Hillsides and pastures; all provinces and Isle of Pines: widely distributed in the West Indies. Native of continental tropical America. Not a true *Pithecolobium*. Perhaps referable to *Zygia* [P. Br.] J. St. Hil. Exp. Fam. Nat. 2: 246. 1805. The type of *Zygia*, which has long priority of publication over *Pithecolobium*, is *Z. arborescens* J. St. Hil., which is the same as *Pithecolobium latifolium* (L.) Benth.

17. PITHECOLOBIUM BERTERIANUM (Balbis) Benth. Lond. Journ.  
Bot. 3: 220. 1844

*Acacia Berteriana* Balbis; DC. Prodr. 2: 470. 1825.

Hillsides and woodlands in dry districts. Oriente, Camagüey, Santa Clara; Hispaniola; Jamaica.

Not a true *Pithecolobium*.

18. PITHECOLOBIUM TORTUM Mart. Herb. Fl. Bras. 114. 1837

*Pithecolobium vincentis* Benth. Lond. Journ. Bot. 3: 222. 1844.

*Acacia lentiscifolia* A. Rich. Ess. Fl. Cub. 469. 1845.

Sand dunes, sandy river-banks, coastal thickets and hillsides near the coast, Santa Clara, Havana, Pinar del Rio, Isle of Pines; St. Vincent; Martinique; Central and South America.

Not a true *Pithecolobium*.

19. PITHECOLOBIUM PREHENSILE (C. Wright) Benth. Trans. Linn.  
Soc. 30: 593. 1875

*Calliandra prehensilis* C. Wright; Sauvalle, Anales Acad. Habana  
5: 406. 1868.

Rocky river-banks, coastal thickets and saline plains, Oriente; Santa Clara. Endemic.

Perhaps a congener of *P. brevifolium* Benth., the type of the genus *Havardia* Small.



## 25. FURTHER NOTES ON COMOCLADIA\*

## 1. COMOCLADIA PINNATIFOLIA L. Syst. ed. 10, 861. 1759

Professor Urban has pointed out to me that Linnaeus, who printed the specific name *pinnatif.*, more likely intended this contraction to mean *pinnatifolia* than *pinnatifida*, as I printed it, following the Kew Index.

## 12. COMOCLADIA PLATYPHYLLA A. Rich.

The species ranges westward in Cuba into the province of Pinar del Rio as far as Corrientes Bay (*Britton & Cowell 9914*).

14. *Comocladia cuneata* nom. nov.

*Comocladia acuminata* Britton, Bull. Torrey Club 37: 349. 1910.

Not *C. acuminata* Moc. & Sessé; DC. Prodr. 2: 65. 1825.

Known hitherto only from the type specimen, this species has recently been collected by Rose, Fitch and Russell (4185) at San Pedro de Macoris, Santo Domingo. The broadly cuneate leaf-bases distinguish it from its relatives.

## 15. COMOCLADIA GLABRA Spreng.

In Flora Portoricensis, Professor Urban refers to this species, the *C. acuminata* Moc. & Sessé, as a variety, and states that it is Porto Rican, rather than Mexican as supposed by DeCandolle.

18. COMOCLADIA DODONAEA (L.) Urban, Symb. Ant. 4: 360.  
15 My 1910; Britton, Bull. Torrey Club 37: 351. 29 J1 1910

The species extends eastward in the Virgin Islands to Tortola (*Britton & Shafer 902*).

## 26. ANOTHER WEST INDIAN DENDROPANAX

*Dendropanax filipes* sp. nov.

A slender, straggling shrub up to 3 m. high. Leaves oblong-ob lanceolate, thin-coriaceous, 12 cm. long or less, 1-3 cm. wide, rather strongly pinnately veined, acutish at the apex, obtuse or acute at the base, the petioles 2-25 mm. long; peduncle very slender, bracted at the base, apparently nodding, 10 cm. long or

\* See Bull. Torrey Club 37: 345-363. 1910.



less; umbel about 12-flowered; pedicels filiform, 8–15 mm. long; flowering calyx only 1.5 mm. high and broad, broadly obconic; petals 1.5–2 mm. long, oblong-lanceolate.

Peckham woods, Upper Clarendon, Jamaica, at about 800 meters elevation, May 22, 1912, *Harris 11057*.

Among the species discussed by me in 1912,\* this most nearly resembles the Cuban *D. cuneifolium*.

## 27. THREE UNDESCRIBED BOURRERIAS†

### *Bourreria mucronata* sp. nov.

A divaricately branched shrub 2 m. high, with very slender branches, the young twigs and branches of the inflorescence appressed-pubescent. Leaves elliptic, 1–3 cm. long, 8–15 mm. wide, coriaceous, acute and mucronate at the apex, narrowed at the base, revolute-margined, reticulate-veined, strongly tuberculate-roughened, shining, and when young hispid above, dull and smooth beneath, the midvein impressed above, prominent beneath, the lateral veins about 5 on each side, the petioles 2–3 mm. long, pubescent when young; inflorescence 3–6-flowered; calyx, in bud, oblong, 3 mm. long, glabrous; corolla unknown; fruiting calyx 3 mm. long, its lobes acutish or obtuse; drupe ovoid-spherical, pointed, 5 mm. long.

Limestone cliff, San Diego de los Baños, Pinar del Rio, Cuba, (*Britton, Earle & Gager 6791*), Sept. 1910. Probably nearest related to *B. setoso-hispida* O. E. Schulz.

### *Bourreria moaensis* sp. nov.

A slender shrub or tree up to 3.3 m. high, glabrous throughout. Leaves obovate or broadly oblanceolate, 10 cm. long or less, 2.5–4.5 cm. wide, coriaceous, revolute-margined, acute or acutish, at the apex, narrowed at the base, the midvein impressed above, prominent beneath, the lateral veins about 6 on each side of the midvein, the petiole stout, only 2–4 mm. long; flowers unknown; fruiting inflorescence stalked, 4 cm. broad or less, 6–8 cm. long, its branches stout; fruiting calyx about 13 mm. long, its ovate acute lobes about as long as the tube; fruit subglobose, 12 mm. in diameter.

Camp La Gloria, south of Sierra Moa, Oriente (*Shafer 8182*), Dec. 24–30, 1910.

\* Bull. Torrey Club 39: 1–14.

† See O. E. Schulz in Urban, Symb. Ant. 7: 45–71; 349.



Apparently nearest related to *B. grandiflora* (Poir.) Griseb., which has smaller, obtuse leaves with much narrower petioles.

***Bourreria Nashii* sp. nov.**

A shrub, about 1 m. high, the young twigs pilose. Leaves obovate to oblong-obovate, 18 mm. long or less, 4-7 mm. wide, coriaceous, revolute-margined, densely rough-papillose and inconspicuously veined above, canescent, reticulate-veined and the midrib prominent beneath, obtuse, retuse or apiculate at the apex, narrowed at the base, the margin papillose-hispid, the pubescent petiole about 1 mm. long; fruits solitary or 2 together, orange-brown, terminal, subsessile, depressed-globose, about 6 mm. in diameter, persistent calyx-lobes ovate-lanceolate, acute, loosely pubescent.

Foothills, between Marmelade and San Michel, Haiti, Aug. 4, 1905 (*Nash & Taylor 1380*).

Nearest related to the Cuban *B. pauciflora* O. E. Schulz.

28. NOTES ON PSYCHOTRIA\*

PSYCHOTRIA LIGUSTRIFOLIA (Northr.) Millsp. Field Col. Mus. 2:  
172. 1906

To the range of this species may now be added BERMUDA, where it is locally abundant, and hitherto referred to *P. undata* Jacq.; FLORIDA: Key Largo (*Curtiss 5501*); CUBA; on coral-rock, Madruga (*Britton & Shafer 776*).

PSYCHOTRIA SULZNERI Small, Fl. Miami 176. 26 Ap 1913  
*Psychotria pulverulenta* Urban, Symb. Ant. 7: 456. 15 Au 1913.

29. NOTES ON VARIOUS SPECIES

JUNIPERUS LUCAYANA Britton, N. A. Trees 121. 1908  
*Juniperus australis* Pilger, in Urban, Symb. Ant. 7: 479. 1913.  
The types of both are from the Bahamas.

THRINAX MICROCARPA Sargent, Gard. & For. 9: 162. 1896  
Western part of Cayo Cruz, Camagüey, Cuba (*Shafer 2800*).  
Not heretofore recorded from Cuba:—South Florida; Bahamas.

\* See Urban, Symb. Ant. 7: 433-477.



MAYTENUS PHYLLANTHOIDES Benth. Bot. Sulph. 54. 1844

Cayo Coco, Cayo Sabinal and Cayo Romano, Camagüey, Cuba (*Shafer 1062, 2507, 2633, 2678*). Not heretofore recorded from Cuba:—Southern Florida; Mexico and Lower California.

CROTON NUMMULARIAEFOLIUS A. Rich. in Sagra, Hist. Cub. 11: 211. 1850

Rocky coastal thicket, Guanica, Porto Rico (*Britton & Shafer 1911*). New to Porto Rico; Cuba.

ACALYPHA ALOPECUROIDEA Jacq. Obs. 3: 196. 1789

Palo Seco, Porto Rico (*Brother Hioram, Oct. 1912*). New to Porto Rico:—Bahamas, Cuba, Hispaniola, Jamaica, Grenada.

CALLICARPA HITCHCOCKII Millsp. Field Col. Mus. Bot. 2: 312. 1909

Alto del Aji, Cayo Romano, Camagüey (*Shafer 2791*). Not previously recorded from Cuba:—Bahamas.

CLERODENDRON (?) CALCICOLA Britton, Bull. Torrey Club 39: 9. 1912

The habitat of this plant, omitted at the place of publication, is limestone rocks, Corrientes Bay, Cuba (*Britton & Cowell 9871*).

LYCIUM CAROLINIANUM Walt. Fl. Car. 84. 1788

Rio Gavelan, Santa Clara (*Britton, Earle & Wilson 6027*) and on Cayo Romano, Camagüey, Cuba (*Shafer 2632*). Not heretofore recorded from Cuba:—Southeastern United States.

STENOSTOMUM MYRTIFOLIUM Griseb. Fl. Br. W. I. 334. 1860

Western part of Cayo Cruz, Camagüey, Cuba (*Shafer 2798*). Not previously reported from Cuba:—Bahamas.

ERNODEA LITTORALIS Sw. Prodr. 29. 1788

In my discussion, in 1908, of the species and races of the genus *Ernodea* Sw. (Bull. Torrey Club 35: 203–208) I remarked that no species had been found in Cuba, but I can now record the typical race of *E. littoralis* Sw. as occurring between Punta Sol and



Molinas, Nipe Bay, Oriente (*Shafer 1794*), and also on Cayo Romano, Camagüey (*Shafer 2621*).

SPERMACOCE KEYENSE Small, *Flora Florida Keys* 141. 11 Au 1913

*Spermacoce floridana* Urban, *Symb. Ant.* 7: 550. 15 Au 1913.

From the printed dates of publication, Dr. Small has four days priority.

ACANTHOSPERMUM HISPIDUM DC. *Prodr.* 5: 522. 1836

Island of Culebrita, Porto Rico (*Britton & Wheeler 280*).

### 30. ASTER IN THE WEST INDIES

Scapose, the scapes monocephalous; leaves rosulate, linear-oblong, pilose.

1. *A. Grisebachii*.

Caulescent, branched, polycephalous.

Rays large, surpassing the involucre.

Leaves, except the basal ones, reduced to small imbricated scales; rootstocks tuberous.

2. *A. adnatus*.

Leaves normal, the upper often small, but distant.

Involucre-bracts densely pubescent, acuminate; inflorescence wand-like; rootstocks tuberous.

3. *A. lucayanus*.

Involucre-bracts glabrous or nearly so, or puberulent; inflorescence paniculate; rootstocks not tuberous.

Not fleshy, or but slightly so, at least the lower leaves flat, linear to spatulate.

Involucre-bracts acuminate, glabrous.

4. *A. bahamensis*.

Involucre-bracts obtuse or merely acutish.

Very densely leafy; involucre-bracts puberulent; rays white.

5. *A. Burgessii*.

Not densely leafy; involucre-bracts glabrous.

6. *A. dumosus*.

Fleshy; leaves all narrowly linear, thick, subterete.

7. *A. Bracei*.

Rays small, little if at all surpassing the involucre.

Stem-leaves lancolate, 6-12 cm. long, 2 cm. wide or less.

8. *A. inconspicuus*.

Stem-leaves linear to linear-oblong.

Stem-leaves elongated-linear; involucre-bracts acuminate.

9. *A. exilis*.

Stem-leaves oblong-linear; involucre-bracts acute.

10. *A. squamatus*.



1. *Aster Grisebachii* Britton, nom. nov.

*Haplopappus marginatus* Griseb. Cat. Pl. Cub. 149. 1866. Not  
*Aster marginatus* H.B.K.

Sandy and gravelly pine-lands, Pinar del Rio and Isle of Pines,  
Cuba.

A species with solitary heads on long, sparingly bracted scapes,  
the rootstocks much-branched, the rosulate linear-oblong leaves  
pilose, the rays bright white.

2. *ASTER ADNATUS* Nutt. Jour. Acad. Nat. Sci. Phila. 7: 82.  
1834

Pine-lands, Great Bahama Island; southeastern United States.

3. *ASTER LUCAYANUS* Britton, Bull. N. Y. Bot. Gard. 4: 143-  
1906

Pine-lands, Great Bahama Island.

4. *Aster bahamensis* Britton, sp. nov.

Stout, fibrous-rooted, slightly fleshy, glabrous, 3-20 dm. high.  
Lower leaves and those of sterile shoots with sheathing petioles  
4-7 cm. long, the blades oblong to linear-oblong or oblong-lanceo-  
late, obtuse or acute, 4-8 cm. long, 5-20 mm. wide, sparingly  
crenate-dentate or entire, narrowed into the petiole, the midvein  
prominent, the lateral veins obscure; upper stem-leaves linear,  
entire, 6 cm. long or less, those of the branches nearly subulate,  
3-12 mm. long; heads numerous, paniculate; involucre nearly  
cylindric, 6-8 mm. high, its bracts linear, acuminate, about 0.7  
mm. wide, green with scarious margins, or the inner merely green-  
tipped; rays purple, 4-5 mm. long; achenes columnar, 2.5 mm.  
long, the angles roughened; pappus brownish, twice as long as the  
achene.

Moist grounds and marshes, Great Bahama, Andros, Eleuthera  
and Cat Island. Type from Barnett's Point, Great Bahama  
(*Britton & Millspaugh 2621*).

5. *Aster Burgessii* Britton, sp. nov.

Rootstock short, thick. Stems clustered or solitary, densely  
leafy, often with many short branches, pubescent, at least above,  
5 dm. high, or less. Lower and basal leaves oblanceolate or  
spatulate, obtuse or acutish, distantly low-serrate, 2-5 cm. long,



6 mm. wide or less, narrowed into slender, ciliate, partly clasping petioles, otherwise glabrous; stem-leaves similar, but narrower and sessile or nearly so, those of the branches 4-10 mm. long; heads numerous, thyrsoïd-corymbose; involucre about 5 mm. high, its bracts in about 4 series, linear, ciliolate or glabrous, obtuse or acutish; rays white, 5-8 mm. long.

Rocky river-banks, Pinar del Rio, Cuba. Type collected on Rio Portales, near Guane, March, 1911 (*Britton, Britton & Cowell 9751*). Erroneously recorded by Grisebach as *Aster carneus* Nees.

6. ASTER DUMOSUS L. Sp. Pl. 873. 1753

Pinelands, high mountains of Santo Domingo; eastern United States.

7. ASTER BRACEI Britton; Small, Fl. Miami 190. 1913

Brackish marshes and savannas, southern Florida, Bahamas, Cuba.

8. ASTER INCONSPICUUS Less. Linnaea 5: 143. 1830

*Erigeron expansus* Poepp.; Spreng. Syst. 3: 518. 1826. Not *Aster expansus* Nees.

Marshes, ditches and roadsides at lower and middle elevations: Cuba; Jamaica; South Florida; Mexico.

9. ASTER EXILIS Ell. Bot. S. C. & Ga. 2: 344. 1824

Wet grounds, provinces of Santa Clara, Havana and Pinar del Rio, Cuba; Andros Island, Bahamas; southeastern and southern United States.

10. ASTER SQUAMATUS (Spreng.) Hieron. Bot. Jahrb. 29: 19. 1901

*Conyza squamata* Spreng. Syst. 3: 515. 1826.

Naturalized along roadsides, especially on Ireland Island and Boaz Island, Bermuda. The plant erroneously listed by Lefroy as *Aster Trifolium* L., was probably this species, misprinted for *A. tripolium* L. Native of southern South America.



## 31. UNDESCRIBED SPECIES OF JAMAICA

**Lasiocroton Harrisii** sp. nov.

A tree, about 8 m. high, the stout twigs densely brown-tomentose when young, bearing prominent leaf-scars. Leaves oblong-elliptic, rather firm in texture, 8-15 cm. long, 7 cm. wide or less, sharply acuminate at the apex, narrowed at the base, sparingly pubescent above, densely pubescent beneath, yellowish-green, somewhat paler beneath than above, pinnately veined, with about 5 veins on each side of the midvein, the margin entire or slightly undulate, the stout, tomentose petioles 10-16 mm. long; fruiting racemes slender, tomentose, equalling the leaves or longer, the slender tomentose pedicels 10-15 mm. long; fruiting calyx tomentose, 4 mm. broad, the sepals ovate, acute; capsule obtusely 3-lobed, 7 mm. broad, 3-4 mm. high, densely brown-tomentose; styles 2 mm. long; stigmas fimbriate; seeds subglobose, 2.5 mm. in diameter.

Peckham woods, Upper Clarendon, Jamaica, September 9, 1912 (*Harris 11192*).

*L. Farwettii* Urban, of Dolphin Head Mountain, Jamaica, differs in having nearly glabrous long-petioled leaves.

**Varronia clarendonensis** sp. nov.

A slender shrub with weak straggling branches, the twigs loosely pilose. Leaves broadly ovate-elliptic, 5-10 cm. long, 3-7 cm. wide, firm-chartaceous in texture, rather strongly pinnately veined, coarsely and sharply dentate, obtuse at the apex, obtuse or subtruncate at the base, loosely pilose beneath, scabrous-pubescent and papillose above, the loosely villous petioles 1.5 cm. long or less; peduncles slender, pilose, 5-8 cm. long; heads globose, densely many-flowered, 2 cm. in diameter; calyx brown-pilose above, its tube about 4 mm. long, its lobes triangular-ovate with linear, pilose, curled tips 5-6 mm. long; corolla about 9 mm. long, its lobes short and broad; stamens about equalling the corolla; filaments filiform; anthers oblong.

Peckham woods, Upper Clarendon, Jamaica, July 7, 1911 (*Harris 10995*).

**Jacobinia** (?) *jamaicensis* sp. nov.

Stem stout, 3-6 dm. high, densely long-villous. Leaves lanceolate to ovate-lanceolate, 6-10 cm. long, 1.5-3 cm. wide, rather firm in texture, densely villous-pubescent on both sides, acuminate at the apex, narrowed to an obtuse base, with villous



petioles 2-4 mm. long; spike terminal, few-flowered; bracts lanceolate, acuminate, villous, about 1.5 cm. long; calyx-teeth narrowly lanceolate, loosely villous; corolla rose-colored, 3.5 cm. long, loosely villous, 2-lipped, the teeth of the lobes short and rounded; filaments slender, nearly as long as the corolla, glabrous; anthers 2.5 mm. long.

Crevices of limestone rocks, Peckham woods, Upper Clarendon, Jamaica (*Harris 10978, type; 11178*).

### 32. UNDESCRIBED CUBAN SPECIES

#### *Copernicia rigida* Britton & Wilson, sp. nov.

A tree up to 6 m. high, with a slender cylindrical trunk. Leaf-blades wedge-shape, 13-15 dm. long, deeply grooved below the middle, bright green above, paler beneath and sometimes armed on the margins of the grooves with small, straight or recurved teeth 1-4 mm. long; leaf margins armed mostly below the middle with numerous recurved, straight, ascending, or sometimes hooked teeth 3-7 mm. long; petiole short, stout, 1-1.5 dm. long, 1-1.4 dm. broad, unarmed; ligule rigid, rhombic-ovate, 2.5-3.5 dm. long, 1.7-2 dm. broad, armed on the margin with ascending, recurved, straight or sometimes hooked teeth 3-12 mm. long, coalescent with and decurrent on the short petiole; inflorescence lax, branches slender, the ultimate ones densely clothed with short hairs; spathes of the inflorescence abruptly tapering to a long, slender acuminate tip; flowers unknown; fruit subglobose, 1.5-1.6 mm. long, 1.4-1.6 mm. broad, brown, shining; old calyx persistent beneath the fruit, the lobes triangular; seed subglobose, 9-11 mm. long.

Type collected in the vicinity of Tiffin, Camagüey, Cuba, November 1-5, 1909 (*Shafer 2895*); also collected at Santa Lucea, Camagüey (*Shafer 971*); Province of Santa Clara (*Britton & Wilson 4563; Britton, Cowell & Earle 10299*).

#### *Copernicia Cowellii* Britton & Wilson, sp. nov.

A small tree, up to 3 m. high, the head globose, about 1 m. in diameter, very dense, the trunk up to 1.7 dm. thick, strictly cylindrical. Leaves many, the blades shining, yellow-green above, covered with a bright white waxy bloom beneath, about 6 dm. long, somewhat wider than long, the younger erect, the older persistent, reflexed; petioles white-waxy, 1 dm. long or less, 3-5 cm. wide, flattened, armed with irregular, curved and somewhat hooked teeth 5-8 mm. long; margins of the leaves with many



recurved teeth 2-3 mm. long, the leaf otherwise unarmed; inflorescence lax, the branches slender, densely clothed with short hairs; spathes of the inflorescence gradually tapering to long acuminate tips; calyx cylindrical, 3-3.5 mm. high, the lobes strongly mucronate; corolla 5-6 mm. long, densely clothed with short, mostly appressed hairs on the outer surface, the lobes prominently grooved within below the middle, the grooves hairy on the margin, longitudinally converging and bearded above; dilated portion of the filaments prominently triangular; carpels truncate at the summit, grooved; styles nearly cylindrical; fruiting panicles about twice as long as the leaves, pendent, glabrous, much-branched, slender, the stalk about as long as the fruit-bearing part; sheath closely appressed, the lower up to 1 dm. long; fruits close together on the ultimate branches of the panicle, subglobose, obovoid, a little longer than thick, yellow when full-grown but not quite ripe, shining, 14-17 mm. long; old calyx-segments persistent under the fruit, triangular-ovate, acute, 2 mm. long; flesh of old ripe fruit very thin; seed smooth, about 12 mm. long; endosperm bony, grooved.

Seedlings have rough-edged leaves green on both sides.

Type collected in savannas near Camagüey, Cuba, April 2-7, 1912 (*Britton, Britton & Cowell 13187*); also collected in the province of Camagüey (*Shafer 508, 1144, 2917*).

#### *Anneslia enervis* sp. nov.

A shrub or small tree 4 m. high, with slender, stiff, somewhat zigzag twigs sparingly pubescent when young, soon glabrous. Leaves very small; pinnae 2, the petiole and petiolules each about 1 mm. long, rather stout; pinnules 2 to each pinna, 2-3 mm. long, obovate, sessile, nerveless, shining, rounded at the apex, oblique at the base; heads nearly sessile in the upper axils, few-flowered; calyx campanulate, 1.5 mm. long, its teeth acute; corolla about 3 mm. long; stamens 6-7 mm. long; legume glabrous, 3-4 cm. long, 5 mm. wide, abruptly tipped at the apex, narrowed from below the middle to the base, the valves subcoriaceous.

Mountains of northern Oriente, Cuba; type from Camp La Gloria, south of Sierra Moa, *Shafer 8274*, December, 1910.

Not closely related to any species known to me, but somewhat resembling *A. collettioides* (Griseb.) Britton [*Calliandra collettioides* Griseb.] of low elevations in dry parts of the same province.



**Belairia parvifoliola** sp. nov.

A slender tree, up to 10 m. high, the twigs copiously armed with dark brown to black subulate spines 1.5-3 cm. long. Leaves short-petioled, the slender rachis puberulent or short-pubescent; leaflets 7-13, oblong to oblong-lanceolate, shining, nearly equally bright green and rather prominently veined on both sides, 8-13 mm. long, 2-3 mm. wide, the base inequilateral, the apex mucronate, the petiolules 0.5 mm. long; legume narrowly oblong, 10-12 mm. long, 3-4.5 mm. wide, narrowed at base and apex, strongly veined, borne on a filiform pedicel 6 mm. long or more.

Coastal woods, thickets and hillsides, southern Oriente, from Guantanamo Bay to Ensenada de Mora. Type, *Britton, Cowell & Shafer 13037*, Ensenada de Mora, March, 1912.

**Meibomia Cowellii** sp. nov.

Root thick and woody; stem slender, stiff, erect, hirsute, 3-8 dm. high, simple, or with few nearly erect hirsute branches. Leaves unifoliolate, short-petioled, oblong, linear-oblong or lanceolate, subcoriaceous, 2-10 cm. long, 2.5 cm. wide or less, obtuse and mucronulate at the apex, obtuse at the base, rather strongly reticulate-veined, finely short-pubescent above, villous-pubescent on the veins beneath, nearly equally green on both sides, the rather stout petioles 2-10 mm. long, the stipules lanceolate, striate, acuminate, 2-4 mm. long, the stipels subulate, about 3 mm. long; panicle narrow, nearly simple, long-stalked, 1-3 dm. long; bracts linear-subulate, 2.5-4 mm. long; pedicels filiform, puberulent, 4-7 mm. long; calyx 2.5-3 mm. long, campanulate, pubescent, lobed to about the middle, the lobes lanceolate, acute; corolla purple, 10 mm. broad; loment short-stipitate, 4-6-jointed, 2 cm. long or less, nearly equally constricted on both margins, the joints oval, about 4 mm. long and 2.5 mm. broad, loosely pubescent, indistinctly reticulate-veined.

Savannas and pine-lands, Pinar del Rio and Isle of Pines, Cuba. Type, *Britton, Britton & Cowell 10090*, from between Pinar del Rio and Coloma, March 16, 1911. Related to *M. angustifolia* (H.B.K.) Kuntze.

**Kieseria cubensis** sp. nov.

A tree, up to 13 m. high, the twigs stout, densely leafy toward the ends. Leaves coriaceous, oblong-obovate, 6-10 cm. long, 3 cm. wide or less, obtuse and rounded or somewhat emarginate at the apex, narrowed to the nearly sessile base; midvein impressed



above, rather prominent beneath, the lateral veins obscure; peduncles solitary in the upper axils, stout, ancipital, 3-5 cm. long, 2-bracted at the top; bracts oblong, obtuse, about 1 cm. long; fruiting pedicels stout, subterete, 1-2.5 cm. long; sepals narrowly oblong, obtuse, 1.5 cm. long, entire; capsule about as long as the sepals, tapering into a stout-subulate beak about 6 mm. long.

Mountains of northern Oriente, Cuba. Type, *Shafer 8121*, from Camp La Gloria, south of Sierra Moa, December 1910. The genus is hitherto known only from South America. The Cuban species most resembles *Bonnetia anceps* Mart., of Brazil. The generic name *Kieseria* Nees, has priority over *Bonnetia* Mart., which is a homonym of *Bonnetia* Schreb.

### 33. A HYBRID PALM

On the sterile "savannas" north and east of Camagüey, Cuba, palms of two species of *Copernicia* abound. The one, *C. hospita*, has grey-green, thin foliage with spiny-toothed petioles about as long as the blades, and elongated, slender panicles; the other, *C. macroglossa*, has bright green, rigid foliage with very short, broad, unarmed petioles, the blades spiny-toothed on the margins of the outermost segments and on the upper surface of the ribs of the undivided part, the stout panicles not much longer than the leaves and the inflorescence with large bracts.

Of the two, *C. hospita* is the more abundant, *C. macroglossa* growing in colonies, more or less surrounded by it. At many places where the two grow together, plants intermediate in foliage characters occur, their leaves with spiny-toothed petioles of various lengths, the blades with sparingly spiny-toothed margins, otherwise smooth, and in color varying from green to grey, the panicles short and the inflorescence lacking the characteristic large bracts of *C. macroglossa*.

Field observations during four days with Mr. John F. Cowell, led us to the conclusion that these intermediate plants are of hybrid origin rather than a third species, as was first suggested.



## 34. PORTLANDIA [P. BR.] L., IN THE WEST INDIES

The type species is *Portlandia grandiflora* L.

1. Leaves cordate or subcordate at base, sessile or nearly so.  
Capsules 1 cm. long or less.  
Leaves orbicular, 2.5 cm. wide or less; corolla yellow;  
flowers sessile or very nearly so. 1. *P. sessilifolia*.  
Leaves elliptic, 5-10 cm. long; corolla pinkish; flowers  
pedicelled. 2. *P. nitens*.  
Capsules nearly 2 cm. long. 3. *P. Harrisii*.
2. Leaves narrowed or rounded at the base, petioled.  
Leaves rounded or obtuse at the apex.  
Leaves elliptic. 4. *P. elliptica*.  
Leaves obovate or oblanceolate.  
Capsule involucrate by bractlets. 5. *P. involucreta*.  
Capsule not involucrate. 6. *P. uliginosa*.
- Leaves acute or acuminate at the apex.  
Calyx-lobes oblong to ovate. 7. *P. grandiflora*.  
Calyx-lobes linear to subulate.  
Capsule 1 cm. long or less; leaves 5-8 cm. long. 8. *P. pendula*.  
Capsule 1.5-5 cm. long; leaves 6-15 cm. long.  
Capsule scarcely angled.  
Leaves ovate to elliptic; calyx-lobes linear;  
corolla 5-7 cm. long. 9. *P. coccinea*.  
Leaves oblong-lanceolate; calyx-lobes long-  
subulate; corolla 2-2.5 dm. long. 10. *P. Lindeniana*.  
Capsule distinctly angular.  
Capsule long-stalked, truncate. 11. *P. daphnoides*.  
Capsule short-stalked, narrowed at both ends. 12. *P. domingensis*.

1. *Portlandia sessilifolia* sp. nov.

A branching resinous shrub about 1.3 m. high, the young twigs short-pubescent, angular. Leaves thick-coriaceous, orbicular, 1.5-3 cm. long, sessile, subcordate, shining above, dull beneath, very indistinctly veined, the margins thick and revolute, their bases connected by a stipular sheath; inflorescence terminal, sessile, subcapitate, several-flowered; pedicels very short; calyx about 8 mm. long, very resinous, the linear lobes about as long as the tube; corolla tubular-campanulate, yellow, 1.5 cm. long; capsule oblong-obovoid, 5-6 mm. long.

Wet mountains of northern Oriente, Cuba. Type from Camp La Gloria, south of Sierra Moa, Cuba, December, 1910 (*Shafer 8190*).

A specimen from between Rio Yamanigüey and Camp Toa (*Shafer 4180*) with much larger elliptic leaves, 11 cm. long or less, but otherwise similar, may, perhaps, be referred to this species.



2. *PORTLANDIA NITENS* Britton, Bull. Torrey Club 39: 10. 1912  
Wet mountains of northern Oriente, Cuba.

3. *PORTLANDIA HARRISII* Britton, Bull. Torrey Club 39: 8. 1912  
On limestone rocks, Peckham Woods, Upper Clarendon, Jamaica.

To the original description the following may now be added from Mr. Harris' subsequent collections and observations: Corolla white, tinged with rose, urn-shaped, about 9 cm. long and 3.5 cm. wide at the mouth, fragrant, the tips of its lobes reflexed; pedicels and calyx-lobes usually claret-colored; calyx-lobes oblong, about 1.5 cm. long and 5 mm. wide; filaments pubescent below; anthers narrowly linear, yellow, nearly 2 cm. long, about half as long as the filaments (*Harris 11209*, Sept. 28, 1912).

4. *Portlandia elliptica* sp. nov.

A slender shrub 3.3 m. high, the young twigs, pedicels and calyx finely pubescent. Leaves elliptic, coriaceous, glabrous, or when young, slightly pubescent, 8 cm. long or less, 2-4 cm. wide, obtuse or rounded at the apex, narrowed at the base, dark green and shining above, bright green and rather dull beneath, the midvein prominent, the lateral veins obscure, the stout petioles 1 cm. long or less, the stipular sheath truncate; inflorescence terminal, sessile, few-flowered; pedicels slender, 5-8 mm. long; calyx 10-12 mm. long, its linear-lanceolate lobes longer than the tube; corolla narrowly campanulate, glabrous, ochroleucous, 2 cm. long; capsule obovoid, 12 mm. long.

Thickets on serpentine rocks, between Baracoa and Florida, Oriente, Cuba, March 15, 1910 (*Shafer 4332*).

5. *PORTLANDIA INVOLUCRATA* Wernham, Jour. Bot. 51: 320. 1913  
Wet parts of northern Oriente, Cuba. As remarked by Mr. Wernham, perhaps not of this genus; the corolla is unknown.

6. *PORTLANDIA ULIGINOSA* Wernham, Jour. Bot. 51: 320. 1913  
Between Rio Yamanigüey and Camp Toa, northern Oriente, Cuba.

7. *PORTLANDIA GRANDIFLORA* L. Syst. ed. 10. 928. 1759

Thickets and hillsides at lower and middle altitudes, in moist districts, Jamaica; St. Thomas (native?); cultivated in Grenada, and in St. Croix.



8. *PORTLANDIA PENDULA* C. Wright; Griseb. Cat. Pl. Cub. 126.  
1866

Pendent on limestone cliffs, Pinar del Rio, Cuba.

A beautiful species, the pendent habit unusual, the branches sometimes drooping to a length of 2 meters or more; the flowers are fragrant.

9. *PORTLANDIA COCCINEA* Sw. Fl. Ind. Occ. 1: 384. 1797

*P. coriacea* Sw.; Spreng. Syst. 1: 708. 1825.

Thickets and hillsides at lower elevations in dry districts, southern side of Jamaica.

10. *Portlandia Lindeniana* (A. Rich.) Britton, nom. nov.

*Gonianthes Lindeniana* A. Rich. in Sagra, Hist. Cub. 11: 10. *pl.* 49  
*bis.* 1850.

*Portlandia gypsophila* Macf. Fl. Jam. 2: 216; Griseb. Fl. Br. W. I.  
324. 1861.

A tree, up to 8 meters high. Leaves chartaceous, oblong-lanceolate, pinnately veined, sharply acuminate at the apex, narrowed at the base, 12–20 cm. long, the petioles about 8 mm. long; flowers solitary in the axils; peduncles about 2 cm. long; calyx-teeth narrowly linear, 2.5–3.5 cm. long; corolla white, 2–2.5 dm. long, the narrowly campanulate limb much longer than the nearly cylindrical tube; capsule oblong-obovoid, 4–5 cm. long, 15–18 mm. thick, smooth, not angled.

Wooded river and stream-banks at lower elevations, province of Oriente, Cuba; Jamaica? Cultivated in Martinique.

11. *PORTLANDIA DAPHNOIDES* R. Graham, Edinb. N. Phil. Jour.  
1840–41: 206

*Gonianthes Sagraeana* A. Rich. in Sagra, Hist. Cub. 11: 11. 1850.

*Portlandia longiflora* Meisn.; Griseb. Cat. Pl. Cub. 126. 1866.

A shrub, about 1.3 meters high. Leaves thin, oblong, narrowed at both ends, rather dull green, pinnately veined, 7–13 cm. long, the petioles 1 cm. long or less; flowers solitary in the axils; peduncles 1–3 cm. long; calyx-lobes linear, 1.5–2 cm. long; corolla yellowish, about 2 dm. long, the campanulate limb about as long as the slender tube; capsule obpyriform, angled, truncate, 2.5–3 cm. long, slender-peduncled.



On rocks, especially along rivers and brooks, at lower and middle elevations, provinces of Oriente, Matanzas, and Pinar del Rio, Cuba.

The use of the name *P. daphnoides* for this species is taken from Graham's description, which does not agree with our specimens in all respects. I have not seen the type specimen. The shrub is abundant in the limestone hills of Pinar del Rio.

12. **Portlandia domingensis** sp. nov.

Foliage similar to that of the preceding species, but the petioles shorter, about 2 mm. long; flowers unknown; capsules short-peduncled, oblong, 5-angled, apparently somewhat fleshy, 4-4.5 cm. long, narrowed at both ends; calyx lobes linear, somewhat broadened at the base, about 1.5 cm. long.

Near San Pedro de Macoris, Santo Domingo, March 26, 1913  
(*Rose, Fitch & Russell 4176*).



## Observations on the behavior of some species at the edges of their ranges\*

ROBERT F. GRIGGS

Various writers on ecology and plant geography have spoken of the behavior of species at the edges of their ranges—of the habitats they affect, of their reproduction, and of their abundance. These statements are of course based on impressions from the experience of the authors, but there are few extensive records of detailed observations on these matters. It is clear that a knowledge of the causes which set the limits to the distribution of species is of fundamental importance to the student of plant geography and it is obvious that the termini of the ranges are the only localities favorable to the study of these conditions. But an understanding of the matter can be reached only after the collection of a large amount of detailed evidence from numerous regions. It is with the desire of contributing one detail toward such a body of evidence that the present observations are published.

The area in which these observations were made is unusually favorable for such studies since a large proportion of the native flora here reaches its territorial limits. 122 species, about 13 per cent. of the native flora, reach, so far as is now known, the limits of their ranges in one direction or another, in the Sugar Grove region. This is a narrow strip of country covering the area of maximum outcrop of a heavy sandstone, the Black Hand Conglomerate, stretching from the edge of the terminal moraine a few miles north of the town of Sugar Grove in Fairfield County, Ohio, southward to the valley of Queer Creek, east of South Bloomington, in Hocking County. The high cliffs and narrow ravines formed in the weathering of this sandstone impart a ruggedness to the country which is largely responsible for its botanical interest, providing suitable habitats for many of its rare plants and at the same time rendering the land unsuitable for agricultural purposes,

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\* Contribution from the Botanical Laboratory of the Ohio State University, no. 79.



thus in a measure insuring their preservation. It is for this reason wilder and more nearly in its aboriginal condition than the less rugged country which surrounds it. Since the time of Sullivant



FIG. 1. *Sullivantia*, south of Sugar Grove

it has been known to the botanists of Ohio as one of the richest collecting grounds in the state. The flora of the northern portion, that lying in Fairfield County, was worked up more than seventy



years ago by John M. Bigelow, an able botanist, thus affording an exceedingly interesting basis for comparison of present with past conditions.

Although the Sugar Grove area lies at the end of the long lobe of the Alleghenian Floral Area which Merriam's\* map shows stretching into northeastern Ohio, the plants which terminate here are by no means all Alleghenian but include species of varied geographical affinity stretching away from the area in all directions as was shown in a preceding paper.†

It must be pointed out at the outset that the list of plants here given as reaching their territorial limits is by no means a complete or final catalogue. From the nature of the case it will be subject to a considerable amount of revision as the flora of the country becomes better known. When the manifold sources of error which enter into the study are taken into consideration the results might almost be said to have been reached by the multiplication of uncertainties. Nevertheless it is believed that present knowledge is sufficient to justify their publication for, however much the status of individual species may be changed by later discoveries, it does not seem likely that the general outlines of the account here presented will require much readjustment. The first source of error lies in the fact that as the flora becomes better known plants which are not now known beyond the borders of this area may be found in adjoining counties, thereby being removed from the list. In view of the fact that the Sugar Grove area has been more thoroughly worked than the surrounding territory the number of these may be somewhat large. Plants new to the area may be discovered and added to the list. But probably more important than changes due to either of the above causes will be the addition of numerous species, now reported from the region, whose ranges are not yet known with sufficient accuracy to enable us to tell whether they here reach their limits or not. In this category are many groups of plants which have not been collected thoroughly enough in Ohio to justify any deductions as to their distribution. Many groups are so difficult of identification that only the deter-

\* Merriam, C. Hart. Life zones and crop zones of the United States. U. S. Dept. Agr. Biol. Survey Bull. 10. 1898.

† Griggs, Robert F. Observations on the geographical composition of the Sugar Grove Flora. Bull. Torrey Club 40: 487-499. f. 1-10. 10 S 1913.



minations of the specialist are dependable. These must be eliminated from consideration by plant geographers because no reliance can be placed on the various local lists which must form, in large measure, the basis of such work. Lastly there is a very large and at present increasing number of plants, the very specific identity of which is not yet understood. These include numerous recently recognized species and some older ones which have not been sufficiently studied. The difficulties occasioned by these deficiencies in our knowledge have limited the work very considerably and because of them I have sought to illustrate my points as far as possible with such well-known and conspicuous species as *Kalmia latifolia* and *Rhododendron maximum*, which are collected and listed by every amateur botanist.

The first question that arises concerning the behavior of a species at the edge of its range is as to its abundance. Do the individual plants become scarcer and scarcer until finally the species fails altogether, or is it common close up to the edge where it suddenly stops short? The species whose ranges terminate in the Sugar Grove area are therefore classified from this point of view in the following table.

ABUNDANCE OF SPECIES ON THE EDGES OF THEIR RANGES

*Plants common in many stations*

<i>Andropogon virginicus</i>	<i>Diospyros virginiana</i>
<i>Aralia spinosa</i> *	<i>Epigaea repens</i>
<i>Aruncus Aruncus</i>	<i>Eupatorium aromaticum</i> *
<i>Ascyron hypericoides</i> <sup>1</sup>	<i>Eupatorium coelestinum</i>
<i>Asplenium pinnatifidum</i>	<i>Eupatorium rotundifolium</i> *
<i>Aster divaricatus</i>	<i>Fraxinus quadrangulata</i> †
<i>Betula lutea</i> *	<i>Gaultheria procumbens</i>
<i>Betula nigra</i> *	<i>Hieracium paniculatum</i>
<i>Carex costellata</i>	<i>Hieracium venosum</i>
<i>Cassia nictitans</i>	<i>Hydrangea arborescens</i>
<i>Castanea dentata</i>	<i>Isopyrum biternatum</i> †
<i>Chimaphila maculata</i>	<i>Juncoides saltuensis</i>
<i>Chrysosplenium americanum</i>	<i>Kalmia latifolia</i>
<i>Circaea alpina</i> *	<i>Koellia incana</i>
<i>Cornus stolonifera</i> (abundant at Columbus at least)	<i>Lechea racemulosa</i>
<i>Cunilla originoides</i>	<i>Lycopodium lucidulum</i>
<i>Cypripedium acaule</i>	<i>Lycopodium lucidulum porophilum</i>
<i>Dasystoma laevigata</i>	<i>Lysimachia quadrifolia</i>
<i>Dentaria heterophylla</i> *	<i>Oxydendrum arborescens</i>
	<i>Panicum polyanthes</i>



<i>Pinus rigida</i>	<i>Stachys cordata</i>
<i>Pinus virginiana</i>	<i>Silene rotundifolia</i> *
<i>Pyrola elliptica</i>	<i>Solidago juncea</i>
<i>Quercus Prinus</i>	<i>Sullivantia Sullivantii</i> *
<i>Rhododendron maximum</i> ‡	<i>Trichostema dichotomum</i>
<i>Rubus odoratus</i>	<i>Tsuga canadensis</i>
<i>Salix amygdaloides</i> †	<i>Unifolium canadense</i>
<i>Sambucus pubens</i>	<i>Viola hirsutula</i>
<i>Saxifraga virginiana</i>	<i>Viola rostrata</i>
<i>Sericocarpus asteroides</i>	

## Common in few stations

<i>Asplenium montanum</i>	<i>Phacelia dubia</i> ‡
<i>Azalea lutea</i> ‡	<i>Phlox stolonifera</i>
<i>Iris cristata</i> *	<i>Quamasia hyacinthina</i> §
<i>Lobelia puberula</i>	<i>Viola rotundifolia</i> *
<i>Pedicularis lanceolata</i>	

## Individuals abundant in one station

<i>Dodocatheon Meadia</i> § ¶	<i>Melampyrum lineare</i> *
<i>Hypericum Drummondii</i> *	<i>Saxifraga pennsylvanica</i> ‡ (probably in other stations as well).

## Rather common

<i>Achroanthes unifolia</i>	<i>Isotria verticillata</i>
<i>Aster macrophyllus</i>	<i>Lobelia leptostachys</i>
<i>Anemone canadensis</i>	<i>Populus tremuloides</i>
<i>Aristida dichotoma</i>	<i>Porteranthus stipulatus</i>
<i>Capnoides sempervirens</i>	<i>Quercus minor</i> *
<i>Chrysopsis mariana</i> *	

## Scarce

<i>Aesculus octandra</i> ‡	<i>Pyrola rotundifolia</i>
<i>Aronia nigra</i>	<i>Scutellaria galericulata</i>
<i>Blephariglottis peramoena</i> *	<i>Smilax echirrata</i>
<i>Lycopodium complanatum</i> *	<i>Valeriana pauciflora</i> §
<i>Lycopodium obscurum</i>	<i>Viburnum dentatum</i>
<i>Passiflora lutea</i>	<i>Viburnum molle</i> .

## Individual plants rare and widely scattered

<i>Azalia macrophylla</i>	<i>Gymnocladus dioica</i> §    **
<i>Asclepias Sullivantii</i>	<i>Lycopodium clavatum</i>
<i>Asclepias variegata</i>	<i>Napaea dioica</i>
<i>Blephariglottis lacera</i>	<i>Parnassia caroliniana</i>
<i>Fraxinus nigra</i>	<i>Psoralea Onobrychis</i>
<i>Gentiana crinita</i>	<i>Stylosanthes biflora</i>

\* Species confined to the southern portion of the area.

† Species reaching their limits immediately to the west of the area.

‡ Species confined to the northern portion of the area.

§ Main body of range ends in Central Ohio but extends locally into Pennsylvania.

¶ Also reported from another station by Bigelow.

|| Not known south of Columbus.

\*\* Fairly common a few miles to the westward.



*Frequency of occurrence not observed*

<i>Bidens aristosa</i>	<i>Panicularia elongata</i>
<i>Eatonia nitida</i>	<i>Rynchospora glomerata</i>
<i>Panicum stipitatum</i>	<i>Solidago erecta</i>

*Plants reported by Bigelow\* but not now known in the area*

<i>Brauneria purpurea</i> .§	<i>Panicularia acutiflora</i>
<i>Cardamine rotundifolia</i>	<i>Panicularia pallida</i>
<i>Carduus virginicus</i>	<i>Trifolium reflexum</i>
<i>Cypripedium Reginae</i>	<i>Trollius laxus</i>
<i>Dasyphora fruticosa</i>	<i>Veratrum Woodii</i>
<i>Lysias orbiculata</i>	

## SUMMARY

Common in many stations.....	58
Common in few stations.....	9
Individuals abundant in one station.....	4
Rather common.....	11
Scarce.....	12
Rare.....	12
Frequency of occurrence not observed.....	6
Not now known from the area.....	11
Total.....	123

It is clear from these lists that in this region the species in which the individuals become scarcer and scarcer until it fails altogether is exceptional. In the majority the individuals are abundant in their respective stations up to the very edge of their ranges.

But one who studies the ranges of species in a broad way rather than in a restricted area, gets a decided impression that the ranges of most species are bordered by a fringe of outlying stations at considerable distances from each other. Many of the most interesting species of the Sugar Grove region are such outliers. Those which are not known elsewhere within approximately one hundred miles are listed below. It may be asserted with some confidence that some of these such as the *Rhododendron* and the *Azalea* really do not occur elsewhere within the boundaries of the state of Ohio, but some of the others have not yet been searched for enough to justify much confidence in their assignment to this category. One of the list, *Silene rotundifolia*, occurs in Jackson County only twenty-five miles south of our area but as its next known station is far beyond the borders of the state, it seems only

\*Florula Lancastricensis. Proc. Medical Convention of Ohio 1841: 49-79. Columbus, 1842.



proper to include it here. Numerous other species must be outliers separated from their nearest stations by smaller intervals, but the distribution of the Ohio flora is not yet well enough known to



FIG. 2. *Blephariglottis peramoena* in flower at Sugar Grove. Plant unusually strong, with unusually large flower clusters.

enable us to pick out these species with sufficient accuracy to justify the attempt. The list of outliers separated by the larger interval includes:



SPECIES	NEXT KNOWN STATION
<i>Achroanthes unifolia</i> . . . . .	Only Ohio Station.
<i>Aralia spinosa</i> . . . . .	Clermont Co.
<i>Asclepias Sullivantii</i> . . . . .	Erie Co.
<i>Asclepias variegata</i> . . . . .	Summit Co.
<i>Asplenium montanum</i> . . . . .	Summit Co.
<i>Azalea lutea</i> . . . . .	Only Ohio Station.
<i>Betula lutea</i> . . . . .	Wayne Co.
<i>Circaea alpina</i> . . . . .	Clarke Co. (75 miles) and Summit Co.
<i>Cypripedium acaule</i> . . . . .	Said formerly to have occurred in Licking Co. immediately to the north.* Nearest station known to me, Medina Co.
<i>Dodecatheon Meadia</i> . . . . .	Clarke Co. (75 miles).
<i>Eupatorium aromaticum</i> . . . . .	Only Ohio Station.
<i>Eupatorium rotundifolia</i> . . . . .	Only Ohio Station.
<i>Hypericum Drummondii</i> . . . . .	Clermont and Ashtabula Counties.
<i>Lycopodium clavatum</i> . . . . .	Geauga Co.
<i>Juncoides saltuensis</i> . . . . .	Mahoning Co.
<i>Melampyrum lineare</i> . . . . .	Lorain Co.
<i>Phacelia dubia</i> . . . . .	Only Ohio Station.
<i>Phlox stolonifera</i> . . . . .	Only Ohio Station.
<i>Pyrola rotundifolia</i> . . . . .	Summit Co.
<i>Polygonum arifolium</i> . . . . .	Wayne Co.
<i>Rhododendron maximum</i> . . . . .	Only Ohio Station.
<i>Silene rotundifolia</i> . . . . .	Hocking and Jackson Counties only.
<i>Sullivantia Sullivantii</i> . . . . .	Highland Co.
<i>Viola hirsutula</i> . . . . .	Only Ohio Station yet known.
<i>Viola rotundifolia</i> . . . . .	Cuyahoga Co.

There are on the other hand many species which are abundant all along the edges of their ranges. The plants in this category contrast strongly with the outliers, which are plants of diverse geographical affinity, in that they belong for the most part to two definite groups: Alleghenian plants here on the western edges of their ranges, and southern plants limited to the poor soils of the uplands. Some of them, such as *Pinus rigida*, are to be found within a few miles almost anywhere that one may choose to enter their ranges, even though the individuals may be somewhat scarce at the very edge. In some of the others the case is not so clear from collections at present available, but all those here included are known from at least three contiguous counties in our region. They are moreover plants which field experience leads me to

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\* Jones, H. L. Flora of Licking Co. Bull. Sci. Lab. Dennison University 7: 85. 1892.





FIG. 3. A small plant of *Epigaea repens* in flower at Sugar Grove

suppose common over much wider areas than is shown by the collections. This list includes:

<i>Andropogon virginicus</i>	<i>Hieracium venosum</i>
<i>Asplenium pinnatifidum</i>	<i>Kalmia latifolia</i>
<i>Aster divaricatis</i>	<i>Lycopodium lucidulum</i>
<i>Aruncus Aruncus</i>	<i>Lycopodium complanatum</i>
<i>Ascyron multicaule</i>	<i>Oxydendrum arboreum</i>
<i>Betula nigra</i>	<i>Pinus rigida</i>
<i>Castanea dentata</i>	<i>Pinus virginiana</i>
<i>Chimaphila maculata</i>	<i>Pyrola elliptica</i>
<i>Cunilla originoides</i>	<i>Quercus Prinus</i>
<i>Daystoma laevigata</i>	<i>Saxifraga virginensis</i>
<i>Epigaea repens</i>	<i>Sericocarpus asteroides</i>
<i>Eupatorium coelestinum</i>	<i>Solidago bicolor</i>
<i>Gaultheria procumbens</i>	<i>Tsuga canadensis</i>
<i>Gyrostachys gracilis</i>	

If now we attempt to determine by analysis the factors which cause the termination of the ranges, our first inquiry is naturally concerning the reproductive functions of the plants under discussion. It has been supposed, somewhat generally, that the reproductive functions of many species fail at the northern or southern edges of their ranges. The failure may occur at any one of several points in the cycle: a plant may not produce flowers in sufficient numbers to maintain its place in plant society; it may



flower freely but fruit sparingly either because of faulty fertilization or because of a short season; conditions while adequate for adult plants may be unfavorable for the development of seedlings. To determine how far these various possibilities restrict the spread of the plants under consideration they have been classified according to the apparent success of the reproductive system as follows:



FIG. 4. *Unifolium canadense* at Sugar Grove. Beds as thick as this are rare in this region. Although flowering freely, the plant does not fruit well

REPRODUCTION OF SPECIES ON THE EDGES OF THEIR RANGES

*Flowering scantily*

*Gaultheria procumbens*\*  
*Isotria verticillata*  
*Passiflora lutea*  
*Phlox stolonifera*\*†

*Pyrola elliptica*\*  
*Pyrola rotundifolia*\*  
*Sambucus pubens*\*†  
*Stylosanthes biflora*

*Fruiting sparingly although flowering freely*

*Aesculus octandra*‡  
*Asclepias variegata*  
*Blephariglottis lacera*  
*Diospyros virginiana*  
*Lycopodium lucidulum porophilum*§

*Lysimachia quadrifolia*  
*Napaea dioica*¶  
*Quercus minor*  
*Rubus odoratus*.  
*Unifolium canadense*

\* Fruit appears to "set" and mature well.

† Species confined to the southern portion of the area.

‡ Species confined to the northern portion of the area.

§ Sporangia comparatively scarce.

¶ Dioecious, only one plant found.



*Flowering freely, fruiting not observed*

<i>Achroanthes unifolia</i>	<i>Hypericum Drummondii</i>
<i>Anemone canadensis</i>	<i>Isopyrum biternatum</i> ¶
<i>Aronia nigra</i>	<i>Iris cristata</i> †
<i>Aster macrophyllus</i>	<i>Polygonum arifolium</i> †
<i>Bidens aristosa</i>	<i>Quamasia hyacinthina</i> ¶
<i>Blephariglottis peramoena</i> †	<i>Scutellaria galericulata</i>
<i>Chrysopsis mariana</i> †	<i>Solidago erecta</i>
<i>Chrysosplenium americanum</i>	<i>Solidago juncea</i>
<i>Dentaria heterophylla</i> †	<i>Stachys cordata</i>
<i>Eatonia nitida</i>	<i>Trichostema dichotomum</i>
<i>Epigaea repens</i>	<i>Valeriana pauciflora</i> §

*Fruiting freely*

<i>Azelia macrophylla</i>	<i>Koellia incana</i>
<i>Andropogon virginicus</i>	<i>Juncoides saltuensis</i>
<i>Aruncus Aruncus</i>	<i>Lobelia puberula</i> †
<i>Ascyron multicaule</i>	<i>Lycopodium lucidulum</i> ††
<i>Azalea lutea</i>	<i>Lycopodium clavatum</i> †††
<i>Capnoides sempervirens</i>	<i>Lycopodium complanatum</i> †††
<i>Carex costellata</i>	<i>Lycopodium obscurum</i> ††
<i>Castanea dentata</i>	<i>Panicum polyanthes</i>
<i>Cunilla originoides</i>	<i>Panicum stipitatum</i>
<i>Cypripedium acaule</i> °	<i>Pedicularis lanceolata</i>
<i>Dasystema laevigata</i>	<i>Phacelia dubia</i> †
<i>Epigaea repens</i>	<i>Porteranthus stipulatus</i>
<i>Dodecatheon Meadia</i> † **	<i>Salix amygdaloides</i> ¶
<i>Eupatorium aromaticum</i> †	<i>Sericocarpus asteroides</i>
<i>Eupatorium coelestinum</i>	<i>Viola hirsutula</i>
<i>Eupatorium rotundifolium</i> †	<i>Viola rotundifolia</i> †
<i>Hieracium paniculatum</i>	<i>Viola rostrata</i>
<i>Hydrangea arborescens</i>	

*Fruiting freely, seedlings also abundant*

<i>Aralia spinosa</i> †	<i>Oxydendrum arboreum</i>
<i>Aster divaricatus</i>	<i>Pinus rigida</i>
<i>Betula lutea</i> †	<i>Pinus virginiana</i>
<i>Betula nigra</i> †	<i>Quercus Prinus</i>
<i>Cassia nictitans</i>	<i>Rhododendron maximum</i>
<i>Circaea alpina</i> †	<i>Saxifraga pennsylvanica</i> †
<i>Gymnocladus dioica</i> § ¶	<i>Saxifraga virginiana</i>
<i>Hieracium venosum</i>	<i>Silene rotundifolia</i> †
<i>Kalmia latifolia</i>	<i>Sullivantia Sullivantii</i> †
<i>Melampyrum lineare</i> †	<i>Tsuga canadensis</i>

|| Not maintaining itself, perhaps only a waif.

¶ Species reaching their limits immediately to the west of the area.

° Many flowers are unfertilized but fruit is common.

\*\* Also reported from another station by Bigelow.

†† Sporangia abundant.



*Pteridophytes, prothallia not observed*

<i>Asplenium montanum</i>	<i>Lycopodium lucidulum</i>
<i>Asplenium pinnatifidum</i>	<i>Lycopodium lucidulum porophilum</i>
<i>Lycopodium clavatum</i> †	<i>Lycopodium obscurum</i>
<i>Lycopodium complanatum</i> †	

*Species abundant by vegetative propagation (scattered through above groups)*

<i>Cypripedium acaule</i>	<i>Lycopodium lucidulum porophilum</i>
<i>Gaultheria procumbens</i>	<i>Phlox stolonifera</i> †
<i>Iris cristata</i>	<i>Unifolium canadense</i>
<i>Lycopodium lucidulum</i>	

*Fruiting yet to be observed*

<i>Aristida dichotoma</i>	<i>Lobelia leptostachys</i>
<i>Asclepias Sullivantii</i>	<i>Panicularia elongata</i>
<i>Cornus stolonifera</i>	<i>Parnassia caroliniana</i>
<i>Fraxinus nigra</i>	<i>Populus tremuloides</i>
<i>Fraxinus quadrangulata</i>	<i>Psoralea Onobrychis</i>
<i>Gentiana crinita</i>	<i>Rynchospora glomerata</i>
<i>Lechea racemulosa</i>	<i>Smilax ecirrhata</i>

## SUMMARY

Flowering scantily.....	8
Fruiting sparingly although flowering freely.....	10
Flowering freely, fruiting not observed.....	22
Fruiting freely.....	35
Fruiting freely, seedlings abundant.....	20
Pteridophytes, prothallia not observed.....	7
Abundant by vegetative propagation, species scattered through the above groups	7
Unobserved.....	14+11, 25
Total.....	134
Duplications.....	12
Net total.....	122

Such a classification to be of the maximum value should have been made by one familiar with the various species throughout the whole extent of their ranges. Species that appear to the writer to fruit abundantly may fruit so much more abundantly in other regions that their fruit in the Sugar Grove area would be scarce by comparison. The wintergreen, *Gaultheria procumbens*, is a case in point. The berries are apparently sufficiently common to supply enough seed for the perpetuation of the species, and the plant would accordingly have been classed as fruiting freely but for the acquaintance of the writer with the same species in New England where the berries are borne in such great profusion—six

† Species confined to the southern portion of the area.



or seven to a stalk—as to make the Ohio plants bearing rarely more than one or two berries and those only on about one plant in ten, seem sterile by comparison. On the other hand some



FIG. 5. *Oxydendrum arboreum* in fruit at Sugar Grove

species flower sparingly throughout their range so that similar behavior at the termini would not be unusual. In making the tables I have classed as fruiting freely all those species whose seed production appeared adequate for their perpetuation.



But allowing for all the changes which might be made in the classification by one of wider field experience than the writer, it seems certain that failure of the reproductive functions is an unimportant factor in the termination of ranges in this region. Most plants normally produce such an enormous quantity of surplus seed that even a considerable falling off in seed production would not necessarily affect the abundance of the species.

The success of the seedlings is apparently much more important than the number of seeds. *Rubus odoratus* is a case in point. Although flowers are produced in abundance the fruit does not set well so that it is usually difficult to find a berry perfect enough to be palatable. In the aboriginal forest this species led a precarious existence on the cliffs and other places unoccupied by trees, where sufficient light and moisture were obtainable. But with the destruction of the forest it is becoming one of the commonest plants of the ravines. It is clear therefore that its failure to fruit well is not a controlling factor in fixing its range.

Vegetative propagation plays of course a role of considerable importance in this connection. The most striking instances are *Phlox stolonifera*, *Unifolium canadense* and the lycopods which would hardly maintain themselves were it not for their stolons and gemmae.

On the other hand it seems safe to assign failure of the reproductive mechanism as the limiting factor in the case of those species which do not fruit well and at the same time are uncommon, being without means of vegetative multiplication. These include only *Asclepias Sullivantii*, *Aseculus octandra*, *Asclepias variegata*, *Blephariglottis lacera*, *Napaea dioica*, *Passiflora lutea*, *Quercus minor* (?), *Stylosanthes biflora* and the lycopods, *L. obscurum* and *L. clavatum*, which although forming large masses by their runners are yet scarce, especially the latter, of which only a single bed has been discovered.

The next question to arise is as to what differences in abundance there may be between the different geographical groups represented in the lists. What differences are there between northern and southern or eastern and western plants? A comparison of the lists given above with those presented in the preceding paper\* gives the data shown in tabular form below.

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\* Griggs, Robert F. Observations on the geographical composition of the Sugar Grove flora. Bull. Torrey Club 40: 487-499. f. 1-10. 10 S 1913.



	Common	Common Few Stations	Abundant One Station	Rather Com- mon	Per Cent. Common	Scarce	Rare	Per Cent. Uncommon	Unobserved	Flower Scantly	Fruit Sparingly	Per Cent. Not Fruiting Well	Flower Freely	Fruit Freely	Seedlings Abundant	Per Cent. Fruiting Well	Not Observed	Total
Alleghenian. . . . .	18	0	1	4	65	4	4	22	7	5	5	28	6	9	5	53	9	39
New England																		
Appalachian. . . . .	11	1	0	0	80	0	0	0	2	0	0	0	1	6	6	93	1	14
Appalachian. . . . .	7	4	0	0	92	0	0	0	1	1	0	8	1	4	3	66	3	12
Carolinian. . . . .	16	2	0	5	68	2	3	15	4	2	4	18	6	11	3	61	6	32
Western. . . . .	3	1	2	0	40	3	4	47	3	0	1	7	5	2	2	60	5	15
Northern. . . . .	2	1	2	2	77	1	0	11	1	0	0	0	3	2	1	66	3	9

This table does not indicate that in this region species behave differently on different edges of their ranges. Except in one case the differences shown are too small to be significant in view of the small numbers involved. The abundance and reproduction of species terminating in this area are evidently matters concerned with the individual peculiarities of the particular species rather than with its geographical position. The large number of rare plants among those from the west is, however, very striking. When this is coupled with the fact that a large proportion of them are known from scattered stations far to the eastward of their main range, it becomes significant.

There is a widely held idea, which owes its origin I believe to Blytt\* though it may be much older, that, whereas a species may be ubiquitous in the center of its range, occurring in all sorts of habitats because highly favored by climate, at its areal limits it will be closely limited to those conditions which are most favorable to it. According to this reasoning we should be best able to determine the conditions most favorable to any given species by observing its behavior on the edges of its range. The theory is so plausible that one would like to accept it and apply it to our plants. But unfortunately certain of our Sugar Grove plants do not seem to behave according to expectations and raise doubts concerning its validity.

The chestnut is one of the most typical of all the "calcifuge" plants and its distribution in central Ohio fulfils expectations in this regard. It is absent from the limestone country about Columbus but appears immediately as one enters the outcrops of sand-

\* I am unable to find the reference to Blytt's paper; see also Cowles, *Physiographic Ecology of Chicago and Vicinity*. Bot. Gaz. 31: 83. 1901.



stone about twenty miles to the eastward. From this point it is abundant all over the sandstone part of the state and is one of the most important timber trees about Sugar Grove. What was



FIG. 6. *Rhododendron* at Sugar Grove. (Photograph by J. E. Hyde.)

my surprise then, on mapping its general range, to find its Michigan stations described in these terms by Beal:\* "Occurs abundantly

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\* Beal, W. J. Michigan Flora 69. Lansing, 1904.



along an outcrop of Helderberg limestone in E. Monroe Co. and Wayne Co., C. F. Wheeler." Thus its preferences in one part of the edge of its range would make it a calciphile and in another part a calcifuge plant.

*Rhododendron maximum* is interesting in this connection. Its typical habitat is the densest shade in deep forests, where it forms impenetrable thickets. This for the most part is its habitat in the Sugar Grove area where it is found at the base of the cliffs in deep ravines on slopes with a northern exposure. In the northern section of the area immediately around Sugar Grove I have never seen it except in such situations. But in the southern section although likely habitats are common enough it is absent except for two isolated patches of small extent. One of these is near "Written Rock" on Clear Creek and the other is at the head of Laurel Run. In both of these stations the plant grows and apparently thrives measurably well as a crevice plant high up *on cliffs with extreme southern exposure* in conditions far different from its supposed optimum.

*Aralia spinosa* was almost exclusively a crevice plant in the primeval forest, occurring high up on the faces of the cliffs and dropping its seeds into the caves below where they sometimes took root, as in Old Man's Cave. Since the timber of the higher slopes has been cut off, the plant has multiplied extraordinarily until it has become a common pest on lumbered hillsides. The manuals credit it with growing in "Damp moist soil in the neighborhood of streams." But in the valley of Queer Creek only a single specimen and that dead, was found in the moist bottom land. Mohr\* describes its habitat in Alabama as "Damp borders of woods and copses." Hilgard,† page 495, describes it as a lowland plant in highly productive calcareous soil and again, on page 515, states that with the *Liriodendron*, black walnut, Kentucky coffee tree, and others which are like it normally lowland plants, it may ascend in calcareous regions into the uplands as well. The rock in whose crevices it occurs in our area is not limestone but a pure sandstone which is sometimes quarried for glass sand; the hillsides which it has invaded are very poor land which was originally

\* Mohr, Charles. Plant Life of Alabama. Cont. Nat. Herb. 6: 640. 1901.

† Hilgard, E. W. Soils. Macmillan Co., 1904.



covered by a mixed forest of scrub and pitch pine, black oak and blueberries. Through the whole region much of the land has been abandoned and not more than half of the houses are now occupied. The crevices in exposed rocks are the poorest of all the habitats in the region and it can be shown that the majority of the chasmophytes are plants which have been crowded out of the more favorable habitats which they would quickly repopulate, as the *Aralia* has done, were their more successful neighbors removed. This very plant indeed, when the forest is removed, gives abundant evidence of the kind of habitat it prefers. It is really a *sun-loving* plant and grows only where sunlight is abundant. In the primeval forest the upper faces of the cliffs were the only situations in which a plentitude of light was available to a plant of such humble stature, so here it developed wherever together with sunlight sufficient water was present.

Even so few examples as these are sufficient to destroy the utility of the theory that at the edges of their ranges, species are confined to the most favorable habitats. Where it describes conditions previously known to obtain, well and good. But it cannot be generalized nor can it serve as a guide to the optimum habitats of plants whose preferences in this matter are unknown. Like much *a priori* reasoning it presents a conclusion which may be true rather than one which must be true. Moreover, another line of *a priori* reasoning might in this case lead us to diametrically opposite conclusions. In the center of its range a plant, being supposedly favored by all the conditions of its environment, is able to compete with other plants at an advantage and maintain a place for itself in various habitats. On its areal limits on the other hand environmental conditions are supposedly less favorable to this species than to others with which it will therefore be compelled to compete at a disadvantage. This may be brought about either by unfavorable physical conditions such as soil, climate, etc., or by the entry into the struggle for place of species absent from the center of the range which have an advantage over the given species in rapidity of growth or the like. The species in question is therefore driven out of the most favorable habitats and must find a place for itself where it can. This is exactly the situation of *Aralia spinosa* which in the dense forest



that originally covered the Sugar Grove region could grow only on the cliffs, where the successful forest trees could neither follow it nor deprive it of its light.

We seem, therefore, to have made little progress in the effort to determine the causes of the termination of ranges. The feeling that it was not caused by such factors as I could observe has also been borne in upon me as I have repeatedly studied the plants in the field. It has been quite impossible to imagine why a given species should be abundant in one valley and absent from the next one only a few miles away when all conditions seemed similar.

It is generally supposed that climatic influences are the most important factors in determining plant ranges. By appropriate manipulation of climatic data it is possible to draw striking parallels with vegetational zones. Thus Merriam\* has constructed maps from temperature data which conform remarkably closely to the life zones of North America. Transeau† likewise by plotting the ratio of evaporation to rainfall has made a map conforming to the forest areas of eastern North America in scarcely less striking fashion. Although dealing with factors to a large extent unrelated to each other, the correspondence of each of these maps with biogeography is so striking as to lead almost irresistibly to the conclusion that each of them represents the causative factor. They are, however, admittedly made to fit the facts of distribution and have not the weight that they would possess if constructed *a priori* by someone unfamiliar with the biogeography of North America. Moreover, it is not possible to state with any confidence the climatic requirements of any given species.

If climate were the principal factor restricting the spread of plants the edges of their ranges should exhibit one of two conditions: (1) Since climate changes vary gradually from place to place the controlling conditions should appear very gradually and the plants in response finding the conditions of life more and more difficult should become scarcer and scarcer and finally fail. This, however, happens comparatively seldom in this region. (2) The range should be fringed with outliers occupying habitats

\* Merriam, C. Hart. Laws of temperature control of the geographic distribution of terrestrial plants and animals. *Nat. Geogr. Mag.* 6: 229-238. 1894.

† Transeau, E. N. Forest centers of eastern America. *Am. Nat.* 39: 875-889. 1905.



where the climatic conditions were locally favorable. This is undoubtedly frequently the case. Bessey's\* finding *Adiantum Capillus-veneris* near a hot spring in South Dakota is a notable example. The presence of *Betula lutea* and some other northern plants in the deep cold ravines of the present area may be set down rather confidently as a local instance. I would not dare, however, to apply this explanation to more than seven of the twenty-five outliers listed above; for the others it seems clearly out of the question.

For many of the plants which terminate here, especially those which I know best because their boundaries cross the area, it is quite beyond my power of analysis to discover any reason why they should find their limits where they do and not go a few miles further. The easiest explanation of my inability to fix upon the reason for the location of their termini is that there is no reason; that they do not occupy ranges fixed by climatic conditions but are in process of adjustment. Observation of these plants seems to indicate that competition with other plant species is more important than climate in fixing the limits of their ranges. The case may be best presented by a few concrete examples:

*Silene rotundifolia* is common in the crevices of rocks regardless of exposure (not on "shaded banks") throughout the southern section of our area whence it extends southward along the western slope of the mountains to Tennessee. It is common up to "Cantwell Cliffs" but here it suddenly stops and has never been found further north. Suitable habitats, however, are by no means lacking.

*Aralia spinosa* is another plant of this sort. This species is of such a character that he who travels the brush, whether he be botanist or not, is forcibly made aware of its presence wherever it grows. It is a common plant over most of the southern states reaching its northern limits in southern Illinois, the Sugar Grove area, and Pennsylvania. It is abundant in the valley of Queer Creek and in some places on Big Pine Creek, occurring on the higher slopes where the timber has been cut off. As already indicated its place in plant society has been greatly enlarged by the lumberman so that it is now much more common than formerly

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\* Bessey, C. E. One thousand miles for a fern. *Asa Gray Bull.* 8: 2-6. 1900.



and its seedlings are taking possession of many cut-over woods. But its terminus is perfectly sharp; not a single individual has been found further northward, although a constant lookout has been kept for it. The increase in available habitats is giving it a continuous range, whereas formerly it occupied only isolated stations in the crevices like *Silene rotundifolia*. This change greatly increases the chances of successful reproduction and the plant gives every evidence of spreading northward. But like *Silene* it has no special means of seed dispersal and its progress is very slow.

A large proportion of the western plants terminating here behave similarly. *Afzelia macrophylla*, for example, is rare in our area having been seen only once by the writer but under circumstances which clearly indicate its powers of invasion, for its seedlings were more than holding their own against the former occupants of the soil. The eastern edge of the range of these species consists of a circle of such outliers located where chance seeds have dropped in advance of the range. The large proportion of western plants which are rare with us and at the same time are known far beyond our area may indicate that these are not merely characteristics of the individual species but that there is a somewhat systematic migration of western plants eastward.

The converse of the same proposition is presented by such a plant as the hemlock, *Tsuga canadensis*. The main body of its range ends in the Sugar Grove region, where it is common, especially in the deepest canyons. It occurs in numerous outlying stations, however, far to the west and south. One of these is in the mountains of western Alabama;\* another is on the Green River in Kentucky; a third,† which is better known, is near Greencastle, Indiana, where it occurs together with the yew on a limestone soil. Since it is usually found on rocks one might suppose that the causes of its termination were physiographic—the absence of suitable habitats in the intervening country. But although most often found on rocks, both sandstone and limestone, it is by no means a chasmophyte by preference but is at its best

\* Mohr, C. Plant Life of Alabama. Cont. Nat. Herb. 6: 34. 1901.

† Coulter, Stanley. Indiana Geol. Surv. Rep. 24: 616. 1899. Since this paper was in type I have found that is by no means the only station in Indiana as is stated by Coulter.



in the richest of deep alluvial bottomland soils as in the canyon of Queer Creek in the southern section of the present area. In the northern section of the area, however, where the valleys are somewhat older in a physiographic sense, the hemlock is restricted to the rocks around the edges of the ravines while the bottom is occupied by a mixed *Liriodendron* forest. A study of the plant societies here has convinced me, however, that it once occupied the bottoms as it still does in the more inaccessible valleys further south, but that it has been driven out of the more favorable habitats by the hardwoods. It seems probable that it once ranged continuously over all of Ohio and Indiana but that it has been displaced except in a few outlying rocky stations where it has been able to maintain itself till the present time. Study of the reproduction of the hemlock forest in the present area would indicate moreover that under present conditions, as modified by man, it will soon disappear from these stations as it has from the surrounding territory. On account of the superficial root-system, seedlings are unable to get a start except in very humid conditions such as obtained in the virgin forest. Wherever the humidity has been lowered by clearing, the hemlock seedlings are quickly dried out and killed both on rocks and in the bottom, while the hardwood trees which spring up beside them thrive where the soil is sufficiently deep.

The reasons for the increased abundance of such a plant as *Aralia spinosa* are of course not natural but artificial, introduced by the advent of man. On first thought one might be inclined to rule out such cases, but clearing and cultivation of the land make little if any change in climatic conditions. Their effect is in changing the conditions of competition between plant species. How profound this influence has been is forcibly brought to our attention every day by our pestiferous weeds, many of which are native species originally present in the forests but in insignificant numbers. All of these are species with some effective means of seed dispersal and their conquest of the country is now so complete that it is impossible to imagine their aboriginal condition. It is only the slow-moving species whose progress can be now studied.

That plant competition often plays a larger part than climatic influences is also indicated by the fact that most plants thrive



and successfully reproduce when planted under conditions widely different from those of their natural habitats if only competing plants are removed. Professor J. H. Schaffner informs me that *Cactus missouriensis* in Kansas at the eastern edge of its range is confined to the dry tops of the hills where nothing else can grow. But when he transplanted it to a rich shaded yard it grew far more rapidly than before and attained twice the size of wild specimens as long as grass was kept away from it.

The case of the hemlock is a good illustration of one very important factor which has not been touched on—the historical factor.\* The reasons that the hemlock occupies its present range are primarily historical. It is here because this particular species and not some other analogous conifer like the Norway spruce was present in eastern North America during the Glacial Period and because it has not yet been completely displaced by the post-glacial flora. It occupies the canyon of Queer Creek not because it is better suited for that situation than any other plant of the region but simply because the invading hardwood forest has not had so good an opportunity to gain a foothold there as elsewhere.

There are thus apparently *tension zones* between different species somewhat similar to the familiar tension zones between plant societies. These zones are as critical in the study of plant geography as are formational tension zones in ecology. For in these zones it can be seen that some species are advancing while others are being beaten back. Just as one can determine the course of ecological succession from the behavior of plant societies in the tension zones so one can determine the trend of geographical movements† by a study of the tension zones at the edge of plant ranges.

And yet there can be no doubt that climatic conditions are of fundamental importance in determining the ranges of plants. It is apparent that plants tend to spread and would finally come to

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\* For a discussion of the importance of the historical factor, see Adams, C. C. The Postglacial dispersal of North American Biota. Biol. Bull. 9: 53-71. 1905.

† Adams (Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull. 3: 115-131. 1902) has insisted that biogeography must be put on a dynamic basis. Bessey, C. E. (Plant migration studies. Univ. Neb. Studies 5: 11-27. 1905) has shown that the forest trees are invading Nebraska from all sides, largely on account of the elimination of prairie fires.



occupy ranges as large as their adaptability to climate would permit, just as stream erosion would reduce all regions to base-level. Under such conditions competition between species would cease to be a factor, for that battle would have been finished and the weaker species eliminated. With competition would disappear the historical factor which is largely a record of the state of the struggle.

At best, however, such conditions obtain only for part of the plants. There are always a large number of species like the cactus cited above which are driven out of the favorable habitats by more aggressive plants but find a place in unfavorable situations where their competitors cannot follow them but which they can endure. Thus the plants of favorable habitats may be limited by climatic factors while those of unfavorable are largely controlled by competition. Accordingly one may find a species dominant at one edge of its range but outcast at the other. As one passes from zone to zone into more and more severe conditions he may find the outcast plants of one region becoming the dominant ones of the next, giving an appearance of complete adjustment to climatic conditions whereas in reality only half the vegetation is controlled by climate.

Where conditions have remained stable such adjustment should be found everywhere but as species approach the limits of their adaptability to climatic conditions their progress may be expected to be increasingly retarded so that as in base-leveling the last stages of the process are exceedingly slow. With our present limited knowledge of plant ranges it would be rash to suppose that complete climatic adjustment of vegetation is as rare as the completion of a cycle of erosion, but it is evident that various factors may intervene to disturb the process before completion. (1) The minor changes brought about by shifting physiography might affect the distribution of such plants as require certain peculiar habits. (2) Whenever and wherever new types of plants, or of animals that feed upon them, are evolved, their entry into the struggle for existence introduces an entirely different set of conditions and throws the whole vegetation\* out of adjustment.

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\* Shreve in a paper entitled "The rôle of winter temperatures in determining the distribution of plants," read before the Botanical Society of America at Atlanta,



Changes of this character in the past are responsible for profound modifications of present phytogeography, such as the extinction of many types of conifers in the northern hemisphere. There is no reason for supposing that evolution has ceased or that its progress is so slow as to make its effect on plant competition unobservable. (3) We know very little about the rapidity of climatic changes but climatic revolutions in the past have wrought great changes in vegetation. It is hardly reasonable to suppose that such changes are not still going forward. It may be doubtful, perhaps, whether they are rapid enough to be discernible in the present day flora, but it is clear that exceedingly slow movements of vegetation may be readily detected by observations of the tension zones between the ranges.

Broad conclusions involving a systematic shifting of plant ranges cannot of course be drawn from study of a single area. But the behavior of the species reaching the edges of their ranges in the Sugar Grove area seems to indicate very clearly that the ranges terminating there are not fixed but are changing. Plants of boreal affinity are apparently being displaced by others from the west and south. This obviously falls into line with the biotic changes which are known to have occurred since the glacial period. The conditions of the tension zones between the species terminating at Sugar Grove find, therefore, their most rational interpretation as a present-day continuation of the floristic movements following the glacial period.

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31 D 1913, reported that the northward and altitudinal extension of the lowland flora in the vicinity of the Desert Botanical Laboratory is checked by winter temperatures. This would of course fall into line with other facts, such as extremely localized ranges and the rich development of endemic forms, which indicate for the flora of the southwest a great age as compared with the comparative youth of the flora of the northeastern states.









# A taxonomic study of the Pteridophyta of the Hawaiian Islands—IV

WINIFRED J. ROBINSON

(WITH PLATES I AND 2)

## LYCOPODIALES

Terrestrial or epiphytic plants with spores produced in sporangia borne in the axils of scale-like leaves.

Homosporous.

Sporangia 1-celled.

Sporangia 2-3-celled.

Heterosporous.

LYCOPODIACEAE.

PSILOTACEAE.

SELAGINELLACEAE.

### LYCOPODIACEAE

Plants with upright or procumbent stems; leaves small, simple, crowded, in 2-several ranks upon the stem; sporangia in the axils of sporophylls, which may be leaf-like or scale-like, these in some species aggregated to form terminal strobili; spores yellow, numerous.

LYCOPODIUM L. Sp. Pl. 1100. 1753

Characters of the family.

Type species: *Lycopodium clavatum* L.

Vegetative leaves uniform.

Sporophylls not aggregated in strobili; stems usually erect.

Stems tufted, often reddish; leaves coriaceous, entire, 6-8-ranked.

Leaves linear-lanceolate, patent, 8-ranked.

*L. erubescens.*

Leaves ovate-lanceolate, appressed, 6-ranked.

*L. Haleakalae.*

Stems not tufted, green; leaves membranaceous, finely serrate, 4-6-ranked.

*L. serratum.*

Sporophylls aggregated in strobili; stems erect or pendulous.

Leaves membranaceous, 3-ranked.

*L. Phlegmaria.*

Leaves coriaceous, in more than 3 ranks.

Leaves 8-ranked; strobili simple, usually recurved.

*L. cernuum.*

Leaves 4-6-ranked; strobili often branched, not recurved.

Leaves linear-lanceolate, 6-ranked; sporophylls lanceolate, decreasing somewhat in size from base to apex of strobilus.

*L. nutans.*

Leaves lanceolate, 4-6-ranked; sporophylls broadly ovate, uniform in size.

*L. phyllanthum.*

Vegetative leaves not uniform.



Stems dorsi-ventral.	<i>L. volubile.</i>
Stems not dorsi-ventral.	
Sporophylls aggregated in terminal strobili.	<i>L. venustum.</i>
Sporophylls not aggregated in terminal strobili.	<i>L. polytrichoides.</i>

LYCOPODIUM SERRATUM Thunb. Fl. Jap. 341. 1784

*Lycopodium varium* Mann, Proc. Am. Acad. 7: 221. 1866. Not Swartz.

*Lycopodium sulcinervium* Spring, Mém. Acad. Roy. Brux. 15: 39. 1842.

*Lycopodium javanicum* Sw. Syn. Fil. 175. 1810.

*Lycopodium sargassifolium* Liebm. Öfvers. Vid. Selsk. Förh. 1847: 41. 1847.

TYPE LOCALITY: Japan.

DISTRIBUTION: On tree trunks in forests at 700 m.–2200 m. elevation; Hawaiian Islands, Japan, India, Philippine Islands, Sumatra, Polynesia, Mexico.

ILLUSTRATIONS: Thunb. Fl. Jap. pl. 38. 1784. Hook. & Grev. Ic. Fil. pl. 37. 1847.

SPECIMENS EXAMINED: Hawaii, *Robinson 218 V*; Oahu, *Heller 2904 C*; *Forbes 1036 BM*; *Forbes BM*; *Knudsen B*; *Robinson 196 V*; Kauai, *Heller 2687 C*; *Knudsen B*; *Robinson 414 V*; *816 V*.

Hillebrand's *L. serratum dentatum* (Hilleb. Fl. Haw. Is. 643. 1888) is represented by one small specimen from Lanai in the Berlin Herbarium; his *L. serratum subintegrum* by a single sterile shoot at Berlin. Forbes's specimen (no number) collected between Punahou and Kaipaupau, Oahu, corresponds with Hillebrand's description of the latter as to size and reddish color.

LYCOPODIUM ERUBESCENS Brack. Fil. U. S. Expl. Exped. 320. 1854

TYPE LOCALITY: Mount Haleakala, Maui, Hawaiian Islands.

DISTRIBUTION: In wet lands, at 2,000 m. elevation, Maui and Kauai, Hawaiian Islands.

ILLUSTRATION: Brack. Fil. U. S. Expl. Exped. pl. 45. 1854.

SPECIMENS EXAMINED: Hawaiian Islands, *Wilkes Expedition I B* (type); *Wilkes Expedition C*; *K*.

This very compact form is well suited to the xerophytic conditions of the high altitudes where it is found.



LYCOPODIUM HALEAKALAE Brack. Fil. U. S. Expl. Exped. 312.  
*pl.* 45. 1854

TYPE LOCALITY: Eeka, W. Maui, Hawaiian Islands.

DISTRIBUTION: Type locality.

ILLUSTRATION: Brack. Fil. U. S. Expl. Exped. *pl.* 45. 1854.

SPECIMENS EXAMINED: *Hillebrand* 153 B.

Hillebrand's specimen is small, but its obtuse, serrated leaves, with an incurved apex, and its greater rigidity distinguish it from *L. erubescens* Brack. and *L. compactum* Hook., which are its nearest allies.

Pritzel, E. & P. Nat. Pflanzenfam. 1<sup>4</sup>: 593. 1900, gives both *L. Haleakalae* and *L. erubescens* as varieties of *L. suberectum* Lowe, but they differ from each other sufficiently to establish their origin from different species at least, if change of habitat should prove that their alpine characters are not specific.

LYCOPODIUM PHLEGMARIA L. Sp. Pl. 1101. 1753

TYPE LOCALITY: India.

DISTRIBUTION: India, Australia, Pacific Islands, Mauritius.

ILLUSTRATIONS: Breyne, Exot. Cent. *pl.* 92. 1678. E. & P. Nat. Pflanzenfam. 1<sup>4</sup>: 600. *f.* 377. 1900.

SPECIMENS EXAMINED: Maui, *Mann* B.

The specimen examined is more slender than the Indian forms, but the material available does not warrant the establishment of a new species.

LYCOPODIUM CERNUUM L. Sp. Pl. 1103. 1753

*Lycopodium curvatum* Gaud. Voy. Freyc. Bot. 284. 1828.

TYPE LOCALITY: India.

DISTRIBUTION: Common in thickets at the edge of forests in the tropics.

ILLUSTRATIONS: Dill. Hist. Musc. *pl.* 63. 1741. E. & P. Nat. Pflanzenfam. 1<sup>4</sup>: 603. *f.* 379. 1900.

SPECIMENS EXAMINED: Maui, *Robinson* 398 V; Oahu, *Forbes* BM; *Hillebrand* B; *Robinson* 53 V; 95 V; 197 V; *Seemann* 1705 B; Kauai, *Heller* 2596 C; *Knudsen* 186 B; Hawaiian Islands, *Hillebrand* B; *Miss Sessions* C.

The specimens of *L. cernuum* in the Hillebrand collection in



the Berlin Herbarium are there separated into two species, *L. crassifolium* and *L. capillaceum*, the former of which is the more robust. It is difficult, however, to determine constant characters which may be termed diagnostic, whether one tries to separate the plants into two species as at Berlin or into seven with Müller (Bot. Zeit. 19: 161. 1861).

LYCOPODIUM NUTANS Brack. Fil. U. S. Expl. Exped. 327. 1854

TYPE LOCALITY: Oahu, Hawaiian Islands.

DISTRIBUTION: On trees, at 600 m.-1,000 m. elevation, rare, Hawaiian Islands.

ILLUSTRATIONS: Brack. Fil. U. S. Expl. Exped. *pl.* 46. 1854.  
PLATE I.

SPECIMENS EXAMINED: Oahu, Nuuanu Valley, *Hillebrand B*; *Robinson 199 V*; W. Maui, Wailua Valley, *Hillebrand B*.

The conspicuous difference between the slender fertile portion which terminates the branch and the broad sterile portion with its stiff coriaceous linear-lanceolate leaves, gives the distinguishing feature which separates *L. nutans* from *L. squarrosum* Forst. In the latter, the transition is gradual between the sterile and fertile areas.

Brackenridge in describing *L. nutans* as a new species closely related to *L. phyllanthum* Hook. & Arn. says: "This is one of the most robust species of the genus. It is very well distinguished from the preceding (*L. phyllanthum*) by its stouter stem, and its thick, nodding spikes; the leaves on the stems also are more crowded and the scales of the spikes are of considerably greater length."

LYCOPODIUM PHYLLANTHUM Hook. & Arn. Bot. Beech. 102. 1832

*Lycopodium pachystachyon* var.  $\beta$  *phyllanthon* Spring, Mém. Acad. Brux. 24: 29. 1848.

TYPE LOCALITY: Hawaiian Islands.

DISTRIBUTION: Pendulous on trees; Hawaiian Islands, Tahiti, Samoa, Borneo, Java, India.

ILLUSTRATION: PLATE 2.

SPECIMENS EXAMINED: Hawaii, *Robinson 263 V*; Maui, *Robinson 389 V*; Oahu, *Heller 2182 C*; *Hillebrand B*; *Knudsen 29 B*;



*Kuntze C*; *Robinson 445 V*; Lauai, *Hillebrand B*; Hawaiian Is., *Forbes BM*; *Lindley C*; *Wilkes Expedition C*.

*L. phyllanthum* has very nearly related species in the Indian *L. macrostachys* Spring, *Mém. Acad. Brux.* 24: 30. 1848, and in the Philippine specimens *Williams 573 C* and *Williams 2916 C*. In most of the Hawaiian specimens, the diameter of the fertile portion is greater than it is in the Indian or Philippine plants.

In none of the specimens examined by the writer were the upper sporophylls of the strobilus "barren and larger, approaching the form of true leaves" as described by Hooker and Arnott (l. c.) but in the Philippine specimens mentioned above the strobilus was somewhat foliaceous.

LYCOPODIUM VOLUBILE Forst. Prod. 86. 1781

TYPE LOCALITY: Australia.

DISTRIBUTION: Australia, New Zealand, Hawaiian, Viti, and Society Islands.

SPECIMENS EXAMINED: Hawaiian Islands, *Menzies K*.

This species is interesting because it resembles *Selaginella* in dimorphic sterile leaves, but has the fertile spike of a true *Lycopodium*. *Menzies* is the only collector known to have found it, and his specimen probably came from Mauna Kea, Hawaii.

LYCOPODIUM VENUSTULUM Gaud. Voy. Freyc. Bot. 283. pl. 22.  
1828

TYPE LOCALITY: Hawaiian Islands.

DISTRIBUTION: At elevations of 800 m.—1200 m., Hawaiian Islands.

ILLUSTRATION: Gaud. Voy. Freyc. Bot. pl. 22. 1828.

SPECIMENS EXAMINED: Oahu, *Forbes BM*; Hawaiian Is., *Hillebrand B*; 128 *K*; *Wilkes Expedition B*; 24 *C*; *K*; 26 *C*.

One of the specimens collected by the Wilkes Expedition, 26 *C*, is reduced in size and has fewer branches from the horizontal stem proportionately than the normal form, *Wilkes 24 C*. This doubtless grew at a higher elevation or in a more exposed locality than is usual for the species. *Hillebrand* makes it a variety, *L. venustum* var. *herpeticum*, but it is not worthy of specific rank.



LYCOPODIUM POLYTRICHOIDES Kaulf. Enum. Fil. 6. 1824

TYPE LOCALITY: Oahu, Hawaiian Islands.

DISTRIBUTION: On trees, at 600–1,000 m. elevation, Hawaiian Islands.

SPECIMENS EXAMINED: Oahu, *Chamisso* B (type); Oahu, Mopala Valley, Kaala Mts., *Forbes* BM; Waiolau Valley, *Forbes* BM; Konahuanui, *Heller* C; Kaala Mts., *Hillebrand* B; *Martens* B; Molokai, *Hillebrand* B; Kauai, *Knudsen* 34 B; Hawaiian Islands, *Hillebrand* 594 B; 598 B; *Menzies* K; *Wilkes Expedition* K.

Chamisso's type is a slender plant about 15 cm. high, while Hillebrand's specimen from Molokai is much branched and about 40 cm. high. The others range between these. All, however, agree in the open angles of the branching, and in the many-ranked aculeate leaves, which bear sporangia in the last two or three divisions of the stem.

#### PSILOTACEAE

Represented in the Hawaiian Islands by the single genus *Psilotum*.

PSILOTUM Sw. Syn. Fil. 187. 1806

Epiphytic or occasionally terrestrial plants; stems upright; roots fleshy; leaves small, scale-like, the sterile simple, the fertile bifid; sporangia borne in the axils of the leaves, 3-celled, opening by three valves from the apex; spores minute, yellow.

Type species: *Lycopodium nudum* L.

Stems triangular; sterile leaves aculeate, minute.

*P. nudum*.

Stems flattened; sterile leaves obtuse.

*P. complanatum*.

PSILOTUM NUDUM (L.) Griseb. Abh. Kön. Gesell. Wiss. Göttingen  
7: 278. 1857

*Lycopodium nudum* L. Sp. Pl. 1100. 1753.

*Hoffmannia aphylla* Willd. in Römer & Ust. Mag. Bot. 6: 17. 1789.

*Bernhardia dichotoma* Willd. in Schrift. Acad. Erfurt. 1802: 11.  
1802.

*Psilotum triquetrum* Sw. Syn. Fil. 187. 1806.

*Psilotum oahuensis* Müller, Bot. Zeit. 14: 238. 1856.

TYPE LOCALITY: Jamaica, B. W. I.

DISTRIBUTION: On ground and on trees, in tropical countries.



ILLUSTRATIONS: Schkuhr, *Krypt. Gew. pl. 165b.* 1809; Plum. *Foug. Am. pl. 170 f. a.* 1705; Dill. *Hist. Musc. pl. 64. f. 4.* 1741 (Dillenius probably never saw the specimen but seems to have copied Plumier's figure).

SPECIMENS EXAMINED: Hawaii, *Robinson 264 V*; Maui, *Robinson 313 V*; 351 V; Oahu, *Eschscholz K*; *Wilkes Expedition N*; *Heller 1989 C*; K; N; *Mann & Brigham 140 N*; *Seemann 1723 K*; Hawaiian Is., *Wilkes Expedition C*; N; *Lindley C*; *Macrae K*.

PSILOTUM COMPLANATUM Sw. *Syn. Fil. 188.* 1806

*Muscus clavatus* Bauhin. *Pinax. 360.* 1671.

*Lycopodium Sabinae-facie* Dill. *Hist. Musc. 445.* 1741.

*Lycopodium digitatum* Dill. *Hist. Musc. 448.* 1741.

*Lycopodium complanatum* L. *Sp. Pl. 1104.* 1753.

*Bernhardia ramulosa* Müller, *Bot. Zeit. 14: 222.* 1856.

TYPE LOCALITY: Jamaica, B. W. I.

DISTRIBUTION: On trees, West Indies, Malaysia, Polynesia, and Hawaiian Islands.

ILLUSTRATIONS: Dill. *Hist. Musc. pl. 59. f. 3.* 1741. Sw. *Syn. Fil. pl. 4. f. 5.* 1806. Schkuhr, *Krypt. Gew. pl. 165b.* 1809.

SPECIMENS EXAMINED: Oahu, *Robinson 11 V*; 20 V; *Wilkes Expedition N*; Kaala Mts., *Wilkes Expedition N*; *Heller 2216 C*; K; N; Ex Herb. *Hooker C*; *Hillebrand 118 K*; *Macrae C*.

#### SELAGINELLACEAE

Plants with upright or procumbent, usually dorsi-ventral, dichotomous stems, one branch exceeding the other in growth; leaves uniform or dimorphous, in the latter case forming a mosaic, the lateral leaves extending horizontally from either side of the stem, the intermediate leaves closely applied to the stem; sporophylls borne at the ends of the branches usually forming strobili, in which the few macrosporangia are in the axils of the basal sporophylls, the more numerous microsporangia in the axils of the terminal sporophylls.

SELAGINELLA Beauv. *Prod. 101.* 1805

Characters of the family.

Type species: *Lycopodium selaginoides* L.

Vegetative leaves uniform; spores rough.

*S. deflexa.*

Vegetative leaves not uniform; spores smooth.



Leaves imbricated; stems 20 cm. or less in length.	<i>S. arbuscula.</i>
Leaves not imbricated; stems more than 20 cm. long.	
Branching flabellate; megasporangia 3-valved.	<i>S. Menziesii</i>
Branching pinnate or apparently so; megasporangia 2-valved.	<i>S. Springii.</i>

SELAGINELLA DEFLEXA Brack. Fil. U. S. Expl. Exped. 332. 1854

TYPE LOCALITY: Hawaiian Islands.

DISTRIBUTION: Rare, on trees, at elevations of 600–2,000 m., Hawaiian Islands.

ILLUSTRATION: Brack. Fil. U. S. Expl. Exped. *pl.* 45. 1854.

SPECIMENS EXAMINED: Maui (Mt. Eeka) *Hillebrand B; C;* Molokai (Wailau) *Hillebrand B;* Kauai, *Hillebrand K; Knudsen B; Johnson B.*

*S. deflexa* is easily distinguished from *Lycopodium serratum* by its backwardly directed spinulose leaves and the shortness of the leaves at the base of the stem which give the shoot the appearance of an inverted cone.

SELAGINELLA ARBUSCULA Spring, Mém. Acad. Brux. 24: 183. 1848

*Lycopodium arbuscula* Kaulf. Enum. Fil. 19. 1824.

*Lycopodium pennigerum* Gaud. Voy. Freyc. Bot. 288. 1828.

TYPE LOCALITY: Oahu, Hawaiian Islands.

DISTRIBUTION: Hawaiian Islands.

SPECIMENS EXAMINED: Hawaii, *Hillebrand B; Robinson 269 V;* Oahu, *Diell C; Heller 1993 C;* (Nuuanu) *Hillebrand B;* (Kahaua) *Hillebrand B; Meyen B;* (Hillebrand's Glen) *Robinson 121 V; 184 V;* Hawaiian Is., *Gaudichaud B; Macrae K; Wilkes Expedition C; Ex Herb. Kew. C.*

The small size of the plants and the closely crowded leaves distinguish *S. arbuscula* from the other species usually found growing with it.

SELAGINELLA MENZIESII Spring, Mém. Acad. Brux. 24: 185. 1848

*Lycopodium Menziesii* Hook. Bot. Misc. 2: 390. 1831.

*Selaginella flabellata* Underw. Minn. Bot. Stud. 1<sup>4</sup>: 793. 1896.

Not Spring.

TYPE LOCALITY: Hawaiian Islands.

DISTRIBUTION: In mountain forests, Hawaiian, Samoan, and Fiji Islands.

ILLUSTRATION: Hook. & Grev. Ic. Fil. *pl.* 200. 1831.



SPECIMENS EXAMINED: Maui, *Robinson* 723 V; Oahu, *Douglas* 30 K; *Forbes* 1016 BM; (Makaha Valley) BM; (Konahuanui) BM; (Kaipaupau) BM; *Hillebrand* B; *Menzies* K; *Wilkes Expedition* 5 C; Kauai, *Heller* 2499 C; 2558 C.

The darker color, and proportionately broader form distinguish this from *S. Springii*, notwithstanding the close relationship existing between *S. Menziesii*, *S. flabellata*, and *S. Springii*.

SELAGINELLA SPRINGII Gaud. Voy. Bonite Bot. Crypt. 340. 1846

*Selaginella Menziesii* Baker, Fern Allies 97. 1887. Not Spring, Mém. Acad. Brux. 24: 185. 1848.

TYPE LOCALITY: Hawaiian Islands.

DISTRIBUTION: In moist localities, at elevations of 600–800 m., Hawaiian Islands.

ILLUSTRATION: Gaud. Voy. Bonite Bot. Crypt. pl. 12. 1846–9.

SPECIMENS EXAMINED: Maui (Waihee) *Hillebrand* B; (Lahaina) *Hillebrand* B; *Robinson* 704 V; Molokai (Wailau) *Hillebrand* B; Oahu, *Forbes* BM; *Chamisso* B; *Heller* 2009 C; 2180 C; *Robinson* 522 V; 528 V; Ex Herb. Mt. Holyoke College C.

Baker (Fern Allies 97. 1887) and Hieronymus (Nat. Pflanzenfam. 1<sup>4</sup>: 678. 1901) both speak of the intergrading forms between *S. Springii* and *S. Menziesii*. The latter, however, recognizes *S. Springii* as a species distinct from *S. Menziesii* though closely related to it. It would not be remarkable if crosses had frequently occurred between these two forms which grow upon wet rocks where there is every facility for such hybridization.

The teeth at the base of the anterior margin of the stem leaves are longer than those of the apical portion, but hardly slender enough to be regarded as cilia as Gaudichaud figures them.

#### SPECIES INQUIRENDA

SELAGINELLA PARVULA Hilleb. Fl. Haw. Is. 648. 1888

TYPE LOCALITY: Hawaiian Islands.

DISTRIBUTION: Oahu (Nuuanu Valley), Hawaiian Islands.

Hillebrand in a footnote to his description of *S. parvula* suggests that it may be a young form of *S. arbuscula*, a suggestion which seems very probably true, from the close similarity of the two plants and the fact that only the one collection of the material has been made.







# INDEX TO AMERICAN BOTANICAL LITERATURE

1907-1913

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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**Andrews, A. L.** Notes on North American *Sphagnum*—V. Bryologist 16: 74-76. S 1913.

**Barrett, O. W.** Some new or little-known Philippine economics. Philip. Agr. Rev. 6: 493-503. pl. 2-II. O 1913.

**Bates, J. A.** My herbarium and its one enemy. Am. Fern Jour. 3: 49-52. 12 Je 1913.

**Benedict, R. C.** *Schizaea pusilla* in its natural surroundings. Am. Fern Jour. 3: 11-13. pl. I. 22 Mr 1913.

**Berger, [A.].** Eine neue *Agave*. *Agave Vilmoriniana* Berger nov. spec. Repert. Sp. Nov. 12: 503. 1 N 1913.  
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**Berry, E. W.** Some paleontological results of the Swedish South Polar Expedition under Nordenskiöld. Science II. 38: 656-661. 7 N 1913.

**Bicknell, E. P.** The ferns and flowering plants of Nantucket—XI. Bull. Torrey Club 40: 605-624. 24 N 1913.  
Includes *Hypericum dissimulatum* and *Crocanthemum dumosum*, spp. nov.

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# BULLETIN

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## CONTENTS

The ferns and flowering plants of Nantucket—XII.	EUGENE P. BICKNELL	71
Phytogeographical notes on the Rocky Mountain region—II. Origin of the alpine flora.	P. A. RYDBERG	89
The propagation of medicinal plants . . . . .	FRED A. MILLER	105
INDEX TO AMERICAN BOTANICAL LITERATURE. . . . .		131

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BULLETIN  
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FEBRUARY, 1914

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The ferns and flowering plants of Nantucket—XII

EUGENE P. BICKNELL

CACTACEAE

OPUNTIA.

In the history of Nantucket botany this cactus bears the distinction of having been the first one of the island's plants to receive formal botanical mention and published record. We do not know that it was ever seen on Nantucket by civilized man prior to its discovery there by Mr. Thomas A. Green, of New Bedford, on whose authority it was announced as a Nantucket plant as long ago as 1833 by Professor Edward Hitchcock in his "Report on the Geology, Mineralogy, Botany and Zoology of Massachusetts." Other plants of Nantucket find record in the same work but the prickly pear, under the name *Cactus Opuntia* L., has priority of place, thus, eighty years ago, marking the starting point of exact Nantucket botany.

On Nantucket this cactus is at the extreme northeastern limit of its range and is native only on that long arm of sand known as Coatue, which reaches along the western side of the harbor protecting it from Nantucket Sound. It abounds there in sandy openings among the low red cedars taking so strong a growth as to form close assurgent clusters sometimes three to five feet across.

Only once have I seen it there when it was in full bloom, on July 13, 1912. Its flowers were in great profusion, and one plant of three and a half feet spread bore about 220 blossoms. The flowers are bright yellow with a conspicuous red center and are

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6.3–7.5 cm. across, pressing out to as much as 9.5 cm.; petals 8–12, mucronate, 2.5–3.2 cm. wide; cluster of stamens 3.8–4.5 cm. in natural spread. The red center of the flower is patterned as a star, its rays tapering out beyond the stamens along the midveins of the petals. Larger stems, 10.5 dm. long, may bear as many as thirty joints, these narrowly oblong to obovate, becoming 18 cm. long and 8 cm. wide, occasionally narrow and trigonous. Fruits often seven, sometimes nine, on one joint, marginal or one or more also lateral, mostly 3.75–4 cm. long, commonly narrowed from apex to base, when lateral sometimes 5.5 cm. long. Base of the plant bulbous, becoming woody and much enlarged; main root horizontal and greatly elongated; a root carefully excavated Sept. 7, 1904 was nine and a half feet in length.

Two species of cactus have been attributed to Nantucket doubtless with reference to the spiny and spineless plants found on Coatae. These are not to be regarded as other than forms or varieties of one species. They do indeed stand well apart in the one character of armature, and it is probably true that some plants always produce spines and that others never do. But the flowers of each are essentially the same, although a close comparison, made on the one occasion when the plants were found in bloom, makes it possible to say that those of the spiny form were quite generally a trifle the smaller with slightly narrower petals, and usually a little more color—the red a shade deeper and the yellow just perceptibly brighter. A very small proportion of the unarmed form bear a few spines, sometimes not more than one or two and only on a single one of the joints.

I have not used any specific name for this cactus believing that two distinct species of *Opuntia* belong to our eastern flora and that it will therefore need to be determined to which one the current names *Opuntia vulgaris* Mill. and *Opuntia Opuntia* (L.) Coult. properly belong. Among the rocky hills on Manhattan Island and beyond, near Van Cortlandt Park, and in Bronx Park, there grows a cactus which is to me not at all the same species as the sand inhabiting littoral plant found on Nantucket. It thrives on rocky knolls in hilly woodland, either quite exposed to the sun or in partial shade, and has smaller flowers, which are light yellow throughout with never the faintest tinge of red, as I



have observed it. It is a smaller plant than the Nantucket species with shorter and more rounded joints of a duller green color and I have never seen on it even the rudiment of a spine nor observed that it ever developed a bulbous woody base or greatly elongated roots. It is also of more prostrate habit than the Nantucket plant.

## LYTHRACEAE

### DECODON VERTICILLATUS (L.) Ell.

No aquatic plant of Nantucket grows up in a greater number of ponds and bog holes than the swamp loosestrife and where it gets a footing it slowly pushes into undisputed possession of the places it chooses to occupy. It is the only shrubby aquatic of the island's ponds, where it makes the outermost fringe of vegetation along many a bushy shore, its wandlike arching and recurving stems forming an airy embankment above the water. In the autumn its foliage becomes as brilliant as it is possible for leaves to be and encircles some of the smaller ponds with a zone of variegated scarlet. The Pout Ponds deep set among the hills make a memorable scene when thus emblazoned.

On Nantucket this plant seems to be always more or less pubescent, the upper part of the stem and the leaves beneath even densely tomentulose with branched or substellate often ferruginous hairs.

New shoots a few inches high May 30, 1909, and just noticeable June 3, 1911; in full flower Aug. 15, 1906.

### LYTHRUM SALICARIA L.

Mrs. Owen's catalogue records "a few plants in danger of extinction near Long Pond." Today, twenty-five years later, a few plants are still to be found there. They grow close to the shore at the "Gut," where I first saw them Aug. 12, 1906, then passing out of bloom. It was in full flower July 10, 1912, and beautifully conspicuous from the bright rose-purple spikes borne by three separated groups of plants. On June 1, 1909, the tallest plants were about six inches high.

The Nantucket plant is the form having the upper stem and the leaves with the bracts and calyx densely white tomentulose—*var. tomentosum* (Mill.) DC.



## MELASTOMACEAE

## RHEXIA VIRGINICA L.

Common in sandy swamps and along pond shores. In fresh flower Aug. 12, 1906; continues to bloom into September. The leaves show considerable variation in form, from lanceolate-oblong and acute, to ovate or, on small plants, even quite orbicular.

## ONAGRACEAE

## ISNARDIA PALUSTRIS L.

Very common in muddy pond holes and ditches.

## \* LUDWIGIA ALTERNIFOLIA L.

Another one-locality plant of Nantucket. It was found Aug. 29, 1904, well established about one of the small ponds at Shimmo Valley farm, bearing abundant fruit and some late flowers.

## \* CHAMAENERION ANGUSTIFOLIUM (L.) Scop.

This tall herb, so conspicuous when in bloom from midsummer till autumn, is not included in Mrs. Owen's catalogue of 1888 although it had become frequent not many years later. It seems to have been first collected as far back as 1886 by Mrs. Cornelia L'Hommédieu near the Agricultural Grounds. Two years later it was found by Mrs. Owen in Polpis, and again, in 1892, by Mrs. Mabel P. Robinson. There is no record that it was anywhere common before 1895, when Mr. Dame reported it as abundant at Gibbs Swamp "appearing after an extensive brush fire," and Mr. Floyd found it well established on the "commons." For these records I am indebted to Mr. Floyd's manuscript notes. Today the plant is rather common, even locally abundant, on the eastern side of the island from Polpis and about Sauls Hills to Tom Nevers Swamp, and along the railroad in the southeast quarter. It does not yet appear to have spread into Shawkemo, Quaise, Pocomo or Squam. Further west it occurs at a few stations in the South Pasture, in Taupawshas Swamp, and near the state road not far beyond the town. On the western side of the island I have met with it near Miacomet Pond (1899), the "Woods" (1904), and Trots Swamp (1912). First flowers July 3, 1912; it sometimes continues to bloom until late in September.



A single plant with white flowers was found in Gibbs Swamp by Mr. Dame in 1895 (F. G. Floyd).

*EPILOBIUM HIRSUTUM* L.

Common in the lower parts of the town and out into the suburbs, often massed along ditches and in the corners of damp lots and low fields; also by the roadside in Shawkemo, the only place where I saw it far out from the town. Mr. Floyd reports that it was found by Mr. Dame in 1895 well established at Gibbs Swamp, where it was very common the following year coming in with the preceding species after an extensive brush fire. According to Mrs. Owen its introduction on the island was in or about the year 1855, when it was raised in a garden in Union Street, subsequently spreading into waste places.

First flowers July 6, 1912; blooming through September.

On the uninhabited southern extremity of Chappaquiddick Island, Marthas Vineyard, a single plant, still in flower, was found Sept. 28, 1912, growing with an abundance of *Chamaenerion angustifolium* in a grove of pines which had been swept by fire early in the same year.

\* *EPILOBIUM PALUSTRE* L.

Rare and local; sphagnum bogs in Squam and west of Sankaty and near Reed Pond, also Tom Nevers Swamp. It appears to flower earlier than *Epilobium lineare*; mature fruit Aug. 13, 1908. Still some flowers Sept. 11, 1907. Collected at one station on Marthas Vineyard. This is the slender little bog plant that has been called var. *monticola* Haussk. Its variations are considerable, however, and take it into forms that are close to typical *palustre* as well as into others that nearly match specimens of var. *labradoricum* Haussk. It is from 1-2 dm. high, erect, often with decumbent base and sometimes stoloniferous, simple with a single terminal flower or well branched, the glabrate leaves numerous and closely ascending or more distant and spreading, sessile or petiolulate, 1-3 cm. long, 1-4 mm. wide, linear-lanceolate to oblanceolate or oval-oblong, either tapering or contracted to the rounded apex, thickish or rather thin; pedicels very slender, mostly elongated, sometimes longer than the pod, again only one quarter its length.



## EPILOBIUM LINEARE Muhl.

Common in bogs. Plants six inches high June 27, 1912; first flowers Aug. 14, 1906; continues to bloom through September.

## \* EPILOBIUM STRICTUM Muhl.

Rare and local in bogs and wet mossy places in open ground. Watts Run bog, Shawaukemmo meadow, shore of Sachacha Pond—only a few plants at each locality. Plants 15 inches high June 15, 1908, and ten inches high July 1, 1912, but showing no flower buds; in flower and with mature fruit Sept. 19, 1899.

## EPILOBIUM COLORATUM Muhl.

Rather common in low grounds or wet places. Plants several inches high June 28, 1912; observed in flower late in September.

## \* EPILOBIUM ADENOCAULON Haussk.

Not rare, occurring in low grounds or damp thickets. Tom Nevers Pond and swamp, Taupawshas Swamp, Shimmo, Coskaty. Freshly in flower Aug. 7, 1906, in flower and with mature fruit Aug. 30, 1904, some flowers Sept. 19, 1899. Plants of pronounced character were collected in Tom Nevers swamp, the leaves 6–9 cm. long by 2–2.5 cm. broad. The flowers are commonly larger and much deeper in color than those of *Epilobium coloratum*.

## OENOTHERA BIENNIS L.

Common in fields and open places, in thickets and woodland and as a weed in waste and in cultivated ground, flowering from midsummer through September. First flowers July 6, 1912. Its widely varying forms seem to hint at more than one species and appear to include crosses with *Oenothera muricata*. There are long pod forms and short pod forms that display marked contrasts. In the former the capsules are tapering linear and rather prominently quadrangular, becoming 4 cm. long and 4–5 mm. wide at the base; in the contrasted form they are commonly 2–3 cm. long and 5–7 mm. wide, less tapering and more abruptly contracted at the apex and with more rounded angles; in both forms the capsules may be either densely pubescent or glabrate. The flowers are commonly 4–5 cm. wide but are sometimes considerably smaller; the largest seen were 6.5 cm. wide on plants that after having been partly cut down had



recovered their growth. A form found on the eastern side of the island was noteworthy from the shiny and bright red-purple sparsely pubescent stem and branches which, with the subglabrate capsules, were viscid to the touch; the flowers and capsules were of medium size, the thin leaves lanceolate, with attenuate base and apex, the lowermost slender petioled.

\* *OENOTHERA MURICATA* L.

Common, especially along shores, often in pure sand, but also in sandy and gravelly spots in all parts of the island. First flowers July 8, 1912; flowering through September.

Professor DeVries who, on his first visit to America, looked over some of my Nantucket and Long Island specimens of this *Oenothera* pronounced them to be essentially the same as the introduced American plant growing in Holland known to him as *O. muricata* L. Miss Vail has recorded (Carnegie Inst. Wash. Publ. No. 81: 74) that "*O. muricata* L. raised from seed received from Professor DeVries from the Holland sand dunes resembled these American plants but were not absolutely identical."

As compared with *O. biennis* this is a lower and more leafy-bracted plant with more numerous and ascending leaves of narrower form and thicker texture and less definitely repand denticulate, the lower with oblanceolate tendency; the general pubescence is softer, denser and more appressed, the longer hairs tending to form a villous or even pilose investiture especially on the capsules. In *O. biennis* the sparser pubescence is harsher and more or less hirsute, the smaller hairs mostly erect and incurved; the seeds are considerably smaller than those of *O. muricata*.

\* *OENOTHERA STRIGOSA* (Rydb.) Mackenzie & Bush.

On June 19, 1910, many plants of this western species were found scattered through a once cultivated field on the Cabot farm in Shimmo valley; they were in full flower and a few bore capsules already 2 cm. in length. Specimens collected agree closely with the types of *O. strigosa* in the Herbarium of the New York Botanical Garden. Doctor Rydberg, who made the comparison with me, concurs in the determination. The plant seems to be new to our eastern flora and must be supposed to have been recently introduced. It was perhaps only transient at the Cabot farm



since it was not to be found there in June of the two years following its discovery. The plants, although well flowered and having stout roots, were unbranched and were rather contracted in habit as if repressed by some unfavorable condition of soil or surroundings. They were 2-4 dm. high, the simple stem sulcate, the crowded leaves rather undersized and erectly ascending, thickish and light green, the lowermost already turning purplish-red, pubescence dense and subappressed, of soft and somewhat silky hairs; flowers at first bright yellow becoming pinkish-red basally or throughout; petals 1.5-2.5 cm. long, 2.2-2.5 cm. wide, obovate, rounded or truncate; hypanthium 2-2.5 cm. long; flower buds abruptly narrowed or rounded to the apex; sepal tips very short. The earlier flowering period as compared with that of our native eastern species is especially to be noted.

Another closely allied *Oenothera*, *O. canovirens* Steele, described from Illinois (Contr. U. S. Nat. Herb. 13: 365. 1911), is not very different from this, but its longer hypanthium and longer sepal tips appear to be well marked distinctive characters, and other differences in the specimens I have seen lead me to think it a valid species. It is clearly not the same as *O. subulifera* Rydb. from Montana\* which is also characterized by long sepal tips.

It may here be recorded that *O. canovirens* also occurs on the Atlantic seaboard. As long ago as Aug. 9, 1906, I collected it at Van Cortlandt, New York City, and put aside specimens under a manuscript name as a new species. These have been deposited in the herbarium of the New York Botanical Garden. My notes record that the flowers were not fragrant as were those of *O. biennis* with which it grew. A less densely pubescent form of *O. canovirens* was collected at Lynbrook, Long Island, July 3, 1910, growing along a new made roadway; the flowers were conspicuous from the reddish orange suffusion towards the base of the petals.

\* *OENOTHERA OAKESIANA* Robbins.

Scarce; found only along a roadside northwest of the town and below the "Cliff." In flower and with small capsules Aug. 4, 1906; mature fruit Sept. 9, 1904. The Nantucket plant agrees closely with the plant of the Hempstead Plains, Long Island.

\* Bull. Torrey Club 40: 66. 1913. *O. strigosa subulata* Rydb. Mem. N. Y. Bot. Gard. 1: 279. 1900.



specimens from both places were used by Doctor MacDougal in his "Mutation Studies," 1904.

\* *Oenothera stenopetala* sp. nov.

Dwarf, 1-4 dm. high, erect, often geniculate at base, simple or sparingly branched, the branches ascending, often surpassing the main stem; root woody, slender and elongated, mostly simple or nearly so; stem pale brown, sometimes slightly reddened below when old, lignescent and terete below, the bark early splitting and exfoliating in thin strips; above, and the branches, somewhat angled decurrently from the insertions of the leaves, closely appressed canescent-puberulent, sometimes thinly short strigillose above. Leaves often erectly ascending, pale green, narrowly oblong to linear-oblong, 4-7 cm. long, 5-10 mm. wide, acute or subacute, the lower tapering into slender petioles, the uppermost and the bracts sessile with tapering base, or, even the bracts also, sometimes short petioled, entire or obscurely repand denticulate, on both surfaces finely white pubescent with appressed hairs; flower buds densely appressed strigillose and downy puberulent with gland tipped hairs; hypanthium very slender, 2-3 cm. long, glandular-puberulent; sepals 7-12 mm. long, glandular-puberulent and subpilose, the apical process subterminal, about 2 mm. long; petals narrowly linear, pale yellow, spreading, at length reflexed, puberulent on the outer surface and often slightly so within, 10-22 mm. long, 1.5-3 mm. wide; stamens longer than the style; filaments becoming 10 mm. long, anthers 3-4.5 mm. long; capsule tapering from the base or from above the middle to a narrowed apex, quadrangular with rounded angles, 2.5-3.2 cm. long, 5-7 mm. wide, when young whitened with a dense appressed subsericeous pubescence becoming appressed pubescent and slightly strigillose.

Type Aug. 15, 1906, in Herbarium New York Botanical Garden.

Found only along the sandy embankments of the railroad beyond the Orange Street crossing, where it was common in 1906 and 1907. In full flower and with some immature pods Aug. 5, 1906; still in flower, and with full sized pods Aug. 15; a few last flowers Sept. 11, 1907. On June 19, 1908, the larger plants were 3-4 inches high.

It is interesting to find that this plant was collected on Nantucket by Morong as long ago as Aug. 31, 1871, as evidenced by a flowering specimen in the Herbarium of the New York Botanical Garden labeled by Mr. Morong's hand "*Oenothera biennis* var.



*parviflora*." Others have also found the plant there, for Mr. Floyd's notes refer to collections as follows: Orange street, 1904, Mrs. Nellie F. Flynn; roadside near Maxcys Pond, 1905, Joseph R. Churchill, both determined as *O. cruciata* Nutt.

Notwithstanding the narrowly linear petals of this the smallest of our *Oenotheras* there can be little doubt that its real affinity is not with *O. cruciata*, a near relative of *O. biennis*, but rather with *O. Oakesiana* with which it agrees closely in pubescence and to some extent in the form of the capsule. *Oenothera cruciata*, which would be quite out of its known range on Nantucket, is an altogether larger and to an extent a glabrate species becoming thinly papillose hirsute with stiff spreading hairs. It differs throughout from the Nantucket plant; the bracts subtending the flowers are broad based, not narrowly tapering or petiolulate; the sepal tips are twice longer; the linear petals are materially shorter, never apparently becoming much more than half the length of the longest in *O. stenopetala*. As compared with *O. Oakesiana*, *O. stenopetala* is a much smaller plant; its pubescence although similar is less dense and canescent, sometimes taking an appressed strigillose character, especially on the broader based and shorter capsule; the cauline leaves are longer petioled and less sinuate or not at all so; the bracts are more narrowed to the base, the sepal tips much shorter and subterminal, the petals different beyond comparison.

An ambiguous *Oenothera*, which grew near *O. stenopetala*, seemed quite intermediate in pubescence and leaf characters between that species and *O. muricata* and appeared like a hybrid between them. The flowers were very small but with the petals quite as broad as long, mostly 10 mm. or less in length and breadth, a few as much as 15 mm. This plant is also suggestive of *O. Oakesiana* but the pubescence is coarser, the leaves more entire, the capsules stouter and less crowded and with more foliaceous bracts and the sepal tips are terminal and very short.

\* *OENOTHERA LAMARCKIANA* DeVries.

Not *O. Lamarckiana* Seringe (1828). See Davis, Bull. Torrey Club 39: 519-533. pl. 37-39. 1912.

The occurrence of this now storied plant on Nantucket as an stray from cultivation has already been reported by MacDougal



(Carnegie Inst. Wash. Publ. No. 81: 6. 1907). It was found in August, 1904, in the neglected yard of a small house on lower Union Street, where it had spread among the grass and weeds and strayed outside the fence into an adjoining waste lot. Inquiry gained the information that a number of years before it had been raised from seed that had been given to the then occupant of the premises. It could be seen that the plant had spread naturally from two small and long undisturbed flower beds now almost obliterated by an incursion of weeds and grass. The specimens submitted to Doctor MacDougal were collected Aug. 29, 1904, bearing flowers and mature fruit. Other specimens were collected Aug. 15, 1906. In September, 1907, it was found that a general clearing up of the locality had almost exterminated the plant and a straggling individual in the yard and one in the adjoining lot were all that could be found. Subsequently, with further alterations in the surroundings, the plant had disappeared. But on a transient visit to Nantucket, Sept. 28, 1912, the same *Oenothera* in full flower was seen in almost complete possession of a small uncared for yard in a built up part of the town.

The flowers are remarkably showy, the petals bright golden yellow, the sepals deep purplish red in marked contrast. The largest corollas were 12.7 cm. across the expanded petals, the smallest less than half that size (6 cm.). No fragrance was perceptible. On bright days they open late in the afternoon closing in the forenoon of the following day. The capsules were 2.8–3.2 cm. long, papillate-hirsute, and glandular-puberulent with minute spreading hairs; seeds 1.5–2 mm. long, distinctly wing angled, wrinkled-lineate and rugulose.

Doctor MacDougal in his "Mutation Studies" of this species took seeds from the Nantucket specimens collected in 1904 and sowed them in sterilized soil in November of the same year. "On Jan. 27, 1904 [1905], 24 plantlets representing the widest diversity observable were transplanted to small pots in accordance with the usual practice. Six of these corresponded quite exactly to the mutant *O. albida* . . . all the other individuals developed in accordance with qualities of *O. Lamarckiana* with a maximum amount of color in the buds and also a maximum number of basal branches of some length" (Carnegie Inst. Wash. Publ. No. 81: 6. 1907).



\* *KNEIFFIA PUMILA* (L.) Spach.

Not uncommon and actually widely scattered on the island, but very local. A few dried up plants were met with in September, 1899, below the "Cliff," where it was not seen again until June, 1910, when it was fairly common. It occurs also in meadows and low grounds in Squam towards Polpis; near the Polpis school-house; in the "Thorn Lot"; about a mile west of the town; at the Weweeder Ponds; the "Woods," at two stations, and by the Sheep Pond in the southwestern corner of the island.

Green buds only June 9, 1909; first flowers June 9, 1911; in full flower and with small pods June 15, 1910; still in bloom July 11, 1912.

Specimens from below the "Cliff," collected June 15, 1910, have reddened stems and flower buds and calyces of a bright purplish red. At all other localities the plants were without any obvious reddish tinge.

*CIRCAEA LUTETIANA* L.

Frequent in thickets on the eastern side of the island from Shawkemo to Squam and Coskaty. First flowers July 11, 1912; mature fruit Sept. 17, 1907; fruit mostly gone Sept. 20, 1907.

## HALORAGIDACEAE

*PROSERPINACA PALUSTRIS* L.

Common in the borders of muddy ponds and in pools and ditches. Just in flower July 2, 1912.

*MYRIOPHYLLUM TENELLUM* Bigel.

In abundance along the muddy borders of a pond west of Madequet ditch, growing in exposed spots as well as among the cat-tails. In full flower July 10, 1912. Mrs. Owen has recorded that it was found by her in Cains Pond in 1858.

*MYRIOPHYLLUM HUMILE* (Raf.) Morong.

Common in ponds and pools or, where the water has receded, on drying mud. At Maxcys Pond, Sept. 12, 1907, the terrestrial form was abundantly in flower and fruit, the submersed form in fruit only, and very sparingly. On Sept. 10, 1899, the form with emersed spikes bore both fruit and flowers. In all three phases of



the plant the carpels, about 1.25 mm. long, were prominently tuberculate or minutely papillose-roughened, often with a smooth dorsal space between two indistinct ridges. Occurs on Tuckernuck.

### ARALIACEAE

#### ARALIA NUDICAULIS L.

Not common and found only in the dense thickets on the eastern side of the island from Shimmo to Polpis, Pocomo and Squam; also at Tom Nevers Swamp, and on Tuckernuck. Just in flower June 2, 1909.

### UMBELLIFERAE

#### HYDROCOTYLE UMBELLATA L.

One of the most common aquatics of Nantucket having found its way into almost all of the fresh water ponds and pools. Also on Tuckernuck. The floating leaves begin to appear by the end of May. In full flower and fruit through September.

#### \* SANICULA MARYLANDICA L.

This is one of the plants of Nantucket that have been found only at a single spot. On July 4, 1912, I came upon a thriving colony of about fifteen plants hidden in the seclusion of a thicket in Squam not far east of Watts Run; they were in full flower and well set with young fruit. This species is frequent in the thickets of Chappaquiddick Island, Marthas Vineyard.

#### \* SANICULA CANADENSIS L.

Also found only at a single station, and only one plant. It grew at the border of a thicket in Squam towards Wauwinet, Aug. 13, 1906, a well-fruited plant nearly 9 dm. high. It is scarcely to be doubted that other plants are to be found among the extensive and almost impenetrable thickets in that part of the island although I have not succeeded in rediscovering it. It occurs on Marthas Vineyard and I know of a single colony on Chappaquiddick Island.

#### \* CONIUM MACULATUM L.

Occasional in waste ground about the wharves and in the outskirts of the town. Some plants were already nearly five feet tall June 4, 1911, the umbels still close and green. In full flower June 29, 1912.



\* *PETROSELINUM HORTENSE* Hoffm.

A weed in a garden, 1897, Mrs. Nellie F. Flynn. Possibly merely persistent after cultivation. A specimen received from Mrs. Flynn was collected Aug. 16, bearing mature fruit.

\* *CICUTA MACULATA* L.

Capaum Pond, May 30, 1909, a single tuft 14 inches high on the west side of the pond back of the beach. Not seen since. Met with at two localities on Marthas Vineyard.

\* *CICUTA BULBIFERA* L.

Mrs. Nellie F. Flynn has sent me for examination a specimen of this species collected Aug. 18, 1899, in a ditch near Shawauk-emmo spring. It is a stout plant, 8.5 dm. tall, in full flower and bearing many clusters of young bulblets. Mrs. Flynn has now no recollection of having seen more than this one plant, the only one known ever to have been collected on Nantucket.

*SIUM CICUTAEFOLIUM* Schrank.

Common about the borders of fresh water ponds and in swamps and ditches. The leaves are well developed at the end of May. First flowers July 11, 1912.

*PTILIMNIUM CAPILLACEUM* (Michx.) Raf.

Abundant in damp places in either fresh or brackish soils. The seedling plants become visible early in June and are in full flower and fruit in September.

\* *AETHUSA CYNAPIUM* L.

Occasional about the wharves and by street sides in the town. On every visit to Nantucket I see it somewhere, but never more than a few plants, and usually at some new locality. Umbels showing white June 4, 1911; first flowers June 10, 1909; in full flower and fruit in September.

\* *ANETHUM GRAVEOLENS* L.

Mrs. Flynn has sent me specimens of this plant collected by her from a large clump growing in a waste spot among the Scallop houses near the harbor shore.



## LIGUSTICUM SCOTICUM L.

In abundance along the shores of Baches Harbor and Polpis Harbor and on the western side of the island at Great Neck and Little Neck. It also grows at the ice houses by Maxcys Pond where it has doubtless come in with eel grass taken from the sea shore. On the south side of the island it was seen only by Madequecham Pond, a single tuft. A dense cluster at Little Neck in 1904 was six feet across. No flowers observed up to the first week in July; fruit in all stages of maturity may be found early in September and flowers until late in the month. Locally common along the shores of Edgartown Harbor, Marthas Vineyard.

## \* CORIANDRUM SATIVUM L.

Well established through an abandoned weedy yard at the south end of the town; in full flower June 28, 1912.

## \* COELOPLEURUM ACTAEIFOLIUM (Michx.) Coult. &amp; Rose.

At Wauwinet many plants of this stout umbellifer are scattered through the low bayberry thickets that clothe the bank above the harbor shore. They were in full flower July 11, 1912, and bore many umbels still undeveloped as well as others heavy with mature fruit. The largest plants were over four feet high. In the same thickets the cow parsnip (*Heracleum*) had long since flowered and was completely dried up. A single large plant of the *Coelopleurum* in flower and with young fruit was found at the border of a low field near the shore on Beach Street, June 6, 1911. It had doubtless been introduced there, more than probably from the Wauwinet locality some eight miles up the harbor. Nantucket seems to be the southernmost point to which this northern plant has made its way.

## \* PASTINACA SATIVA L.

A casual weed of fence borders and waste ground. It is of frequent occurrence by roadsides south of the town and about Milestone farm but is not often met with elsewhere; near Millbrook swamp Aug. 9, 1906. First flowers June 12, 1909, June 19, 1910.<sup>9</sup>



## HERACLEUM LANATUM Michx.

Common all along the harbor in the northeastern quarter of the island from Shimmo to Wauwinet, growing up among the shrubbery back of the beaches and in the shore thickets; too common and vigorous among the rarer native plants on Rattlesnake bank; Polpis; west of Sankaty. Tuckernuck. First flowers June 2, 1909; conspicuously in bloom June 7, 1908; a few last flowers June 29, 1912.

## DAUCUS CAROTA L.

Very abundant, whitening fields and pastures through July, August and September. The green umbels begin to unfold about the middle of June and the flowers become noticeable early in July. First flowers June 26, 1910, June 27, 1912; umbels frequently pink.

## CORNACEAE

## CHAMAEPERICLYMENUM CANADENSE (L.) Asch. &amp; Graebn.

*Cornus canadensis* L.

Rare, but abundant at one locality in Shawkemo near Quaise where in a damp shaded thicket it fairly carpets the ground; it occurs also, but sparingly, in a thicket in Polpis. First flowers June 4, 1909; in full flower June 7, 1908.

## CYNOXYLON FLORIDA (L.) Raf.

*Cornus florida* L.

Not rare among the extensive thickets in Squam where I have come upon it at perhaps half a dozen stations, single trees or a few together, except in one instance where as many as thirty, most of them in poor condition, formed a close group. The trees are mostly well matured but not over ten or twelve feet high. At Beechwood in Polpis it is more numerous and of freer growth, the larger trees having attained a height of certainly 18-20 feet. I have seen it elsewhere on Nantucket only near the state road a mile or so west of Siasconset, where a dense thicket conceals a cluster of several old trunks of widespread branchment but not over 4-5 feet high, the lower branches nearly prostrate. At Beechwood it was in full flower June 12, 1909. A group of small trees was found on Tuckernuck, June 17, 1911.



\* *CORNUS AMOMUM* Mill.

Fringing a brook along the north side of Trots swamp; a second locality is at Capaum Pond where there are several thick clusters near the shore on the west side of the pond. Cymes just appearing June 10, 1908; in full flower July 12, 1910; ripe fruit Sept. 12, 1907.

*NYSSA SYLVATICA* Marsh.

A common tree on the eastern side of the island, wanting over much of the western side; small trees grow on Coatue. Tuckernuck. It is ordinarily not taller than 8-10 feet, although trees 15 feet high are not uncommon; in Pocomo are groups of larger trees over twenty feet in height, and in Beechwood are some that are certainly not less than 30-35 feet high, equalling in height the tallest red maples. Probably there are no taller native trees anywhere on Nantucket. The trunks of these were not as thick as those of lower trees on Pocomo where the largest seen was 28 inches in circumference. A still stouter trunk of a not particularly tall tree in Quaise was 35 inches around one foot above the base. Coming into leaf June 3, 1909; anthers visible but not yet mature June 8, 1911, June 15, 1908; in full flower and with small green fruit June 20, 1910.







Phytogeographical notes on the Rocky Mountain region  
II. Origin of the alpine flora\*

P. A. RYDBERG

When studying the flora of a certain region or district, one naturally asks himself the following questions: What is the origin of these plants? Where did they come from? How did they come there? Where else are they found? Why are they found there and not in adjacent territory? Why are they there and not in other similar regions? Why are other plants found in similar regions and not there? Many other similar questions might be asked and none of them could be satisfactorily answered. We can only make suggestions and surmises. Some answers may seem satisfactory to us now, as others may have seemed satisfactory to generations gone by; others may seem merely probable, and still others not even so. The alpine regions of the Rockies are merely small isolated spots, when the whole mountain range is considered. They can be compared with a number of small islands, now surrounded (so far as many of the species are concerned) by barriers insurmountable, more so even than islands in an ocean could ever be. It is far easier to tell what an alpine plant is (and I have already in a former paper tried to give a definition thereof) than to tell how it came there. If we had only endemic species to deal with, we should perhaps explain its existence by a spontaneous generation or as something originated from a related species, which exists or has existed in the subalpine region below. The belief in a spontaneous generation, at least so far as the higher plants or animals are concerned, is now generally discarded. The derivation from related species of the subalpine region is in many cases a satisfactory explanation of the existence of many endemic alpine species but not of all. But how shall we explain the existence of the same plant in the alpine regions of Colorado and the Alps in

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\* In this paper the sedges have been omitted, as they have not yet been worked up. Without an authentic determination of the species, it is risky to discuss such a critical genus as *Carex* in a phytogeographical paper.



Europe, as for instance *Potentilla nivea*, *Lloydia serotina* and *Viola biflora*? This question leads to other related ones. Has a species originated only once or can the same plant arise at the same time or at different times at two or more isolated localities? Are the individuals of *Potentilla nivea*, now growing in Colorado, in the Alps, in Scandinavia, in Greenland, etc., offsprings of the same parent *Potentilla nivea* living ages ago, or did the species originate independently at the different places? In the case of *Potentilla nivea*, I rather think that it is monotypic and has had a much more general distribution than it now has, for it is a common plant in the arctics. But this is not the case with *Viola biflora*, which is not an arctic plant. Until lately the only localities known in this country were in Colorado, but now it is known also from Alaska.

It is not, however, impossible that some so-called species have had a polytypic origin. *Primula farinosa* is a plant of the Alps, northern Europe, northeastern America, and apparently the same plant is found in south Chile to Terra del Fuego. In both cases, however, the plant itself or else the parent plant, from which it originated, must have had a much greater distribution than it now has. We know of many plants which in earlier periods have been distributed over much greater territory than they now are, as for instance *Ginkgo biloba* and *Taxodium distichum* were once found in Europe, while they now are restricted, the former to northeastern Asia and the latter to the southern United States.

It was stated before that many of the alpine plants of the Rockies are also arctic or subarctic, and as far as the Rockies are concerned the seeds could be carried by wind and animals from mountain top to mountain top, as the stretches are not so far, the mountain chain running north and south, but this would not be a satisfactory explanation in Europe and Asia where the principal chains run east and west and at a great distance from the arctic. Another explanation must therefore be given. The most plausible and most generally accepted theory concerning the origin of the alpine flora is the following. In the glacial periods, the regions in front of the ice-sheet became unfit for the woody vegetation and in fact for all plants except the arctic-alpine elements. The forest receded south in front of the advancing ice. The temperature in the mountain regions south thereof became lower and lower, the



glaciers increased and extended downwards and the forests receded down the mountain sides. At last the foothills and even the plains of northern Europe, Asia and America received an alpine-arctic climate and bore mostly arctic vegetation. As the ice sheet receded, the climate became more temperate, the forest again took possession of the land and the arctic plants were partly driven towards the pole, partly up the mountains, until in our days they are confined to the arctic regions and the highest mountain tops, where they have become isolated. In America the glacial drifts did not reach as far south as Colorado, but evidently the temperature during the glacial epoch must have been low enough, so that the local glaciers of the Rockies may have covered most of the mountains, and the great plains and the foothills surrounding them undoubtedly had an arctic or subarctic climate at that time. Many of the arctic plants had originated before the glacial period and had spread over the two continents. Some of these still exist on both, others might have died out on one of the continents, but remain on the other. Some might become exterminated in the mountain regions while continuing their existence in the arctic regions, or vice versa. Some, after isolation, might have changed in the course of time and developed into new species. This is perhaps more common in the case of the alpine than of the arctic plants. The arctic-alpine plants may therefore be classified in the following categories.\*

1. Circumpolar arctic-alpine or glacial plants, found in the arctic as well as in the mountain regions of both continents.

2. Eurasian arctic-alpine or glacial plants, found only in the mountains of the Old World and the arctic regions. Some of these may be:

(a) European arctic-alpine or glacial plants, with the center of distribution in the Alps;

(b) Asiatic arctic-alpine or glacial plants, with the center in the Altai.

3. American arctic-alpine or glacial plants, confined to the mountains of the New World and the arctic.

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\* Here I do not include the alpine plants of tropical regions, which must be considered altogether by themselves.



4. Eurasian alpine plants, found in the mountains of the Old World, but not in the arctic regions. The principal subdivisions of this group are:

(a) Alpestrian, endemic plants of the European Alps, including the Pyrenees and the Caucasus;

(b) Altaic, north Asiatic alpine plants.

5. American endemic alpine plants. The principal regions of these are the following:

(a) Sierra Nevada, including the Cascade Mountains, which latter, however, contain an intermixture of some elements belonging to the next;

(b) Rocky Mountains, including the San Francisco Mountains and the other ranges of Arizona, New Mexico and northern Mexico;

(c) White Mountains. Most of the plants of this region belong to the arctic-alpine group, but endemic alpine plants are not wholly lacking, as for instance, *Potentilla Robbinsiana* and *Sieversia Peckii*.

6. Circumpolar arctic plants, not found in the mountains.

7. Eurasian arctic plants, which do not concern us at all.

8. American arctic plants.

9. Subarctic and

10. Subalpine plants, which encroach on the arctic and alpine regions.

#### CIRCUMPOLAR ARCTIC-ALPINE OR GLACIAL PLANTS

These species probably had originated before or during the glacial epochs. In some cases the origin probably was somewhere in the Old World, in others in the New World. Of course, we cannot know, but we may surmise. The region which contains the most numbers of certain groups of species may probably be the place where this group originated (*i. e.* the home of the parent species) and where the individual species sprang from. As for instance, there is a group of arctic-alpine species of *Potentilla* with ternate leaves white-wooly beneath. *Potentilla nivea* is the most generally distributed species of the group; it is also the first and best known. Where is the probable ancestral home of this species? The species is found in Europe, rather common in the Scandinavian mountains,



but not so common in the Alps. It is the only species of the group there. It is, therefore, not probable that its ancestry came from that region. The group is represented in both North America and Asia by several species. The American species, except *P. nivea* and *P. uniflora*, are rather local, and are modified to adapt themselves to local conditions. Both *P. nivea* and *P. uniflora* as well as *P. villosa* (found in the northwestern corner of this continent) are found in Asia, together with several others of the group. *P. nivea* itself is common there in the mountains as well as in the arctic, while it has been collected only at a few places in the Rockies of Colorado. It is therefore probable that the group originated in Asia.

Let us now discuss the plants of this category. The following plants are common to the arctic regions of both continents, the Alps, and the Rockies as far south as Colorado. Most of these are also found in Asia. Those with a star are also found in the subalpine regions.

* <i>Phleum alpinum</i>	<i>Salix reticulata</i>
* <i>Trisetum subspicatum</i>	<i>Oxyria digyna</i>
* <i>Deschampsia caespitosa</i>	* <i>Bistorta vivipara</i>
<i>Poa cenisia</i>	<i>Silene acaulis</i>
* <i>Poa alpina</i>	<i>Thalictrum alpinum</i>
<i>Festuca supina</i>	<i>Ranunculus pygmaeus</i>
* <i>Festuca ovina</i>	<i>Draba fladnizensis</i>
* <i>Festuca rubra</i>	<i>Muscaria adscendens</i>
<i>Juncus triglumis</i>	<i>Potentilla nivea</i>
<i>Juncus castaneus</i>	* <i>Astragalus alpinus</i>
* <i>Juncoides spicatum</i>	<i>Campanula uniflora</i>
<i>Lloydia serotina</i>	<i>Myosotis alpestris</i>

Some of these species extend into mountains situated so far south that they could not have been connected with the arctic regions even in the glacial times. The existence of these species there has to be explained in some other way. In most cases their seeds were probably carried by birds or other animals or by the wind. Included among such plants are the following:

*Lloydia serotina*, a typical arctic-alpine plant, is found not only in the arctic regions, the mountains of northern Europe and Asia, the Alps, the Rockies and the Sierra Nevada, but also in



mountains farther south, as the Pyrenees, the Caucasus, the Himalayas, and, in America, in the San Francisco Mountains, Arizona. Like most bulbiferous plants, it does not readily propagate by seeds, but when these are formed, they may easily be distributed by the wind on account of their flatness.

*Juncooides spicatum* has about the same distribution except that it is not found in the Himalayan region. The seeds of this species must have been carried by birds as they are too heavy to be carried by wind.

*Poa alpina* extends south to the Sierra Nevada (Spain), the Appennines, and the Himalayas, and *Trisetum subspicatum* and *Phleum alpinum* extend in America south through the mountains of Mexico, Central and South America. As these grasses also are subalpine, their seeds have probably been distributed by animals.

The following two species are common to the arctic regions of both hemispheres, to the Rockies, and to the Asiatic mountains, but not found in the Alps: *Draba glacialis* and *Anemone parviflora*.

*Saxifraga cernua* and *Campanula uniflora* are circumpolar glacial plants, but do not reach the Alps. They are found in America as far south as Colorado and Utah. Either these plants are of American origin and have extended their range over northern Europe, or else they have perished in the Alps.

The same may be said about *Micranthes hieracifolia*, although it does not reach the southern Rockies.

*Aster alpinus* is a glacial plant found both in the Alps and the Altai, rare in the Rockies and lacking altogether in the Scandinavian mountains.

Some of the circumpolar glacial plants, although they are found on this continent, are found neither in the southern Rockies nor in Sierra Nevada, although they are found in both the Alps and the Altai. Such are:

*Cerastium alpinum*

*Chondrosea Aizoon*

*Erigeron alpinum*

*Micranthes nivalis*

The first two are, however, represented by related endemic species.

A few of these circumpolar plants are found in the Alps, but neither in the Altai nor in the southern Rockies, as for instance



*Tofieldia palustris*. This is found in Great Britain, Scandinavia, northern Russia, the Alps, the Pyrenees and the Ural. Notwithstanding the fact that it is less distinctly arctic-alpine than for instance *Lloydia serotina* and has been collected in the lowland as far south as Two Harbors, Minnesota, it has not been collected in the Rockies south of northern Montana.

#### ASIATIC ARCTIC-ALPINE OR GLACIAL PLANTS

*Dasystephana glauca* is a distinctly Asiatic glacial plant, but also found in western North America, coming down south as far as Montana.

#### AMERICAN ARCTIC-ALPINE OR GLACIAL PLANTS

A large number of the alpine plants of the Rockies are strictly American glacial plants, i. e., found both in the mountains and the arctic regions of this continent but not in the mountains of the Old World.

1. In many cases they are there represented by closely related plants. In such cases the history of the plant might be the following:

(a) That the parent plant had a circumpolar distribution before or during the earlier part of the glacial period and the two related species developed independently from it;

(b) That the Old World plant existed on both continents during the glacial epoch and became modified after isolation on this side; or

(c) That the American plant existed and became modified abroad.

Here I give a list of such plants and the nearest relatives in the Old World.

AMERICAN	EUROPEAN	ASIATIC
* <i>Calamagrostis purpurascens</i>	<i>C. arundinacea</i>	
<i>Salix glaucops</i>	† <i>S. glauca</i>	
<i>Salix chlorophylla</i>	<i>S. phyllicifolia</i>	
* <i>Alsinopsis propinqua</i>	<i>A. verna</i>	

\* Those starred are also subalpine and subarctic.

† *Salix glauca* and *Rhodiola rosea* are also found in northeastern America, but not in the Rockies.



AMERICAN	EUROPEAN	ASIATIC
<i>Alsinopsis quadrivalis</i>	<i>A. verna</i>	
<i>Alsinopsis Rossii</i>	<i>A. verna</i>	
<i>Anemone zephyra</i>	<i>A. narcissiflora</i>	<i>A. narcissiflora</i>
<i>Ranunculus affinis</i>		<i>R. pedatifidus</i>
<i>Smelowskia americana</i>		<i>S. calycina</i>
<i>Rhodiola integrifolia</i>	† <i>R. rosea</i>	
<i>Leptasea austromontana</i>		<i>L. bronchialis</i>
* <i>Potentilla quinquefolia</i>	<i>P. nivea</i>	<i>P. nivea</i>
<i>Potentilla nipharga</i>	<i>P. nivea</i>	<i>P. nivea</i>
<i>Vaccinium oreophilum</i>	<i>V. Myrtillus</i>	
<i>Androsace carinata</i>	<i>A. Chamaejasme</i>	<i>A. Chamaejasme</i>
<i>Androsace albertina</i>	<i>A. Chamaejasme</i>	<i>A. Chamaejasme</i>
* <i>Swertia palustris</i>	<i>S. perennis</i>	<i>S. perennis</i>
<i>Amarella monantha</i>	<i>A. tenella</i>	<i>A. tenella</i>
<i>Amarella plebeia</i>	<i>A. Amarella</i>	<i>A. Amarella</i>
<i>Dasystephana Romanzovii</i>	<i>D. Froelichii</i>	<i>D. frigida</i>
<i>Condrophylla americana</i>	<i>C. prostrata</i>	<i>C. prostrata</i>
<i>Polemonium pulcherrinum</i>		<i>P. humile</i>
<i>Erigeron simplex</i>	<i>E. uniflorus</i>	<i>E. uniflorus</i>
<i>Erigeron melanocephalus</i>	<i>E. uniflorus</i>	<i>E. uniflorus</i>
<i>Artemisia saxicola</i>	<i>A. norvegica</i>	
<i>Artemisia spithamea</i>		<i>A. borealis</i>

Many of the endemic American glacial plants—or rather alpine-arctic plants, for most of them undoubtedly originated after the glacial period—are evidently derived from existing circumpolar glacial plants. Such are:

AMERICAN GLACIAL	CIRCUMPOLAR GLACIAL
<i>Deschampsia curtifolia</i>	<i>D. caespitosa</i>
<i>Poa arctica</i>	<i>P. cenisia</i>
* <i>Festuca saximontana</i>	<i>F. ovina</i>
<i>Agropyron biflorum</i>	<i>A. caninum</i>
<i>Cerastium Behringianum</i>	<i>C. alpinum</i>
<i>Draba andina</i>	<i>D. glacialis</i>
<i>Draba oligosperma</i>	<i>D. glacialis</i>

Some of these arctic-alpine plants had probably the same



parents as some existing circumpolar-arctic plants. While one offspring has remained arctic, *i. e.* has not spread south during the glacial period or else has died out in the alpine regions, the other has become both alpine and arctic with a purely American distribution, or else the latter has developed from the former since glacial time. Such plants are:

NORTH AMERICAN ARCTIC-ALPINE	CIRCUMPOLAR ARCTIC
<i>Chrysosplenium tetrandrum</i>	<i>C. alternifolium</i>
<i>Antennaria media</i>	<i>A. alpina</i>
* <i>Antennaria umbrinella</i>	<i>A. alpina</i>

A few strictly arctic plants have for some reason spread into the Rockies, their existence there being a little hard to explain. Among these may be mentioned *Phippsia algida*, which has been collected in one place in Colorado. It is otherwise not known out of the arctic. *Sagina nivalis* has been found in Colorado; otherwise only in the arctic regions of America and in the Scandinavian mountains.

The following are truly endemic American arctic-alpine plants without any close relatives as far as I know elsewhere:

<i>Ranunculus hyperboreus</i>	* <i>Erigeron compositus</i> and its close relatives, viz.
<i>Aragallus podocarpus</i>	* <i>Erigeron multifidus</i>
* <i>Vaccinium caespitosum</i>	<i>Erigeron trifidus</i>

The following are probably derived from subarctic or subalpine species:

* <i>Calamagrostis Langsdorffii</i> †	<i>C. canadensis</i> , American, subalpine and boreal.
* <i>Alsine laeta</i>	<i>A. longipes</i> , American, subarctic, subalpine and boreal.
* <i>Kalmia microphylla</i>	<i>K. glauca</i> , eastern American, subarctic and boreal.
* <i>Senecio cymbalarioides</i>	<i>S. aureus</i> , eastern American, boreal.

† This is also found in subarctic Scandinavia.



## AMERICAN ENDEMIC ALPINE PLANTS

More than one third of the alpine plants of the Rockies are endemic and if the subalpine element found just over the timberline, or occasionally higher up, is included, this proportion is increased to about half of all the species. Several of these are apparently derived from circumpolar glacial or arctic plants.

SOUTHERN ROCKIES	CIRCUMPOLAR GLACIAL OR ARCTIC
<i>Deschampsia alpicola</i>	<i>D. caespitosa</i>
<i>Ranunculus Macauleyi</i>	<i>R. nivalis</i>
<i>Parrya platycarpa</i>	<i>P. macrocarpa</i>
<i>Leptasea chrysantha</i>	<i>L. Hirculus</i>
<i>Muscaria delicatula</i>	<i>M. caespitosa</i>
<i>Muscaria micropetala</i>	<i>M. caespitosa</i>
<i>Saxifraga debilis</i>	<i>S. rivularis</i>
<i>Saxifraga simulata</i>	<i>S. cernua</i>
<i>Potentilla modesta</i>	<i>P. nivea</i> (perhaps through <i>P. quinquefolia</i> )

NORTHERN ROCKIES	CIRCUMPOLAR GLACIAL OR ARCTIC
<i>Salix nivalis</i>	<i>S. reticulata</i>
<i>Draba lonchocarpa</i>	<i>D. nivalis</i>
<i>Muscaria monticola</i>	<i>M. caespitosa</i>
<i>Micranthes Rydbergii</i>	<i>M. hieracifolia</i>
<i>Micranthes crenatifolia</i>	<i>M. nivalis</i>
<i>Spathularia Vreelandii</i>	<i>S. stellaris</i>
<i>Phyllodoce empetriformis</i>	<i>P. coerulea</i>
<i>Phyllodoce glanduliflora</i>	<i>P. coerulea</i>
<i>Cassiope Mertensiana</i>	<i>C. tetragona</i>

SOUTHERN AND NORTHERN ROCKIES	CIRCUMPOLAR GLACIAL OR ARCTIC
<i>Micranthes rhomboidea</i>	<i>M. nivalis</i>
<i>Micranthes arnoglosa</i>	<i>M. nivalis</i>
<i>Taraxacum scopulorum</i>	<i>T. arcticum</i>
<i>Salix saximontana</i>	<i>S. reticulata</i>

Others have no close relative on this continent, but may have the same origin as some Old World plants. A list of these is here given with the nearest relatives abroad.



NORTHERN ROCKIES	EUROPEAN	ASIATIC
<i>Salix Dodgeana</i>	<i>S. retusa</i>	
<i>Alsine americana</i>		<i>A. dichotoma</i>
<i>Leptasea Van Bruntiae</i>		<i>L. bronchialis</i>
<i>Drymocallis pseudorupestris</i>	<i>D. rupestris</i>	
<i>Eritrichium elongatum</i>	<i>E. nanum</i>	<i>E. villosum</i>

SOUTHERN ROCKIES	EUROPEAN	ASIATIC
<i>Condrophylla Fremontii</i>		<i>C. humilis</i>
<i>Anthropogon barbellatum</i>	<i>A. ciliatum</i>	
<i>Eritrichium argenteum</i>	<i>E. nanum</i>	<i>E. villosum</i>

Still other species are probably derived from, or have the same origin as, American glacial or American arctic plants.

#### SOUTHERN ROCKIES

<i>Poa pudica</i>	<i>P. arctica</i> , glacial
<i>Festuca minutiflora</i>	<i>F. brachyphylla</i> , glacial
<i>Salix pseudolapponum</i>	<i>S. glaucops</i> , glacial
<i>Alsine polygonoides</i>	<i>A. laeta</i> , glacial
<i>Cerastium Earlei</i>	<i>C. Behringianum</i> , glacial
<i>Caltha rotundifolia</i>	<i>C. biflora</i> , subarctic
<i>Draba pectinata</i>	<i>D. andina</i> , glacial
<i>Rhodiola polygama</i>	<i>R. integrifolia</i> , glacial
<i>Polemonium delicatum</i>	<i>P. pulcherrimum</i> , glacial
<i>Castilleja Haydeni</i>	<i>C. pallida</i> , arctic

#### NORTHERN ROCKIES

<i>Agropyron andinum</i>	<i>A. biflorum</i> , glacial
<i>Agropyron latiglume</i>	<i>A. biflorum</i> , glacial
<i>Salix cascadiensis</i>	<i>S. arctica</i> or <i>S. anglorum</i> , arctic
<i>Cerastium pulchellum</i>	<i>C. Behringianum</i> , glacial
<i>Caltha leptosepala</i>	<i>C. biflora</i> , subarctic
<i>Caltha cheledoni</i>	<i>C. biflora</i> , subarctic
<i>Phacelia Lyallii</i>	<i>P. sericea</i> , glacial
<i>Polemonium parviflorum</i>	<i>P. pulcherrimum</i> , glacial
<i>Erigeron pedatus</i>	<i>E. multifidus</i> , glacial



## NORTHERN AND SOUTHERN ROCKIES

<i>Bistorta linearifolia</i>	<i>B. bistortoides</i> , glacial
<i>Acomastylis turbinata</i>	<i>A. Rossii</i> , arctic
<i>Acomastylis sericea</i>	<i>A. Rossii</i> , arctic
<i>Mertensia nivalis</i>	<i>M. lanceolata</i> , glacial
<i>Castilleja occidentalis</i>	<i>C. pallida</i> , arctic

Many of the alpine plants of the Rockies have their nearest relatives among the subalpine or mountain plants of the region. Such are

## NORTHERN ROCKIES

ALPINE	SUBALPINE
<i>Potentilla perdissecta</i>	<i>P. diversifolia</i>
<i>Potentilla decurrens</i>	<i>P. diversifolia</i>
<i>Pseudocymopterus Tiedestromii</i>	<i>P. montanus</i>
<i>Bupleurum purpureum</i>	<i>B. americanum</i> (related to <i>B. ranunculoides</i> of Europe)
<i>Phacelia alpina</i>	<i>P. heterophylla</i>

## SOUTHERN ROCKIES

<i>Avena Mortoniana</i>	<i>A. americana</i>
<i>Poa Pattersonii</i>	<i>P. crocata</i>
<i>Eriogonum xanthum</i>	<i>E. flavum</i>
<i>Aquilegia saximontana</i>	<i>A. brevistyla</i>
<i>Thlaspi coloradense</i>	<i>T. glaucum</i> (also closely related to <i>T. alpestre</i> of Europe)
<i>Thlaspi purpurascens</i>	<i>T. glaucum</i> (also closely related to <i>T. alpestre</i> of Europe)
<i>Cheirinia amoena</i>	<i>C. Wheeleri</i>
<i>Cheirinia nivalis</i>	<i>C. Wheeleri</i>
<i>Cheirinia radiata</i>	<i>C. asperrima</i>
<i>Aragallus foliolosus</i>	<i>A. reflexus</i>
<i>Primula angustifolia</i>	<i>P. Broadheadae</i>
<i>Phlox condensata</i>	<i>P. caespitosa</i>
* <i>Mertensia Bakeri</i>	} † <i>M. lanceolata</i>
* <i>Mertensia lateriflora</i>	
* <i>Mertensia Parryi</i>	
* <i>Mertensia viridula</i>	
<i>Besseya alpina</i>	<i>B. plantaginifolia</i>
<i>Achillea subalpina</i>	<i>A. lanulosa</i>

† Those marked with braces constitute groups of closely related species.



## SOUTHERN AND NORTHERN ROCKIES

<i>Poa Lettermannii</i>	<i>P. crocata</i>
<i>Poa rupicola</i>	<i>P. crocata</i>
<i>Anemone tetonensis</i>	<i>A. globosa</i>
<i>Drymocalis pumila</i>	<i>D. glandulosa</i>
<i>Solidago decumbens</i>	<i>S. oreophila</i>
<i>Solidago ciliosa</i>	<i>S. scopulorum</i>

The following alpine plants have no close relatives and seem to have originated in the Rockies:

<i>Agropyron Scribneri</i>	<i>Oreoxis alpina</i>
* <i>Claytonia megarrhiza</i>	<i>Oreoxis Bakeri</i>
<i>Paronychia pulvinata</i>	<i>Oreoxis humilis</i>
<i>Ranunculus adoneus</i>	<i>Polemonium viscosum</i>
<i>Ranunculus stenolobus</i>	<i>Polemonium Grayanum</i>
<i>Delphinium alpestre</i>	<i>Polemonium confertum</i>
<i>Gormannia debilis</i>	<i>Polemonium speciosum</i>
<i>Telesonix Jamesii</i>	<i>Polemonium mellitum</i>
<i>Telesonix heucheriformis</i>	<i>Polemonium Brandegei</i>
<i>Potentilla saximontana</i>	<i>Douglasia nivalis</i>
<i>Potentilla minutiflora</i>	<i>Douglasia montana</i>
<i>Potentilla tenerrima</i>	<i>Tonestus pygmaeus</i>
<i>Trifolium nanum</i>	<i>Tonestus Lyallii</i>
* <i>Trifolium Parryi</i>	<i>Xylorrhiza coloradensis</i>
<i>Trifolium montanense</i>	<i>Xylorrhiza Brandegei</i>
<i>Trifolium salictorum</i>	<i>Rydbergia grandiflora</i>
<i>Trifolium Brandegei</i>	<i>Rydbergia Brandegei</i>
* <i>Trifolium dasyphyllum</i>	<i>Artemisia scopulorum</i>
* <i>Trifolium lividum</i>	<i>Artemisia Pattersonii</i>
* <i>Trifolium stenolobum</i>	<i>Artemisia Parryi</i>
<i>Trifolium attenuatum</i>	<i>Senecio Holmii</i>
<i>Trifolium bracteolatum</i>	<i>Senecio taraxacoides</i>
<i>Angelica Grayi</i>	<i>Senecio Soldanella</i>
	<i>Senecio petrocallis</i>
	<i>Senecio Porteri</i>

## AMERICAN ARCTIC PLANTS

Many plants which have their main distribution within the arctic regions of North America are also found in the northern



Rockies; only a few of these extend far enough south to reach the boundary of the United States. In other words, only a few of them reach Montana and still fewer northern Idaho.

<i>Salix alexensis</i>	<i>Artemisia Richardsoniana</i>
<i>Salix arbusculoides</i>	<i>Artemisia arctica</i>
<i>Salix Barrattiana</i>	* <i>Achillea borealis</i>
<i>Salix Drummondiana</i>	* <i>Achillea multiflora</i>
* <i>Tofieldia coccinea</i>	* <i>Senecio lugens</i>
<i>Micranthes foliolosa</i>	<i>Potentilla emarginata</i>
<i>Erigeron grandiflorus</i>	<i>Amarella arctophila</i>
<i>Erigeron lanatus</i>	<i>Amarella propinqua</i>
<i>Erigeron unalaschensis</i>	<i>Mertensia Drummondii</i>
<i>Antennaria alpina</i>	<i>Castilleja pallida</i>
<i>Antennaria monocephala</i>	

Some of these arctic plants have a circumpolar distribution, as the following:

<i>Juncus biglumis</i>	<i>Muscaria caespitosa</i>
<i>Juncoides arcticum</i>	<i>Micranthes nivalis</i>
<i>Juncoides hyperboreum</i>	<i>Cardamine bellidifolia</i>
<i>Juncoides arcuatum</i>	<i>Mairania alpina</i>
<i>Androsace septentrionalis</i>	<i>Cassiope tetragona</i>
<i>Saxifraga rivularis</i>	<i>Pedicularis lanata</i>
<i>Draba nivalis</i>	<i>Pedicularis Oederi</i>
<i>Draba alpina</i>	<i>Pedicularis flammea</i>

The following are Asiatic-American arctic plants extending into the Canadian Rockies:

<i>Cheirinia Pallasii</i>	<i>Potentilla villosa</i>
<i>Potentilla uniflora</i>	<i>Campanula lasiocarpa</i>

#### SUBALPINE PLANTS

Besides these, there are many of the subalpine plants which occasionally are found above timber line. If the sedges, which I have not yet recorded, are excepted, the list contains 80 such species. There is no need of giving the list in this connection. If I should discuss in a subsequent paper the subalpine region, such a list would there find its place.

\* Mostly subarctic-subalpine.



The alpine plants of all classes in the Rocky Mountains number about 250 species. The subalpine plants, which sometimes are found in the alpine region, are if the sedges are added over 100 in number. Hence about 350 species of flowering plants, or between 6 and 7 per cent. of the Rocky Mountain species, are growing within the alpine region.

NEW YORK BOTANICAL GARDEN







## The propagation of medicinal plants\*

FRED A. MILLER

An understanding of the best methods of propagating medicinal plants is essential to their successful cultivation. Their cultivation or commercial production is not a new industry, in fact certain phases of it are extremely old, though poorly developed. However long some of them have been continued under cultivation, there are still many phases of their propagation which have never been investigated. Repeated crop failures in the production of henbane in England have occurred during the past thirty years, and still the most recent reports continue to mention the uncertainty of germination without any attempt at explanation.

This condition is now changing, and the last few years have seen a more general and widespread interest in the thorough investigation of a rather selected list of drug plants than was hitherto experienced. The organized efforts of the United States Department of Agriculture are conducive to the continuation of this interest. England, Germany, and Austria have not been slow in following the example of the United States, and are now advocating the national support of comprehensive drug plant investigations.

The success of these investigations must of necessity depend upon the readiness with which supplies of seeds and plants can be obtained, and the ease with which they may then be propagated. The means of propagating medicinal plants need not differ in the main from those employed for other economic forms. Seedsmen, nurserymen, florists and gardeners all have their special and well-perfected systems of propagation for their respective classes of plants. The questions involved in these systems are not only those for increasing the number of individual plants, but also those involving the blooming and fruiting periods, harvests, markets, special crops, improvements, and breeding operations. Any

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\* A Thesis presented to Purdue University toward the degree of Master of Science.



method of propagation which does not augment these conditions is soon abandoned. Also, in the case of medicinal forms, the problems of propagation, though essential of solution, are only supplementary to other more valuable and interesting ones. The improvement of drug plants through selective breeding and hybridization, their successful cultivation upon a commercial scale, with the involved questions of practical and economic production, are more attractive, but in the end are all dependent upon successful propagation.

With medicinal plants it is many times difficult to obtain sufficient materials from which to propagate. Isolated, restricted, and many times unknown regions of production, make it almost impossible to obtain either seeds or plants. Even syndicates and sometimes government control have so monopolized these regions that they are practically inaccessible to the individual investigator. In an effort to obtain sufficient material with which to evolve certain problems upon the cultivation and improvement of the more valuable drug plants, difficulties were soon encountered in locating reliable sources of supply. Any study of the methods of propagation must therefore consist of, first, the obtaining or locating of suitable materials and, second, the various methods by which these may be successfully propagated and perpetuated. The first part of this discussion will, therefore, deal with probable sources of seeds and plants and the second with their propagation.

A thorough search has been made in an effort to locate the best and most probable sources for these materials. The results are given under the following five divisions:

- I. Commercial samples and shipments of crude drugs.
- II. Crude drug merchants.
- III. Individuals living in or near producing regions, or others carrying on investigations with similar plants.
- IV. Public and private botanical gardens, experiment stations and other institutions.
- V. Commercial seedsmen and nurserymen.

A discussion of these sources together with results obtained follows in the foregoing order.



## I

From commercial samples and shipments of crude drugs in which the aerial parts of the plants are used, germinable seeds are often obtainable. Many lots of drugs must be examined, however, and large numbers of questionable seeds examined and tested. In addition to furnishing material for planting, this procedure also serves as a valuable means of accurately identifying some crude drug of questionable origin. The age of seed from this source is always unknown and considerable time must be allowed for possible failures in germination. Among the forms of which seed may be obtained in this manner are American wormseed (*Chenopodium ambrosioides*), angelica (*Angelica atropurpurea*), anise (*Pimpinella Anisum*), arnica (*Arnica montana*), belladonna (*Atropa Belladonna*), broom tops (*Cytisus scoparius*), buchu (*Barosma betulina*), cannabis indica (*Cannabis sativa*), capsicum (*Capsicum fastigiatum*), caraway (*Carum Carvi*), cardamom (*Elettaria Cardamomum*), castor bean (*Ricinus communis*), celery seed (*Apium graveolens*), cevadilla (*Schoenocaulon officinale*), coca (*Erythroxylum Coca*), colchicum (*Colchicum autumnale*), colocynth (*Citrullus Colocynthis*), conium (*Conium maculatum*), coriander (*Coriandrum sativum*), fennel (*Foeniculum vulgare*), goats' rue (*Galega officinalis*), grains of paradise (*Amomum Melegueta*), henbane (*Hyoscyamus niger*), jumbul seed (*Abrus precatorius*), larkspur (*Delphinium Consolida*), Levant wormseed (*Artemisia pauciflora*), lobelia (*Lobelia inflata*), nux vomica (*Strychnos Nuxvomica*), parsley seed (*Apium Petroselinum*), passion flower (*Passiflora incarnata*), poppy heads (*Papaver somniferum*), scullcap (*Scutellaria lateriflora*), senna (*Cassia acutifolia* and *C. angustifolia*), serpentaria (*Aristolochia Serpentaria* and *A. reticulata*), staphisagria (*Delphinium Staphisagria*), stramonium (*Datura Stramonium*).

Germination tests have been made upon a number of the above forms as follows:

American wormseed.....	
Angelica.....	Fair germination.
Anise.....	
Arnica.....	Three tests. No results.
Belladonna.....	About 50 per cent. germination.
Broom tops.....	No results.
Buchu.....	5 per cent. germination.



Cannabis indica . . . . .	100 per cent. germination.
Caraway . . . . .	
Cardamom . . . . .	Two tests. No results.
Celery seed . . . . .	
Cevadilla . . . . .	One test. About 25 per cent.
Coca . . . . .	Four tests. No results.
Colchicum . . . . .	Three tests. About 5 per cent. from one.
Colocynth . . . . .	Most tests give from 5-10 per cent. germination.
Conium . . . . .	50 per cent. germination or over.
Coriander . . . . .	
Fennel . . . . .	
Goat's rue . . . . .	One test gave 5 per cent. germination.
Grains of paradise . . . . .	
Henbane . . . . .	Most tests give 5 per cent. germination, or more.
Larkspur . . . . .	100 per cent. from most tests.
Levant wormseed . . . . .	No results from 2 tests.
Lobelia . . . . .	
Nux vomica . . . . .	No results from 5 tests.
Parsley seed . . . . .	
Passion flower . . . . .	One test gave 3 per cent. germination.
Poppy heads . . . . .	All tests gave 100 per cent. germination.
Scullcap . . . . .	One test out of three gave about 5 per cent. germination.
Senna . . . . .	Most tests gave fair germination.
Serpentaria . . . . .	No results from 2 tests.
Staphisagria . . . . .	One test gave 3 per cent. germination.
Stramonium . . . . .	All tests gave 50 per cent. germination, or more.

Large numbers of seeds were used in most of these tests, and the conditions governing germination were varied to suit the requirements, in so far as they could be determined. It is to be noted that germination in most cases was low. Table IV gives details on most of these plants and on certain other miscellaneous drug plants.

## II

Dealers in crude drugs will many times lend valuable assistance in searching for and supplying seeds and plants. Importers with foreign representatives and the foreign merchants themselves will sometimes request their agents and collectors to assist in such matters. No great diversity of forms, however, can be secured through these sources. They are restricted to those of which the seed constitutes the medicinal part, or to those in which the seeds are likely to appear with other plant parts. The forms thus obtainable are mostly included in the preceding list, though better seeds are sometimes furnished by the dealers upon special request for fresh material.



## III

It is sometimes possible to locate individuals in different countries who have become interested in the collection of rare seeds and plants. Such sources are extremely questionable. While some individuals can furnish much good material, there are others who, though expressing much interest, cannot be depended upon to supply the proper species. Numerous instances of this have been recorded, an example of which may be noted where an enthusiastic druggist of Texas supplied fine specimens of *Monarda* for henbane, which he claimed was growing luxuriantly in his section of the state.

Local drug collectors may be considered here rather than with crude drug merchants. More strictly speaking, they are a class by themselves with many peculiarities and limitations. They are mostly illiterate persons, who take instructions poorly and disregard them when once in the field. A close personal association with many of them has revealed the fact that they are only capable of accurately identifying a very small number of medicinal plants. These usually occur among the monotypic genera and, when two or more closely related species are in question, are usually collected indiscriminately. One of the most intelligent collectors observed repeatedly brought in specimens of various species of *Asclepias*, upon requests and instructions for *Apocynum cannabinum* and *Apocynum androsaemifolium*. *Apocynum cannabinum* when finally located was supplied upon requests for both of the two species. Only recently a negro quack, who is held in high repute by the colored element of a considerable section, supplied *Apocynum androsaemifolium* upon request for *Leptandra virginica*. Another form supplied for *Asclepias tuberosa* will have to be grown to maturity before it can be identified. One collector was shown potted specimens of golden seal (*Hydrastis canadensis*), and stone root (*Collinsonia canadensis*), and failed to recognize either of them. Twin leaf (*Jeffersonia diphylla*) is repeatedly offered by local dealers for genuine golden seal. Both the leaf and root structures of these forms are quite distinct.

## IV

In so far as their collections will permit, the botanical gardens and other similar institutions are of great value in supplying



materials. Usually their collections of medicinal plants are comparatively small, but those which are obtainable are of high quality, and correctly classified. The liberal spirit of some of these stations is now restricted in some instances by government control. Such is the case with the buchu (*Barosma betulina*) of South Africa. To obtain seeds of this form direct from the Transvaal a long and tedious routine of grants, permits, etc., is necessary before they are allowed to be sent out of the country. On the other hand, such places as the Jamaica Public Gardens, Jamaica, the Kew Royal Gardens near London, England, the Royal Botanic Garden of Calcutta, India, the Botanic Garden and Museum of Natural History of Pará, Brazil, the Botanic Garden at Georgetown, British Guiana, and many others in foreign localities are usually willing to exchange or contribute materials for experimental purposes. Of no less distinction and willingness in this respect are the gardens at New York and St. Louis, the Office of Seed and Plant Introduction, and the Bureau of Plant Industry of the United States Department of Agriculture. However, it frequently happens that these excellent and widely separate stations fail to have the materials desired. At present, this condition exists with some unusually desirable species of the genus *Artemisia*.

## V

Commercial seedsmen and nurserymen have so far proven the best sources of supply, though they do not always maintain the highest standards of nomenclature. It is encouraging in this respect to note a growing tendency on their part to list more of their materials under the specific technical names. However, great numbers of varietal or trade names are annually introduced through these channels, which cause much confusion and uncertainty. Sooner or later many of these must be reduced to synonymy. Much time and energy is consumed in varietal tests for determining these synonyms, and any movement which will reduce their number must be greatly appreciated. What is most desired in this respect is the retaining of the native and introduced forms under their original names, or at least the recording of varieties in such a manner that the original parents can be traced, and the pedigrees of the supposed new forms accurately obtained.



The catalogues of the most prominent seedsmen and nurserymen from the United States, England, France, Germany, and Japan have been examined for medicinal plants. In such an examination it was necessary to have clearly in mind some means of deciding whether or not a given form should be classed medicinal or non-medicinal. Certain limitations must be exercised in such a distinction, and a conservative rather than a general attitude should be maintained. To follow the inclinations and suggestions of some authors would mean the consideration of an almost unlimited number of plants as possessing medicinal value. Practically, the list should not greatly exceed three hundred in number, and of these there are many included which are of doubtful value. In Bulletin No. 2, California State Board of Forestry, entitled "Pharmacal Plants and Their Culture," there is a context of one hundred and fifty-four pages, eight of which treat of the cultivation of medicinal plants in California. A portion of this small space is given up to such forms as sage, horehound, rosemary, marjoram, and dandelion. The greater bulk of the publication is taken up with a list of "Native and Introduced Medicinal and Poisonous Plants." The inclusion in this list of such forms as sugar maple, box elder, maidenhair fern, common edible mushroom (*Agaricus campestris*), wind flower, columbine, pawpaw, banana, garden beet, clematis, persimmon, California poppy, strawberry, holly, lemon, puffball, sorrel, cinquefoil, yucca and even corn, can hardly be explained. If such plants as the foregoing are to be considered medicinal, the list of three hundred would quickly grow to six hundred or more.

Based upon such a liberal classification, all seedsmen and nurserymen could be said to list medicinal plants regularly, and in large numbers, while as a matter of fact they list but very few. Certainly such a classification is not advisable, from either a practical or a scientific standpoint. The list which has been used as a means of dividing this material into medicinal and non-medicinal contains three hundred and eighty different forms, and includes all those that are commonly used by prominent manufacturers of pharmaceutical preparations.



A LIST OF SEEDSMEN AND NURSERYMEN WHOSE CATALOGUES HAVE BEEN  
EXAMINED FOR MEDICINAL PLANTS, AND THE NUMBERS OF SUCH  
FORMS LISTED BY THEM

Name of Firm	Location	Number Medicinal Forms Listed
Bash's Seed Store	Indianapolis, Ind.	25
P. J. Berckmans Co.	Augusta, Ga.	20
A. T. Boddington	New York City	12
Bobbink & Atkins	Rutherford, N. J.	53
Benary, Ernst	Erfurt, Germany	68
Biltmore Nursery	Biltmore, N. C.	45
W. Atlee Burpee & Co.	Philadelphia, Pa.	18
California Nursery Co.	Niles, Cal.	26
Childs, John L.	Floral Park, N. Y.	17
Dreer, Henry A.	Philadelphia, Pa.	47
Elliot Nursery	Pittsburgh, Pa.	33
Ferry, D. M., & Co.	Detroit, Mich.	4
Fottler, Fiske, Rawson Co.	Boston, Mass.	17
Gillett, Edward	Southwick, Mass.	58
Glen St. Mary Nurseries	Glen St. Mary, Fla.	6
Gregory & Son	Marblehead, Mass.	3
Isaac House & Son	Bristol, England	5
Peter Henderson & Co.	New York City	21
Horsford's Nurseries	Charlotte, Vt.	35
Haage & Schmidt	Erfurt, Germany	158
Kelway & Son	Langport, England	10
Medical Nursery	Calcutta, India	50
Livingston Seed Co.	Columbus, Ohio	4
C. C. Morse & Co.	San Francisco, Cal.	8
T. V. Munson & Son	Denison, Texas	4
Monroe Nursery Co.	Monroe, Mich.	16
Henry Mette	Quedlinburg, Germany	58
Oregon Nursery Co.	Salem, Ore.	10
Roumanille Lafayette père & fils	St. Remy de Provence, France	28
John A. Salzer Seed Co.	La Crosse, Wisc.	27
J. M. Thorburn & Co.	New York City	52
Vaughan's Seed Store	Chicago, Ill.	35
Watkins & Simpson	London, England	24
J. D. Webster	Chichester, England	15
Yokohama Nursery Co.	Yokohama, Japan	6

Based upon the number of important species listed, method and accuracy of nomenclature, class of material and general attitude the above list could be reduced to nine as follows: Haag & Schmidt, Benary, Mette, Medical Nursery, Gillett, Thorburn, Biltmore Nursery, Dreer, and Bobbink & Atkins. Materials have been obtained from five of these, and from eight of the others.



The following discussion will consider not only the propagation of this material, but also such related problems as continued growth, productivity, commercial value, hardiness, habitat, and ease of transplanting, cultivating, and harvesting.

The methods of propagation have been those of standard use. Corbett (4) divides these methods into the natural and artificial. The natural methods include reproduction by seeds, spores, rootstocks, stolons, suckers or root sprouts, bulbs, corms, and tubers. The artificial methods consist in reproduction by cuttings, layering, grafting, and budding. Necessary adjuncts to all of these methods are suitable greenhouses, cold frames, hot beds, and open field accommodations.

Propagation from seeds has been practiced wherever possible, and must in nearly all cases precede other methods. Seed propagation, however practical it may be, will not serve all purposes. In breeding experiments and improvement selections, it is often very desirable to multiply individual specimens by other means. Inbreeding for the purpose of obtaining uniform strains is often a long and laborious method, while vegetative reproduction would give the same results in a shorter interval of time. Latent tendencies are more quickly and accurately eliminated, necessary seed production is avoided, as well as the saving of much time in seeding and transplanting.

Open field methods of seeding have been found impracticable and in many cases impossible with many medicinal forms. This condition necessitates a wide deviation from most normal methods of cropping and leads to the necessary development of specialized systems. Little of an agricultural nature has been developed with these forms. Farwell (8) says that belladonna, henbane, digitalis, and aconite can be grown as easily as potatoes. Turner (23) gives directions for growing henbane, which are too general to be of any value. Saunder's (19) statements on the germination of seeds of medicinal plants are general, and include no methods or actual data. Henkel (10) says that digitalis offers no difficulties in cultivation, and advises sowing in the open field or in seed beds. True (22) advocates open field planting of digitalis. Kraemer (13), in his brief notice on seed germination, discourages open field sowing. Open field sowings of henbane, belladonna and digitalis have been



made for three successive years on well-prepared ground, and all have resulted in complete failures. Not enough plants for experimental purposes were obtained by the most careful attention.

Continued failures from open sowing of henbane are reported from England. Thirty years ago Holmes called attention to the difficulties in the cultivation of henbane. He mentioned the uncertainty of the crop in England, and the peculiarities in the germination of the seed. Again (11) in 1905 he mentions the uncertainty of the crop. Ransom (17) in 1902 claims that it is difficult to obtain a good crop of this drug in Britain. Henkel (10) later calls attention to the uncertainty in seed germination. Turner (23) in his directions for growing henbane is encouraging in the extreme. In his opinion it is not a difficult crop to handle. Repeated tests in the open field have resulted in failures. Fair germination was obtained in one instance, but the seedlings could not compete with common weeds until large enough for cultivation. Seed tests carried on under glass indicate that germination is of high percentage, uniform and fairly regular for seeds from different sources.

With some of the older drugs in cultivation, propagation and cultural systems have been highly developed. Examples of this may be found in the excellent notes of Weddell (24) on the nurseries, cultivation, harvesting and curing of coca, of Lumsdaine (15) on the cultivation of nutmegs and cloves in Bencoolen, of Eatwell (7) on the methods of cultivation, collecting, and curing of opium, and the influence of soil and climate upon the yield and quality of the product, and of DeVry (6) on cinchona.

There are few authentic data or directions, however, upon the propagation and cultivation of the more important forms which are adapted to this country. This list might well include such forms as belladonna, henbane, stramonium, digitalis, arnica, larkspur, valerian, santonica, veratrum, hellebore and others. It is evident that methods would have to be developed to suit the conditions of soil and climate, and at the same time be varied to meet the purposes of the work. That is, commercial production might be possible under a system which would be worthless for experiments on plant breeding and improvement.

In the following discussions the questions of propagation have



been taken up in conjunction with other problems, and have only been developed as progress might demand. The work has been done for the purpose of determining the practicability of growing certain drug plants upon a commercial scale, and the possibility of improving them through an application of the methods of plant breeding. All seed tests have been of a practical nature, and but little of the great mass of material upon the effects of various reagents and influences upon germination has been used. This material so far seems to have resulted in no new general laws applicable to commercial growers. Experiments upon the effects of light and darkness (Heinricher, 9) upon seed germination, temperature (Reynolds, 18) in relation to germination, treatment with warm water (Jensen, 12), sterilization of soil (Stone & Smith, 21), copper sulphate treatment (Bréal & Giustiniani, 2), electrical effects (Monahan, 16), soaking in chlorine water (Spatschil, 20), soil temperature (Brown, 3), action of ether and chloroform (Becquerel, 1) and delayed germination (Crocker, 5), have resulted in many data but few generalizations. Specific gravity tests, sterilized soils and the sulphuric acid treatment (Love & Leighty, 14), have been used successfully and might be recommended for practical purposes. The forms under consideration and the results so far obtained are as follows:

#### DIGITALIS

More or less uncertainty exists as to the exact botanical source of this drug. The comparative medicinal value of the leaves from wild and cultivated forms, and the disputed methods of collection, curing and packing are unsettled questions of considerable importance. The comparative value of the many species and horticultural varieties, their ease of culture, relative yield of crude drug, their flowering periods, hardiness and duration of growth are additional problems which must be investigated before the genus can be made to yield its best to the manufacture of medicine.

Open field sowing was tried several times during two successive years. These tests were carried out both under practical field conditions and in ideally prepared seed beds. The results were complete failures and open seed sowing under field conditions



cannot be recommended. After this preliminary work, the open field methods were abandoned for the more reliable greenhouse methods.

Seeds of twenty-seven varieties were obtained for experimental plantings. These were germinated (see Table I) in seed pans under glass, and transplanted to flats as soon as the second leaves were visible. These flats were retained in a cool greenhouse of 50 degrees night temperature, and 60 degrees day temperature, until March 1, when they were transferred to cold frames. The sashes of these frames were of double glass construction, and required little attention until the latter part of April. Then the sashes had to be removed during the day to prevent burning of the foliage, and to thoroughly harden off the young seedlings before transplanting to the field.

Transplanting to the open field was done mostly by inexperienced labor, and during dry weather accompanied by strong winds. The inexperienced labor was used as a means of determining the transplanting qualities of these forms, and the unfavorable weather only rendered this test more severe. After transplanting, the young plants were watered twice on consecutive days, and then left to the influence of natural conditions. Cultivation was commenced early, and repeated frequently throughout the growing season. The soil was a poor, stiff, clay loam, but all forms of the digitalis made excellent growth, as is evidenced by the amount of dry leaf produced by some average individual plants. Some of these yielded as follows:

*Digitalis maculata Iveryana*, a strong and robust form, 392 grams, *Digitalis gloxiniioides* 170 grams, *Digitalis Ivery's spotted* 209 grams, and *Digitalis alba* 1,721 grams. In obtaining the comparative yield (see Table I) of all the varieties, ten average plants were selected, and all the leaves collected from them, and thoroughly air dried. The figures representing comparative yield of *Digitalis alba*, *D. purpurea* and *D. canariensis*, Watkins; *D. sibirica*, *D. lanata*, and *D. ambigua*, Horsford; and *D. gloxiniaeflora rosea*, Dreer, are all low on account of early collection. Those for the other forms, however, are accurate enough for all practical purposes. The comparative toxicity as given in the table is based upon figures obtained by the one hour frog heart method for testing *Digitalis*



and its preparations. The value "one" represents the greatest toxicity, while the numerical increase indicates a proportional decrease in toxicity. Thus the weakest sample tested (*Digitalis gloxiniaeflora alba*) has a toxicity of 6.3.

Another object of the *Digitalis* study was to test the effects of hybridization upon medicinal value. For this work, it was very desirable to bring the various species and varieties into flower as soon as possible. Early seed sowing augmented by a rather rapid growth in the greenhouse and by a slow hardy growth in the cold frames, as well as by a late and unusually favorable season, resulted in a number of flowering plants from several species and varieties (see Table II). For the purpose of obtaining early flowering plants upon which to begin the work of inbreeding and hybridization, a number of one year old plants were purchased from A. T. Boddington. These began flowering early, and furnished material throughout the season. Various combinations were tried, a number of which were successful, and seedlings are already being propagated in an effort to bring them into flower the first year. Thus any breeding operations can be annually continued or discontinued as the results may indicate, whereas these forms under the usual conditions of propagation would require two years to reach maturity.

It has also been noted that a small number of annual forms have appeared in the late plantings of several species and varieties, and especially where large numbers of plants were used. In all cases these have been inbred. The resulting progeny of these inbred annuals will be closely observed for the reappearance of annual forms.

Root division and propagation of lateral buds have both been tried with several varieties of *Digitalis* (see Table III). It was hoped that clonal varieties could be obtained in this manner. Uniformity of individuals and their behavior to varied soil and climatic conditions could then be studied with greater accuracy. Lateral buds, with and without roots, were carefully removed. Those removed during summer, fall and winter were extremely hard to start, whether they bore roots or not. Sand proved to be the best material for this purpose. However those made in early spring from plants left in the open have yielded a large percentage of



plants. Side cuttings, with and without roots, made February 21, 1913, had rooted in sand in the greenhouse March 20, 1913.

#### BELLADONNA

The propagation of belladonna was first attempted through open field sowing. Successive trials under varied field conditions with seed from several different sources resulted in complete failures. Fall sowing of imported seed upon a carefully prepared seed bed gave the following result. Seed planted September 3, 1912, fair germination October 21, 1912. Seed collected from growing plants August 15, 1912, planted September 3, 1912, fair germination October 21, 1912.

Greenhouse conditions were then tried, which were practically the same as those for digitalis, except that the seed pans used were more carefully protected from alternate degrees of moisture and dryness. See Table IV for germination data, and Tables V and VI for the influence of certain seed treatments upon germination.

The belladonna seedlings transplant with considerable ease and with practically no loss. Damping off is not so frequent as with digitalis and henbane. Sterilized soil and careful watering greatly reduce this trouble in all cases. The belladonna seedlings were retained in the greenhouse in flats until well established, and were then transferred to the cold frames. This was done on some occasions as early as March 19. Observations at this time showed a temperature of 46 degrees inside the frames, with the outside temperature below freezing. Outside night temperatures of 18 degrees caused no injury to the seedlings under the unprotected double glass sash. Seedlings transplanted directly into the frames in stiff clay soil made slower growth than those in the better soil of the flats, but produced hardier and more stalky plants, which transplanted to the open with much greater ease and certainty. They also made better subsequent growth than those in the flats. They required much less attention while in the frames, having to be watered only occasionally, while those in the flats dried out rapidly as the season advanced, and demanded considerable attention. Seedlings retained in the greenhouse in flats until May 10 were tender and succulent and wilted badly when transferred to the open field. From thirty to forty per cent. were lost



during this second transplanting, while with those from the cold frames this loss was scarcely appreciable.

The successful propagation of the belladonna plant was only a necessary preliminary procedure to other more important problems. It was desired to observe this form under cultivation, to study its commercial production and the possibilities of developing a strain which would produce a uniformly higher yield of alkaloids than the ordinary commercial drug.

The first of these problems was accomplished through seed propagation. No difficulty was experienced in obtaining an abundance of plants after indoor methods of propagation were adopted. Large luxuriant plants were obtained from seed sown March 8, 1912, and were flowering by July 12. It is interesting to note here that the plants which had been transplanted directly from the seed pans to the poor soil in the cold frames were the first plants to commence flowering. The plants at this time (July 12) were from two to three feet tall, and much branched. Ransom (17) says that belladonna grown in England from seed sown in early spring produces little if any herb worth cutting the first year.

It is now believed that two profitable harvests can be obtained during one growing season, from plantings made January 1st of the same year. The belladonna plant is an herbaceous perennial, but on account of its susceptibility to winter killing in this climate, it may have to be grown as an annual. 1724 plants were left in the open without protection as a test for hardiness and as a means of obtaining individual plants of unusual hardiness from which to develop a strain more adapted to this climate. September 24 the entire herbaceous portion was removed from 1414 of these plants, the remaining 310 being left undisturbed. Twelve clumps of roots were lifted November 7, 1912, and placed in the cold frames with no protection except the double glass sash. The sash was put on at this time, and left closed until March 31, 1913, when the plants were first observed. At this time they were all bearing vigorous sprouts. Those left in the open were showing no growth on this date. These were again observed May 1, and the following conditions noted:

Number of plants, from which herbaceous portion had been removed, showing growth, 44.



Number of plants, which had been left undisturbed, showing growth, 307.

The second object of the belladonna investigation, viz., the attempt to produce a strain which would yield a uniformly higher percentage of alkaloids than the commercial drug, involves another method of propagation. In this case, individual plants must be examined for their property of yielding certain percentages of alkaloids. It is desirable to propagate promising individuals in such a manner that the high yielding character will be uniformly transmitted to the offsprings. As yet it is not known how such a character behaves. Alkaloids are not essential products of metabolism, and the inheritance of the property of producing a large percentage of such products is indeed questionable.

To investigate this point, both seed and vegetative propagation of pure strains must be practiced. The behavior of the character in these pure strains and their progeny will throw much light on the possibility of developing, propagating, and maintaining high yielding varieties through the practice of breeding.

If the property of an individual plant to produce a definite amount of alkaloids when grown under uniform conditions, behaves in the same manner as many external characters, the propagation of pure bred strains by the vegetative method should yield uniformly according to selection.

To test this possibility, it was necessary to follow the methods of the florist in the propagation of cuttings in sand. This was done both in the greenhouse and in the open under cheese cloth shade. In the greenhouse the open sand bed was tried as well as the glass-covered bed recommended by Bailey. The open bed was also tried, with the cheese cloth shade. The best results in the greenhouse were obtained with the open bed under the influence of a mild bottom heat, and very careful watering. Sterile sand had to be used to prevent a total loss of the cuttings from the attack of a very small white worm, which fed on the lower ends of the cuttings, and prevented callousing until decay would commence. The best outdoor results were obtained from the use of the cold frames protected with cheese-cloth shades. Top cuttings made from the more mature wood of the open grown plants strike root more readily than those from the tender succulent wood of plants grown in the greenhouse.



Table III gives results obtained by the vegetative method of propagation for belladonna and other miscellaneous forms. Open field seeding has been found practical for such forms as stramonium (*Datura Stramonium*), cannabis indica (*Cannabis sativa*), larkspur (*Delphinium Consolida*), and lappa (*Arctium Lappa*). This list can probably be greatly enlarged as other forms are tested.

Various species and varieties of the genus *Datura* are being investigated in the same manner as belladonna and digitalis. Fifty individual plant assays have been made from plantings of *Datura Stramonium* and *Datura Tatula*. These indicate that the application of plant breeding methods to the improvement of medicinal plants may be successful, and extremely practicable. Averages of 50 per cent. and 60 per cent. have been obtained from the progeny of selected parent plants of *Datura Stramonium* and of 49 per cent. and 62 per cent. from *Datura Tatula* as compared with averages of 28 per cent. and 35 per cent. obtained respectively from wild plants of these two species. Individual plants have been found which assay as high as 65 per cent. for the *D. Stramonium* and 77 per cent. for *D. Tatula*. Such individuals are used for propagating purposes. Again, as in the case of belladonna, it is a question of inheritance that must determine the method of propagation or the advisability of attempting to perpetuate these high yielding individuals for commercial purposes.

In the foregoing, propagation has only been considered as a necessary preliminary procedure to other more comprehensive problems. A sufficient number of methods for propagating various classes of plants has been developed to suit the present need of medicinal plant growers. These have been largely the result of certain demands upon well-established horticultural forms, and their extended use is only a matter of application.

Their application herein described has furthered investigations not otherwise possible. The results obtained from their application, the continuation of other related problems, and the objects in view, have all been stated. The related problems such as commercial production, the testing of different species and varieties, and their improvement by breeding and selection, have an unquestionable economic value, the solution of which will lend



TABLE I  
FIELD RECORD

Species or Varieties	Source	Date Planted	Date Germinated	Per Cent. Germination	Date First Transplanting	Number Plants Used	Date Second Transplanting	Number Transplanted to Field	Number at End of Season, 10-31-12	Samples Collected	Per Cent. Loss in Drying	Comparative Toxicity	Comparative Yield of Dry Drug
		1912	1912		1912		1912			1912			gm.
<i>Digitalis purpurea rosea</i> . . . . .	Boddington	2-6	2-15	90	3-13	440	5-20	396	358	9-15	82	1.3	1,845
<i>Digitalis purpurea rubra</i> . . . . .	Boddington	2-6	2-15	70	3-18	330	5-21	264	226	9-15	82	1.5	1,656
<i>Digitalis lanata</i> . . . . .	Boddington	2-6	2-19	60	3-12	209	5-25	88	87	9-19	76	1.0	1,008
<i>Digitalis</i> Ivery's spotted . . . . .	Ferry	2-29	3-11	60	3-29	330	5-24	264	244	10-11	86	1.8	2,090
<i>Digitalis</i> mixed . . . . .	Salzer	3-7	3-18	90	4-2	330	5-25	176	153	10-18	82	2.5	1,755
<i>Digitalis</i> sp. . . . .	Yokohama	3-5	3-18	80	4-5	330	5-23	264	239	10-18	81	3.0	1,495
<i>Digitalis lutea</i> . . . . .	Benary	3-22	4-1	60	4-11	330	5-22	264	256	11-1	70	2.1	554
<i>Digitalis macranthus</i> . . . . .	Benary	3-22	4-1	70	4-11	330	5-23	264	231	11-1	67	2.6	430
<i>Digitalis Buxbaumi</i> . . . . .	Benary	3-22	4-1	70	4-10	330	5-23	264	253	11-1	74	1.6	994
<i>Digitalis purpurea maculata superba</i> . . . . .	Benary	3-22	4-1	60	4-11	330	5-25	176	168	11-1	77	1.6	1,360
<i>Digitalis purpurea</i> . . . . .	Oregon	2-19	3-1	60	4-1	1390	5-10	1300	952	7-14	76	3.0	425
		1911	1911										
<i>Digitalis alba</i> . . . . .	Watkins	11-22	12-1	90	1-30	345	5-20	264	193	7-25	78	2.3	391
<i>Digitalis purpurea</i> . . . . .	Watkins		12-1	90	1-30	351	5-25	88	83	7-25	80	3.0	312
		1912	1912										
<i>Digitalis canariensis</i> . . . . .	Watkins	1-4	1-15	70	2-15	440	5-21	264	244	8-15	47	1.6	266
<i>Digitalis monstrosa</i> . . . . .	Watkins	2-7	2-15	80	3-15	440	5-20	396	349	9-15	84	2.6	1,150
<i>Digitalis sibirica</i> . . . . .	Horsford	2-8	2-19	80	3-11	220	5-21	396	380	7-28	72	1.8	149
		1911	1911										
<i>Digitalis lanata</i> . . . . .	Horsford	12-20	12-28	40	2-6	99	5-25	176	173	7-28	76	1.3	219
<i>Digitalis ambigua</i> . . . . .	Horsford	12-21	12-29	40	2-14	200	5-21	264	243	7-29	66	1.8	173
		1912	1912										
<i>Digitalis gloxiniioides</i> . . . . .	Horsford	2-7	2-16	80	3-4	450	5-20	616	552	9-16	82	1.5	1,850
<i>Digitalis gloxiniaeflora rosea</i> . . . . .	Dreer	1-8	1-19	80	2-15	100	5-20	264	213	8-19	74	2.0	664
<i>Digitalis monstrosa</i> . . . . .	Dreer	2-7	2-15	90	3-1	511	5-20	428	394	9-15	82	1.8	1,645
<i>Digitalis grandiflora</i> . . . . .	Dreer	2-7	2-19	60	3-27	330	5-24	264	220	9-19	68	3.0	351
<i>Digitalis maculata Iveryana</i> . . . . .	Boddington	1-17	1-25	80	2-13	333	5-21	264	228	8-35	84	1.6	1,050



TABLE I (Continued)

## FIELD RECORD

Species or Varieties	Source	Date Planted	Date Germinated	Per Cent. Germinated	Date First Transplanting	Number Plants Used	Date Second Transplanting	Number Transplanted to Field	Number at End of Season, 10-31-12	Samples Collected	Per Cent. Loss in Drying	Comparative Toxicity	Comparative Yield of Dry Drug
<i>Digitalis gloxiniaeflora purpurea</i> ..	Boddington	1-30	2-10	70	3-7	440	5-20	352	318	9-10	84	1.5	1,815
<i>Digitalis gloxiniaeflora lutea</i> .....	Boddington	1-30	2-13	60	3-6	440	5-22	264	262	9-13	74	1.6	882
<i>Digitalis gloxiniaeflora lilicina</i> ....	Boddington	2-6	2-14	80	3-8	440	5-22	308	272	9-14	80	1.6	1,715
<i>Digitalis gloxiniaeflora alba</i> .....	Boddington	2-6	2-15	80	3-16	330	5-24	308	224	9-15	82	6.3	1,475
<i>Digitalis purpurea alba</i> .....	Boddington	2-6	2-15	80	3-12	440	5-20	396	334	9-15	84	1.6	1,855

TABLE II

## DATES OF FLOWERING AND NUMBER OF PLANTS IN FLOWER

Variety	Source	Date Planted	Jul. 15	Jul. 20	Jul. 25	Jul. 30	Aug. 10	Aug. 10	Sep. 1	Sep. 20	Oct. 15	Used
<i>Digitalis lanata</i> .....	Horsford	1911 12-20						1		2	2	97
<i>Digitalis ambigua</i> .....	Horsford	12-21	1	17	35	49	54	87	151	217	220	233
<i>Digitalis canariensis</i> .....	Watkins	1912 1-4									2	224
<i>Digitalis gloxiniaeflora lutea</i> .....	Boddington	1-30		1	1			3	11	68	95	386
<i>Digitalis purpurea rosea</i> .....	Boddington	2-6						1				358
<i>Digitalis purpurea alba</i> .....	Boddington	2-6					1					334
<i>Digitalis gloxinioides</i> .....	Horsford	2-7					4		5	9	10	383
<i>Digitalis monstrosa</i> .....	Watkins	2-7					1	2			2	349
<i>Digitalis grandiflora</i> .....	Dreer	2-7		1	2		5	32	113	189	239	240
<i>Digitalis sibirica</i> .....	Horsford	2-8								6	20	294
<i>Digitalis Iverys spotted</i> .....	Ferry	2-29									1	344
<i>Digitalis sp.</i> .....	Yokohama	3-5									5	239
<i>Digitalis macranthus</i> .....	Benary	3-22		2	3		16	81	161	217	222	231
<i>Digitalis lutea</i> .....	Benary	3-22								1	3	256
<i>Digitalis Buxbaumi</i> .....	Benary	3-22							1	7	25	319



TABLE III  
PROPAGATION BY CUTTINGS

Name	Source	Number Started	Date Started	Number Rooted	Date Rooted	Method
Belladonna . . . . .	Field plants	26	1912 7-31	0	1912	Greenhouse, open sand bed.
Belladonna . . . . .	Field plants	17	8-3	1	8-19	Greenhouse, open sand bed.
Belladonna . . . . .	Field plants	24	8-1	0		Greenhouse, open sand bed.
Belladonna . . . . .	Greenhouse plants	76	5-14	73	6-6	Greenhouse, bottom heat.
Belladonna . . . . .	Greenhouse plants	25	8-1	0		Greenhouse, bottom heat.
Belladonna . . . . .	Greenhouse plants	35	8-14	0		Greenhouse, bottom heat.
Coleus control . . . . .	Greenhouse plants	6	8-14	4	8-26	Greenhouse, bottom heat.
Coleus control . . . . .	Greenhouse plants	19	8-22	0		Greenhouse, bottom heat.
Coleus control . . . . .	Greenhouse plants	28	8-22	0		Greenhouse, bottom heat.
Coleus control . . . . .	Greenhouse plants	5	1-30	0		Greenhouse, bottom heat.
Coleus control . . . . .	Greenhouse plants	121	1-22	0		Greenhouse, glass covered bed.
Coleus control . . . . .	Greenhouse plants	49	1-29	0		Greenhouse, open sand bed.
Coleus control . . . . .	Greenhouse plants	42	1-29	0		Greenhouse, open sand bed.
Coleus control . . . . .	Field plants	220	9-4	107		Cold frames, cheese cloth shades.
Coleus control . . . . .	Field plants	180	9-6	101		Cold frames, cheese cloth shades.
<i>Digitalis canariensis</i> . . . . .	Field plants	50	6-10	19	6-29	Greenhouse, open sand bed.
<i>Digitalis canariensis</i> . . . . .	Field plants	40	7-13	0		Greenhouse, cheese cloth shade.
<i>Digitalis canariensis</i> . . . . .	Field plants	21	7-31	0		Greenhouse, open sand bed.
<i>Cytisus scoparius</i> . . . . .	Greenhouse plants	20	5-8	12	6-29	Greenhouse, open sand bed.
<i>Cytisus scoparius</i> . . . . .	Greenhouse plants	55	6-29	30	8-30	Greenhouse, open sand bed.
Nasturtium control . . . . .	Greenhouse plants	7	6-29	6	7-8	Greenhouse, open sand bed.
<i>Cereus grandiflorus</i> . . . . .	Crude drug	36	6-5	18	6-29	Greenhouse, open sand bed.
Marshmallow . . . . .	Field plants	11	7-31	11	8-19	Greenhouse, open sand bed.
<i>Solanum Dulcamara</i> . . . . .	Field plants	7	8-5	4	8-30	Greenhouse, open sand bed.
Vanilla . . . . .	Greenhouse plants	21	6-20	14	8-20	Greenhouse, open sand bed.
<i>Digitalis</i> . . . . .	Field plants	6	2-21	4	3-18	In sand under bell glass.



TABLE IV  
SEED GERMINATION

Name	Source	Date Planted	Date Germinated	Germination	Conditions
<i>Atropa Belladonna</i> .....	Greenhouse	12-21-11	1-24-12	Good	Greenhouse
<i>Atropa Belladonna</i> .....	Comm. sample	12-11-11	1-26-12	Uneven—fair	Greenhouse
<i>Atropa Belladonna</i> .....	Greenhouse	1- 4-12	2- 9-12	Good	Greenhouse
<i>Atropa Belladonna</i> .....	Comm. Lot.	2- 9-12	3- 1-12	Fair	Greenhouse
<i>Atropa Belladonna</i> .....	Comm. Lot	2-19-12	3- 8-12	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Dept. Agri.	1-10-12	2-20-12	Very good	Greenhouse
<i>Atropa Belladonna</i> .....	Dept. Agri.	2-20-12	3-10-12	Fair	Greenhouse
<i>Atropa Belladonna</i> .....	Aug. & Geo. Fischer	2-26-12	3-21-12	Good	Greenhouse
<i>Atropa Belladonna</i> .....	Cult. plants	12-24-12	12-20-12	Good	Greenhouse
<i>Atropa Belladonna</i> .....	Haag & Schmidt	2-22-13	3-23-13	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Select plant	2-25-13	3-19-13	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Select plant	2-25-13	3-19-13	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Select plant	2-25-13	3-19-13	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Select plant	2-25-13	3-27-13	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Select plant	2-25-13	3-27-13	Poor	Greenhouse
<i>Atropa Belladonna</i> .....	Aug. & Geo. Fischer	9- 3-13	10-21-12	Fair	Open field
<i>Atropa Belladonna</i> .....	Cultivated plants	9- 3-12	10-21-12	Fair	Open field
<i>Nicandra physaloides</i> .....	Haag & Schmidt	2-22-12	3- 7-12	Good	Greenhouse
<i>Hyoscyamus niger</i> .....	Benary	2-22-12			
<i>Hyoscyamus niger</i> .....	Benary	3-22-12	4- 3-12	Fair	Greenhouse
<i>Hyoscyamus niger</i> .....	Aug. & Geo. Fischer	3-22-12			
<i>Hyoscyamus niger</i> .....	Aug. & Geo. Fischer	2-12-12	2-23-12	Good	Greenhouse
<i>Hyoscyamus niger</i> .....	Aug. & Geo. Fischer	2- 7-12	2-14-12	Good	Greenhouse
<i>Hyoscyamus niger</i> .....	Haag & Schmidt	2-25-12		No result	Greenhouse
<i>Hyoscyamus niger</i> .....	Haag & Schmidt	2- 7-12		No result	Greenhouse
<i>Hyoscyamus niger</i> .....	Yokohama, Japan	2-25-12	3-20-12	Fair	Greenhouse
<i>Hyoscyamus niger</i> .....	Yokohama, Japan	3-14-13	4- 3-13	Poor	Greenhouse
<i>Hyoscyamus</i> sp.....	Watkins & Simpson	5- 5-13		No result	Greenhouse
<i>Hyoscyamus</i> annual.....	Cultivated plant	5- 3-13	3-27-13	Good	Greenhouse
<i>Hyoscyamus orientalis</i> .....	Haag & Schmidt	2-10-13	2-27-13	Poor	Greenhouse



TABLE IV (Continued)

## SEED GERMINATION

Name	Source	Date Planted	Date Germinated	Germination	Conditions
<i>Hyoscyamus muticus</i> . . . . .	Wheeler & Son	2-24-13	3- 8-13	Fair	Greenhouse
<i>Hyoscyamus muticus</i> . . . . .	Aug. & Geo. Fischer	3-20-12		No result	Greenhouse
<i>Hyoscyamus</i> sp. . . . .	Vaughn	4-15-10		No result	Greenhouse
<i>Glycyrrhiza glabra</i> . . . . .	Haag & Schmidt	4-30-12	5- 9-12	Very poor	Greenhouse
<i>Glycyrrhiza glabra</i> . . . . .	Haag & Schmidt	12-24-12	1- 2-13	Poor	Greenhouse
<i>Bryonia alba</i> . . . . .	Haag & Schmidt	12-24-12		No result	Greenhouse
<i>Bryonia dioica</i> . . . . .	Haag & Schmidt	12-24-12		No result	Greenhouse
<i>Cinchona officinalis</i> . . . . .	Haag & Schmidt	2- 8-13	3-28-13	Poor	Leaf mould
<i>Cinchona Calisaya</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Leaf mould
<i>Cinchona succirubra</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Leaf mould
<i>Erythroxylum Coca</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Leaf mould
<i>Veratrum album</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Leaf mould
<i>Veratrum viride</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Leaf mould
<i>Veratrum nigrum</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Leaf mould
<i>Colchicum autumnale</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Greenhouse
<i>Gentiana lutea</i> . . . . .	Haag & Schmidt	2- 8-13		No result	Greenhouse
<i>Laurus Cinnamomum</i> . . . . .	Haag & Schmidt	2- 8-13		No result	
<i>Santalum album</i> . . . . .	Haag & Schmidt	2-10-13		No result	
<i>Strychnos Nux-vomica</i> . . . . .	Haag & Schmidt	2-10-13		No result	
<i>Convolvulus Scammonia</i> . . . . .	Haag & Schmidt	2-10-13	2-18-13	Poor	
<i>Citrullus Colocynthis</i> . . . . .	Haag & Schmidt	2-10-13	3-28-13	Poor	
<i>Piper nigrum</i> . . . . .	Haag & Schmidt	2-10-13		No result	
<i>Quillaja Saponaria</i> . . . . .	Haag & Schmidt	2-10-13		No result	
<i>Scilla maritima</i> . . . . .	Haag & Schmidt	2-10-13		No result	
<i>Aloe ferox</i> . . . . .	Haag & Schmidt	2-10-13		No result	
<i>Archangelica officinalis</i> . . . . .	Haag & Schmidt	3-14-13		No result	Greenhouse
<i>Anthemis nobilis</i> . . . . .	Haag & Schmidt	3-14-13	3-19-13	Good	Greenhouse
<i>Arnica montana</i> . . . . .	Haag & Schmidt	3-14-13	3-21-13	Fair	Greenhouse
<i>Levisticum officinale</i> . . . . .	Haag & Schmidt	3-14-13		No result	Greenhouse
<i>Pyrethrum cinerarifolium</i> . . . . .	Haag & Schmidt	3-14-13	3-24-13	Good	Greenhouse
<i>Carthamus tinctorius</i> . . . . .	Haag & Schmidt	3-14-13	3-18-13	Good	Greenhouse
<i>Foeniculum vulgare</i> . . . . .	Haag & Schmidt	3-14-13	3-24-13	Good	Greenhouse



TABLE IV (Continued)

## SEED GERMINATION

Name	Source	Date Planted	Date Germinated	Germination	Conditions
<i>Elettaria Cardamomum</i> .....	Comm. Sample	12-27-12		No result	Greenhouse
<i>Delphinium Staphisagria</i> .....	Comm. Sample	12-27-12	1-20-13	Poor	Greenhouse
<i>Grindelia robusta</i> .....	U. S. Dept. Agr.	2-11-13	2-15-13	Good	Greenhouse
Insect flowers.....	Comm. Lot	2-11-13		No result	Greenhouse
<i>Strophanthus</i> sp.....	Comm. Lot	2-19-13		No result	Greenhouse
<i>Strophanthus</i> sp.....	Comm. Lot	2-19-13	3-5-13	Poor	Greenhouse
<i>Althaea officinalis</i> .....	U. S. Dept. Agr.	2-22-13	3-5-13	Good	Greenhouse
<i>Berberis Aquifolium</i> .....	Commercial	3-10-13	4-3-13	Fair	Greenhouse
<i>Conium</i> sp.....	Comm. Lot	5-5-13	3-20-13	Good	Greenhouse
<i>Theobroma Cacao</i> .....	Jamaica	3-14-13		No result	Greenhouse
<i>Valeriana officinalis</i> .....	Dreer	3-27-13		Good	Greenhouse
<i>Apium Petroselinum</i> .....	Comm. Lot	4-4-13	4-17-13	Good	Greenhouse
<i>Amomum Melegueta</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Apium graveolens</i> .....	Comm. Lot	4-4-13	4-16-13	Good	Greenhouse
<i>Coriandrum sativum</i> .....	Comm. Lot	4-4-13	4-18-13	Good	Greenhouse
<i>Chenopodium ambrosioides</i> .....	Comm. Lot	4-4-13	4-21-13	Good	Greenhouse
<i>Carum Carvi</i> .....	Comm. Lot	4-4-13	4-17-13	Fair	Greenhouse
<i>Delphinium Staphisagria</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Lobelia inflata</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Foeniculum vulgare</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Foeniculum vulgare</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Schoenocaulon officinale</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Pimpinella Anisum</i> .....	Comm. Lot	4-4-13		No result	Greenhouse
<i>Citrullus Colocynthis</i> .....	Comm. Lot	5-1-12		No result	Greenhouse
<i>Aristolochia Serpentaria</i> .....	Comm. Lot	5-2-12		No result	Greenhouse
<i>Schoenocaulon officinale</i> .....	Comm. Lot	5-8-12	7-8-12	Poor	Greenhouse
<i>Amomum Melegueta</i> .....	Comm. Lot	5-8-12	5-20-12	Fair	Greenhouse
<i>Strophanthus</i> sp.....	Comm. Lot	5-8-12			Greenhouse
<i>Datura ferox</i> .....	Haag & Schmidt	5-28-12	6-4-12	Good	Greenhouse
<i>Strophanthus Kombe</i> .....	Comm. Sample	6-18-12			Greenhouse
<i>Strophanthus hispidus</i> .....	Comm. Sample	6-18-12			Greenhouse
<i>Citrullus Colocynthis</i> .....	Comm. Sample	6-18-12	7-8-12	Poor	Greenhouse



TABLE V  
EFFECT OF SEED AND SOIL TREATMENT ON GERMINATION

Name	Date Planted	Date Germinated	Germination	Treatment
Belladonna.....	2-6-12	3-2-12	Good	Water
Belladonna.....	2-5-12	3-5-12	Good	Warm water
Belladonna.....	2-7-12	2-26-12	Very good	Warm water
Belladonna.....	2-7-12	2-26-12	Very good	Warm water
Belladonna.....	2-5-12	3-25-12	Good	Warm water
Belladonna.....	2-6-12	3-2-12	Poor	Untreated

TABLE VI  
CONCENTRATED SULPHURIC ACID TREATMENT FOR BELLADONNA

	Planted	Germ.	No. Seed-ling	Date	No. Seed-ling	Date	No. Seed-ling	Date	No. Seed-ling	Date	No. Seed-ling
Untreated.....	1913 2-14	1913		1913 3-13	3	1913 3-19	3	1913 3-28	14	1813 4-8	24
Treated 5 mi.....	2-14	3-5	2	3-13	4	3-19	10	3-28	27	4-8	36
Treated 10 mi....	2-14	3-5	3	3-13	11	3-19	46	3-28	125	4-8	138
Treated 15 mi....	2-14			3-13	3	3-19	15	3-28	32	4-8	31

much to the demands for better and more precise medicinal products.

INDIANAPOLIS, INDIANA.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1910-1914

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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- Brooks, C.** Some apple diseases and their treatment. New Hampshire Agr. Exp. Sta. Bull. 157: 3-32. f. 1-30. Ap 1912.
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- Charabot, E.** Formation and distribution of odorous products in plants. *Am. Jour. Phar.* 85: 550-554. D 1913.
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- Clute, W. N.** The production of new forms in *Rudbeckia*. *Am. Bot.* 19: 131-134. N 1913.
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### CONTENTS

Seed development in the genus *Peperomia*. (Plates 3-6.) [*To be concluded.*]  
G. CLYDE FISHER 137

The morphological relationships of the Florideae and the Ascomycetes.  
B. O. DODGE 157

INDEX TO AMERICAN BOTANICAL LITERATURE. . . . . 203

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BULLETIN  
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MARCH, 1914

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Seed development in the genus *Peperomia*\*

G. CLYDE FISHER

(WITH PLATES 3-6 AND A TEXT FIGURE)

The abnormal embryo sac is doubtless the most interesting feature of the development of the ovule and seed in the genus *Peperomia*. The first sixteen-nucleate embryo sac, found in Angiosperms, was that discovered by Campbell (6) in 1899, in *Peperomia pellucida*. Johnson (30), in 1900, first described the origin and development of the endosperm in *P. pellucida*. He showed that the mature embryo sac of this species contains one egg, one synergid, six nuclei which are cut off singly about the periphery of the sac and which finally degenerate, and eight nuclei which fuse to form the endosperm nucleus. Campbell (7), in 1901, confirmed the work of Johnson in all these features, except the number of synergids, which he thought might often be two. Schnegg (64), in 1902, reported a sixteen-nucleate embryo sac in *Gunnera*, a genus of the Haloragidaceae not at all closely related to *Peperomia* of the Piperaceae. Johnson (32), in 1902, showed that two species of the closely related genus *Piper* have typical eight-nucleate mature embryo sacs. In 1907, Johnson (34) described a new type of mature embryo sac in *Peperomia hispidula*, which likewise contained one egg and one synergid, but in which all the remaining fourteen nuclei fuse to form the endosperm nucleus. Ernst (21), in 1908, reported a sixteen-nucleate sac in *Gunnera macrophylla*. In 1908, Brown (4) reported, for three more

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\* Botanical Contribution from The Johns Hopkins University, No. 35.

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species of *Peperomia*, embryo sacs essentially similar to that of *P. pellucida*, and also discovered evanescent walls following the first and second nuclear divisions in the sac. Miss Stephens (70), in 1909, described sixteen-nucleate embryo sacs for three different genera of the Penaeaceae, a family not closely related to the Piperaceae or the Haloragidaceae. Modilewski (50 and 52), in 1909 and 1911, found sixteen-nucleate sacs in two species of the Euphorbiaceae, which again are not closely related to any family in which this type of embryo sac had hitherto been found. Johnson (35), in 1910, reported a typical eight-nucleate sac in another species of *Piper*. Samuels (59), in 1912, extended the work of Schnegg and of Ernst on the genus *Gunnera*.

Since 1899, sixteen-nucleate embryo sacs, in which the arrangement of nuclei differs considerably in the different species, have therefore been found to occur in at least a half-dozen genera, distributed among four very distantly related families of Angiosperms.

In pursuit of additional evidence upon the significance of the abnormal embryo sac in the genus *Peperomia*, a study of the development of several species, not hitherto investigated, was undertaken. The species studied were: *P. reflexa* A. Dietr., *P. verticillata* A. Dietr., *P. scandens* Ruiz & Pav., *P. metallica* Lind. & Rod., *P. Fraseri*, var. *resediflora* C. DC., *P. blanda* HBK., *P. galioides* HBK., and *P. Langsdorffii* Miq. (?).

*Piper tuberculatum* Jacq., an arborescent species belonging to a very closely related genus, was also examined.

Most of the material used in this study was from Jamaican plants. It was in part collected from living plants in Jamaica,\* and in part—the chief portion—from Jamaican plants growing in the greenhouse of The Johns Hopkins University at Homewood, which were brought back by The Johns Hopkins University Botanical Expedition of 1910.

The plants of *Peperomia scandens* and *Piper tuberculatum*, from which flower-spikes were collected, were directly determined by Dr. Casimir de Candolle from portions of the plants sent to

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\* The material was collected and fixed at Cinchona by Professor D. S. Johnson on visits made to Jamaica in 1903, 1906, and 1910. The expedition of 1903 was aided by a grant from the Botanical Society of America, that of 1906 from the Bache Fund, and that of 1910 from The Johns Hopkins University.



him. The plants of *Peperomia reflexa*, *P. verticillata*, *P. metallica*, *P. blanda*, and *P. galioides* were carefully compared with herbarium specimens of these species, which had been determined by the same authority. The material of *P. Fraseri*, var. *resediflora* was obtained from a plant, labeled *P. resedaeflora*, in the greenhouse of the "Pflanzenphysiologisches Institut" in Munich.

The material of the species which is here referred to as *Peperomia Langsdorffii* Miq. (?) was secured from a plant growing in the greenhouse of The Johns Hopkins University. This plant was obtained from the New York Botanical Garden, and their plant was secured from the "Königlichen Botanischen Garten," Dahlem, Germany, where it is known as *Peperomia humilis* (Vahl) A. Dietr., which is there considered to be equivalent to *Peperomia Langsdorffii* Miq. After an examination of a specimen of the Johns Hopkins plant and one of the New York plant, Dr. Casimir de Candolle thinks it can not be referred to *P. Langsdorffii* Miq., but that it is very probably a new species. However, in the absence of any other name, the plant will be referred to in this paper as *P. Langsdorffii* Miq. (?)

The material was killed and fixed in medium chromo-acetic, in acetic acid and absolute alcohol, or in Flemming's fluid. The first mentioned was generally the most satisfactory.

The stains used were Haidenhain's iron-alum haematoxylin, counterstained in Orange G; and Flemming's triple. The former combination was more satisfactory for the younger stages, while the latter was better for the later stages, in which the embryo and endosperm were formed.

For the sake of clearness, each species will be described separately, after which the general considerations will be taken up.

#### PEPEROMIA REFLEXA A. Dietr.

*Peperomia reflexa* A. Dietr., being typical of the series of Peperomias studied, will first be considered somewhat in detail. Part of the material of this species was collected on rocks at 5,000 feet elevation near Cinchona, where it grew on the dry south side of the Blue Mountains of Jamaica. Most of the material, however, was collected from two plants in the greenhouse of The Johns Hopkins University at Homewood. One of the greenhouse plants



had been brought from Jamaica and the other had been collected by Professor C. J. Chamberlain in March, 1908, at Xalapa, Mexico.

The flower in this species consists of two stamens and a single carpel, which is sessile in the axil of a peltate bract (FIG. 4). These bracts, which are homologous with leaves, rather closely resemble in shape the peltate leaves of some other species of the genus (*e. g.* those of *P. arifolia*).

There is no evidence—not even rudiments—of calyx or corolla. The flowers are borne upon a terminal spike, which measures 15–25 mm. in length and 1.5–2.0 mm. in diameter. The flowers are arranged in such a close cylindrical spiral or helix that a cross-section of the spike frequently shows from five to seven flowers in almost the same plane. In the early stages the flowers are completely covered by the overlapping bracts, the upper edge of each bract being outside—a necessary result of the acropetal mode of development of flowers and bracts on the spike. In each carpel is borne a single, orthotropous ovule, with a single integument (FIG. 4). The sessile stigma, with its numerous finger-like papillae, is limited to the anterior or lower part of the carpel, the stylar canal opening just above the stigma.

The bracts and their axillary flowers have their origin in the periblem, and their development, so far as observed, very closely coincides with that described by Schmitz (63) for *P. urocarpa* Fisch. & Mey. (= *P. ionophylla* Griseb.).

The flowers are not only initiated in acropetal succession, but they reach maturity in the same order, there being a great deal of difference between those at the base and those at the apex of the spike, especially in the earlier stages of development. In this character the flowers of *Peperomia* are to be distinguished from those of the genus *Piper* in so far as the species examined in this study are concerned. In the latter the flowers originate acropetally on the spike, but they all reach maturity at practically the same time.

As is characteristic for all xerophytic species seen by the writer, each flower with its subtending bract is sunk in a depression in the inflorescence axis. The depth of the depression may practically equal, or even slightly exceed, the height of the ovule; and this relation obtains without much change from the time the



primary archesporial cell is differentiated until about the time of pollination. About this time the nucellus begins to increase in size by the development of perisperm, and the diamond-shaped border of the cup increases in height around the developing fruit, until at maturity the fruit projects about one third of its length (FIG. 17). Sometimes the margin of the cup extends out practically as far as the outer end of the ripe fruit. The borders of these cups constitute ridges between the flowers, and the tops of these ridges and also the peduncle of the spike are rather thickly beset with simple, sharp-pointed hairs (FIG. 18). Each of these hairs consists of four to eight cells, including the basal cell, arranged uniseriably, and measures from .15 mm. to .3 mm. in length. Among these hairs on the rachis and on the peduncle of the spike, and also on the carpels and bracts, there are glandular trichomes each consisting of three cells—a basal cell belonging to the epidermis, a short stalk-cell, and an enlarged terminal cell which usually has the shape of a much-flattened oblate spheroid, or door-knob (FIG. 18). As Haberlandt (26, pp. 444-455) suggests, these trichomes probably serve for the excretion of water (as hydathodes), or at least for the absorption of water. According to Solereder (69), hydathodes of this kind occur not only in *Peperomia*, but also in the related genera *Saururus* and *Piper*.

Large oil-cells are present in the rachis, bracts, and carpels. Starch grains are abundant in the rachis and bracts.

The anthers, as in all other species of *Peperomia*, are bilocular. The masses of archesporium in the stamen, when fully differentiated, show about twenty-five cells in cross-section. The tapetum, which is organized very early, consists of a single layer of cells. This layer entirely lines the pollen sac, and thus completely surrounds the male sporogenous tissue. At first it is rather thin, but the cells increase in size until they are quite large, reaching their greatest relative size about the time of the formation of the tetrads of microspores (FIG. 19). The walls of the pollen sacs are three cells thick—the epidermis, the endothecium, and a more or less complete and very thin layer inside the endothecium. This is exclusive of the tapetum. The microspores are formed by the time the primary archesporial cell in the nucellus of the same flower has cut off the parietal cell. The walls of the micro-



spores immediately become somewhat thickened. The microspores, which are uninucleate at first, become binucleate before the nucleus of the embryo sac mother-cell of the same flower divides. The walls of the pollen grains increase in thickness, and become roughened on the outside. Their nuclei do not divide further before germination. The mature microspore is therefore binucleate, and no cross-wall is formed between the nuclei. The tapetum and the thin layer of cells just inside the endothecium have practically disappeared by the time the microspores have become binucleate and the endothecium has become fully developed. The pollen is shed sometime after the embryo sac of the same flower becomes eight-nucleate and before it becomes sixteen-nucleate. This is later than it occurs in *P. pellucida* (Johnson, 30). Very few pollen-tubes were seen, and none of those seen were in good condition. The details of the germination of the pollen were not made out.

The embryo sac and seed develop in a manner closely similar to that described by Campbell (6 and 7) and by Johnson (30) for *P. pellucida*. The primary archesporial cell is single and subepidermal (FIG. 1). It divides to form a tapetal cell, and the definitive archesporial cell,\* or the embryo sac mother-cell, as it has sometimes been called (FIG. 2). At the time of this division of the primary archesporial cell, the integument has grown about half-way up to the apex of the nucellus. The tapetal cell by repeated division gives rise to a cap of parietal cells. This cap of tapetum becomes two or three cells thick before the nucleus of the embryo sac mother-cell divides, and three cell-layers in thickness is about the limit of its development (FIG. 3).

The reduction of chromosomes probably occurs in the first two divisions of the nucleus of the embryo sac mother-cell, as is indicated by the presence of synapsis before the first division (FIG. 5). In this respect the behavior is the same as that reported by Johnson for *P. hispidula*.

The nucleus of the embryo sac mother-cell divides into two (FIG. 6), and these two divide into four nuclei (FIGS. 7, 8), which usually at least are arranged tetrahedrally—that is, the four

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\* The definitive archesporial cell is to be distinguished from the primary archesporial cell which is the parent of the definitive archesporial cell plus the tapetal or parietal cell.



nuclei occupy the four corners of an imaginary tetrahedron (FIG. 7). The central part of the embryo sac, from this stage onward, is occupied by a large vacuole. As was shown by Brown (4) in *P. Sintenisii* and in *P. arifolia*, and by Brown and Sharp (5) in *Epipactis*, the nuclei resulting from the first two divisions of the nucleus of the embryo sac mother-cell are frequently separated by more or less complete rudimentary or evanescent walls (FIGS. 6, 8). It is possible that these rudimentary walls are always formed following the first two divisions of the nucleus of the embryo sac mother-cell, but that they are so evanescent that they are not often seen. No case was found in which the wall following the first division had persisted until the second division, and the walls following the second division, so far as observed, always disappeared before the third division in the embryo sac.

Each of the first four nuclei divides, thus giving rise to eight nuclei (FIG. 9), which are scattered in the peripheral layer of cytoplasm surrounding the large central vacuole. No signs of separating walls were seen at this stage.

Each of these eight nuclei divides, thus giving rise to sixteen free nuclei in the embryo sac, distributed in the same way as were the eight (FIG. 10). Soon after this stage is reached, a portion of the cytoplasm near the micropyle, together with a nucleus, is cut off by a wall from the rest of the sac, and becomes the oosphere or egg (FIGS. 13, 14). A smaller portion of the cytoplasm very near the egg, together with a nucleus, is cut off by a wall and becomes a synergid, the only one formed in the sac (FIG. 14). It is probable that the egg and synergid arise from sister nuclei, but no definite evidence of this was seen. Of the remaining nuclei, a number varying from six to eight in different embryo sacs is cut off singly from the rest of the embryo sac by saucer-shaped walls (FIG. 13). A small portion of cytoplasm is cut off with each of these nuclei. These peripheral nuclei, as they were called by Johnson (30), take no further part in development and finally degenerate, being crushed by the developing endosperm. The remaining nuclei, varying from six to eight in different embryo sacs, become grouped together, usually near the center of the embryo sac (FIG. 11), and fuse to form the endosperm nucleus (FIG. 12). The number of nuclei taking part in the formation



of the endosperm nucleus, and consequently the number of peripheral nuclei left over, may vary to a greater extent than to the limits observed. The endosperm nucleus is formed in essentially the same manner as that of *P. pellucida* (Johnson, 30).

The embryo sac evidently enters upon a resting stage after four nuclei are formed and before these divide into eight. This is indicated by the fact that a much larger proportion of four-nucleate sacs were found in the preparations than of two-nucleate or eight-nucleate sacs. A number of slides, containing all stages from the definitive archesporial cell to the mature embryo sac, were carefully examined, and an accurate count made to determine this proportion, with the following result: *six* two-nucleate sacs, *thirty-five* four-nucleate sacs, and *seven* eight-nucleate sacs. The significance of this relation will be considered in the general discussion.

In nearly all the cases which were at a stage where this could be determined, it was observed that the endosperm nucleus divides before the male nucleus actually fuses with the nucleus of the egg (FIGS. 13, 14). In most instances, however, the male nucleus was present in the egg, where it usually remained for a considerable time before fusing with the egg nucleus. The presence of the male nucleus in the embryo sac may produce a stimulus which causes the endosperm nucleus to begin its development. This would seem to be in accord with Czapek's (15, p. 127) statement that the swelling of the ovary, in plants, after pollination, is caused by certain soluble substances (*hormones*) emanating from the pollen. The first division of the endosperm nucleus and all subsequent divisions of the resulting endosperm nuclei are mitotic, as is shown by the presence of typical spindles, etc. It is true that the equatorial plate is very broad in these spindles, a condition probably correlated with the presence of the large number of chromosomes contributed by the six or eight constituent nuclei fusing to form the endosperm nucleus, but this was not determined by counting.

Each division of the endosperm nucleus is followed by a cell-wall from the start, the first wall being parallel with the long axis of the fruit or nearly so (FIG. 13). The endosperm continues its development until, in the mature fruit, there is a mass showing about twenty-five cells in median longitudinal section (FIG. 16),



and which is usually almost spherical in shape except for the depression in the micropylar side occupied by the undifferentiated embryo. The nucleus of each cell of the endosperm usually contains several nucleoli, the number observed varying from one to six.

After the male nucleus has fused with the nucleus of the egg, the development of the embryo begins. The fertilized egg divides to a two-celled embryo by a wall longitudinal to the nucellus (FIG. 15). The cells of the embryo continue to multiply until, in the apparently mature seed, there are about twenty cells in a median longitudinal section. The mature embryo shows no differentiation externally in any way except that it is somewhat flattened on the micropylar side. No suspensor is formed, and there is no indication of cotyledons or other organs (FIG. 16).

#### PEPEROMIA VERTICILLATA A. Dietr.

*Peperomia verticillata* A. Dietr., as used by C. de Candolle (9), is listed in the Index Kewensis as *P. pulchella* A. Dietr., while the name *P. verticillata* A. Dietr. is given as a synonym.

Part of the material for the study of this species was collected near Cinchona, Jamaica, where the plants grew on rocks and trees, at an elevation of 5,000 feet. But most of the material was collected in the greenhouse of The Johns Hopkins University from two plants which had been brought from Jamaica.

The flower-spikes of *P. verticillata* average fully three times as long as those of *P. reflexa*, with a range of two to nine centimeters in length. They are much less fleshy, and this condition, together with other characters of the plant, indicates that it is less strongly xerophytic in structure than the species first considered. The flowers, which are very similar to those of *P. reflexa*, are not nearly so closely crowded on the mature spike, but are loosely scattered along the axis. The bracts, trichomes, and oil-cells of the inflorescence axis resemble those of the former species. In this species the starch grains are strikingly abundant in the bracts.

The development of the stamen and pollen showed no essential difference from that of the former species, although the tapetal cells were larger and more conspicuous here (FIG. 19).

The development of the carpel and ovule, from the differentia-



tion of the primary archesporial cell (FIG. 20) to the practically mature fruit, is essentially the same as in *P. reflexa*, except for some anomalous cases, which will be described later. The nucleus of the embryo sac mother-cell shows synapsis before it divides. Evanescent walls frequently more or less completely separate the nuclei in the two-nucleate and four-nucleate stages of the embryo sac. The mature embryo sac contains sixteen nuclei (FIG. 21). An egg and one synergid are cut off from the rest of the sac. Of the remaining fourteen nuclei, at least six are individually cut off as peripherals, and at least six others fuse together to form the endosperm nucleus. There can be very little doubt that the combined number of peripheral and endosperm nuclei is fourteen as it is in *P. reflexa*, and the number of each probably varies, as it does in that species.

As in *P. reflexa*, relatively many more four-nucleate embryo sacs were found than two-nucleate or eight-nucleate ones, thus indicating that there is a resting stage after the sac becomes four-nucleate.

The abnormal lobing of the ovules is the most interesting feature in the development of this species. A very large percentage of the ovules do not develop in the manner typical for this genus, but become more or less lobed (FIGS. 22-27). The carpel, which encloses an abnormal lobed ovule, seems altogether normal. The irregularity is confined to the nucellus and integument. Instead of the simple, ellipsoidal ovule, usual in *Peperomia*, we often have a two-lobed structure, one lobe developing an embryo sac and the other usually remaining sterile (FIGS. 23-27). The notch between the fertile and sterile lobes does not extend clear to the base of the ovule, but only about one half to three fourths of the distance (FIGS. 23, 27)—so that this lobing may be looked upon as a forking or branching of the ovule, somewhat similar to that reported by Hofmeister (29) in *Morus alba*.

The sterile lobe is generally larger than the fertile lobe, so that less than half of the tissue of the ovule takes part in the formation of the seed. The fertile lobe is the only part of the ovule which develops an integument (FIG. 25), and this integument may vary greatly. In normal, unlobed ovules the integument is two cells thick except at the apex where it is thicker around the micropyle.



In the abnormal, lobed ovules, it is frequently more than two cells thick, is usually irregular in shape, and is often more or less incomplete. The fertile lobe develops into a ripe seed, which is more or less deformed by the presence of the sterile lobe. The latter may cause a flattening of one side of the seed, or there may be a depression in one side of the seed due to its presence (FIG. 27). The sterile lobe is always more or less cut up into smaller lobes, and this subdivision is extremely irregular and often very complex. The sterile lobes often contain large oil-cells, which are regularly found in the carpels, bracts, and rachis, but are not present in the normal ovules, nor in the fertile lobes of these lobed ovules.

Frequently, in young ovules, one or more of these sterile lobes appear potentially able to form an embryo sac, as indicated by their shape, their affinity for certain stains, and sometimes by the presence of cells which appear to be sporogenous in character. In fact a few cases were found in which the two lobes of the ovule were fertile, each having an embryo sac and a separate integument. But no ovule was found in which more than one embryo had been initiated. In this respect, the phenomenon resembles the similar abnormality in *Morus alba* (Hofmeister, 29) in which, in all the investigated cases, the ovules aborted after the egg apparatus was formed.

The flower-spikes which showed this abnormality were all obtained from the two plants in the greenhouse at the Botanical Garden of The Johns Hopkins University. No such cases were found in the Jamaican material. It may be concluded that the greenhouse environment was responsible for the phenomenon, but this seems improbable when we take into consideration the fact that almost nothing of this kind was seen in the half dozen other greenhouse species which were studied in detail. On one plant of *P. verticillata*, which grew in the greenhouse, nearly one half of the ovules were of this lobed sort. In fact, in some spikes of this plant every ovule was lobed or branched. On the other plant, a very much smaller proportion of the ovules showed this abnormality.

Whether these abnormal structures have more than a teratological significance is difficult to determine. Their relative abun-



dance may indicate that they have some phylogenetic suggestion. It may be an approach to a condition of more than one ovule in a carpel, and may be of atavistic significance.

More than one ovule in a carpel was the prevailing condition in the ancestors of the Piperaceae, if the theory of Lotsy (42, pp. 487-513) or of Hallier (27) be accepted, for both these authors believe that the Piperaceae have descended from the Magnoliaceae. Of this latter family of ten or eleven genera, all but one genus (*Illicium*) have more than one ovule in each carpel. And the same thing is true, if we accept the phylogenetic view embodied in the classification of the Engler-Gilg Syllabus (18, p. 157). The Saururaceae, which according to that grouping is the lowest family of the Piperales, has multiovulate carpels, and the carpels of certain of the Casuarinaceae, the family next below the Piperales, may sometimes contain two ovules.

Schwere (65), working on *Taraxacum*, found a case in which two embryo sacs developed in one nucellus, each giving rise to a normal embryo. Phylogenetically considered, he pointed out that we have here one megasporangium with two megaspores, and he considers it an atavistic appearance, an illustration of Hofmeister's ingenious and masterly work on the genetic relationship between Phanerogams and Cryptogams.

Hofmeister (29) considered the abnormal division of the nucellus in *Morus alba* as a monstrosity, although it was of frequent occurrence. The cases of *Morus* differ from those of *Peperomia* in that the two parts or lobes of the nucellus of the former are always both enclosed by the same inner integument, while in the latter the two parts or lobes of the nucellus are never enclosed by the same integument.

Braun (3) refers to these cases of *Morus* (Hofmeister, 29) as false polyembryony (*unächte Polyembryonie*), and they have been so classified by later authors (Ernst, 19; Coulter & Chamberlain, 14). The reason for this is not plain, for there is no statement in Hofmeister's brief description that any embryos were really initiated. Since no case was found in *P. verticillata*, in which more than one embryo was initiated in the ovule, it is inappropriate to consider this a case of polyembryony, or pseudo-polyembryony, as it has been called.



In *Coffea arabica*, Hanausek (28) found actual polyembryony, as he called it, in which two to three embryos were formed in branches of the nucellus, one embryo developing in each branch. The abnormal branching of the nucellus in *Coffea* resembles that in *P. verticillata*, although the storage material in the former is endosperm, while in the latter it is chiefly perisperm.

This case of *Coffea*, that of *Taraxacum*, mentioned above, and other similar cases have been classed under pseudopolyembryony by later writers, but since they are cases of the occurrence of more than one embryo in a single seed, no good reason is apparent for calling the phenomenon *false* polyembryony. It is true that these cases, in which more than one embryo arises in one nucellus—each in a separate embryo sac—are quite different from the ordinary cases of polyembryony, but they do not differ from them in the essential character of polyembryony, that is, the initiation of more than one embryo in one ovule.

Two ovules, each surrounded by a separate inner integument, each containing an embryo sac, and both inside a common outer integument, were described and figured by Schacht (60, *pl. 3, f. 18*) in *Orchis Morio*. Braun (3) was of the opinion that these twin ovules, as he called them, arose by division of the nucellus, rather than by a growing together of two nucelli. He was led to this view by the appearance inside of the common outer integument of two entirely separate inner integuments.

In *Monotropa Hypopitys*, Schacht (60, p. 40) found a quite similar case, in which two embryo sacs filled with endosperm were surrounded by a single integument.

The case of *Orchis latifolia*, described and figured by Schleiden (62, p. 599, *pl. 6, f. 2*), is, as suggested by Strasburger (72), doubtless to be interpreted in the same way as Schacht's twin ovules in *Orchis Morio* (60).

Strasburger (72) described a case, similar to that found in *Orchis Morio*, in a closely related orchid, *Gymnadenia conopsea*, in which each of the two embryo sacs already contained an embryo.

Luerssen (43, p. 296) mentioned a similar case, which he found in *Iris sibirica*.

While the abnormally branched or lobed ovules in *Peperomia verticillata*, *Monotropa*, *Morus*, *Coffea*, *Iris*, *Gymnadenia*, and



*Orchis* resemble one another in the occurrence of two embryo sacs in one nucellus, there are, with respect to the integuments, at least four different classes: (1) That represented by *Peperomia* in which each fertile lobe of the nucellus has an independent single integument, (2) That represented by *Monotropa* in which both embryo sacs are surrounded by the same single integument, (3) That represented by *Morus*, the ovules of which have two integuments, in which both embryo sacs are within the same inner integument, (4) That represented by *Gymnadenia* and *Orchis* in which each lobe has a separate inner integument but both lobes are within a common outer integument. It seems that in cases like *Morus* and *Monotropa* we have two gametophytes developed within a single megasporangium, although divided or forked, for it is still all inside of the single integument, or inside the inner integument, if there be two. And it may be but a step from this to cases like *Peperomia* and *Orchis*, which, if they have more than teratological significance, probably either represent an approach to a condition of more than one ovule in a carpel, or they constitute atavistic appearances of a similar condition.

#### PEPEROMIA SCANDENS Ruiz & Pav.

The material for the study of *Peperomia scandens* Ruiz & Pav. was collected in the greenhouse of The Johns Hopkins University at Homewood, from a plant brought from Jamaica. In its native habitat, the plant commonly grows at low altitudes as an epiphyte upon the trunks of trees.

The flower-spikes of *P. scandens* are about the same length and about the same diameter as those of *P. reflexa*. The most obvious differences are that the mature fruits of the former are hardly at all sunk in the axis, while those of the latter are deeply sunk (FIGS. 4, 17, 32, 33), and that the fruits of the former have long, curved beaks, while those of the latter have only very short straight beaks. The carpel of *P. scandens* is sessile in the axil of a peltate bract, which closely resembles those of the two preceding species. Up to the sixteen-nucleate stage of the embryo sac, the carpel is sunk in the spike to such a depth that the stigma and beak of the carpel barely project outside the surface. At this stage, the stalk of the bract is entirely sunken in a separate cavity just below the one



containing the carpel, only the shield-like top of the bract being outside. It is not until after the embryo sac is mature that the developing fruit is pushed out. The flowers and consequently the fruits are just about as much crowded in this species as they are in *P. reflexa*. There are no hairs on the rachis between the flowers as there are in *P. reflexa*, but there are a few on the peduncle of the spike. The absence of hairs on the rachis, together with the exserted fruits and thinner epidermis, indicates that this species is less xerophytic than *P. reflexa*. In all essential particulars the flowers and fruits of *P. scandens* closely resemble those of the two preceding species.

In the development of the stamen and pollen, this species very closely coincides with that of *P. verticillata*.

The development of the carpel and ovule, from the differentiation of the primary archesporial cell to the practically mature fruit, is essentially the same as in *P. reflexa*. The nucleus of the embryo sac mother-cell goes into synapsis before division. Evanescent cell-walls frequently appear between the nuclei following the first and second divisions in the embryo sac (FIGS. 28-31). The mature sac contains sixteen nuclei, of which one becomes the egg and one becomes the single synergid (FIG. 34). Of the remaining fourteen nuclei, a number varying from six to nine are cut off as peripherals, and there is little doubt that the endosperm nucleus is made up by the fusion of the remainder of the fourteen, although in many cases the number could not be positively determined.

The difficulty in determining the exact number of nuclei which fuse to make up the endosperm nucleus in any species of *Peperomia* studied by the writer, lies in the fact that usually, if not always, a part of the nucleoli fuse during the process of fusion of the nuclei. The nucleoli are excellent indicators of the number of component nuclei as long as they remain distinct. But it is comparatively rare that one finds in his preparations complete groups of fusing endosperm nuclei in which no nucleoli have yet fused. It is true that the lobes of the endosperm nucleus and the relative size of the nucleoli can frequently be relied upon to indicate to what extent fusion has proceeded, but not after the fusion is complete.

A resting stage evidently occurs in this species after the embryo sac has reached the four-nucleate stage, as shown by the relatively



greater number of four-nucleate sacs than of two-nucleate or eight-nucleate ones. In forty-two ovules, taken at random, *ten* two-nucleate, *thirty* four-nucleate, and *twelve* eight-nucleate sacs were found.

PEPEROMIA METALLICA Lind. & Rod.

The material for the study of *Peperomia metallica* Lind. & Rod. was obtained from a plant growing in the greenhouse of The Johns Hopkins University at Homewood.

In the original description of this plant by Rodigas (58), there was no description of the flowers, and it seems that none has been published since.\* In fact Linden and Rodigas were not absolutely sure that the plant was a *Peperomia*, although they named it and described it as such. The flowers, however, leave no doubt that the plant is a true *Peperomia*. They are borne on a spike, which varies from 3.5 cm. to 7.5 cm. in length, and which is rather slender, resembling that of *P. verticillata* in size, and the flowers are loosely scattered along the spike and are only slightly sunken in the axis. The rachis is smooth except for the presence of hydathodes very similar to those in the other species of *Peperomia*. The flower consists of two stamens and a single carpel, the latter being sessile in the axil of a peltate bract, which very closely resembles those of the other species of the same genus studied by the writer. The anthers are bilocular; the stigma is sessile and penicillate; and the carpel contains a single orthotropous ovule. In fact, the whole flower and all its parts closely resemble those found in other *Peperomias*.

The development of the carpel and ovule, from the differentiation of the primary archesporial cell up to the four-nucleate stage of the embryo sac, is essentially the same as that observed in *P. reflexa*. The nucleus of the definitive archesporial cell or embryo sac mother-cell shows synapsis before division.

A striking abnormality was observed in this species. The single plant, cultivated in the greenhouse of The Johns Hopkins University, when flowering in the autumn of 1912 bore only four or five spikes each of which was interrupted by a zone of small vegetative leaves, as shown in FIG. 35. Flowers are borne on the

\* Dr. Casimir de Candolle writes me that his unpublished manuscripts contain a diagnosis of this species including the flowers.



spike both above and below this zone of leaves, being more distant from each other just above the zone than they are below it. In other words, in the arrangement of the flowers, the part of the spike above the leaves as well as the part below the leaves resembles a whole normal spike of this species, that is, it is much as though there were one normal spike above another. In this respect these abnormal interrupted spikes remind one of the similar, though normal, phenomenon in *Callistemon*, the inflorescence axis of which continues to grow after flowering and produces a zone of vegetative leaves and later another zone of flowers, and so on. An approach to this condition is normally found in *Ananas sativa*, in which the inflorescence axis continues to grow and produces vegetative leaves above the fruits. This phenomenon has also been found as an abnormality in *Pinus* and *Larix*. But in neither of these cases, so far as known to the writer, is there a second zone of flowers formed, as there is in *Callistemon* and in *Peperomia metallica*.

Dr. Casimir de Candolle writes me that these interrupted spikes are not present in his two herbarium specimens of *P. metallica*. And further, he thinks that the peculiar spikes constitute a teratological case, of which he has found striking examples in several species of *Piper*, and also in some *Peperomias*. In *P. Fraseri* C. DC. (*P. resedaeflora* Lind. & André), particularly, he has seen some spikes in which a few scattered bracts were replaced by small undeveloped vegetative leaves.

At a subsequent blooming of the plant in the greenhouse at Homewood, only six of the abnormal spikes appeared, while at least twice that number were normal. One of the abnormal ones showed the small vegetative leaves scattered considerably along the axis. A close examination of the interrupted zone shows that a few of the leaves have flowers in their axils.

The writer believes with De Candolle that these abnormal spikes have only teratological significance.

#### PEPEROMIA FRASERI var. RESEDIFLORA C. DC.

The flower-spikes of *Peperomia Fraseri* var. *resediflora* C. DC. (*P. resedaeflora* Lind. & André), which were used in this study, were collected by Professor D. S. Johnson in 1901 in the greenhouse of the "Pflanzenphysiologisches Institut" in Munich.



This species is peculiar for a *Peperomia*, in that it has compound flower-spikes. In the genus *Peperomia*, which comprises some four hundred species, nearly all have the flowers in simple spikes. But in this species the flowers are borne in conical panicles with a central axis and numerous lateral branches, the flowers being sessile in the axils of bracts and limited in their distribution to the branches of the inflorescence, except the apical portion of the central axis, as is usual in paniculate inflorescences.

The development of the carpel and ovule, from the definitive archesporial cell, or embryo sac mother-cell stage, up to the sixteen-nucleate embryo sac stage, coincides very closely with that of *P. reflexa*. In several cases rudimentary or evanescent walls were clearly visible in the two- and four-nucleate stages.

#### PEPEROMIA BLANDA HBK.

The material for the study of *P. blanda* HBK. was collected in the greenhouse of The Johns Hopkins University at Homewood.

The development of the embryo sac, from the embryo sac mother-cell stage to the 16-nucleate stage, closely resembles that of *P. reflexa*. Evanescent walls were seen in the two- and four-nucleate stages (FIG. 36). The number of peripheral nuclei cut off in the mature sac is about eight and seems to vary above and below this number.

This species differs from the others examined in this study, in that the stigma is both above and below the external opening of the stylar canal and is not limited to the anterior or lower part of the carpel.

Two cases were found in which the ovule was lobed in a manner similar to those of *P. verticillata*. And three cases were observed in which there were two ovules in one carpel. These lobed ovules and twin ovules doubtless have the same significance as the lobed ovules of *P. verticillata*.

Baillon (2, p. 140) calls attention to an approach to the anatropous condition in the ovules of this species and states that the ovule is inclined toward the anterior side of the ovary. An examination of a number of ovules, however, shows that this feature is not constant. In fact, the ovules are usually inclined toward the axis of the inflorescence, that is, toward the *posterior* side of the ovary, but the micropyle may be either anterior or posterior to the apex of the ovule.



## PEPEROMIA GALIOIDES HBK.

The flower-spikes for the study of *P. galioides* HBK. were collected in the greenhouse of The Johns Hopkins University at Homewood. The plant from which they were obtained was collected near Cinchona, in the Blue Mountains of Jamaica, where it grew on the crags on the flank of John Crow Peak.

The development of the embryo sac, from the stage of the definitive archesporial cell, or embryo sac mother-cell, to the sixteen-nucleate embryo sac, is essentially the same as that of *P. reflexa*. Evanescent walls were seen in the four-nucleate stage.

## PEPEROMIA LANGSDORFFII Miq. (?)

The material used in the study of *P. Langsdorffii* Miq. (?) was collected in the greenhouse of The Johns Hopkins University at Homewood. According to the Berlin Botanical Garden, the plant is a native of the West Indies and the northern part of South America.

The development of the embryo sac, from the embryo sac mother-cell stage to the two-nucleate embryo sac, is essentially the same as that of *P. reflexa*. Evanescent walls were observed in the two-nucleate embryo sac.

## PIPER TUBERCULATUM Jacq.

The only species of the genus *Piper* examined in this study was the arborescent species *P. tuberculatum* Jacq. The flower-spikes were collected from a tree twenty feet in height, which was growing in the forest on the flanks of John Crow Peak at about 5,300 feet altitude, near Cinchona, in the Blue Mountains of Jamaica. Part of the material was collected and fixed in June, 1906, by Professor D. S. Johnson. The remainder was collected from the same tree by Mr. Jonas Walker, caretaker of the Cinchona Gardens, at intervals from July 8 to October 30, 1912, and as collected it was immediately put into a solution consisting of four per cent. formalin in seventy per cent. alcohol,\* in which it remained for several weeks, after which time it was run up through the alcohols as though it had been fixed.

In this species the flower consists of four stamens and a single

\* The formula for this solution was kindly furnished to me by Dr. Charles J. Chamberlain.



pistil, which is sessile in the axil of a short, club-shaped, hairy bract. At the apex of the ovary there are three short spreading stigmas, and this indicates that the pistil is compound, consisting in its morphological origin of three carpels. In each ovary there is borne a single, orthotropous ovule with two integuments (FIG. 41). The anthers are four-locular. There is no evidence—not even rudiments—of calyx or corolla. The flowers are borne on long slender spikes, which bear a close resemblance to those of many *Peperomias*.

The flowers are closely crowded on the spike. While it is true that they are initiated acropetally, they do not reach maturity in this succession, but all mature at practically the same time. In this latter particular they differ from those of the genus *Peperomia*.

The development of the embryo sac in *Piper tuberculatum* is closely similar to that described by Johnson (32 and 35) for *Piper medium*, *Piper umbellata*, and *Piper Betle* var. *monoicum*.

The primary archesporial cell is single and it is subepidermal (FIG. 37). This cell divides transversely, the upper cell being a parietal or tapetal cell, and the lower cell being the definitive archesporial cell (FIG. 38). The parietal or tapetal cell divides to form a layer four or five cells thick in the mature nucellus. The definitive archesporial cell develops directly into the embryo sac, without cutting off any megaspores.

The nucleus of the definitive archesporial cell, or embryo sac mother-cell (FIG. 39), divides to two (FIGS. 40, 41), and these two divide to four nuclei (FIG. 42). These divisions are not followed by walls, even evanescent ones. The nuclei of the embryo sac at the four-nucleate stage always have the linear arrangement or a close approach to it (FIG. 42). Not a single case of tetrahedral arrangement, as is found in *Peperomia*, was observed. Each of the four nuclei divides once more, giving rise to an eight-nucleate embryo sac, which contains an egg, two synergids, two polar nuclei, and three antipodals (FIG. 43). Thus it very closely resembles those found in other species of *Piper* and is typical of those found in the vast majority of angiosperms which have been investigated. There is some evidence that one of the male nuclei takes part in the formation of the endosperm nucleus.



# The morphological relationships of the Florideae and the Ascomycetes

B. O. DODGE

(WITH THIRTEEN TEXT FIGURES)

In recent years our knowledge of the structure and life processes of many species of algae and fungi has been increased by general morphological studies frequently supplemented by critical cytological investigations. The later literature contains a vast amount of data bearing more or less directly on the question of the phylogenetic relationship of the Florideae and Ascomycetes. Harper has clearly distinguished between the questions of morphological relationship and those relating to the special functional activities of the initial organs of the ascocarp.

In the present paper I shall still further discuss the morphology of the various reproductive structures of the Florideae and Ascomycetes in the light of my recent observations on the trichogynes and ascogonia in various members of the Ascobolaceae and related forms (37). Practically all the recently accumulated evidence favors the view that the Ascomycetes are a monophyletic group and have been derived from the red algae. I have brought together in the form of diagrams the results of both recent and older work bearing on this question. The transition from the conditions in the red algae to those in the Collemaceae as described by Stahl (86) has been made much clearer by the work of Miss Bachmann (2, 3) in her studies on *Collema pulposum*.

Brefeld's doctrine that the Ascomycetes have been derived from the Phycomycetes through the evolution of the sporangium into the ascus is of course untenable, though in a somewhat modified form it has been recently revived by Bucholtz (21), who regards *Endogone* as a true Phycomycete in which the fruit resulting from the fusion of the nuclei from two unequally differentiated sex cells is a "zygosporocarp." The short time in which the sex nuclei travel together as a pair out of the oögonium directly into the sac-like outgrowth of the oögonium where they fuse, suggests to Bucholtz a primitive binucleated condition such as might have



existed just previous to the inauguration of the habit of conjugate nuclear division which leads to the fusion of the nuclei in the ascus of such Ascomycetes as *Galactinia*, *Acetabula*, and *Pyronema* according to Claussen (26).

The question as to the relationship of the outgrowths of the fertilized egg, ascogenous hyphae, in the Ascomycetes and oöblastema filaments in the red algae is fundamental for the understanding of the phylogeny of the two groups, and it is a question that has been much neglected. It is a conspicuous and well-established fact that it is an essential character of the eggs in both groups to give rise to more or less complex filamentous outgrowths immediately after fertilization. De Bary (5), although he suspected from what he knew of the mildews that the ascus must in all cases be an outgrowth of the fertilized egg, was unable to trace the connection in *Pyronema*. Kihlman (57) succeeded in making out this connection and it was thus established that the asci are regularly the end members of outgrowths of the oögonium, although Brefeld, in spite of the fact that all subsequent investigations based upon the careful use of microtome sections proved the contrary, continued to insist that the asci might arise from the same hyphae as the paraphyses. Curiously enough Blackman and Welsford (12) notwithstanding the abundant evidence to the contrary in other cases, and the fact that they find a well-developed ascogonium at the origin of the ascocarp, arrive at the conclusion that in *Polystigma* the asci do actually arise from the vegetative hyphae. Fisch (41) recognized the difference between the purely vegetative clusters of hyphae which penetrate the stomata and the trichogynes which are found surrounded by these "respiratory hyphae" (FIG. 1, D). The trichogyne could be distinguished on account of its size and the characteristic changes occurring in it on the application of reagents. Blackman and Welsford (12) have recently reinvestigated this species and are unable to discover that the ascogonium ever develops a trichogyne which grows outward through a stoma, although they figure a trichogyne-like hypha directed outward toward a stoma. They suspect that the trichogyne described by Fisch was merely one of the vegetative hyphae crowding through the stoma just as they do in *Gnomonia*, where Brooks (17) calls them trichogynes that are now sexually function-



less and have probably taken on a respiratory function. It is difficult to understand how Fisch could have figured such perfect ascogonia and trichogynes without having before him the actual structures in question. That he did see ascogonia is attested by the very similar structures figured by Blackman and Welsford and it is not altogether clear how an ascogonium which lies at the very center of the developing perithecium could be uncoiled and forced practically to the wall as they describe unless it were concerned in the production of the ascogenous hyphae which as a fact come to occupy much of the central space of the perithecium.

The first convincing proof that the asci develop from the hyphae arising from the ascogonium was furnished by Janczewski (56) for *Ascobolus furfuraceus* (FIG. 9, B), and shortly afterwards Borzi (15) found practically identical conditions prevailing in *Ascophanus pilosus* (*Lasiobolus equinus*). Undoubted connections between ascogonia and asci have been traced in a number of species. Among the forms in which this connection has been quite satisfactorily established we may note the following: *Sphaerotheca Castagnei* (De Bary, 1863), *Ascobolus furfuraceus* (Janczewski, 1871), *Lasiobolus equinus* (Borzi, 1878), *Pyronema confluens* (Kihlman, 1883), *Sphaerotheca Castagnei* (Harper, 1895), *Ascobolus furfuraceus* (Harper, 1896), *Laboulbenieae* (Thaxter, 1896), *Pyronema confluens* (Harper, 1900), *Poronia punctata* (Dawson, 1900), *Pertusaria communis* (Baur, 1901), *Gymnoascus candida* (Dale, 1903), *Phyllactinia corylea* (Harper, 1905), *Ascodesmis nigricans* (Claussen, 1905), *Humaria granulata* (Blackman & Fraser, 1906), *Thelebolus stercorarius* (Ramlow, 1906), *Thecotheus Pelletieri* (Overton, 1906), *Lachnea stercorea* (Fraser, 1907), *Aspergillus herbariorum* (Fraser & Chambers, 1907), *Baeomyces roseus* (Nienberg, 1907), *Usnea barbata* (Nienberg, 1907), *Ichmadophila aeruginosa* (Nienberg, 1907), *Aspergillus repens* (Dale, 1909), *Ascophanus carneus* (Cutting, 1909), *Gnomonia erythrostoma* (Brooks, 1910), *Leotia chlorocephala* (Brown, W. H., 1910), *Lachnea scutellata* (Brown, W. H., 1911), *Pyronema confluens* (Claussen, 1912), *Ascobolus carbonarius* (Dodge, 1912), *Laboulbenia chaetophora* (Faull, 1912), *Collema pulposum* (Bachmann, 1913), *Xylaria tentaculata* (Brown, H. B., 1913), *Lachnea cretea* (Fraser, 1913).

It is certainly one of the best established facts in the mor-



phology of the Ascomycetes that the asci arise from outgrowths of the ascogonia and that the paraphyses do not originate in the same manner or from the same cells. A further interesting feature in this connection is found in the fact that, in certain forms like *Pyronema*, the mildews, *Ascobolus furfuraceus*, *Lasiobolus equinus*, etc., only one cell gives rise to ascogenous hyphae, while in *Thecotheus* (70), *Ascophanus carneus* (27), *Ascobolus glaber* (31), *A. carbonarius* (37), *Lachnea cretea* (44), and in the lichens (FIG. 7), so far as this process has been noted (9, 32, 65, 3), there are several ascogenous cells in the ascogonium.

As noted above, De Bary (5) discovered that the apothecium of *Pyronema* originates from a rosette of paired swollen hyphae, and his figures show correctly the general form of these hyphae and the tube-like structures connecting the pairs. Bornet and Thuret published their account of fecundation in the red algae in 1867 (14) and gave the name trichogyne to the receptive elongation of the carpogonium. The following year we have the first clear statement of the morphological resemblance between the reproductive structures of the red algae and the Ascomycetes as represented by *Pyronema*. Sachs (75) noted the likeness of the oögonium with its trichogyne to the corresponding structures in the Florideae and likewise the similarity of the fruit body of the Ascomycetes to that of such forms as *Lejolisia* (FIG. 6, F). He also pointed out the difference between the antheridia of *Pyronema* and those of the red algae. Judging from Sachs' repeated references to De Bary in this connection it is not at all unlikely that it was De Bary who originally pointed out these similarities, for in 1870 (4) he states very clearly the evidence upon which a relationship between the two groups might be assumed. He showed also how it might be possible to derive the Ascomycetes from such forms as *Peronospora*, but at this time he maintained that the evidence at hand was not sufficient to justify a conclusion in favor of either hypothesis. His latest attitude on this question may perhaps be inferred from a note by Sachs (76) where it is said in reference to the derivation of the Ascomycetes from the Rhodophyceae: "von den Rhodophyceen sind die Ascomyceten (oder wenigstens die Discomyceten) abzuleiten, worauf vorwiegend die Procarpien beider hinweisen"; to which is added the footnote, "soweit ich



privatim unterrichtet bin, war sowohl De Bary wie Schmitz dieser Annahme zugeneigt."

Woronin, Janczewski, De Bary, and Borzi do not specifically identify the tapering end of the ascogonium in *Ascobolus* as a trichogyne though they give no other interpretation of this very important structural feature of the egg apparatus, and Sachs' classic figure of *A. furfuraceus* represents the fertilization as occurring by means of a pollinodium which applies itself to the tip of the many-celled ascogonium, though this conception has by no means been held by all subsequent students of the form. Stahl's work on the lichens established beyond question the existence of trichogynes fertilized by free spermatia, and this is probably the most important discovery bearing on the relationship of the two groups.

Among the Ascomycetes the trichogyne is most characteristically developed in the Laboulbenieae. The variability in the form of the trichogynes in this group is almost without limit. They may be one-celled structures as in *Stigmatomyces Baeri* (FIG. 2, G), recalling the trichogyne of *Batrachospermum* (FIG. 4, B), or they may be multicellular spirally coiled and branched as in *Compsomyces verticillatus* (FIG. 2, I). Some of them are very similar to the trichogyne of *Pyronema* (FIG. 2, D), as in *Zodiomyces vorticellarius* (FIG. 2, J), where the spermatia remain attached to the stalk, and the trichogyne is therefore a structure active in seeking out the spermatia.

*Ascodesmis*, a form closely related to *Pyronema*, furnishes a further example of a reduced trichogyne. Claussen (25) finds that the end cell of the short spiral coil of the ascogonium functions as a trichogyne (FIG. 2, E). It is not especially different in structure from the other cells of the ascogonium.

Kihlman (57) did not consider the tapering end of the ascogonium of *Melanospora* as a trichogyne (FIG. 2, K) for the reason that he was unable to find that it fused with any hypha representing an antheridium. Miss Nichols (64), however, reports in *Hypocopra* and *Ceratostoma* (FIG. 2, C), other members of the same group, that the end cell of the ascogonium does connect with an antheridium.

Fraser and Chambers (46) find that the ascogonium of *Asper-*



*gillus herbariorum* is provided with an end cell that functions as a trichogyne in certain cases. They think this form is becoming apogamous, but this fact would not, in their opinion, affect the question of the homologies of the cells at the end of the archicarp.

I have described a form of archicarp in *Ascobolus carbonarius* which in its origin is entirely unlike any hitherto known in the Ascomycetes. I refer to the common form of the species which produces abundant spore-like bodies, "conidia," on long stalks, and not to the form *A. mirabilis* (37) of Dangeard. This latter strain which I have since isolated and grown several months in pure cultures produces the ascogonium directly from the mycelial hyphae only rarely producing conidia, and then only in very old cultures. Other interesting abnormalities in the archicarp crop out frequently in this strain. I have not been able to follow the development of these abnormal forms but they do not seem to give rise to normal apothecia.

The typical ascogonia of *A. carbonarius* develop apothecia in about two weeks. As described (37), most frequently the ascogonium arises directly from what appears to be an asexual conidium which germinates forming a coiled portion. The original germ tube thus becomes the stalk of the archicarp at the end of which is formed a second coil of extremely large cells composing the ascogonium proper, and from this is derived by sudden constriction of the end cell a long irregularly coiled trichogyne (FIG. 1, E) which in general is not very unlike the trichogyne of *Collema pulposum* (FIG. 1, C) described by Miss Bachmann (2, 3). When grown in artificial media the trichogyne winds about in the medium or on its surface somewhat irregularly and in many cases the long end cell comes in contact with other conidia on long stalks, which I have called antheridial conidia (FIGS. 1, E, and 3, B). The trichogyne end coils itself tightly about this antheridial conidium in such a manner as to indicate that there is a definite attraction between them. The resemblance of the antheridial conidia here to the spermatia of Miss Bachmann's *Collema* (FIGS. 1, C, and 3, D) is direct and striking. I do not know that any of these conidia of *A. carbonarius* function as asexual bodies in distributing the species. They do not become detached from their stalks and are not oriented as we should expect functional conidia



to be. The conidia of *Lachnea abundans* are very loosely attached to erect aerial conidiophores and germination takes place as soon as they are brought into a fresh medium. In my cultures these conidia of *A. carbonarius* never function in any other way than that described. They never produce mycelia directly. Aborting ascogonia do sometimes grow out vegetatively into long hyphae but such growths are recognizable at once and would not be mistaken for trichogynes. The trichogyne is a hypha of very uniform diameter terminating rather bluntly and without branches (FIG. 1, E).

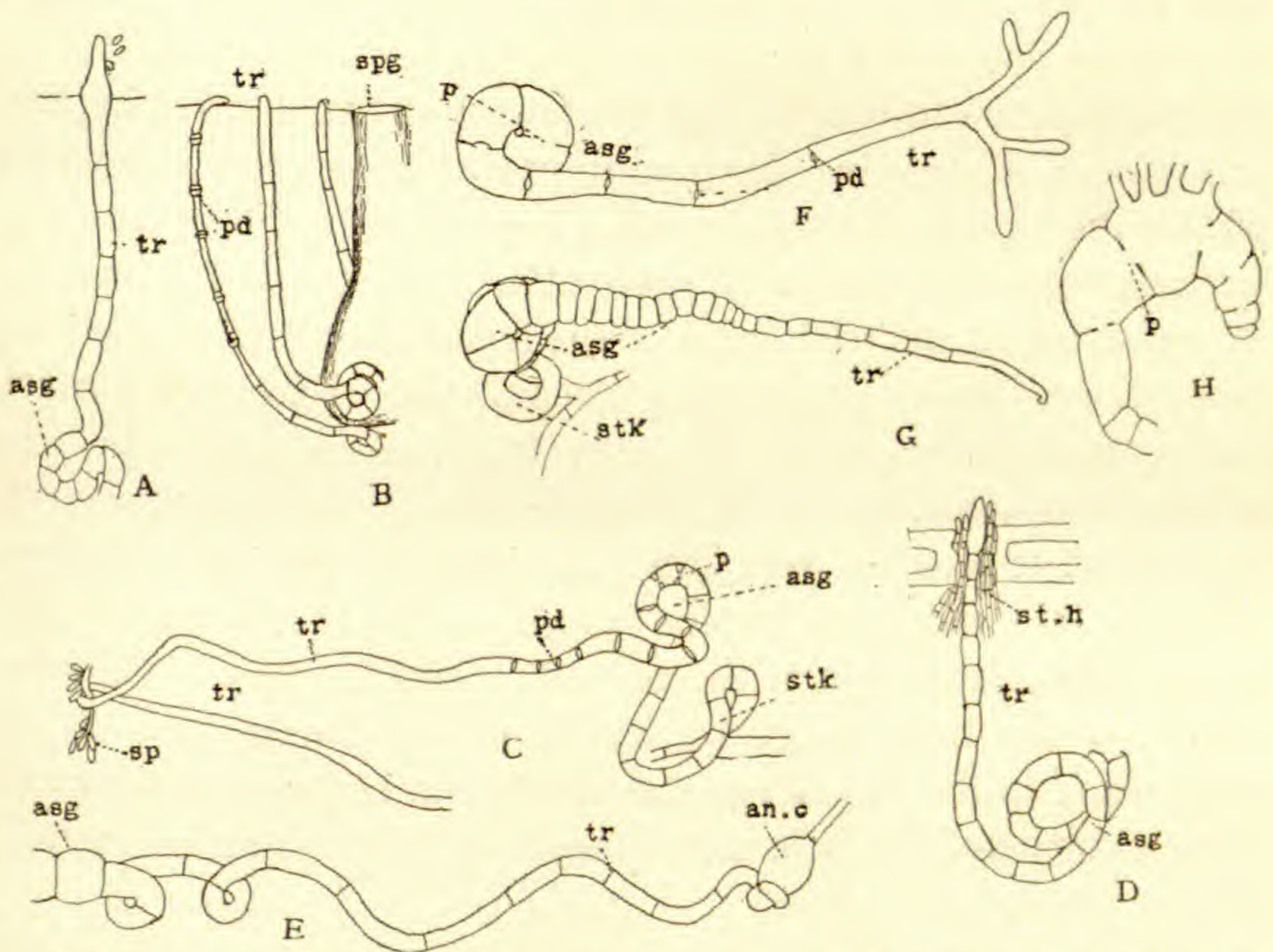


FIG. 1. Septate trichogynes of Ascomycetes. A. *Collema microphyllum*; B. *Physma compactum*; C. *Collema pulposum*; D. *Polystigma rubrum*; E. *Ascobolus carbonarius*; F. *Lachnea cretea*; G. *Lachnea melaloma*; H. *Ascobolus furfuraceus*. asg, ascogonium; an.c, antheridial conidium; p, pore in cross wall; pd, callous pad; spg, spermogonium; st.h, sterile hyphae; stk, stalk of ascogonium; tr, trichogyne. A, B, Stahl; C, Bachmann; D, Fisch; F, Fraser; H, Harper; E, G, original.

The importance of Miss Bachmann's work on *Collema pulposum* can scarcely be overestimated since it furnishes perhaps the most convincing evidence in support of the view that the spermatia of the lichens are sexual organs and that their trichogynes are morphologically equivalent to those of the red algae and of *Pyro-*



*nema*. Miss Bachmann finds that the spermatia of *C. pulposum* are not borne in spermogonia as they are in the forms described by Stahl and others, but are borne singly or in small numbers on branches from the vegetative hyphae imbedded deeply in the thallus (FIGS. 1, C, and 3, D). These spermatia never find their way to the surface of the thallus and commonly remain loosely attached to the spermatiphores. The general character of the fertile branch is not unlike that of other Collemas (FIG. 1, A and B) except as to the structure of the trichogyne and its behavior in fertilization. The specific attraction which the spermatia have for the trichogyne is positively proved by the fact that the trichogyne does not bore outward to the surface of the thallus but is compelled to wind in and out among the vegetative hyphae and colonies of algae in order to connect with the spermatia isolated within the thallus. Several trichogynes may be found growing towards the same cluster of spermatia. The somewhat swollen receptive cell of the trichogyne of the lichens heretofore described (FIG. 1, A) is well adapted for its purpose. Extensive surface area and stability are provided by its increased diameter. In *Collema pulposum*, by virtue of the certainty with which the tip is directed toward the spermatia, no such provision is necessary. However, the receptive surface here is probably much increased by the great elongation of the end cell, which in some cases occupies over one half the entire length of the trichogyne. Wolff (94) describes the end cell of the trichogyne in *Graphis elegans* as being extremely long. In fact no septa were found in the vertical portion of the trichogyne.

The trichogyne of *Lachnea stercorea* (FIG. 2, B) described by Miss Fraser (45) represents another type intermediate between those of *Pyronema* and *Collema*. It is a thick five- or six-celled outgrowth of the oögonium and curves downward fusing with a long irregular club-shaped cell which Miss Fraser believes is an antheridium.

The trichogynes in the lichens, *Ascobolus carbonarius*, and *Lachnea stercorea* are quite as strongly developed as the corresponding organs in the red algae. The land habit has, however, led to their reduction and even disappearance in many forms of Ascomycetes.



The ascogonium of *Lachnea scutellata* (Woronin, 96, W. H. Brown, 19) is not known to have a trichogyne. These authors examined only the comparatively well-developed young fruits and were of course unable to determine the exact form of the archicarp.

Miss Fraser's latest paper (44) describes the trichogynes of *Lachnea cretea* (FIG. I, F) as long and branching. No antheridium was found and Miss Fraser regards the form as wholly apogamous. The archicarps of *L. cretea* as described are very similar to those of *L. abundans*, which I have been able to grow and bring to maturity in great numbers in artificial cultures. In *L. cretea* the cross walls are sometimes perforated but later these perforations

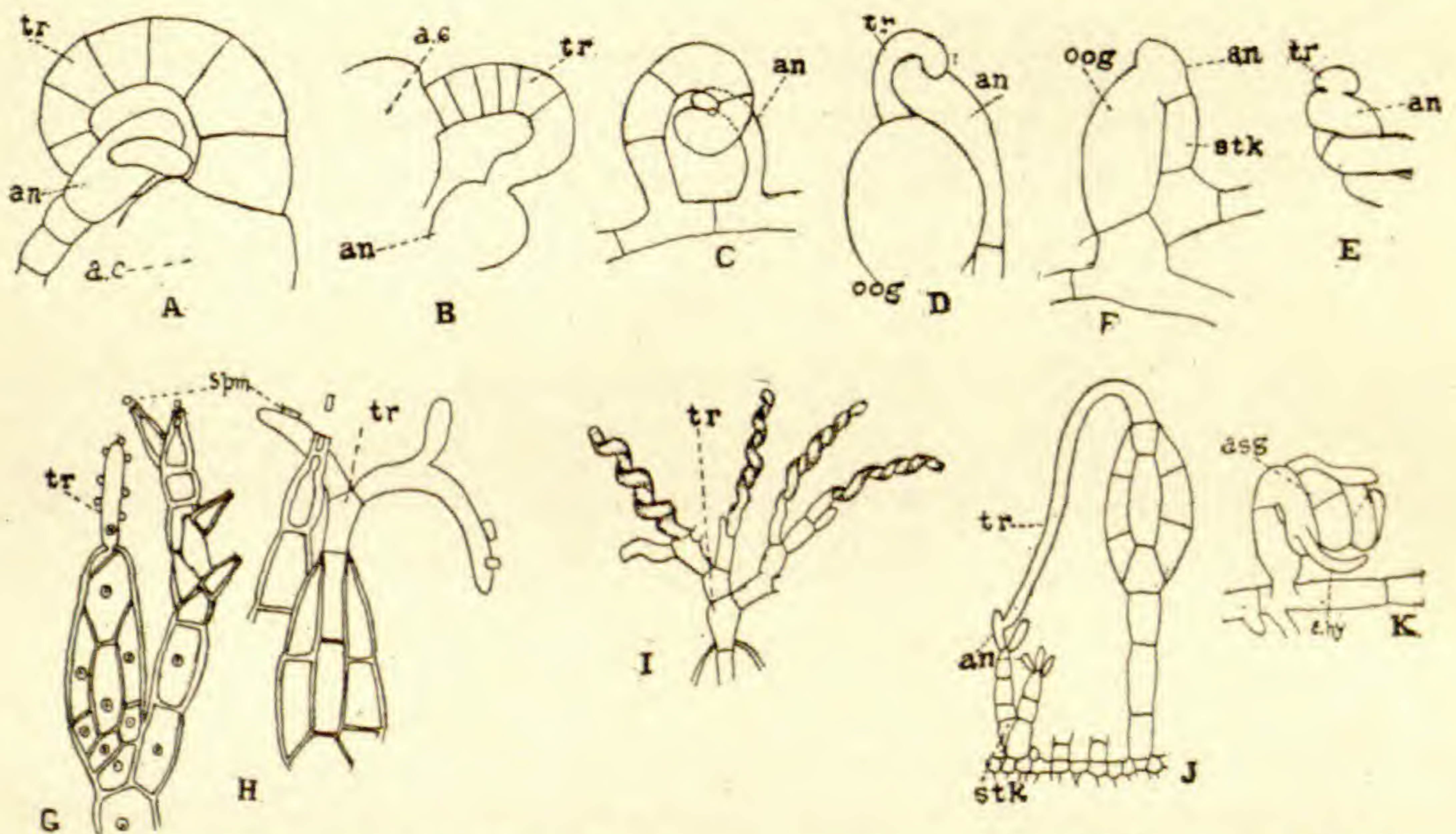


FIG. 2. The upper row shows a further reduction of the trichogyne and a correspondingly nearer approach of the antheridium to the oögonium. A. *Ascobolus magnificus*; B. *Lachnea stercorea*; C. *Ceratostoma*; D. *Pyronema*; E. *Ascodesmis*; F. *Sphaerotheca*; G-J. Four types of trichogynes found in the Laboulbeniaceae. G. *Stigmatomyces Baeri*; H. *Laboulbenia cristata*; I. *Compsomyces verticillatus*; J. *Zodiomyces vorticellarius*; K. The ascogonium of *Melanospora parasitica* without a trichogyne. a.c, ascogenous cell; an, antheridium; asg, ascogonium; e.hy, enveloping hyphae; spm, spermatium; stk, stalk; oog, oögonium; tr, trichogyne. A, original; B, Fraser; C, Nichols; D, F, Harper; E, Claussen; G, H, I, J, Thaxter; K, Kihlman.

are closed by thick pads. Miss Fraser believes that the antheridium has only recently disappeared. Branching trichogynes are not, however, confined to the Laboulbeniaceae as stated by this author. Stahl (86) figures a branched trichogyne in *Collema microphyllum*, Lindau (59) describes and figures such a form in



*Lecanora subfusca*, and Harper (53) figures a two-branched trichogyne in *Pyronema*. Miss Bachmann (3) also describes and figures a branch which is given off from the ascogonium at least very close to the base of the trichogyne in *Collema pulposum*.

The Tulasnes (90) mention the existence of an ascogonium in *Lachnea melaloma*. I have grown this form abundantly in cultures on agar media and find an archicarp of striking proportions. The long stalk, the many-celled coiled ascogonium prolonged into a trichogyne-like portion (FIG. 1, G), likewise the great irregularity and variety of forms which it shows in this species suggest a relationship with *Ascobolus carbonarius*. It may be even more

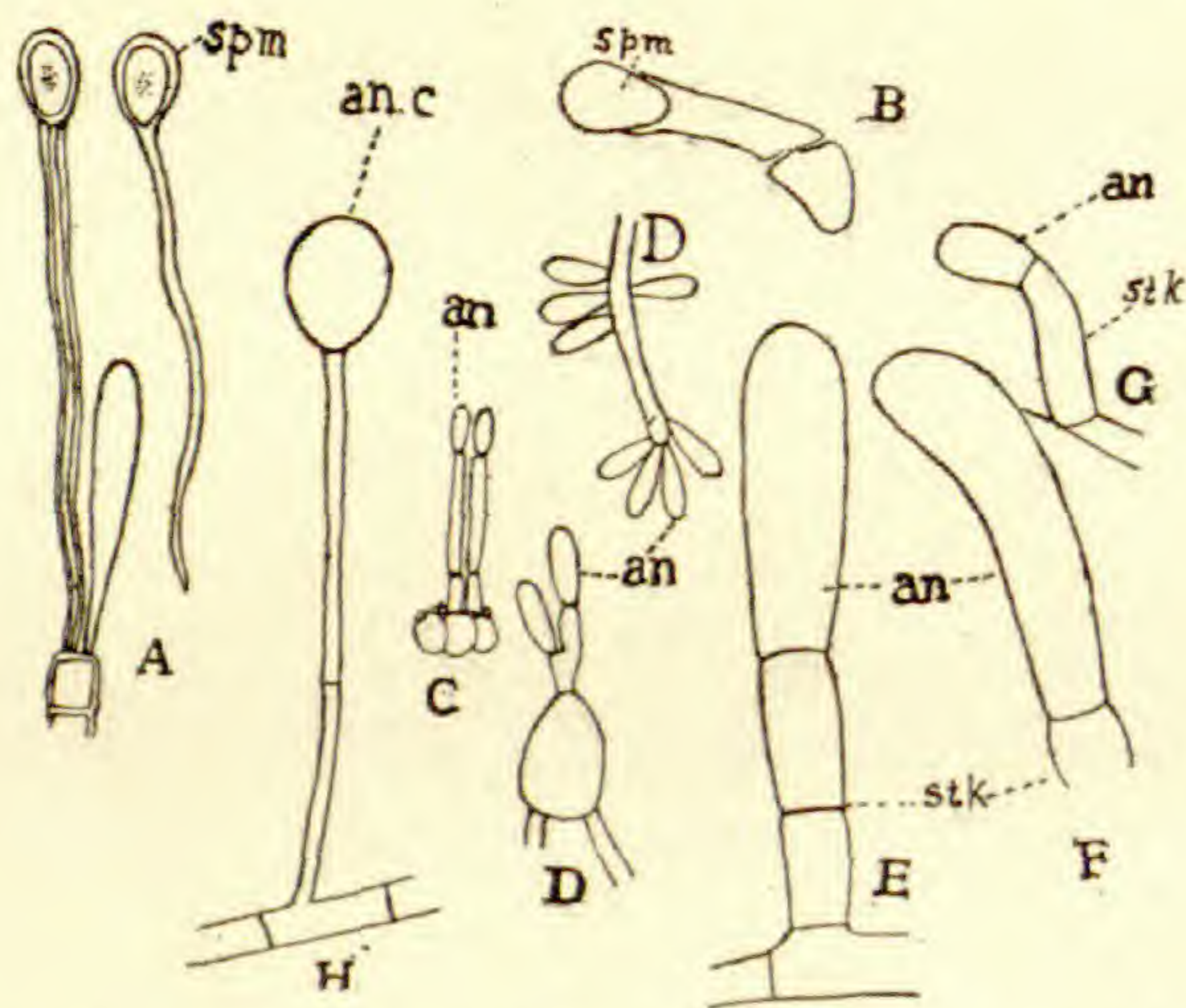


FIG. 3. Antheridia and spermatia. A. *Corallina officinalis*; B. *Delesseria sanguinea*; C. *Collema microphyllum*; D. *Collema pulposum*; E. *Ascobolus magnificus*; F. *Pyronema*; G. *Sphaerotheca*; H. *Ascobolus carbonarius*. an, antheridium; an.c, antheridial conidium; spm, spermatium; stk, stalk. A, Guignard; B, Svedelius; C, Stahl; D, Bachmann; F, Tulasne; G, De Bary; E, H, original.

closely related to the strain *A. mirabilis* since it produces no conidia, chlamydospores, or any asexual spore bodies whatever. The Tulasnes (90) figured conidia for *Pyronema*; later (89) they referred them to *Lachnea melaloma*. They undoubtedly were mistaken in both cases, as I find no such spores in my cultures. The archicarp of *Lachnea melaloma* frequently branches either in the region representing the trichogyne, or well back near the basal portion. In the latter case the branching is somewhat dichotomous. There is also a marked tendency to dichotomous branching in the vegetative hyphae.

As compared with the trichogynes of the Ascomycetes in



general the trichogyne of the red algae is a rather simple structure of quite constant type, being nothing more than an outgrowth or prolongation of the egg cell into a narrow tube. In certain cases, as in *Batrachospermum* (FIG. 4, B), it is a short club-shaped body projecting but little from the carpogonium. In *Nemalion*, *Lia-gora*, *Helminthora*, belonging to the Helminthocladiaceae, and perhaps in a majority of the species, it is a much longer thin filament (FIG. 4, F), which may be curved slightly to one side (FIG. 4, A). Somewhat more complicated are the trichogynes of *Dudresnaya*, *Polyides*, *Bonnemaisonia*, etc., where it is an extremely long and thread-like organ, several times spirally coiled near its base (FIG. 5, C). Some question exists as to whether or not the trichogyne possesses a nucleus of its own and is therefore an independent cell unit. It is commonly held that the trichogyne is simply an outgrowth of the egg cell, and that it is morphologically equivalent to the receptive spot in the egg of *Oedogonium*, *Vaucheria*, etc. Davis (34) claims that the trichogyne of *Batrachospermum* is provided with a chromatophore and nucleus of its own although there is no septum cutting them off from the egg. This has been denied by Osterhout (69) and Schmidle (77), and by Lewis (58) for *Griffithsia Bornetiana* also. Yamanouchi (97) is very positive in his assertion that the trichogyne of *Polysiphonia* has a distinct nucleus.

No cases have been reported where a septum is found between the carpogonium and its trichogyne before fertilization. After fertilization it is commonly found that the egg is cut off from the trichogyne by a thickening of the narrow connecting portion, and Sturch (87) asserts that in *Harveyella mirabilis* a septum is laid down after fertilization between the trichogyne and carpogonium (FIG. 4, E). Harper has described the replacement of the wall, broken down during fertilization, for *Pyronema* (53). A similar method of blocking off trichogyne cells after fertilization has been described by Stahl, Baur, and Miss Bachmann for the lichens, and by Miss Fraser for *Lachnea cretea*. In many forms of the algae the carpogenic branch originates beneath the surface of the thallus. In such cases the trichogyne growing out obliquely from the carpogonium turns directly outward and penetrates any convenient opening between the surrounding filaments (FIG. 4, A). The object to



be gained is primarily to reach the surface, just as it is in the species of lichens described by Stahl (FIG. 1, A and B).

The most obvious difference between the Ascomycetes and red algae is found in the absence in the latter of anything like free cell formation. The ascus is the most characteristic and unique structure of the Ascomycetes. As De Bary and most of the earlier students of the group recognized, the process of free cell formation as found in the ascus is typically different from any

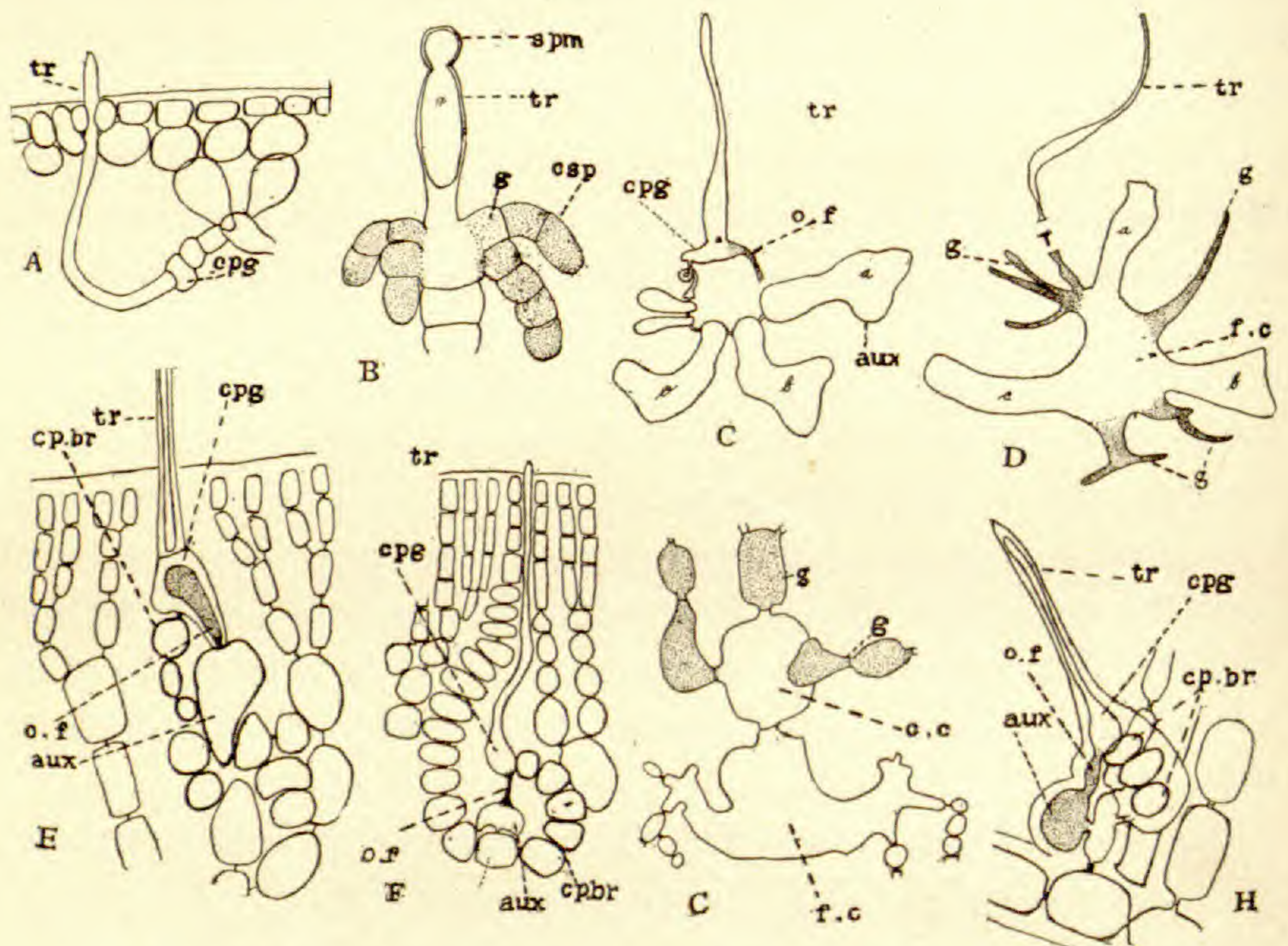


FIG. 4. Procarpic branch and outgrowths from the carpegonium in the red algae. A. *Halymenia ligulata*; B. *Batrachospermum moniliforme*; C, D, *Erythrophyllum delesserioides*; E. *Harveyella mirabilis*; F, G. *Prionitis Lyallii*; H. *Antithamnion Plumula*. *aux*, auxiliary cell; *c.c.*, central cell; *cp.br.*, carpegogenic branch; *cpg*, carpegonium; *csp*, carpospore; *f.c.*, fusion cell; *g*, gonimoblast; *o.f.*, oöblastema filament; *spm*, spermatium; *tr*, trichogyne. A, Bornet; B, Davis; C, D, Twiss; E, Sturch; F, G, Daines; H, Phillips.

other method of spore formation known in the fungi. And the morphological characters of the ascus constitute the main difficulty in all attempts to derive the Ascomycetes from the Florideae. Recent cytological studies (Harper, 51) have emphasized the differences between free cell formation and the progressive cleavage found in sporangia, and Dangeard's discovery of nuclear fusion in



the young ascus (31) has seemed to indicate its resemblance to teleutospores and basidia rather than to any structures in the red algae. Dangeard first described the formation of the ascus in *Pustularia vesiculosa* as involving the fusion of two separate hyphae at their tips, a condition that was found later to actually be the method of origin of the binucleated basal cell in the aecidium cup of the rusts. Although Dangeard immediately corrected his error one can not doubt that it has been largely responsible for his whole theory of the sexuality and origin of the Ascomycetes. His views in this connection have received much attention and need not be considered further here, but the morphological features of the process by which an ascus is formed from the penultimate cell of a "hook" or "crosier" are so characteristic and of such widespread occurrence among the Ascomycetes as to warrant more careful examination than has been given to them. This sort of structure occurs in genera as widely separated as *Collema*, *Usnea*, *Lachnea*, *Morchella*, *Tuber*, *Aspergillus*, and *Pyronema*. In all some thirty-five species have been figured as showing the ascus formed in this manner, and nearly all conform to the same type. Harper (53), who first figured conjugate nuclear division in the hook, and others have given a great deal of attention to this phenomenon and have fully discussed the necessity for some such arrangement as a means of providing that the nuclei which fuse in the ascus shall not be sister nuclei. The manner in which the crosier may become modified seems to be almost without limit, but the fundamental principle is maintained with a very few exceptions. Faull (40) claims to have examined over thirty species and finds that the ascus arises from the penultimate cell invariably in eleven of them. In other forms he describes the omission of the wall which ordinarily cuts off the end cell so that in such cases the terminal cell gives rise to the ascus, although the hook is well represented with its tip curved down. Modifications of the hook by proliferation, the growing out of the end cell to form a second hook, or the fusion of the terminal cell with the antipenultimate cell are variations which have also been described. W. H. Brown (19, 20), McCubbin (61), Claussen (26), Fraser (43), and others have described further ways in which the crosier may be modified.



So far the crosier has not been homologized with any structure in the life history of the red algae. It seems to me that the possible relations of its characteristic features and the resulting fusion of non-sister nuclei to the secondary fertilizations of Schmitz deserve careful consideration as I shall point out in more detail later.

If one assumes that the outgrowth from the oögonium in *Sphaerotheca* represents simply a large, well-nourished ascogenous hypha, then a perfect type of crosier occurs here also. The ascus, according to Harper (52), is formed from the binucleated penultimate cell of this outgrowth (FIG. 8, A). Uninucleated ultimate and antipenultimate cells are regularly formed.

A few forms have been reported in which it is claimed that the ascus arises directly from the end cell of the ascogenous hypha without any bending over of the terminal portion. Maire (60) describes such a process in *Galactinia succosa*. The asci of *Penicillium* are described by Brefeld (16) as arising in rows from cells of the ascogenous hyphae. The same is true for *Exoascus* (Dangeard, 31). Thaxter (88) and Faull (39) have described the formation of the asci from the egg in several species of the Laboulbeniaceae. Here the ascogenous cell buds out directly into a large number of asci. Faull suggests several possible homologies for the cells developed from the germination of the egg, but he by no means makes clear their relationships to the parallel stages in the red algae.

Ramlow (73) points out that the ascus in *Thelebolus* arises directly from a large binucleated cell of the ascogonium the other cells of which are uninucleated. In some cases the ascogenous cell is the subterminal cell.

H. B. Brown (18) has recently reported that the asci of *Xylaria* are simply outgrowths from the end cells of the much-branched ascogenous hyphae. His description is however very brief and should perhaps not be quoted as proof of a departure from the general method of ascus formation.

Dangeard's (31) separation of the Ascomycetes into two groups, the so-called "rectascées" and "curveascées," is not supported by the observations of Fraser and Chambers (46), Dale (29, 30), Brooks (17), and Blackman and Welsford (12), who report the



formation of the crozier in such forms as *Aspergillus*, *Gymnoascus*, *Gnomonia*, and *Polystigma*.

A number of cases have been reported where the end cell bends down and fuses with the cell below the ascus, so that in this way a new cell is formed containing two nuclei which may later fuse and form a new ascus. W. H. Brown (19, 20) noted such cases in *Leotia*, *Geoglossum*, and *Lachnea scutellata*; Fraser (43) in *Humaria rutilans*; and Claussen (26) in *Pyronema*.

The relations of the outgrowths of the egg in those red algae in which secondary fertilizations occur to the so-called auxiliary cells have been the subject of extensive study since the time of Schmitz, and there yet remain many unsolved questions both as to the position and morphological character of the auxiliary cells and the cytological features of the fusion of the egg outgrowths with them. Schmitz called these filaments proceeding from the fertilized egg oöblastema filaments. They are to be distinguished from the gonimoblasts which produce spores directly. Their general resemblance to ascogenous hyphae is certainly striking, as Oltmanns (68) pointed out, and it is strange that it has not been more specifically discussed. Both are outgrowths of the fertilized egg or its equivalent. Schmitz made clear their nature and method of development in the red algae, but Oltmanns claims that Schmitz was mistaken in his interpretation of the fusions of the oöblastema filaments with the auxiliary cells as repeated sexual processes.

Schmitz's classification of the Florideae based largely on the morphology of their reproductive organs at once superseded the older systems of Nägeli (62) and Agardh (1). Daines (28), a pupil of Setchell, has analyzed the data upon which the present classification is based and describes very briefly and clearly the characters of the different groups as generally accepted to-day. There are five main groups:—Nemalionales, Gigartinales, Rhodomeniales, Ceramiales, and Cryptonemiales.

In Schmitz's simplest group are found the well-known forms *Batrachospermum*, *Nemalion*, etc. In these forms vegetative envelopes for the mass of carpospores are almost or entirely wanting (FIG. 6, A). The sporogenous cells, gonimoblasts, grow out from the fertilized egg as short filaments which become septate and give rise at once and without secondary fusions to masses



of carpospores. In certain species, such as *Dermonema dichotomum* (Schmitz 81), the sporogenous filaments form a complex system which develops wholly within the thallus, producing numerous clusters of carpospores separated by sterile tissue (FIG. 6, B). There can be no question in these forms as to the essential facts of their sexual reproduction. It has been described in *Nemalion* (Wolfe, 93) and in *Batrachospermum* (Osterhout, 69). The spermatium nucleus penetrates the trichogyne and passes down to the carpogonium where it unites with the egg nucleus.

The remaining four groups, Gigartinales, Rhodymeniales, Ceramiales, and Cryptonemiales, in which a conjugation between the outgrowths of the carpogonium and an auxiliary cell occurs, do not differ materially among themselves for the purposes of our discussion, except perhaps as to the time and place of the development of the auxiliary cell, this cell being most closely connected with the carpogenic branch in the Gigartinales, while in the Ceramiales it may be entirely independent of, but paired with, the branch which bears the egg cell. In the former we have a secondary fusion of a very simple type. Sturch (87) has described the formation and development of the procarpic branch of *Harveyella mirabilis*. This species is parasitic upon one of the larger red algae and is interesting to us because of its lack of chlorophyll. The curved carpogenic branch is composed of four cells and a basal cell which functions as an auxiliary cell. This is a large cell well supplied with nourishment. After fertilization and after the trichogyne has been cut off by a septum, as claimed by Sturch, the carpogonium grows out into a slender filament which unites with the auxiliary cell below, and from this a central cell is formed which gives rise to sporogenous hyphae (FIG. 4, E). The process in such a case in which the cells below the egg become involved by secondary fusions in the development of a spore fruit may be more similar to that in the lichens, *Ascobolus carbonarius*, etc., where we have the ascogenous hyphae developing from cells far back from the trichogyne, than has hitherto been supposed. The breaking down of the cross walls of the ascogonium in the lichens (Baur, 8, 9; Darbishire, 32; Bachmann, 3) and the formation of pores in the cross walls in the ascogonia of *Ascobolus* (Harper, 50), *Ascophanus carneus* (Cutting, 27), and *Lachnea cretea* (Fraser, 44),



may have the same significance as the development of the egg outgrowth and its fusion with the basal cell or cells of the procarpic branch in such forms as *Harveyella*, *Dudresnaya coccinea* (FIG. 5, E), *Polyides*, and *Erythrophyllum* (FIG. 4, C, D). This topic will be referred to further below.

In *Wrangelia* (Zerlang, 98) the outgrowth from the carpogonium appears to be a sac-like structure connecting with the basal cell of the procarpic branch and forming the so-called central cell from which the sporogenous filaments arise.

In many species of the red algae the lower cells of the procarpic branch become involved in extensive cell fusions which follow fertilization. This is well shown by Twiss (91) for *Erythrophyllum delesserioides* which, as he points out, is one of the Gigartinaceae. The procarpic branch consists of seven or eight cells, the lower three of which are very large, considerably elongated and well nourished. Above these are three much smaller cells but of about the same shape, while the next cell is minute and triangular, and is connected with the carpogonium by a coiled slender portion. After fertilization, presumably, the oöblastema filament grows out and connects with the lowest of the three large cells, which is the auxiliary cell (FIG. 4, C). Then occur the intimate fusion of all three cells and the giving off of gonimoblast filaments from all parts of this fusion cell (FIG. 4, D), very much as in the lichens (FIG. 7) and certain other Discomycetes (37, 44, 27), as just noted, where several cells of the ascogonium become connected by pores in the cross walls and ascogenous hyphae arise from the portions corresponding to each of the original cells. In *Erythrophyllum*, *Gigartina*, and other members of the Gigartinaceae the sporogenous hyphae form an extensive branching system penetrating the thallus so that a somewhat spherical swollen spore fruit is finally developed, perhaps corresponding to such an ascocarp as that of *Penicillium*.

It is a striking and characteristic fact for both the Ascomycetes and red algae that in these cases the spore-bearing filaments should arise from several rather than one cell, and that these cells are connected by pores in the one case and oöblastema filaments in the other. Ascogenous hyphae, gonimoblasts of the *Batrachospermum* type, oöblastema filaments, and even those fusions between



cells of the ascogonium are all to be considered morphological equivalents arising by reduplication at different stages out of some primitive type of egg outgrowth such as we find in the gonimoblasts of *Nemalion*.

Phillips (72) has shown that the cystocarp formation in a number of species of the Rhodymeniales differs from that in the Gigartinales in that the auxiliary cell is derived from the basal cell of the carpogenic branch or is its sister cell. The conjugating tube or outgrowth from the carpogonium is very similar to that found in *Harveyella*.

Yamanouchi (97) has described in some detail the development of the fusion cell in *Polysiphonia* by the union of the auxiliary cell with the basal cells of the carpogenic branch and other adjacent sterile cells. He claims that the union between the carpogonium and the fusion cell takes place by means of a specially formed connecting "auxiliary" cell. In the Gigartinales and Rhodymeniales the carpogenic branch is so curved over as to bring the carpogonium into the near neighborhood of the auxiliary cell.

In *Callithamnion*, a type of the group Ceramiales, the entire process of fertilization and the secondary fusions between the carpogonium and the auxiliary cells has been studied by Oltmanns (68). Paired auxiliary mother-cells are formed on either side of the main axis. One of the mother-cells divides, the lower portion giving rise to the short procarpic branch. At the same time a basal cell is cut off from each mother-cell, leaving the auxiliary cells above (FIG. 5, A). After fertilization the carpogonium grows out into two short oöblastema filaments each of which unites with an auxiliary cell carrying over a daughter nucleus of the fertilized egg. The auxiliary cell now contains two nuclei, the original auxiliary cell nucleus and a daughter nucleus of the fertilized egg. Cell division takes place cutting off the auxiliary cell nucleus below, leaving only the descendant of the egg above (FIG. 5, B), from which the sporogenous filaments are developed. The nuclei of the auxiliary cells degenerate without taking any part in spore formation.

A very simple and clear description of cystocarp formation in *Prionitis Lyallii* has been given by Daines (28). The curved, five- or six-celled carpogenic branch is entirely imbedded in the



thallus through which the trichogyne penetrates to the surface (FIG. 4, F). The auxiliary cell is derived from the lower cell of one of the sterile filaments and is brought into connection with the carpogonium by a short oöblastema. Daines was unable to discover that this filament united with any other cell as in the case of other species of the Grateloupiaceae described by Berthold, and since procarpic branches and auxiliary cells are borne in pairs Daines concludes that this species should be placed with the Ceramiales.

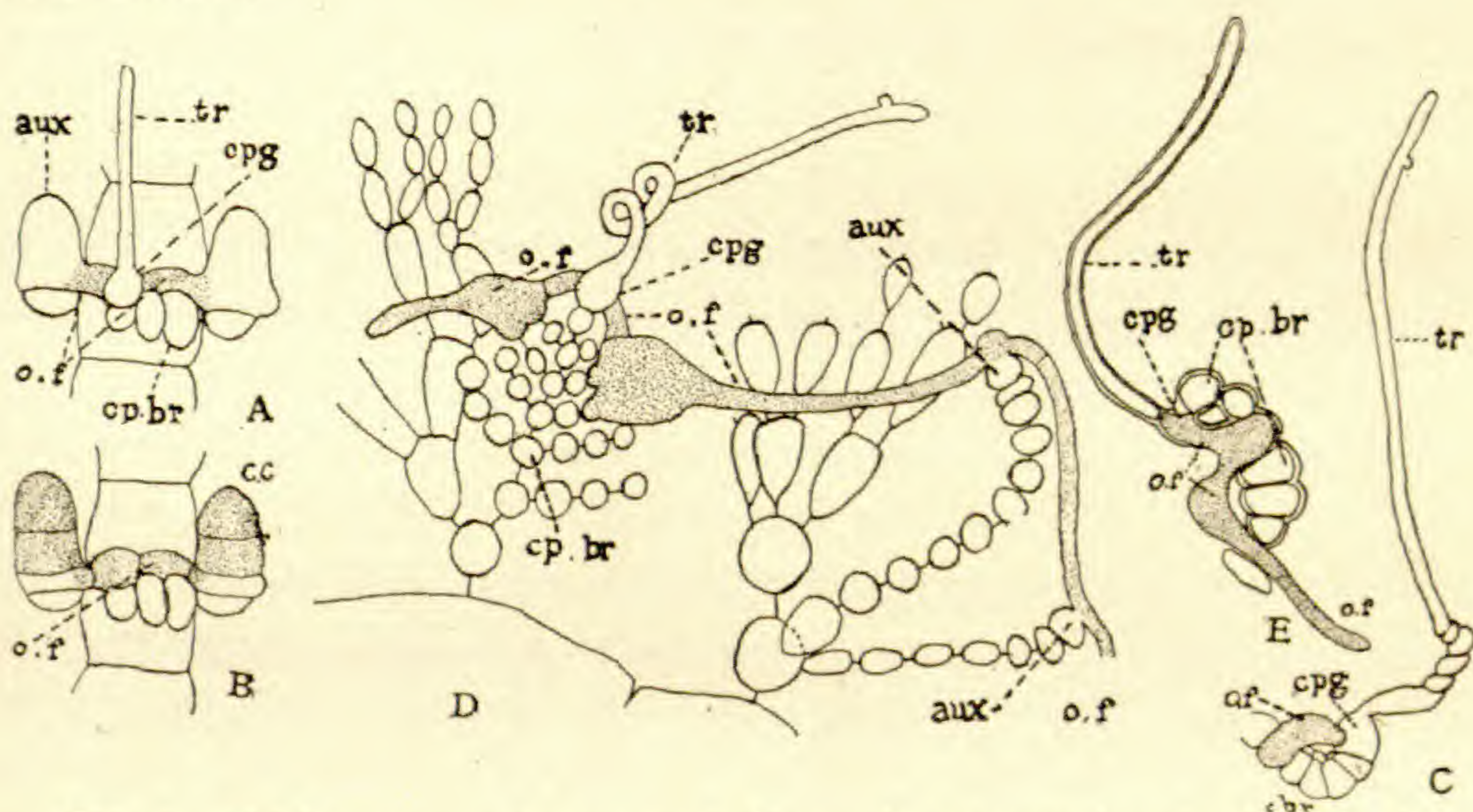


FIG. 5. Trichogynes and outgrowths from the carpogonium in the red algae. A, B. *Callithamnion corymbosum*; C, D. *Dudresnaya purpurifera*; E. *Dudresnaya coccinea*. *aux*, auxiliary cell; *cp.br*, carpogenic branch; *cpg*, carpogonium; *o.f.*, oöblastema filament; *tr*, trichogyne. A, B, D, E, Oltmanns; C, Schmitz.

Vastly more complex and perhaps furnishing still more evidence as to the ancestry of the Ascomycetes are the Cryptonemiales, the forms upon which Schmitz based his theory of secondary sexual fusions.

The procarpic branch in *Cruoriopsis cruciata* (Schmitz, 78, 80) is imbedded within the thallus but its trichogyne extends out beyond the surface. Near these procarpic branches other filaments are developed which Schmitz called "procarps without trichogynes." The end cells (auxiliary cells) of these branches remain imbedded in the thallus and do not grow out into trichogynes. After the fertilization of the procarp there now grows out from its under part an oöblastema filament which branches freely and spreads widely inside of the thallus and "fertilizes the procarp



of the second sort" by fusing with the end cell. These same oöblastema filaments then go on to other procarps of the second sort. Each of these "fertilized" auxiliary cells sends out only one or two rows of from two to four carpospores. Oltmanns (67) says only one simple two- to four-celled spore chain arises from each of these secondary fusions, and we thus have a very interesting parallel to the conditions in the ascogenous hyphae, where from each vegetative nuclear fusion a single ascus results with typically eight spores.

Among the Cryptonemiales Schmitz notes interesting minor differences in the manner in which the auxiliary cells develop after the secondary fusion. In *Dudresnaya* (FIG. 5, C, D), *Polyides*, *Petrocelis*, etc., after fusing with the distant auxiliary cell the oöblastema filament becomes cut off from it and the sporogenous cells arise from the part corresponding to the section of the oöblastema cell. Schmitz saw no nuclear fusions here, and each cell seems to maintain its individuality in a large degree. In *Calosiphonia* the contents of the oöblastema cell go over to the auxiliary cell. Here the outgrowths or gonimoblasts giving rise to the spores arise from the portion originally belonging to the auxiliary cell. In this second case Schmitz believes that the nucleus of the oöblastema cell goes over to the auxiliary cell, but he could have seen no real movement. In *Gloiosiphonia* the entire cell contents of the oöblastema cell except the plasma membrane pass over into the auxiliary cell. There is an intimate fusion of the cytoplasm, and in this case Schmitz believes that the two nuclei unite in what he calls the "second sexual process." He describes the protoplasm of the oöblastema cell as moving over and combining intimately with that of the auxiliary cell, leaving the other empty except for the plasma membrane, and in this case believes that a nuclear fusion actually occurs. Oltmanns denies that there are ever any nuclear fusions here, but he figures the oöblastema cell as empty and holds that the protoplasm and nuclei pass to the auxiliary cell.

Schmitz may be wrong; the next step, however, in the developmental stages which he describes would be the fusion of the nuclei, and with a nuclear fusion under such conditions we should have a further point of resemblance to the young ascus.



It is not impossible that in these secondary cell fusions we should seek for an explanation of the puzzling vegetative nuclear fusions in the ascus. The reported fusion between the end cell of the ascogenous hypha and the cell just below the ascus would perhaps serve the same purpose as would the fusion of the end cell of the oöblastema filament with some other cell of the procarpic branch in case no auxiliary cell were available. Since Oltmanns (68) confirms Schmitz's account as to the cell fusions in *Dudresnaya* and *Gloiosiphonia* the facts here may be taken as fairly well established. His further claim that the nucleus of the auxiliary cell in *Dudresnaya*, *Callithamnion* and *Gloiosiphonia* degenerates, as noted above, after having taken a position as far away as possible from the oöblastema nucleus certainly needs further confirmation. Oltmanns' figures are quite diagrammatic and the successive stages in the disintegration of the vegetative auxiliary cell nucleus are not represented at all. The division stages also by which the fertilized egg nucleus is claimed to multiply and furnish daughter nuclei for further growth are not shown. It is to be remembered that the disintegration of a nucleus and the taking of its cytoplasm by another nucleus as claimed by Oltmanns is entirely without analogy elsewhere in connection with fertilization processes either in the plant or animal kingdom. We certainly need more evidence as to the nuclear phenomena occurring in connection with these secondary fertilizations of Schmitz and the possibility that we shall here find the explanation of the nuclear fusions in the ascus is surely worth considering.

The obvious similarities between ascocarps and cystocarps have doubtless been the most common ground for assuming a relationship between the Ascomycetes and the Florideae. As noted above Schmitz did not consider the form of the mature cystocarp as having great phylogenetic significance. In each of the main divisions of the red algae as we now understand them we find considerable variation in the characters of the fruit body. In the Nemaion group for example we find all stages from the completely unprotected glomerulus of carpospores without sterile filaments (FIG. 6, A) up to well-formed cystocarps with surrounding protecting hyphae. In *Scinaia* (FIG. 6, C) the cystocarp corresponds in form and method of development to a typical pyreno-



carpic fruit body. The protective envelope is developed from the outgrowths from the basal cells of the carpogenic branch. *Wrangeia* is another comparatively simple type but the interpretation of its cystocarp may be open to question. The gametophytic protective filaments are quite definitely disposed about the masses of carpospores. The large and complex carpospore fruits of *Gigartina*, *Erythrophyllum*, etc., the so-called nemathecium, may be regarded as cleistocarpic and, as noted, may correspond to the ascocarp in *Penicillium*. Such nemathecium are found in the com-

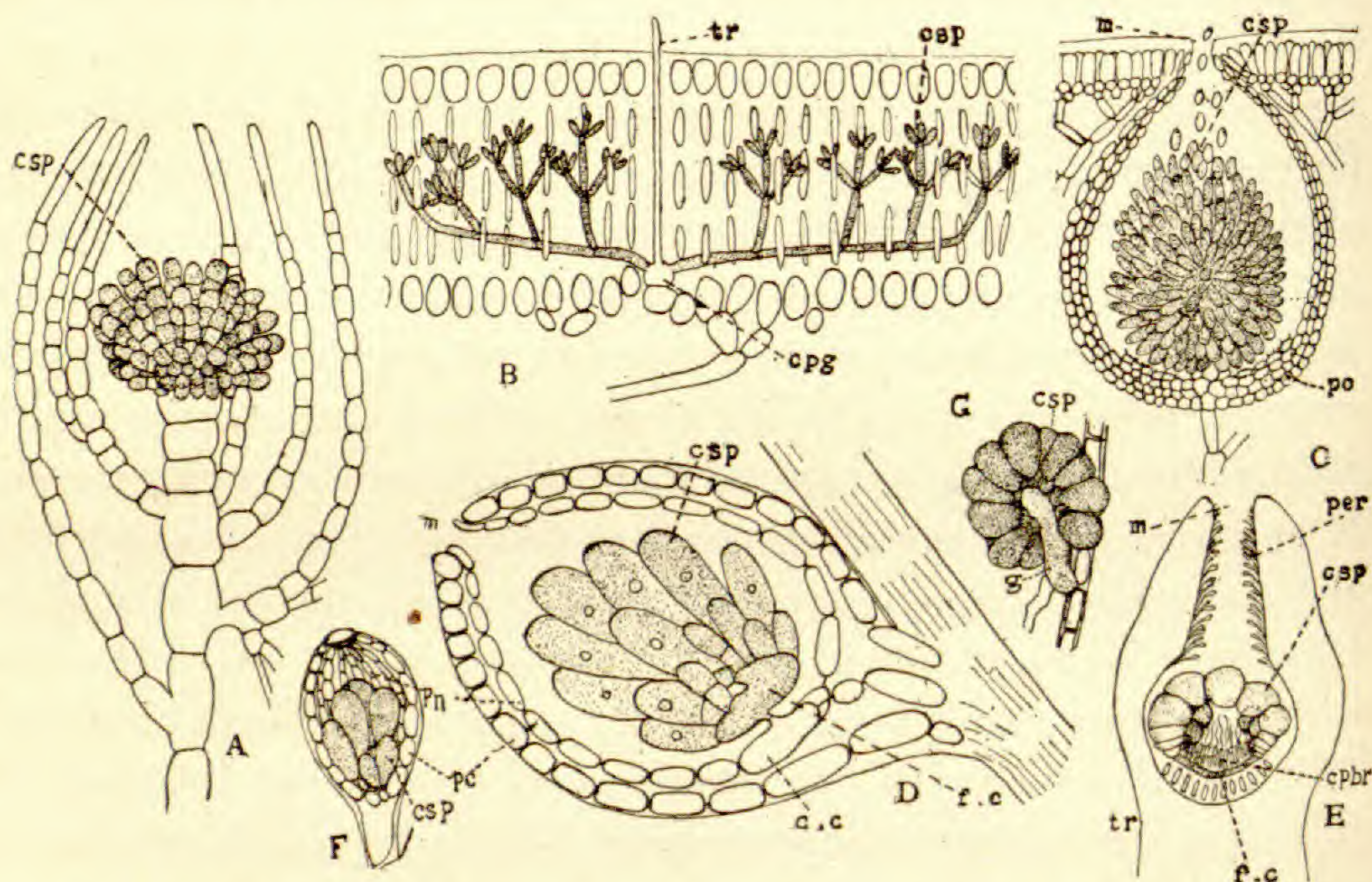


FIG. 6. Cystocarps of red algae. A. *Nemalion multifidum*; B. *Dermonema dichotomum*; C. *Scinaia furcellata*; D. *Polysiphonia*; E. *Corallina mediterranea*; F. *Lejolisia*; G. Spore group, *Polyides*. *c.c.*, central cell; *cpg*, carpogonium; *csp*, carpospore; *f.c.*, fusion cell; *pc*, enveloping filaments or pericarp; *pn*, paranematal filaments or paraphyses; *m*, opening of cystocarp; *per*, periphyses; *tr*, trichogyne. A, Farlow; B, C, Schmitz; D, Phillips; E, Solms-Laubach; F, Bornet; G, Thuret.

paratively simple as well as in the highest groups of the red algae. The conceptacle of *Corallina* (FIG. 6, E) is a structure presumably formed before the development of the procarpic branches, and can not perhaps properly be compared with the ascocarp of the Ascomycetes.

It has been assumed, probably without sufficient grounds, that the cleistocarp is the primitive ascocarp of the Ascomycetes, because in the great majority of cases so far as now known the



ascocarps are in their younger stages more or less closed structures. Practically all authors have made the characters of the ascocarp the basis for subdividing the group, though E. A. Bessey (11) accepts the results of Miss Bachmann's work as further evidence of the possible primitive character of *Collema*, and C. E. Bessey (10) has rearranged his classification of the Ascomycetes placing the "Discolichens" with the Laboulbeniales as transition groups connecting the Ascomycetes and the red algae.

Persoon (71) distinguished between angiocarpous and gymnocarpous forms of fungi. *Mucor*, *Scleroderma*, *Thelebolus*, and *Tuber* are "Angiocarpi," and *Phallus*, *Agaricus*, *Boletus*, *Helvella*, *Ascobolus*, and *Tremella* are "Gymnocarpi." Fries (47, 48) distinguished between the Pyrenomycetes and Discomycetes by the characters of the hymenial layer and the form of the mature fruit. He did not concern himself with the morphology and development of the early stages of the ascocarp as did De Bary (6) who realized that many Discomycetes have entirely closed fruit bodies in their younger stages. *Ascobolus furfuraceus* is the familiar example of this sort of ascocarp (FIG. 9, B). De Bary emphasized the fact that the form of the mature fruit is not a final proof of relationship. The gymnocarpous forms may become cleistocarpous or vice versa. De Bary was uncertain whether the primitive Ascomycetes had closed or open ascocarps and did not regard the method of development in *Ascobolus* as proof of the primitive character of the cleistocarp.

Brefeld (16) held that all ascocarps are cleistocarpous in their youngest stages. Schroeter (82) divided the Ascomycetes into three groups accordingly as they are gymnocarpous from the first, *Pyronema*, *Helvella*, etc.; or first closed, then later opening up, Pezizaceae in general; and third, the more or less permanently closed Pyrenomycetes. In recent years more attention has been paid to the actual form of the youngest obtainable fruits. Fischer (42) and Bucholtz (22-24) have studied a number of the Tuberineae and find that in many cases the hymenium is at first exposed and only later becomes closed over by the infolding of the peridium.

Dittrich (35) and Durand (38) find that certain Helvellineae are cleistocarpous at the time the hymenium is being organized.



In certain species of *Lachnea*, as noted above, the hymenium is at no time enclosed by the peridium. All these observations are quite contrary to the views that have been commonly held. The significance of the rather delicate web of hyphae covering the hymenium of *Geoglossum*, *Mitrula*, *Spathularia*, *Microglossum*, *Cudonia*, etc., according to Dittrich and Durand, can not be regarded as entirely clear and the question whether the ascocarps in these cases are cleistocarpous at first can only be settled by further study of

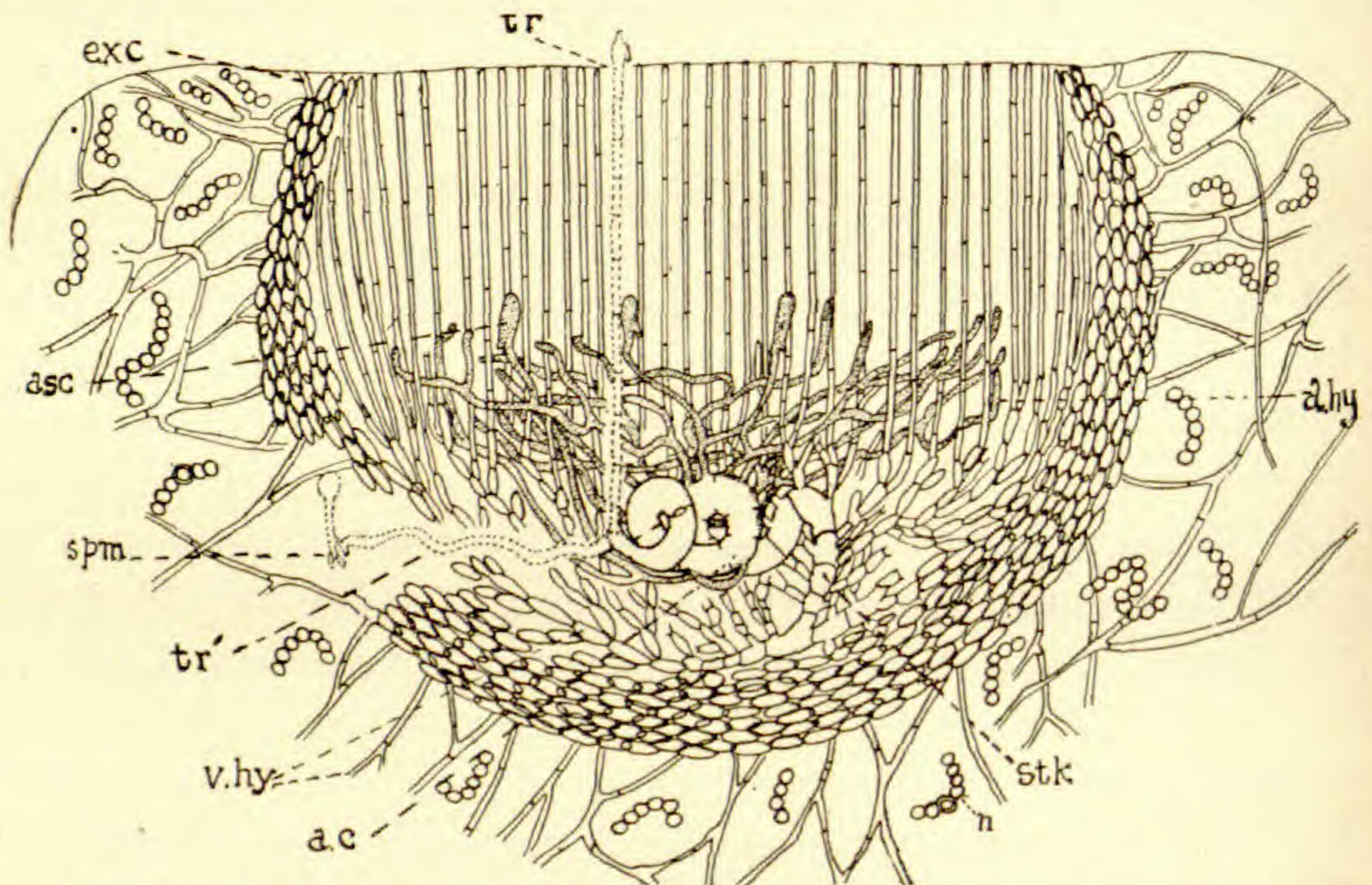


FIG. 7. Apothecium of the Collemas showing the difference between the trichogynes of *C. microphyllum* and those of *C. pulposum*. The trichogyne, *tr*, of *C. microphyllum*, represented by dotted lines, is perpendicular to the surface of the thallus; the trichogyne, *tr'*, of *C. pulposum*, also represented by dotted lines, lies more or less horizontally in the thallus. The figure shows that paraphyses arise from the vegetative hyphae, *v.hy*, as well as from the stalk, *stk*, of the ascogonium and that ascogenous hyphae, *a.hy*, arise from several cells of the ascogonium which are connected by broad pores in the cross walls. *a.c*, ascogenous cells; *asc*, ascus; *exc*, excipulum; *n*, *Nostoc* colonies; *spm*, spermatia; *stk*, stalk of ascogonium. After Stahl, Bachmann, and others.

earlier stages. The real question as to whether an ascocarp is to be classed as open or closed in its early stages depends on whether the young hymenial layer arises endogenously as in *Ascobolus furfuraceus* (FIG. 9, B), or is from the first free and exposed as in *Pyronema* (FIG. 11, B).

Authors have commonly recognized at least four types of



ascocarp: (1) the typical angiocarp or cleistocarp of Schroeter's Plectascineae with no hymenial layer or paraphyses in parallel arrangement, and the perithecium of the Erysiphaceae (FIG. 8, A) which bursts irregularly; (2) the discocarp or apothecium, the type commonly supposed to be possessed by most Discomycetes, for example, the well-known fruit body of *Ascobolus furfuraceus* (FIG. 9, B) where the hymenium is at first entirely closed over and is later exposed by the expansion of the asci and growth of the paraphyses; (3) the pyrenocarp of the vast majority of Pyrenomycetes typically provided with an ostiole through which the spores are expelled (FIG. 8, C); (4) the true gymnocarp, such as that of *Ascodesmis*, *Pyronema* (FIG. 11, B), *Ascobolus magnificus* (FIG. 11, A), *Lachnea stercorea* (FIG. 10), *L. scutellata*, and the Exoasci.

The use of such terms as angiocarpous, pseudo-angiocarpous, hemi-angiocarpous, etc., has come to be quite loose. As noted, Persoon (71) divided the fungi into two groups on the basis of the form of the mature fruit. De Bary and other morphologists of his time extended the use of the term angiocarp to those immature fruit bodies in which the hymenial layer is covered by a peridium. The term angiocarp, or cleistocarp, has long been used to distinguish the closed type of fruit in various classes of plants, and the older writers from Persoon on describe fungi in which the hymenium is enclosed by a peridium or rind as angiocarpous. As it is always possible to determine whether the asci (and paraphyses, if present) arise endogenously this use of the term is perfectly clear and should be maintained. The distinction between cleistocarpic, discocarpic, and gymnocarpic must be based on the method of origin of the hymenial layer rather than merely on the question as to the envelopment of the ascogonium. Most ascogonia are very soon more or less covered by enveloping hyphae. The real distinction lies between such forms as *Ascobolus furfuraceus* (FIG. 9, B) in which the hymenial layer arises endogenously, and *Pyronema* and *Ascobolus magnificus* (FIG. 11, A) in which it is from the first superficial and exposed. To ignore the question of the exogenous origin of the hymenium in the case of those Ascomycetes in which the ascogonium has been described as enclosed in its very early stages, is without any morphological



justification. Even though the ascogonium be completely enclosed at first, if the hymenial layer subsequently develops superficially the ascocarp must certainly be described as discocarpous and not properly cleistocarpous at any stage. Illustrations of permanent cleistocarps are the well known types *Sphaerotheca*, *Chaetomium fimeti*, *Aspergillus*, *Elaphomyces*, etc. Illustrations of those that are gymnocarpous and then become closed are *Tuber excavatum*, *Balsamia* (FIG. 8, D), *Choiromyces*, and *Hydnocystis*.

Two types of cleistocarps have been distinguished. We may take the mildews as well known cases of the first type whose method of development has been fairly clear since De Bary's time. The sporophyte proper which develops from the fertilized egg remains enclosed in a gametophytic envelope, the perithecium (FIG. 8, A), which finally bursts irregularly when the spores are ready to germinate. The second type of cleistocarp, which is open at first but later becomes closed by the growth of the peridium (FIG. 8, D), has been carefully investigated by Fischer (42) and Bucholtz (22-24). In a number of the Tuberineae at the time when the hymenium is first recognizable as such it is freely exposed to the exterior. Later by a process of infolding and the active growth of a peridium it becomes entirely enclosed. Bucholtz (23) believes that the mature form of the fruit body, for example, whether it is angiocarpous or gymnocarpous, is in a great measure determined by the environment and is not a basis for determining phylogeny. Bucholtz calls this second type of cleistocarp "pseudoangiocarp" and proposes to use the term "hemiangiocarp" to distinguish the abnormal forms of *Tuber puberulum* where in rare cases the young hymenium is entirely covered at first by a very delicate web of hyphae which extends out from the peridium proper. He agrees with Dittrich and Durand that any Discomycete in which the ascogonium is enveloped by sterile hyphae is in its ontogeny in fact cleistocarpous, yet in his treatment of the Tuberineae he entirely ignores the possibility that ascogonia may yet be found in them which are surrounded at an early stage by a layer of enveloping hyphae, and classes such forms as *Tuber excavatum* as gymnocarpous, or pseudoangiocarpous, as he prefers to call them. As I have noted it is of little importance whether or not the ascogonium is enveloped in its



early stages providing the asci and hymenium develop superficially, as he claims is the case in certain of these hypogaei (FIG. 8, D).

In spite of the vast amount of work that has been done by Woronin, Fisch, Frank, Gilkinet, Kihlman, Oltmanns, Nichols, and others on the origin and morphology of the pyrenocarp it is not clear just how the ostiole originates. These authors give us no concise account of this feature. We find in the Pyrenomycetes forms like *Chaetomium fimeti* which are permanently cleistocarpous as well as the great mass of forms which have a characteristically developed ostiole, and the conditions here are parallel

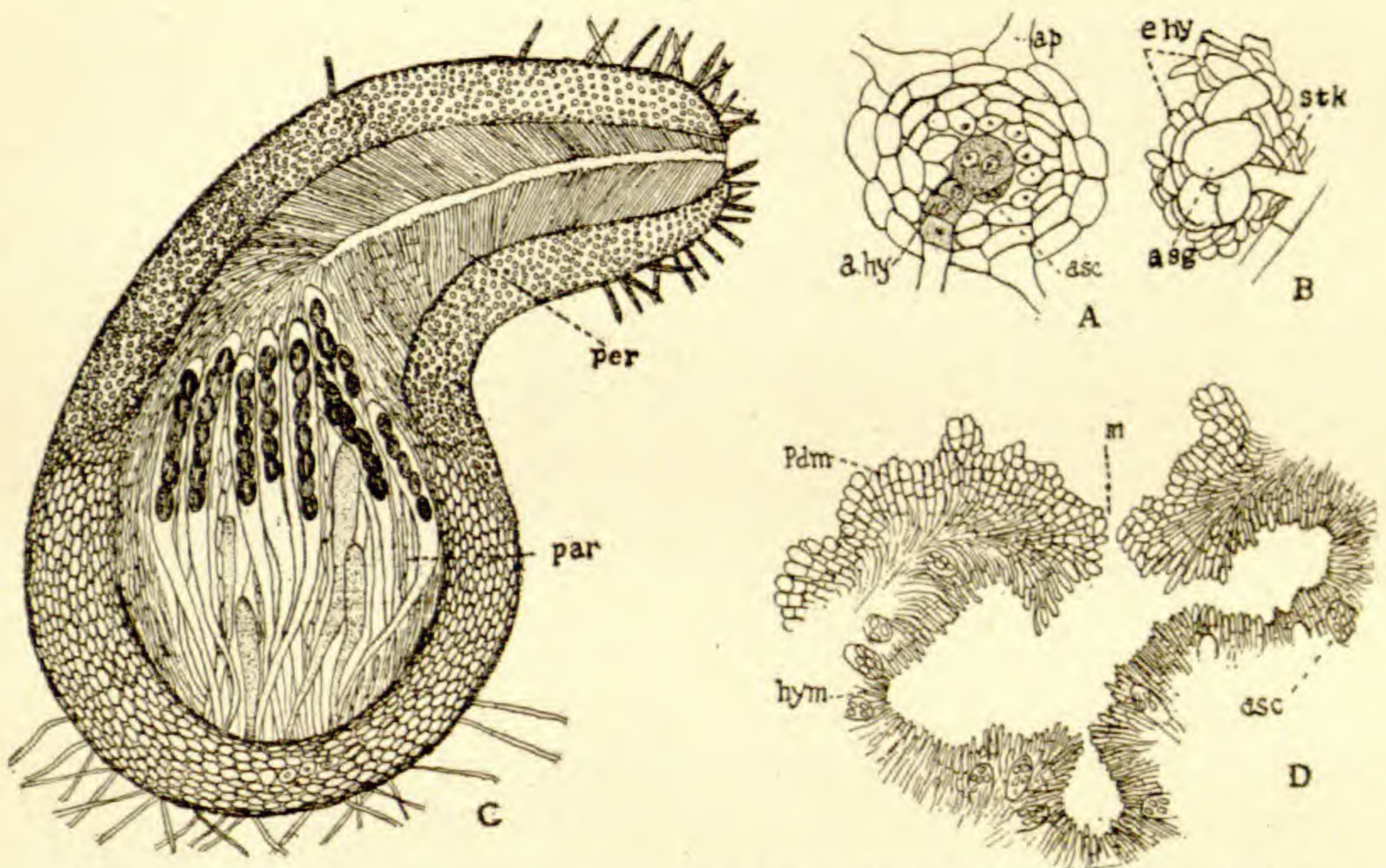


FIG. 8. Ascocarps of Ascomycetes. A. *Sphaerotheca*; B. Young stage of *Melanospora parasitica*; C. *Sordaria fimiseda*; D. *Balsamia*. *a.hy*, ascogenous hyphae; *asg*, ascogonium; *ap*, appendages; *e.hy*, enveloping hyphae; *m*, opening of the fruit body; *par*, paraphyses; *per*, periphyses; *stk*, stalk. A, Harper; B, Kihlman; C, Woronin; D, Bucholtz.

in an interesting way to those in *Ascobolus*, where we have forms like *A. furfuraceus* which is at first cleistocarpous and later becomes wide open, and other forms like *A. magnificus* which is a discocarp from the start. The development of the pyrenocarp has been followed out by Kihlman (57) in *Melanospora*, by Oltmanns (66) in *Chaetomium*, and by Miss Nichols (64) in *Hypocopra* and *Cerato-stoma*, and we know that in these forms some sort of a primordium or



ascogonium is present and that these primordia are completely surrounded by a closely packed layer of enveloping hyphae (FIG. 8, B), but this does not at all settle the question as to how the ostiole originates or even whether the hymenium is endogenous in its origin. Miss Nichols says that the ascogonium of *Ceratomyces* gives rise by cell division to a mass of cells from which asci finally develop, and that the ostiole results from the schizogenetic rupture of the wall at the papillate apex. The interesting account of the development of the ostiole in the region of the base of the archicarp as given by Kihlman for *Melanospora* needs confirmation. According to this account the opening of the ascocarp is at a point which in all other cases is at the center of its base.

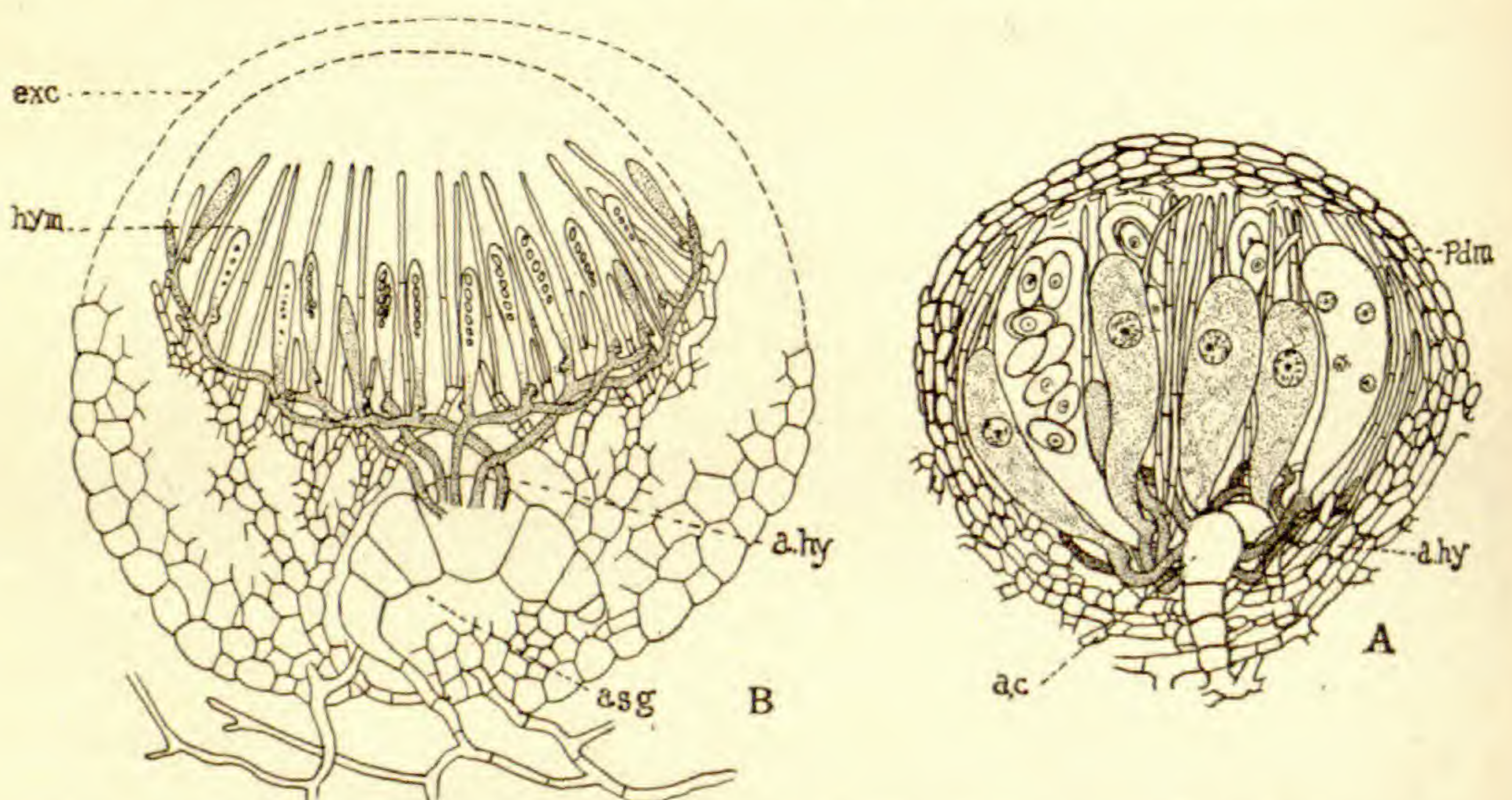


FIG. 9. Discocarps of *Ascobolus*. A. *Ascobolus Winteri*; B. *A. furfuraceus*. *a.c.*, ascogenous cell; *asg*, ascogonium; *a.hy*, ascogenous hyphae; *exc*, excipulum; *hym*, hymenium; *pdm*, periderm. A, original; B, adapted from Sachs.

Two types of apothecia have also been commonly recognized. First, those like *Pyronema* (FIG. 11, B), in which the hymenium is exposed from the beginning; and second, those like *Ascobolus furfuraceus*, in which the hymenium originates endogenously and later becomes exposed by the bursting of the apothecial envelope (FIG. 9, B). The method of the development of the apothecium of *Pyronema* as representing the first type is certainly well known. No excipulum is formed and the paraphyses and asci form a uniformly superficial naked layer (FIG. 11, B). *Ascodesmis nigricans* is an even more simple and open type of fruit body. The apothecium of



*Lachnea stercorea* (Fraser, 45) is at no time cleistocarpous, although Miss Fraser does describe and figure sterile hyphae enclosing the lower part at least of the ascogonium. The hymenial layer is however exposed from the first (FIG. 10). *Lachnea scutellata* (W. H. Brown, 20) evidently develops along much the same lines judging from Brown's figures and description, "when the hymenium is first formed it is covered by the younger setae of the cortex . . . ."

*Ascobolus magnificus* is a further example of the first type. I have already briefly described this species (36) from material grown on the natural substratum and it has since been cultivated on artificial media for several months where the structures giving rise to the apothecium have been more carefully investigated. Although it does not always fruit abundantly in these cultures still a large number of primordia have been obtained and many apothecia have been grown to maturity. The stages passed through give an excellent illustration of a type in which the hymenium is never fully enclosed. The young fruits lie directly on the surface of the agar where they may be carefully studied and I have had no difficulty in arriving at a positive conclusion that in every normal case the ascogonium is prolonged into a rather thick septate trichogyne whose end cells come down over or coil about the end of a club-shaped antheridium which is provided with a stalk of variable length, usually one to three cells. I was not able to make out the antheridium in my earlier studies on specimens gathered in nature. The archicarp and antheridium as far as I have been able to determine do not arise from the same hypha but from hyphae either running along parallel or crossing at an angle much the same as De Bary and Harper found in the mildews. In several cases two functional ascogonia were seen in sections of young apothecia but I suspect that these are merely accidentally included in the same fruit body. Several cases have been observed also where two ascogonia lie exposed close together on the surface of the agar and I have seen not uncommonly two or three additional non-functional antheridia growing near the young fruits.

The ascogonium is exceedingly large, rising upward above the surface of the agar in its younger stages, and if undisturbed is found maintaining a somewhat vertical position in the young apothecium. It not infrequently happens that the ascogonium falls over on the



antheridial branch so that it is not always possible to determine the exact origin of the antheridium and it may possibly in some cases arise from the same hypha that produces the ascogonium. The trichogyne is sharply differentiated from the ascogonium and is not merely a tapering elongation of it such as is found in *Ascobolus Winteri* and *A. immersus*. It is more nearly like Miss Fraser's figure of *Lachnea stercorea* (FIG. 10). It is usually composed of about seven or eight cells, the end cell being much longer, and curved about the antheridium. FIG. 11, A, gives one an idea of the general arrangement and relationships of the ascogonium, trichogyne, antheridium, and the parent hyphae. The "enveloping hyphae" arise almost entirely from the mycelial hyphae on either side of the ascogonium and antheridium and not merely from the stalk of the ascogonium as they do quite exclusively in *Ascobolus Winteri*. Ascogenous hyphae begin to grow out of the ascogenous cell sometimes even before any "enveloping hyphae" have made their appearance and at no time are the primordia and the ascogenous hyphae completely surrounded by a peridial layer. Paraphyses, "enveloping hyphae" and ascogenous hyphae grow upward together. The apothecium is entirely similar to *Pyronema* in this respect. FIG. 11, A, is a somewhat diagrammatic representation of a young apothecium. It will be perceived by a comparison of FIG. 10 of *Lachnea stercorea* and this figure of *Ascobolus magnificus* that these two species are very similar indeed except for the colored spores of the *Ascobolus* and the hairs on the apothecium of the *Lachnea*. Their sexual reproduction and the development of the apothecia differ in no important particular. As noted Brown's figures of a young apothecium of *Lachnea scutellata* show that this species develops in the same way.

The behavior of the sterile or enveloping hyphae in forming the apothecium of *Ascobolus magnificus* is quite different from what it is in *A. furfuraceus*, and resembles more nearly what takes place in *Lachnea stercorea*. The archicarp is considerably raised above the surface of the medium by its long stalk very much as are the archicarps of *Pyronema*. The first growth of "enveloping hyphae" is seen to take place about the time the ascogenous hyphae make their appearance as papillae on the ascogenous cell. Sterile hyphae



arise from the parent hyphae of both sex organs, as well as from the stalk of the archicarp. I have not found that the stalk of the antheridium gives rise to any enveloping hyphae. At first these sterile hyphae grow upward from all sides of the ascogonium. They are very coarse strands which branch profusely, some scattering branches wandering up and over the trichogyne and ascogenous cell, but at no time is there a weft or layer of hyphae completely surrounding the ascogenous cell such as is formed in *Ascobolus furfuraceus*, *A. carbonarius*, etc. The inner branches of the enveloping hyphae give rise to the paraphyses. I have been able to trace connections between the enveloping hyphae that arise

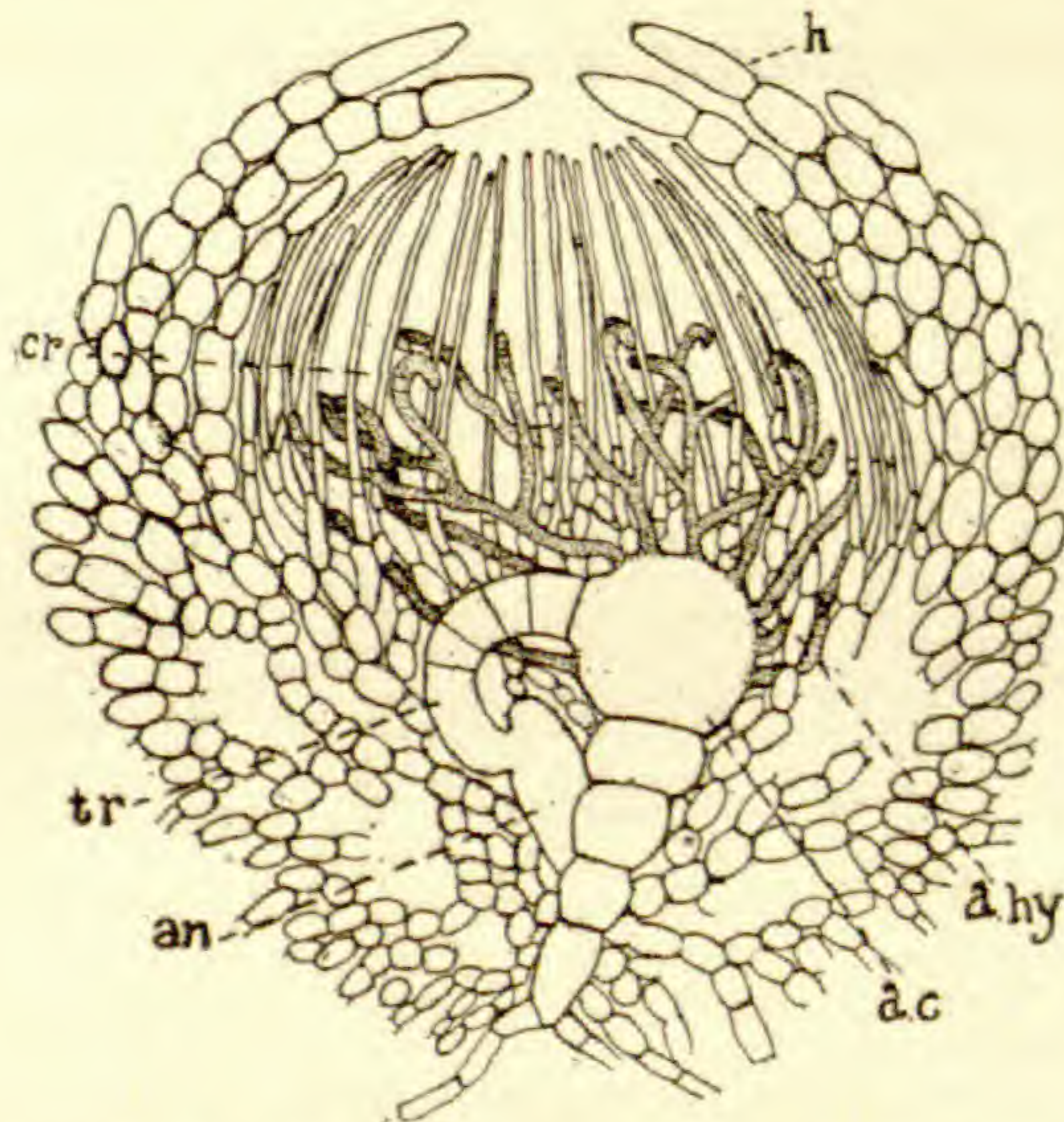


FIG. 10. Gymnocarp of *Lachnea stercorea*. *a.c.*, ascogenous cell; *a.hy*, ascogenous hyphae; *an*, antheridium; *h*, hairs; *par*, paraphyses; *cr*, crosier; *tr*, trichogyne. After Fraser.

from the parent mycelial hyphae and the paraphyses in many cases, but I believe that many paraphyses likewise arise from the branches of the ascogonium stalk. In sections of young apothecia just visible without a lens we find immediately above the ascogenous cell a number of somewhat parallel hyphae running vertically upward. Some of these are ascogenous hyphae, others are paraphyses or hyphae which have pushed in among the ascogenous hyphae and which by further branching will give rise to paraphyses. The two kinds are easily distinguished by the larger nuclei of the ascogenous hyphae and the fact that in sections  $10\ \mu$  or more thick the ascogenous hyphae are easily



traced back to the ascogenous cell. There is at this time (FIG. 11, A) no perithecial layer such as is to be found in *A. furfuraceus* at such a stage. The outer hyphae are now becoming more compact and some of them begin to grow inward forming what in appearance is an inrolled margin, covering in part the hymenial layer which as I have stated is visible from the first and remains exposed throughout the development. The narrowness of the opening above the hymenium at this time led me to erroneously describe the young fruit as "at first closed, then opening by a pore" (36). Microtome sections and careful examination of large numbers of specimens grown on the surface of agar media in plate cultures have made it clear that the hymenium is never closed over; in fact the ascogonium is not more "protected" than are

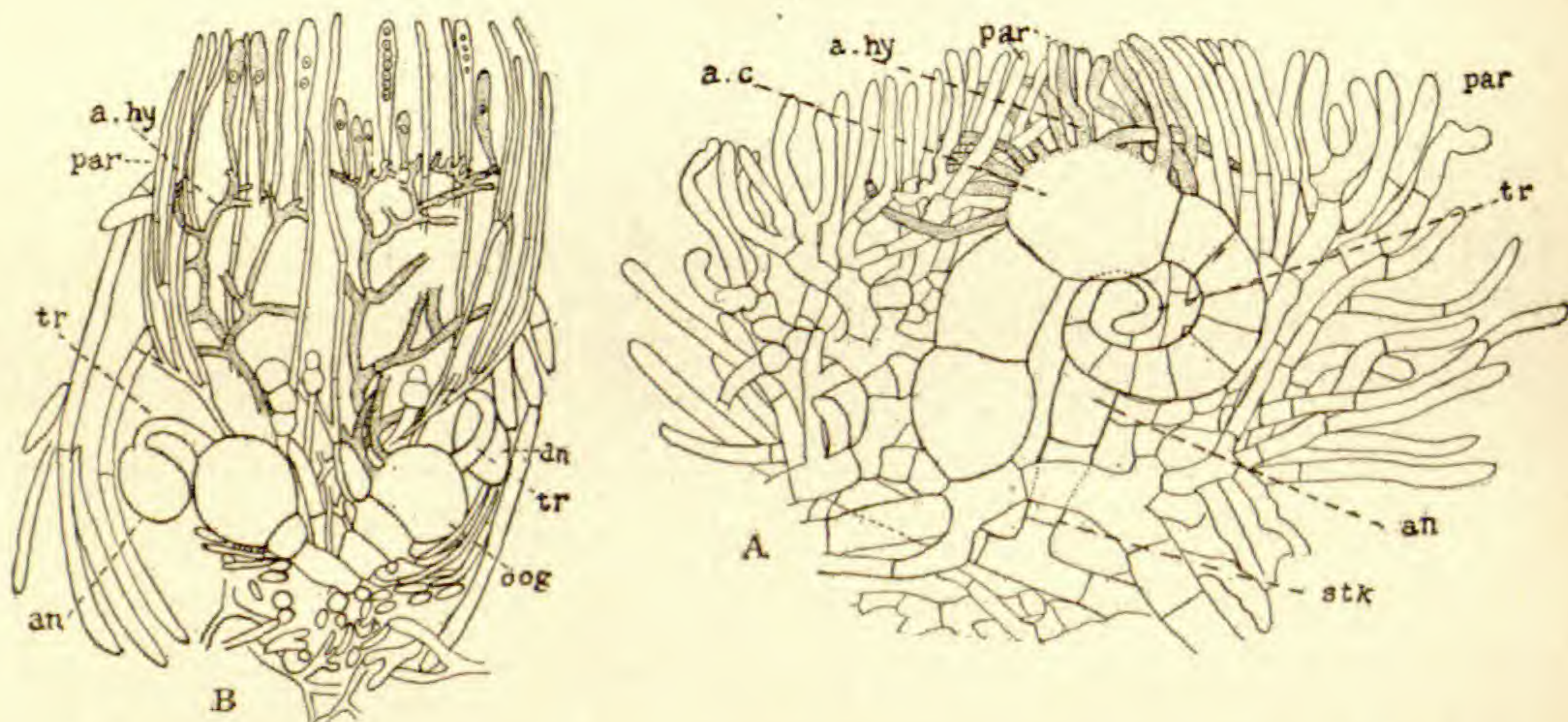


FIG. 11. Gymnocarps. A. *Ascobolus magnificus*; B. *Pyronema confluens*. a.c., ascogenous cell; a.hy, ascogenous hyphae; an, antheridium; oog, oögonium; par, paraphyses; stk, stalk; tr, trichogyne; A, original; B, Harper.

the ascogonia of *Pyronema*. Sections of older apothecia show that there is a well-developed sterile margin, the "excipulum," the outer cells of which strongly refract the light thus making a beautiful snow white margin which is inrolled at first (FIG. 12) but later as the hymenium broadens becomes expanded or even reflexed (FIG. 13).

The second type of apothecium which is at first closed and later opens is illustrated by the familiar figures of *Ascobolus furfuraceus*. Not only is the ascogonium entirely enclosed at an early stage but the young hymenial layer is completely covered by



a well-developed layer of pseudoparenchymatous cells. The growth of the asci and the pushing out of the paraphyses break this layer above the hymenium irregularly and this sterile portion is forced back and becomes the excipulum of the apothecium (FIG. 9, B).

*Lachnea cretea* (Fraser, 44) and *Lachnea abundans*, which I have had the opportunity to study in artificial cultures for some time, are entirely enclosed or cleistocarpous in their younger stages and are only opened by the thrust of the paraphyses upward as in the case of *Ascobolus furfuraceus*. My sections of the young apothecium of *Ascobolus Winteri* (FIG. 9, A) and of *A. Leveillei* show that the hymenium is well covered by a solid wall of hyphae. Even in stages when the spores of some asci are nearly mature this wall is still unbroken and it appears that the asci themselves in their elongation may be the chief agency in bursting open the ascocarp, especially in *A. Winteri*. In this species the ascogonium lies well down at the bottom of the apothecium (FIG. 9, A). The ascogenous hyphae grow out from only one cell of the ascogonium as rather thick short hyphae.

W. H. Brown's figures of young fruit bodies of *Lachnea scutellata* certainly indicate that in this species the hymenium is slightly exposed from the first. His diagram shows that the inner branches of certain hyphae produce the paraphyses, while the outer branches of these same sterile hyphae are prolonged into the hairs which fold in over the hymenium in younger stages. Bucholtz describes what I take to be very much the same condition for *L. leucotricha*, although he claims the young fruit is angiocarpous on account of the extremely delicate web of hyphae that surrounds the whole fruit in its earlier stages. *Lachnea stercorea* (FIG. 10) as described by Miss Fraser is gymnocarpous from the first. Miss Fraser states that the ascogonium is enclosed by enveloping hyphae although the young hymenium is not. Her figures show only the stalk of the ascogonium surrounded by sterile hyphae. *Sphaerosoma* may prove to be gymnocarpous at first, although there seems to be a lack of complete agreement in the descriptions of this form by Rouppert (74), Setchell (84), and Seaver (83).

In *Ascobolus Winteri* it is only rarely that any enveloping hyphae arise from the mycelial hyphae giving rise to the asco-



gonium. All sterile hyphae, paraphyses and secondary mycelium originate as the result of the branching of hyphae which grow out from the base of the ascogonium—from the cells below the ascogenous cell, which I have called the stalk of the archicarp (FIG. 9, A). The ascogonium is quickly and completely enclosed by a thick protective layer. This peridium is not broken open at the apex of the young fruit by the upward thrust of the paraphyses but remains entirely closed until the spores are ripe and the asci then push their way up through the enveloping layer. The young hymenium is not exposed to view by the breaking open of an outer wall. The first appearance of the young fruit is that of a smooth globular structure, and later one discovers the tips of asci pushing up between the cells of the upper surface. Sections of entirely closed fruits often show several well formed asci with the eight spores nearly ready for dispersal (FIG. 9, A). The hypothecium is rather poorly developed. The asci often arise from a point below the ascogenous cell since the ascogenous hyphae grow downward as well as upward. My diagram shows to what a large extent the asci occupy the inner space of the fruit. *Ascobolus immersus* and *A. Leveillei* have much the same sort of ascocarp and originate from the same kind of an ascogonium. From the data just given it is plain that further subdivisions of the two main types of apothecia can be distinguished.

According to Overton (70) the fruit body of *Thecotheus* is a compound apothecium. Baur (8, 9), Darbishire (32), and others have described many species of lichens in which several ascogonia take part or are present at least in the formation of each apothecium. *Ascodesmis* and *Pyronema* are the well-known cases where the rosette of sex organs arises as the result of the dichotomous branching of single hyphae. Ramlow (73) concludes that where more than one ascus is found in *Thelebolus* this came about by accidental inclusion of two or three ascogonia in the same fruit, thus simulating what one frequently finds in *Helotium citrinum* and *Pyronema confluens* although in the latter form each of the fusing apothecia is in itself compound.

If we apply these data as to the method of origin of the ascocarp in estimating the value of current classifications of the Ascomycetes we must conclude that the arrangement in a linear series of the



Plectascineae and Perisporiaceae with cleistocarps, the Pyrenomycetes with pyrenocarps, and the Discomycetes with apothecia or discocarps is quite misleading. Considering the vast number of types whose development is yet unknown it would be premature to attempt a final arrangement of the groups along new lines, but in view of the overwhelming evidence in favor of the Floridean origin of the group the possibility that the apothecium as found in the lichens is primitive must certainly be considered. It should be borne in mind, however, that there are Pyrenomycetes like *Polystigma* and pyrenomycetous lichens like *Pyrenula* with primitive types of archicarps and spermatia. The character and rela-



FIG. 12



FIG. 13

FIG. 12. Apothecia of *Ascobolus magnificus*. Photomicrograph of young fruit bodies grown on agar, showing the pore-like opening at the apex and the fluffy white exterior; at this stage no "hooks" or young asci are to be found. Magnified three times.

FIG. 13. Apothecia of *Ascobolus magnificus*, both young and mature fruits, natural size. The brilliant white margin shown in this photograph is very characteristic of this species.

tive development of the trichogyne is perhaps to be regarded as more significant in determining phylogeny than the form of the ascocarp.

The evidence furnished by the trichogyne with all its variations in the Laboulbeniaceae and the other Ascomycetes seems to be sufficient ground for assuming that the Ascomycetes have been derived from the Florideae. Vuillemin (92) would derive them from the ancestors of the Florideae, perhaps from some form



as far back as *Coleochaete*, and from this remote origin would have two parallel lines of development, one leading up to the red algae, the other to the Ascomycetes. This is leaving to the "tendencies to parallelism" the entire explanation of the obvious similarities of the various other structures in both groups. Bucholtz (21), concentrating his attention on the possible evolution of the ascus in such a case as *Endogone*, also explains the trichogyne as due to accidental "parallelism" in development.

We can arrange a series of the forms best known as to their development which shows a progressive shortening of the trichogyne and a corresponding reduction in the number of the antheridia and their gradual shifting towards a position nearer the oögonium: *Collema microphyllum*, *Physma compactum*, *Collema pulposum*, *Ascobolus carbonarius*, *Thecotheus Pelletieri*, *Ascobolus magnificus*, *Lachnea stercorea*, *Pyronema*, *Ascodesmis*, *Sphaerotheca*.

In *Collema microphyllum* the spermatia are developed at some distance from the trichogyne which is active only in reaching the surface of the thallus. The spermatia are borne to the trichogyne through the agencies of water and wind. In *Physma compactum* the trichogynes grow up around the spermogonium. The spermatia are separated from the trichogynes by only a short distance, and the apothecium is developed within or around the old spermogonium. In *Collema pulposum* we find the antheridial branches scattered throughout the thallus, the spermatia remain loosely attached to the stalk and the trichogyne has become the active structure in seeking out the spermatium. The old spermatophore and trichogyne may or may not become included within the space occupied by the apothecium (FIG. 7). In *Ascobolus carbonarius* the antheridial conidia are distributed at various places through the mycelium bearing the ascogonium and are never set free from the stalk. Instead of clusters of spermatia being borne on one stalk we find only a spore-like "antheridium." The trichogyne grows out to the "antheridium" in much the same way as in *Collema pulposum*. The entire archicarp is finally enclosed in the enveloping hyphae in the early development of the apothecium. Here too we find a much larger number of antheridia than trichogynes developed. A further stage in this reduction and shortening of the trichogyne is found in *Ascobolus magnificus*, where generally



only one antheridium is developed in close proximity to the ascogonial branch. The trichogyne is a much thicker structure of about eight short cells, but it has sufficient length to reach the antheridium to which it applies itself. The trichogyne of *Lachnea stercorea* is somewhat shorter than that of *Ascobolus magnificus*, having about one half as many cells. It apparently fuses with the antheridium without first coiling partly about it. From this stage to *Pyronema* is but a short step where the trichogyne is reduced to one long cell, which we may imagine arose by omitting the cross walls. Reduction has gone on still further in *Ascodesmis*, where the antheridium coils tightly about the ascogonium and the trichogyne is reduced to one short cell. The final step we find in *Sphaerotheca* where the male nucleus travels directly from the antheridium into the oögonium without the aid of any intervening structure.

There are a number of forms in which the ascogonium is prolonged into a trichogyne, although no antheridium is known to exist. In many of the forms in which the trichogyne is most prominent as a multicellular structure at the end of the archicarp we find that several cells of the ascogonium give rise to ascogenous hyphae. In all of the lichens in which this feature has been studied several cells of the ascogonium are connected by large openings and all the cells so connected are ascogenous cells (FIG. 7). Three or four of the first cells beyond the stalk of the ascogonium of *Ascobolus carbonarius* are ascogenous. Cutting (27) states that several cells of the ascogonium in *Ascophanus carneus* give rise to fertile hyphae. Overton (70) has reported the same for *Thecotheus*, and Miss Fraser (44) for *Lachnea cretea*. I have no doubt that the same is true in *L. abundans* and *L. melaloma* although I have not as yet determined this point fully. The list of forms with more than one ascogenous cell is as follows: the lichens, *Ascobolus carbonarius*, *A. pusillus*, *A. glaber*, *Saccobolus*, *Ascophanus carneus*, *Thecotheus Pelletieri*, *Lachnea cretea*, *L. abundans*, *L. melaloma*, *Aspergillus*, *Gymnoascus*, *Ascodesmis* (?).

In *Ascobolus furfuraceus*, *Lachnea scutellata*, *Lasiobolus equinus*, and *Pyronema*, only one cell of the ascogonium bears ascogenous hyphae. In *Lasiobolus pulcherrimus* there is but one ascogenous cell, though the ascogonium is prolonged into a structure of seven



or eight cells. Arranging these forms with only one ascogenous cell in the order of the complexity of the archicarp we find the following series: *Lasiobolus pulcherrimus*, *Ascobolus furfuraceus*, *A. immersus*, *Lachnea scutellata*, *Lasiobolus equinus*, *Ascobolus Winteri*, *A. Leveillei*, *Pyronema*, *Thelebolus*, *Sphaerotheca*.

If we compare the second and third groups above, especially *Ascobolus carbonarius* with *A. furfuraceus* we may get some light on the nature of the entire ascogonium in the latter species, that is, on the question whether the part beyond the ascogenous cell is to be considered morphologically as a trichogyne.

It is certainly very difficult to attempt to homologize the crossier and nuclear fusions in the young ascus with the oöblastema and auxiliary cells and fusions of the *Dudresnaya* type, but it is clear that both involve the same physiological or nutritive conditions. After the fusion of the oöblastema filaments with the auxiliary cells which are gorged with nourishment we find the conditions required for the production of well nourished filaments producing spores. The vegetative nuclear fusions in the ascogenous hyphae provide a large amount of nuclear substance to maintain the "nucleo-cytoplasmic equilibrium" of a large spore mother-cell. In other words the secondary fertilizations of the red algae provide conditions suitable to the formation of groups of carpospores just as the hook phenomena and nuclear fusions in the Ascomycetes lead to the production of ascospores.

We must consider the outgrowths of the carpogonium in all forms of the red algae as homologous structures. The question as to whether or not reduction occurs at the germination of the fertilized egg in *Nemalion* is not necessarily a vital one in this connection. The oöblastema filaments of the *Dudresnaya* group are then homologous with the sporogenous hyphae of *Dermonema*, *Nemalion*, etc., although they do not give rise, for example in *Gloiosiphonia*, directly to carpospores. In the Ascomycetes, *Dudresnaya*, and *Gloiosiphonia* both ascospores and carpospores are produced only after secondary fusions have occurred, and the suggestion is strong that the ascogenous hyphae are homologous with the oöblastema filaments. The very short oöblastema outgrowths in *Harveyella*, *Erythrophyllum*, *Prionitis*, correspond to the long much branched oöblastema of *Dudresnaya*, and among the



Ascomycetes we have the greatest variation in the relative development of the ascogenous hyphae.

It is of course of vital importance to determine where the spermatium nucleus unites with the egg, in view of the fusions between the cells of ascogonia followed by many nuclear divisions such as Miss Bachmann observed. Each of the several fused cells gives rise to ascogenous hyphae (FIG. 9). One sexual act has served to fertilize several cells, exactly as in *Dudresnaya* the fertilization of a single egg ultimately leads to the production of several masses of carpospores.

The hypothetical cases described by Schmitz to provide for possible variations in the reproductive processes which might later be discovered are suggestive. He imagined that the "second sexual act" might by degeneration disappear entirely, leaving conditions just what they are in the primitive forms like *Nemalion*. In case of a failure in the first sexual act due to non-development of spermatia Schmitz conceived that the spermatium mother-cell might grow out into a branched or unbranched male hypha which could perhaps fertilize the auxiliary cell (cf. Sachs' figure of *Ascobolus furfuraceus*). In such cases the carpogonium in time would probably not develop a trichogyne and might even tend to disappear. In case the spermatium mother-cell were not formed the carpogonium itself might grow out directly into male hyphae which could bring about the same end result, the fusion with the auxiliary cell, which might be either an end cell (*Dudresnaya purpurifera*) or an intercalary cell (*D. coccinea*). Schmitz saw a similarity between the Collemaceae and the Cryptonemiaceae but believed that reduction had in some cases already occurred to the extent that the spermatia were no longer developed. In other cases the first sexual act has been entirely suppressed, the second only functioning. This case would correspond to that of the Exoascaceae as we know them. Having in mind the scolecite or ascogone of *Ascobolus* and *Lasiobolus* with the curiously branched hypha, the pollinodium, coiling about its upper end as described by Woronin, Borzi, and Janczewski, Schmitz conceived the ascogenous cell, "the mother-cell of the ascogenous hyphae," to be homologous with the auxiliary cell in the Cryptonemiaceae which is fertilized by the "second sexual act." Reduction in other



cases has gone on so far that the second sexual process has also disappeared so that the auxiliary cell, ascogenous cell itself, whether it can be distinguished from ordinary hyphae by its special form or not, may give rise directly to the spore fruit (*Thelebolus*, *Teichospora*). These speculations of Schmitz regarding the sexuality of the Ascomycetes do not apply to the facts as since worked out and are treated much as Heydrich's theory (54) of the origin of the tetraspore mother-cell is today. Not knowing of the nuclear fusion in the ascus it did not occur to Schmitz that the ascogenous hyphae of *Ascobolus* were to be compared to the oöblastema filaments. He considered them merely as equivalent to the gonimoblasts growing out of the fertilized auxiliary cells to produce carpospores. To him each cystocarp of *Dudresnaya* would be represented by an apothecium, the one or two rows of carpospores in *Cruoriopsis* would be much reduced cystocarps. The apothecium should, however, correspond to a whole nemathecium of *Dudresnaya* cystocarps packed together in one compound fruit. The fruit of *Cruoriopsis* would in reality be a very good counterpart of the apothecium of *Ascobolus magnificus*, *Pyronema*, or *Collema*. One sexual process, or several independent and equal in *Pyronema*, followed by a large number of secondary fusions (auxiliary cells with oöblastema, nuclear or cell fusions at the end of the ascogenous hyphae) gives rise to what we know as the spore fruits of the Ascomycetes.

The attempt to connect the Ascomycetes with the red algae on the basis of superficial resemblances between the ascocarp and cystocarp is entirely misleading. Schmitz pointed out that this system as proposed by Agardh (1), in which the characters of the thallus and cystocarp were made the basis of classification, was entirely inadequate for the purpose of showing phylogenetic relationships. The system proposed by Schmitz, slightly modified by Oltmanns and recently analyzed by Daines, makes no use whatever of the characters of the mature cystocarp in circumscribing the five large groups into which the Florideae are subdivided. This new system is based almost entirely on the morphology of the outgrowths of the fertilized egg together with the origin and disposition of the auxiliary cells and the development of the fusion and central cells. A practical example of the application of these



principles is furnished by Sturch (87) who transfers the genus *Harveyella* from the Nemalionales to the Gigartinales on the basis of the method of development of the procarp and the formation of the auxiliary cell, *i. e.* processes that are concerned with fertilization and the development of the sporophyte. Twiss (91) would transfer *Erythrophyllum* to the *Gigartinaceae* and Daines (28) *Prionitis* to the *Ceramiales* for like reasons. De Bary and Janczewski maintained on the same ground that the nature of the ascogonium and the method and degree of its development rather than the form of the mature ascocarp furnish the best basis for the determination of homologies in the Ascomycetes.

New data as to the morphology of the ascogonium and trichogyne are accumulating rapidly. Investigation of a great number of species ranging from the gelatinous Collemaceae to the dry Cladoniaceae, or the hard and black Graphidiaceae, including both discomycetous and pyrenomycetous forms, discloses the fact that a vast majority of these fungi are provided with trichogynes, and where no such structure has been found, an ascogonium has generally been more or less clearly recognized. It is not improbable that further research will disclose many other interesting transition forms such as we now find in *Collema pulposum*, *Ascobolus carbonarius*, and *Ascobolus magnificus*.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1913

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- Banker, H. J.** Type studies in the Hydnaceae—VI. The genera *Creolophus*, *Echinodontium*, *Gloiodon*, and *Hydnodon*. Mycologia 5: 293-298. 25 N 1913.
- Bitter, G.** Eine neue *Parmelia* (subgeneris *Hypogymnia*) aus der argentinischen Provinz Salta. Repert. Sp. Nov. 12: 515. 15 D 1913.  
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Includes eight new species.
- Blackwelder, E.** Origin of the Bighorn dolomite of Wyoming. Bull. Geol. Soc. Am. 24: 607-624. pl. 28-35. 22 D 1913.  
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- Blodgett, F. H.** College work in plant pathology. Plant World 16: 304-314. N 1913.



- Blumer, J. C.** A northern prickly pear. *Plant World* **16**: 210-212. J1 1913.
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Includes *Russula crenulata*, *R. Murrillii*, and *R. bicolor*, spp. nov.
- Butler, O.** A note on the significance of sugar in the tubers of *Solanum tuberosum*. *Bull. Torrey Club* **40**: 110-118. *pl.* 2 + *f.* 1, 2. 7 Ap 1913.
- Cannon, W. A.** A note on a chaparral-forest relation at Carmel, California. *Plant World* **16**: 36-38. Ja 1913.
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- Davis, B. M.** A much desired *Oenothera*. *Plant World* **16**: 145-153. *f.* 1-4. My 1913.
- Elmer, A. D. E.** Four score of new plants. *Leaflets Philip. Bot.* **5**: 1751-1853. 18 Au 1913.
- Elmer, A. D. E.** *Loranthus* from Mount Urdaneta. *Leaflets Philip. Bot.* **6**: 1959-1971. 29 N 1913.  
Includes eleven new species.
- Elmer, A. D. E.** Rubiaceae from Mount Urdaneta. *Leaflets Philip. Bot.* **5**: 1855-1905. 12 S 1913.  
Includes twenty-five new species.
- Elmer, A. D. E.** Seven oaks from Mount Urdaneta. *Leaflets Philip. Bot.* **6**: 1981-1986. 6 D 1913.  
Includes *Quercus Lipacon*, *Q. Copelandi*, and *Q. bicolorata*, spp. nov.
- Evans, A. W., & Hooker, H. D., Jr.** Development of the peristome in *Ceratodon purpureus*. *Bull. Torrey Club* **40**: 97-109. *f.* 1-26. 7 Ap 1913.
- Fink, B., & Smith, W. D.** Botanical instruction in the high schools of Ohio. *Miami Univ. Bull.* **XI. 12**: 3-39. Au 1913.



- Foxworthy, F. W.** Dipterocarpaceae from the Agusan region. Leaflets Philip. Bot. 6: 1949-1958. 21 N 1913.  
Includes *Dipterocarpus subalpinus*, *D. obconicus*, *D. Malibato*, *Hopea Malibato*, *Shorea Malibato*, and *Vatica mindanensis*, spp. nov.
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- Griffiths, D.** Behavior, under cultural conditions, of species of cacti known as *Opuntia*. U. S. Dept. Agr. Plant Ind. Bull. 31: 1-24. pl. 1-8 + f. 1. 30 D 1913.
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- Harvey, E. M.** The action of the rain-correcting atmometer. Plant World 16: 89-93. Mr 1913. [Illust.]
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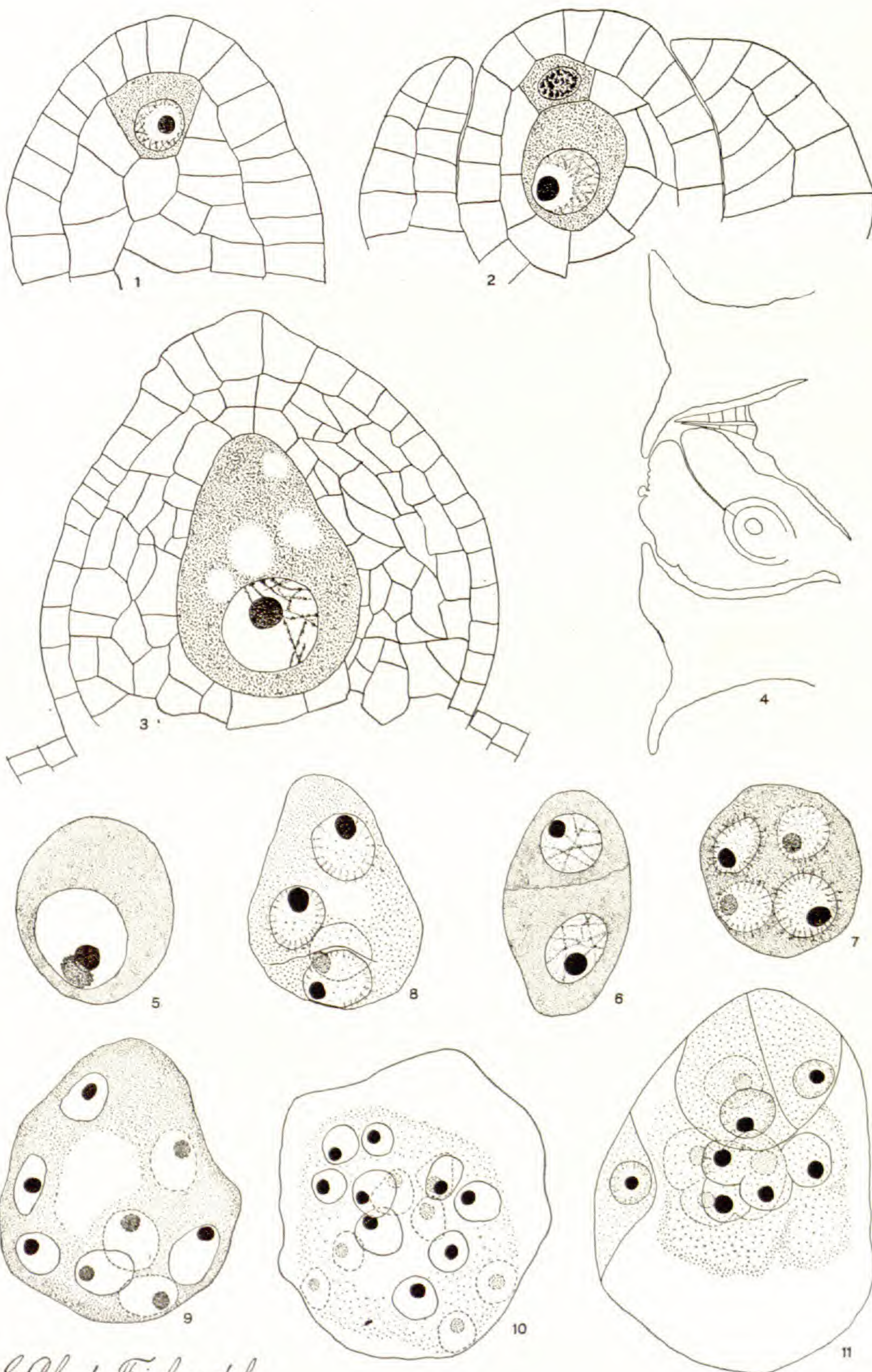
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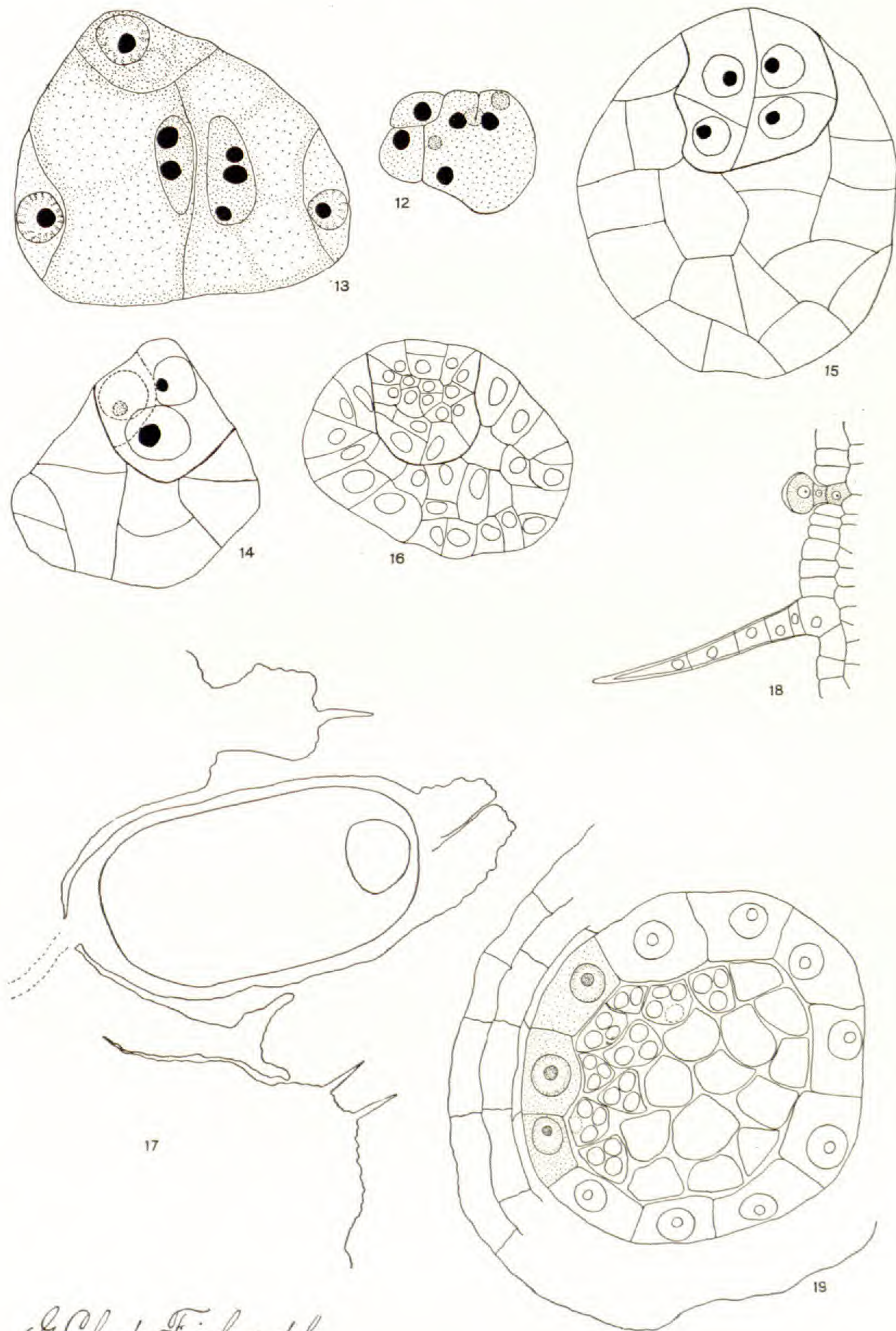




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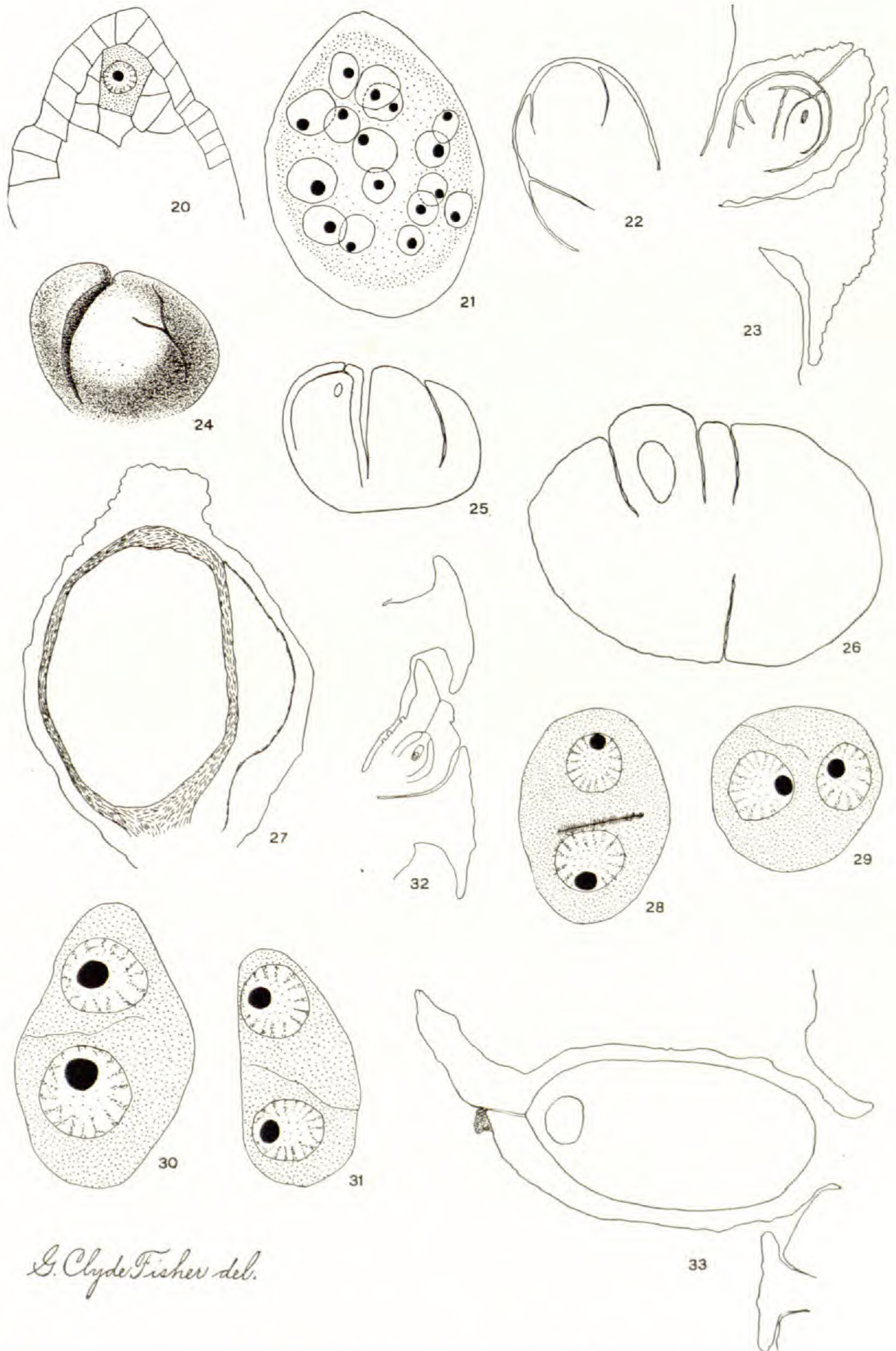




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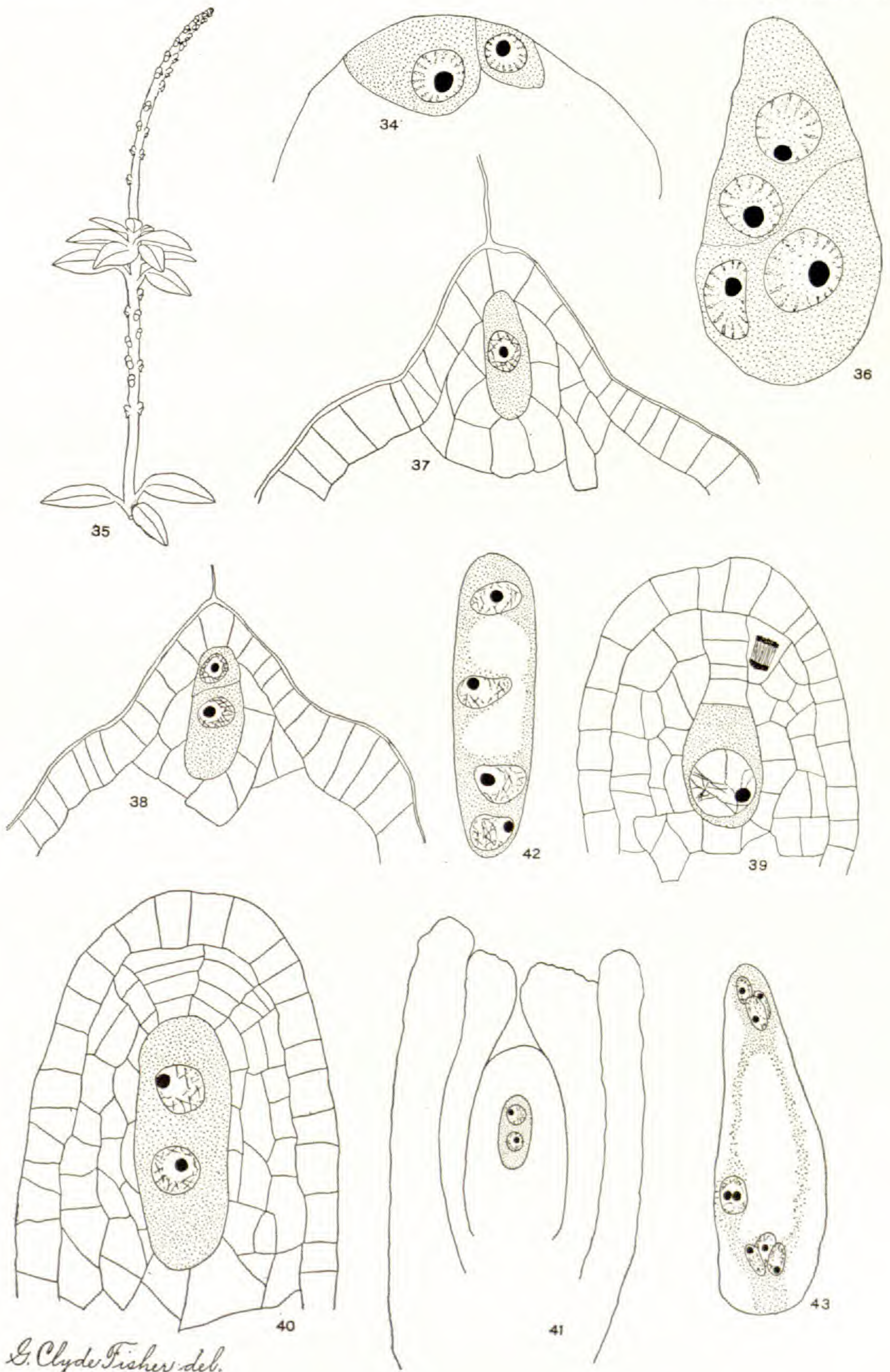




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# BULLETIN

OF THE

# TORREY BOTANICAL CLUB

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### CONTENTS

The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession . . . . . ROLAND M. HARPER 209

Seed development in the genus *Peperomia*. (Plates 3-6.) [*Concluded.*] G. CLYDE FISHER 221

On the relationship between the number of ovules formed and the number of seeds developing in *Cercis* . . . . . J. ARTHUR HARRIS 243

INDEX TO AMERICAN BOTANICAL LITERATURE. . . . . 257

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APRIL, 1914

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The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession

ROLAND M. HARPER

(WITH FOUR TEXT FIGURES)

In eastern North Carolina, where the geographical term "pocosin" is used more frequently than in all the rest of the world, it means a flat wet place with peaty soil, usually remote from large streams, with a scattered growth of trees, mostly *Pinus serotina*, and a dense shrubby undergrowth.\* In South Carolina and Georgia this term is almost unknown,† but it reappears in the coastal plain of Alabama, with a very different meaning.

In a chapter contributed by E. Q. Thornton to Prof. Tuomey's second report on the geology of Alabama, published in 1858 (p. 244), we find the following interesting bit of information:

"East of this place [Troy] is a small scope of country of peculiar appearance, known as the Pocosson settlement. The vallies, which have the rank luxuriant growth of a swamp, are surrounded on three sides by a ridge of snow-white sand, which seems to have been heaped up by the tides on a sea-shore. The only occupant of the hills is a scrubby oak covered with long moss. The soil is exceedingly unproductive, and soon wears out by cultivation."

\* See Bull. Torrey Club 34: 361-363. 1907; C. A. Davis, N. C. Geol. Surv. Econ. Paper 15: 149-150. 1910; L. W. Stephenson, N. C. Geol. Surv. Vol. 3: 280. pl. 24B. 1913.

† Miss E. F. Andrews (see Torrey Club 13: 64-66. 1913) wrote me early in 1913 that she had heard the term applied to certain "large flowery swamps" in the vicinity of Albany, Georgia, where she used to live; and the government soil survey of Dougherty County, Georgia, published in October, 1913, indicates a "Percosin Creek" a few miles west of Albany, but says nothing about any application of the name to vegetation. Still more recently (March, 1914) I have heard of an occurrence of the term in West Florida.

[The BULLETIN for March (41: 137-208. pl. 1-6) was issued 22 Ap 1914]



In Dr. Eugene A. Smith's description of Pike County in his report on the agricultural features of Alabama (Tenth Census U. S. 6: 151; Geol. Surv. Ala., Report for 1881 and 1882, p. 522. 1884) these observations of Thornton's are briefly referred to. About the same time, in the 9th volume of the Tenth Census (p. 528), Dr. Charles Mohr published some more definite information about the vegetation of the same place, as follows:

"PIKE COUNTY.—On the broad ridges which form the divide between the waters of the Pea and Conecuh rivers, upon a purely sandy soil, are found, within the forest of long-leaved pine, tracts with strictly-defined outlines from a half mile to several miles in width, covered with a dense vegetation of small trees and shrubs peculiar to the perpetually moist and cool hummocks\* of the coast. The soil covered with this growth presents no unusual features; it is as poor and arid as that covering the rest of these heights. Surrounded on all sides by pine forests, not a single pine tree is seen within the limits of these glades, called by the inhabitants 'pogosines,' an Indian name the meaning of which I was unable to learn.

"The trees are of small growth, the willow oak, the water oak, beech, red maple, and black gum rarely rising to a height of more than 30 feet among the sourwoods, junipers, hornbeams, hollies, papaws, fringe trees, red bays, and other trees of the coast. These glades verge upon deep ravines from which issue large springs, and from this fact I conclude that, below their sandy, porous soil, strata must exist perpetually moistened by subterranean waters near enough to the surface to supply the moisture necessary to support such a luxuriant vegetation."

There seems to be no reference to this interesting place in Dr. Smith's report on the geology of the coastal plain of Alabama (1895), or in Dr. Mohr's Plant Life of Alabama (1901). In the summer of 1906 Dr. Smith and the writer were in Pike County together for a short time, and heard some accounts of the "pocosin," which led Dr. Smith to make his first visit to it a little later.

In 1910 a soil survey of Pike County was made by W. E. Tharp, of the U. S. Department of Agriculture, and W. L. Lett and W. E. Wilkinson, representing the State; and on the map accompanying their report, published in December, 1911, the location of the pocosin is shown, probably for the first time, but there is not a word about it in the text. Stranger still, its soil is not differentiated on the map from that of the surrounding country ("Norfolk coarse sand"), although it does differ in at least one important particular.

---

\* Dr. Mohr doubtless wrote "hammocks," as he did in his Plant Life of Alabama 17 years later, but it was evidently changed to "hummocks" in Washington, as it was throughout the 5th and 6th volumes of the same series, except on the maps, and one or two places in the text that escaped the proof-readers. (See Geol. Surv. Ala. Monog. 8: 83. 1913.)



Guided by the map just mentioned, the writer visited the spot on November 6, 1912, and March 27, 1913, and made a rough quantitative study of its vegetation. An incessant rain at the time of the first visit interfered somewhat with note-taking and made photography out of the question, but conditions were more satisfactory the second time, when the views here published were taken. A brief mention of it, with the only photograph of its vegetation hitherto published, appeared last summer in my report on the forests of Alabama.\*

The so-called pocosin (Dr. Mohr's description above quoted implies the existence of several such areas, but I know of only one) embraces a hundred acres or more, mostly in Section 7, T. 9 N., R. 22 E., in the midst of a few square miles of undulating sandy country on the east side of Walnut Creek, about half way between Troy and Brundidge, and about 50 miles south of the fall-line and 100 miles from the Gulf coast. The pocosin itself is practically untouched by civilization, except for having one or two little-used roads through it, but the surrounding sandy country is partly under cultivation. As observed by Thornton, however, the sand is much less productive than the loamy soils which prevail elsewhere in Pike County and other parts of the southern red hills or Eocene region of the coastal plain. Where not cultivated it bears a vegetation much like that of the sand-hills of Georgia,† but the soil is evidently a little richer in mineral plant food than that of the average sand-hill, as shown by the prevalence of *Pinus echinata* and the scarcity of *Pinus palustris*.‡

In the following list of sand-hill plants growing around the pocosin the trees, shrubs and herbs are arranged as nearly as possible in order of abundance, but the data are not sufficient for assigning percentages to them. Evergreens are indicated by heavy type.

## TREES

<b>Pinus echinata</b>	Hicoria glabra
Crataegus Michauxii?	Quercus stellata
Quercus Catesbaei	Quercus marylandica
Quercus cinerea	Nyssa sylvatica
Quercus Margaretta	<b>Pinus palustris</b>

\* Geol. Surv. Ala. Monog. 8: 99-100, 160-161. June, 1913.

† See Ann. N. Y. Acad. Sci. 17: 82-89. 1906.

‡ This is in a narrow belt of the coastal plain where the long-leaf pine is very rare. See Geol. Surv. Ala. Monog. 8: 99. 1913.



## SHRUBS AND VINES

**Batodendron arboreum**  
*Ceanothus americanus*  
**Gaylussacia dumosa**  
*Asimina parviflora*

**Osmanthus americana**  
*Chionanthus virginica*  
**Gelsemium sempervirens**

## HERBS

**Opuntia vulgaris**  
*Pteridium aquilinum*  
*Afzelia pectinata*  
*Kuhnistera pinnata\**  
*Solidago odora*  
*Stenophyllus ciliatifolius\**  
**Polypodium polypodioides**  
**Iris verna**  
*Triplasis americana\**  
*Ionactis linariifolius*

*Cracca virginiana*  
*Chrysopsis aspera?*  
*Coreopsis major Oemleri*  
**Tillandsia usneoides**  
*Sorghastrum secundum†*  
*Siphonochia sp.*  
*Pitcheria galactioides\**  
*Astragalus villosus\**  
*Warea cuneifolia‡*

## LICHENS

*Cladonia sp.*

This vegetation, like that on typical sand-hills, is not very dense, as shown by one of the accompanying illustrations (FIG. 1). Apparently about one third of the woody plants (counting individuals, not species) are evergreen.

The pocosin itself seems to center around the precipitous heads of a few small tributaries of Walnut Creek, but its vegetation, except in the bottoms of the ravines, is not at all of a swamp character, the statements of Thornton and Mohr to the contrary notwithstanding. Its soil was doubtless originally the same as that of the surrounding sandy country, but it is now covered and more or less mixed with a thin layer of humus, derived from the trees and protected from desiccation and oxidation by their shade, as in other dense forests the world over. In this forest there is a characteristic faint odor of sour humus (corresponding approximately with the raw humus of Warming§ or more closely with the upland peat of Coville||), as in the mountains of North Carolina

\* These five species do not seem to have been found so far inland in Alabama before. Three of them are Leguminosae.

† Apparently not previously reported from Alabama. (See Ann. N. Y. Acad. Sci. 17: 300. 1906.) But in September, 1912, I found it in considerable abundance in the pine-barrens of Clarke, Monroe and Baldwin Counties.

‡ Another addition to the Alabama flora, its previously known range being from South Carolina to Florida.

§ Oecology of Plants, 62-63. 1909.

|| U. S. Dept. Agr. Bur. Plant Industry Bull. 193: 32-34. F 1911; Jour. Wash. Acad. Sci. 3: 84-86. F 1913.



and many other places where humus accumulates on a soil that is poor in animal life or not intrinsically very fertile. The boundary between the pocosin and sand-hill vegetation is not very sharp, but it is comparatively easy to fix it definitely enough for statistical purposes. In attempting to make a quantitative analysis of the vegetation, however, one encounters a difficulty in that it is a many-storied forest, in which there seem to be all gradations in



FIG. 1. Sand-hill vegetation near the pocosin, with *Pinus echinata*, *Quercus Catesbaei*, *Crataegus*, *Batodendron*, etc.

size between large trees and shrubs, and it is not exactly right to include both trees and shrubs in the same list for the purpose of calculating percentages. The following list is divided into more classes than usual, and the relative position of the species within each class is approximately correct, but it gives no idea of the relative abundance of species in different classes. The illustrations, however, partly make up for this. (FIGS. 3, 4.)

LARGE TREES

*Quercus laurifolia*  
*Hicoria glabra?*  
*Tilia heterophylla?*  
***Magnolia grandiflora***  
*Fagus grandifolia*

*Quercus alba*  
*Prunus serotina*  
*Fraxinus americana?*  
*Quercus velutina*



## SMALL TREES

<i>Osmanthus americana</i>	<i>Acer floridanum</i>
<i>Persea Borbonia</i>	<i>Prunus umbellata?</i>
<i>Quercus</i> sp.*	<i>Bumelia lanuginosa</i>
<i>Ostrya Virginiana</i>	<i>Crataegus Michauxii?</i> (toward edges)
<i>Batodendron arboreum</i>	<i>Quercus Margaretta</i> (toward edges)
<i>Cornus florida</i>	<i>Cercis canadensis</i>
<i>Viburnum rufidulum</i>	<i>Oxydendron arboreum</i>
<i>Prunus caroliniana</i>	<i>Ilex opaca</i>
<i>Crataegus</i> sp.	<i>Amelanchier</i> sp.

## SHRUBS

<i>Hamamelis virginiana</i>	<i>Callicarpa americana</i>
<i>Chionanthus virginica</i>	<i>Aesculus Pavia</i>
<i>Sebastiania ligustrina</i>	<i>Kalmia latifolia</i>
<i>Aralia spinosa</i>	

## WOODY VINES

<i>Vitis rotundifolia</i>	<i>Rhus radicans</i>
<i>Bignonia crucigera</i>	

## HERBACEOUS VINES

<i>Smilax pumila</i>	<i>Dioscorea</i> sp.
<i>Mitchella repens</i>	

## ORDINARY HERBS

<i>Trillium Hugerii</i>	<i>Viola</i> sp.
<i>Asarum arifolium</i>	<i>Sanicula</i> sp.
<i>Galium uniflorum</i>	<i>Dasystoma quercifolia</i>
<i>Polygonatum biflorum</i>	<i>Carex floridana</i>
<i>Solidago odora</i> (toward edges)	<i>Opuntia vulgaris</i>
<i>Monotropa uniflora</i>	<i>Conopholis americana</i>
<i>Panicum</i> sp.	

## EPIPHYTES

<i>Polypodium polypodioides</i>	<i>Tillandsia usneoides</i>
---------------------------------	-----------------------------

## BRYOPHYTES AND THALLOPHYTES

<i>Thuidium</i> sp.	<i>Clavaria</i> sp.
---------------------	---------------------

It is interesting to note that among 57 species here listed as growing in the pocosin there is only one fern, and such large families as Gramineae, Cyperaceae, Leguminosae and Com-

\* An unidentified—and probably undescribed—oak, somewhat similar in appearance to *Q. marylandica* Muench. and *Q. arkansana* Sarg., but apparently more closely related to *Q. nigra* L. (*Q. aquatica* Walt.), *Q. myrtifolia* Willd. (as that species is commonly interpreted), and *Q. microcarya* Small. I have never seen anything like it elsewhere. It grows mostly toward the edges of the pocosin, but not in the sand-hill vegetation. It is one of the commoner species there, as indicated by its position in the list, and it is difficult to understand how Dr. Mohr overlooked it if he visited this same spot, unless he was there only in winter, when it was leafless. (FIG. 3.)



positae are also represented by only one species each. There are five oaks (the same number as in the surrounding sand-hill area) three representatives of the Ericales, and three colorless saprophytes or root-parasites, namely, *Monotropa*, *Conopholis* and *Clavaria*.

Although there are no quantitative figures to show it, just about half of this vegetation is evergreen. It is very similar to



FIG. 2

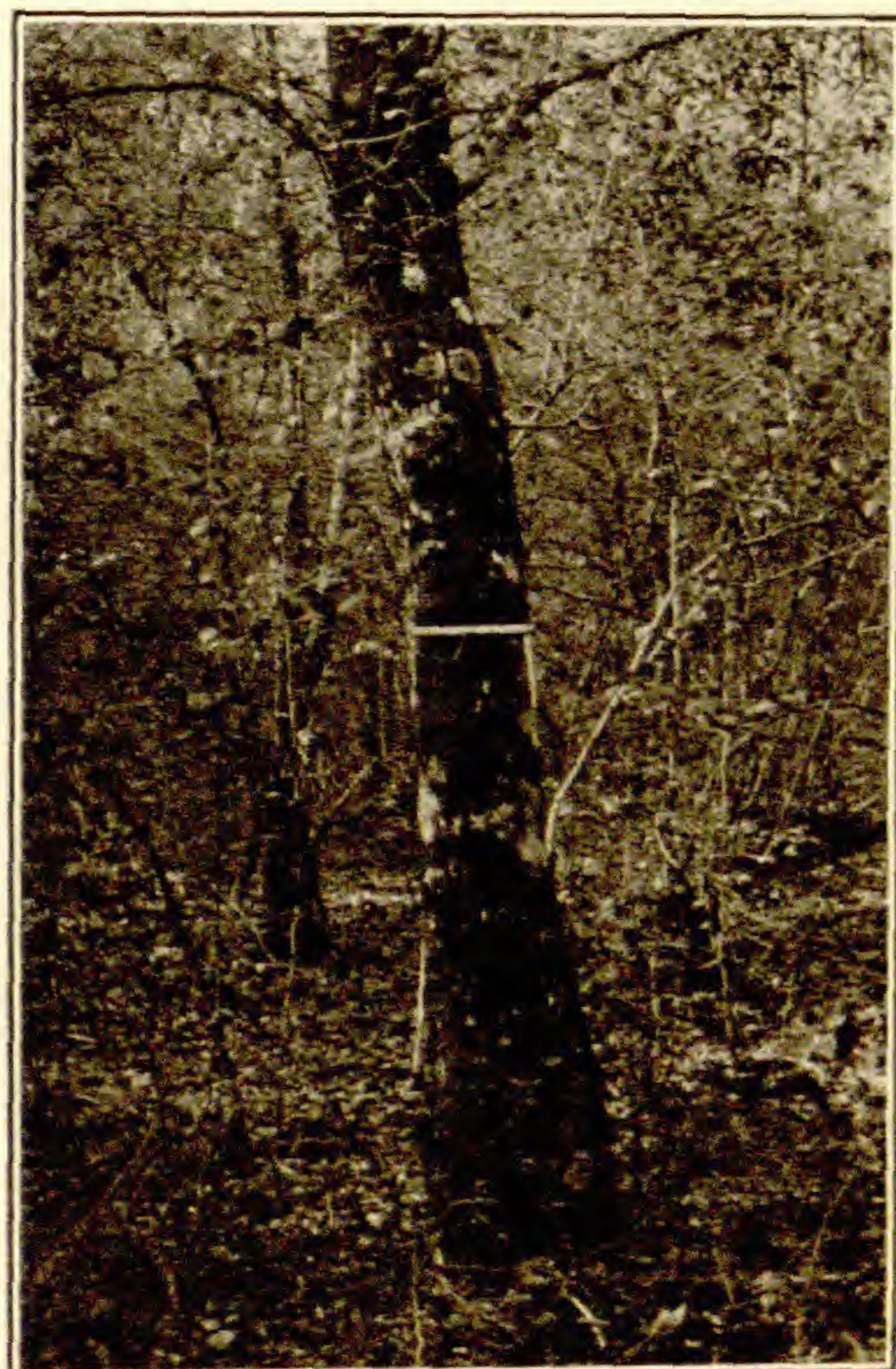


FIG. 3

FIG. 2. Scene on sandy road just outside of the pocosin. Flowering branches of *Quercus stellata* in upper left corner; *Quercus Catesbaei* at right, bearing many dead leaves of the preceding season.

FIG. 3. Trunk of the undescribed *Quercus* (34 inches in circumference, breast-high, and about 30 feet tall) in the pocosin near its eastern edge.

that of some of the sandy hammocks of Georgia and Florida;\* and it may be more or less of an accident that the name *pocosin* was applied to this place by the early settlers instead of *hammock*.†

\* See Ann. N. Y. Acad. Sci. 17: 98-102. 1906; Bull. Torrey Club 38: 515-517. 1911.

† If the early immigrants had come from the southeastward instead of northeastward they would doubtless have been familiar with hammocks, which are more prevalent nearer the coast.



The proportion of evergreens is usually somewhat larger in the hammocks nearer the coast, however. The more remote relationships of this vegetation may be indicated by saying that it is intermediate in character between the deciduous forests that are common on rich uplands in the moderately humid parts of the North Temperate zone, and the "sclerophyllous forests" of Warming and other European ecologists.

A list of the characteristic plants of the ravines will complete the description of the pocosin vegetation. They are about as follows (the arrangement being the same as in the two preceding lists):

## TREES

<i>Osmanthus americana</i>	<i>Cornus florida</i>
<i>Magnolia grandiflora</i>	<i>Symplocos tinctoria</i>
<i>Ilex opaca</i>	<i>Hicoria alba</i>
<i>Liriodendron Tulipifera</i>	<i>Fagus grandifolia</i>
<i>Magnolia glauca</i>	

## SHRUBS

<i>Kalmia latifolia</i>	<i>Ilex coriacea</i>
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## HERBS

<i>Asarum arifolium</i>	<i>Smilax pumila</i>
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## MOSSES

*Thuidium* sp.

Evergreens are decidedly in the majority here.

Previous visitors to this place have been more or less mystified by the occurrence of such luxuriant vegetation in such sandy soil. The explanation is doubtless the same as for other sandy hammocks, and is very simple to one familiar with conditions in South Georgia and Florida.

The pocosin area, exclusive of the ravines, was presumably at some time in the past covered with the same sort of sand-hill vegetation that now partly surrounds it. Vegetation of a denser, more "climactic"\* type must have gradually spread from the creek valley up the ravines to their heads, and then out across the

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\* This adjective, derived from *climax*, is rarely if ever seen in botanical literature, but some such word seems to be needed. Some ecologists have been using *climatic*, an entirely different word, to convey essentially the meaning here intended; while many use *climax* and *mesophytic* more or less interchangeably, which seems to be a perversion of the original meaning of the latter.



sand, making more humus all the time, and crowding out the intolerant sand-hill plants, as in normal succession the world over; and it is probably still spreading slowly but surely. The pocosin vegetation is simply the climax for that type of soil, while the sand-hill vegetation is the pioneer.

In explaining this succession there is one environmental factor that must not be lost sight of. Most of the plants in the pocosin,



FIG. 4. Typical pocosin vegetation. *Magnolia grandiflora* (the largest trunk), *Osmanthus*, *Batodendron*, *Prunus caroliniana*, etc. Ground covered with undecayed leaves.

as in other hammocks, are very sensitive to fire. Fire often sweeps through the upland pine-oak-hickory woods that are common on the better soils of the same region, but the sand-hill vegetation is ordinarily too sparse and open to carry a ground fire any distance, so that it protects the pocosin vegetation on three sides from any fires which may originate in the surrounding country. Protection on the remaining side is afforded by the swamps and bottoms of Walnut Creek, or the broken topography. The hammocks of the Altamaha Grit region of Georgia are similarly protected from fire by the creek swamp on one side of them and the sand-hills on the other, and this protection has been an essential factor in determining their present vegetation.\*

Finally this Alabama pocosin throws valuable light on the

\* See Bull. Torrey Club 38: 524-525. 1911.



relation of evergreens to soil and succession. Although a great deal has been written about the phenomena of succession in various parts of the world, no one yet seems to have published any satisfactory short definition of pioneer and climax vegetation by which they may be recognized wherever found, without knowing the species; and consequently every ecologist has his own views on these points, and perhaps no two of them agree exactly. It is probably pretty generally agreed that normal succession (biotic succession of Cowles\*) involves enrichment of the soil in some way; and as evergreens, in temperate climates at least, are well known to be most abundant in the poorer soils,† I supposed until about two years ago that no typical climax forest could contain any evergreens; and that view has found expression in my writings. Closely connected with that belief was one which seems to be still very generally held, namely, that for every (climatic) *region* there is *one* climax type of vegetation toward which all others are tending. I am now pretty well satisfied, however, that almost every type of *soil* has its own characteristic pioneer and climax vegetation, more or less distinct from those of other types.

The proportion of evergreens in a given habitat or region seems to be correlated with the amount of available potash (and perhaps other minerals) in the soil,‡ and therefore should not be affected much by the sort of succession whose essential feature is the accumulation of humus, or the progress of nitrification. Although an admixture of humus is indeed believed to increase the availability of the mineral plant foods in soil, a soil totally lacking in potash or lime would gain none of these ingredients from humus formed in place. It is even possible that in soils deficient in soluble minerals—as is the case with most sandy and peaty soils—and protected from fire like our pocosin, a considerable proportion of the potash within reach of the roots of trees is locked up for several years at a time in the dead leaves which lie on the ground undecayed, and thus the proportion of evergreens may actually increase with succession, as it does in the present case, where the ravines have the most evergreens and the sand-hills the fewest.

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\* Bot. Gaz. 51: 171-180. 1911; Ann. Assoc. Am. Geogrs. 1: 12-19. 1912.

† See Rep. Mich. Acad. Sci. 15: 197. 1914.

‡ See Geol. Surv. Ala. Monog. 8: 28-29; Torreya 13: 140, 141, 143; Bull. Torrey Club 40: 398. 1913.



(In the pine-barrens frequent fires return the potash, etc., quickly to the soil, while in calcareous or clayey soils there are usually many earthworms, centipedes, snails, bacteria or other soil organisms which assist greatly in converting the leaves into humus.\*) Another successional factor which doubtless tends to diminish the availability of mineral nutrients in the soil is the denser shade of the climax vegetation; for this lowers the temperature of the soil in summer and probably makes the groundwater level more constant, besides diminishing evaporation and eremacausis.

Although no chemical analysis of the pocosin soil has been made, it is evident from a casual inspection that it consists mostly of siliceous sand, and must be rather poor in soluble minerals, like the sandy hammocks of Florida. The climax vegetation of the more clayey soils in the same region is found on river-banks, bluffs, and sides of ravines, where fire is kept away pretty well by the topography; and it differs considerably from that of the pocosin. The following list, of trees only, is a generalized one for the upland climax forests of the whole southern red hill region of Alabama. The species are arranged approximately in order of abundance, as before.

Liquidambar <i>Styraciflua</i>	<i>Ostrya virginiana</i>
<b>Pinus Taeda</b>	<i>Oxydendron arboreum</i>
<i>Liriodendron Tulipifera</i>	<i>Acer floridanum</i>
<i>Fagus grandifolia</i>	<i>Fraxinus americana</i>
<i>Quercus alba</i>	<i>Tilia heterophylla?</i>
<i>Cornus florida</i>	<b>Quercus nigra</b>
<b>Magnolia grandiflora</b>	<i>Cercis canadensis</i>
<b>Pinus glabra</b>	<i>Halesia diptera</i>
<i>Hicoria alba</i>	<i>Magnolia acuminata</i>
<i>Magnolia macrophylla</i>	<i>Quercus rubra</i>
<b>Ilex opaca</b>	<b>Symplocos tinctoria</b>
<i>Nyssa sylvatica</i>	<i>Magnolia pyramidata</i>

Most of the species in this list are common also to the pocosin, but their relative abundance is different, and the proportion of evergreens is considerably less, being probably not over one third or one fourth. Evergreens naturally differ somewhat among themselves in their soil requirements, and it happens that the

\* Mr. Coville's valuable paper on the formation of leaf-mold (Jour. Wash. Acad. Sci. 3: 77-89. 1913) should be consulted in this connection.



two pines here listed prefer richer soils than all the other southern pines and some deciduous trees.

Although it is digressing a little from the scope of this paper, it is interesting to note that the hammocks and river-bluffs of the Altamaha Grit region of Georgia\* differ from each other in much the same way that the pocosin does from the bluffs, etc., just mentioned. Both hammocks and river-bluffs are covered with climax forests, but the soil is sandy in one case and loamy in the other, which makes considerable difference in the vegetation. From the frequency numbers which have been published in the work cited, it appears that 79.6 per cent. of the trees and 30.5 per cent. of the shrubs in the hammocks are evergreen; while the corresponding figures for river-bluffs are 37 and 15; a difference whose significance was not suspected until long after these Georgia lists were published. The sand-hills which border the Georgia hammocks and protect them from fire have been estimated in the same way to have 28.2 per cent. of their trees and 48.3 per cent. of their shrubs evergreen.

#### SUMMARY

This so-called pocosin (which has little in common with the typical pocosins of North Carolina) is a many-storied climax forest of a type characteristic of dry sandy soils in the coastal plain of Alabama, Georgia, and northern Florida. The accumulation of humus—and consequently the development of climax vegetation—began in ravines, and has been favored by the protection from fire afforded by the sparseness of the surrounding pioneer vegetation.

Something like half of the woody plants of the pocosin are evergreen, which is evidently a larger proportion of evergreens than in the case of the pioneer vegetation of the same soil and of the climax vegetation of soils richer in mineral plant food in the same region and elsewhere.

Each fundamentally different type of soil seems to have its own characteristic pioneer and climax vegetation; and the proportion of evergreens in this case—if not in many others—increases with normal succession, owing probably to the lowering of soil temperatures during the growing season, and to the locking up of plant food in undecayed leaves or sour humus, among other things.

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\* Ann. N. Y. Acad. Sci. 17: 98-109. 1906.



# Seed development in the genus *Peperomia*\*

G. CLYDE FISHER

(WITH PLATES 3-6 AND A TEXT FIGURE)

[Concluded from page 156]

## GENERAL DISCUSSION

Whether the sixteen-nucleate embryo sac of *Peperomia* is to be regarded as primitive, depends upon the homologies assumed or proved for the various structures found in this unusual type of embryo sac. In view of this, and since no axial row of megaspores is formed, the first question that naturally arises is whether the first four nuclei in the embryo sac are the morphological equivalents of four megaspore nuclei.

It is quite generally agreed that the cells of the axial row in the nucellus formed by the division of the definitive archesporial cell in most Angiosperms are homologous with those having a similar development in Gymnosperms; in both cases they are almost universally known as megaspores. There exists a further homology, although not quite so close, between the megaspores of Angiosperms and Gymnosperms and those of the heterosporous Pteridophytes. The tetrads of microspores, also, in all of these groups are homologous with one another, and, in a slightly different degree, with the megaspores in the same group. The evidence for these views has been well presented by Strasburger (73, 75), Overton (55, 56), Juel (36), Körnicke (40), Coulter (13), and others.

That the first four nuclei in the embryo sac of *Peperomia* are homologous with megaspore nuclei seems equally clear. The following facts indicate the correctness of this conception:

(1) The cell, the nucleus of which gives rise to these first four nuclei, may be considered, without valid objection, a megaspore mother-cell. It is developed in the position of the axial row. It is derived from a single primary archesporial cell, which cuts off

\* Botanical Contribution from The Johns Hopkins University, No. 35.



a single tapetal cell. In fact, its position and whole antecedent development, being so closely similar to that so generally found in Angiosperms, constitute a strong bit of positive evidence for the view that it is a megaspore mother-cell.

(2) As is evidenced by the occurrence of synapsis in the nucleus of the definitive archesporial cell, preceding its division, the two divisions by which these four nuclei are formed are the reduction divisions, as is the case in the last two divisions in the formation of the megaspore nuclei in all other plants in which they are formed—so far as they have been investigated. In rare cases like that of *Alchemilla speciosa* (Murbeck, 53, 54; Strasburger, 74), in which apparent megaspore-formation occurs without reduction of chromosomes, there is no sexual fusion in the initiation of the embryo which is later developed in the embryo sac. Therefore, as Strasburger contends, such abnormal cases can not be considered examples of true megaspore-formation. The presence of the reduction divisions is considered by some workers as sufficient evidence for the acceptance of the theory of the homology of the megaspores of Angiosperms with those of the Gymnosperms and the higher Pteridophytes. It should mean as much in *Peperomia* as it does elsewhere in heterosporous plants.

(3) The tetrahedral arrangement of these first four nuclei points more strongly to the homology in question than does the linear tetrad, or axial row, arrangement, which occurs in nearly all seed-plants, both Gymnosperms and Angiosperms—since a tetrahedral arrangement of the microspores is found in nearly all heterosporous plants and in the megaspores of all heterosporous Pteridophytes. The linear tetrad of megaspores is universal in the Cycadales, the Coniferales, and the Ginkgoales, in all investigated cases known to the writer; but Juel (36) found a close approach to the tetrahedral arrangement in the megaspores of *Larix sibirica* as a general rule, the typical axial row being seldom found. The tetrahedral arrangement of megaspores is not altogether unknown in Angiosperms, having been observed in *Fatsia japonica* by Ducamp (17). Transitions between the axial row and the tetrahedral arrangement have been observed in *Aralia racemosa* by Ducamp (17), in *Garcinia* by Treub (77), in *Burmannia Championii* by Ernst and Bernard (22), in *Cynomorium*



by Juel (37), and in *Smilacina stellata* by McAllister (45). The case of *Smilacina* is particularly interesting here since the four megaspores show various transitions between the typical axial row and the tetrahedral arrangement. Moreover, after the megaspores are formed and unmistakably separated by walls, the walls disappear. The megaspore nuclei now become the first four nuclei of the embryo sac, and at this stage they assume the tetrahedral arrangement very similar to that in the four-nucleate embryo sac of *Peperomia*. It is not only in *Peperomia* that the first four nuclei of the embryo sac are arranged tetrahedrally, but this is likewise true in all genera in which sixteen free nuclei are formed in the embryo sac—namely, in *Gunnera* (Schneegg, 64; Ernst, 20, 21; Modilewski, 48; Samuels, 59), in *Sarcocolla* (Stephens, 70), in *Brachysiphon* (Stephens, 70), in *Penaea* (Stephens, 70), and in *Euphorbia* (Modilewski, 49, 51, 52).

(4) The fact that the tetrad is always complete in number of nuclei in *Peperomia* makes the homology seem rather more probable in this genus than it is in plants in which the axial row is incomplete, as for example, in one consisting of three cells instead of four.

(5) Eleven species of *Peperomia* have been shown to have sixteen nuclei in the mature embryo sac. In addition to the six here investigated are: *P. pellucida* (Campbell, 6), *P. hispidula* (Johnson, 34), *P. Sintenisii*, *P. arifolia*, and *P. Ottoniana* (Brown, 4). No species has been found to have any other number. As Brown (4) points out, the presence, in the mature embryo sac of *Peperomia*, of the larger number of nuclei than in the sac of ordinary Angiosperms, is in harmony with the view that more megaspore nuclei are concerned in the formation of the *Peperomia* type of embryo sac.

(6) The fact that all four nuclei divide, or germinate, can not militate against the theory that they are homologous with megaspore nuclei, because there are cases in which megaspores are undoubtedly formed and in which they all germinate—that is, the nuclei all divide. This is true, for example, in *Crucianella* (Lloyd, 41), in *Smilacina stellata* (McAllister, 45), and sometimes in *Epipactis* (Brown & Sharp, 5). And then there are intermediate cases in which one or more of the non-functional mega-



spore nuclei divide, e. g. in *Cercis Siliquastrum*, *Phaseolus multiflorus*, and *Erythrina Crista-galli*—all three investigated by Guignard (24). Another interesting case of this kind was found in *Scilla* (McKenney, 46).

(7) That all four nuclei take part in the formation of one embryo sac can not constitute a valid objection to the view, because there are cases where megaspores are undoubtedly formed and in which all four participate in the formation of one embryo sac, as in *Smilacina stellata* (McAllister, 45), and sometimes in *Epipactis* (Brown & Sharp, 5), the walls following the first two divisions of the megaspore mother-cell being evanescent in both cases. In the former case the megaspores are frequently arranged in an axial row, but as was mentioned above, the arrangement is very often an intermediate condition between the axial row and the tetrahedral arrangement, while in *Epipactis* the megaspores always have the linear arrangement.

In *Euphorbia procera* and *E. palustris* (Modilewski, 49, 52) and in the Penaeaceae (Stephens, 70), the quadripolar grouping of the nuclei in the mature embryo sac furnishes a strong bit of evidence that the embryo sac in each of these cases is a composite structure derived from the equivalents of four megaspore nuclei. The same may be true of *Peperomia*, which has the same number of nuclei in the mature embryo sac, even though the nuclei do not have the quadripolar grouping.

(8) Another significant piece of evidence is that there is a resting period following the second division in the embryo sac—that is, following the four-nucleate stage. This was observed in every species of *Peperomia* which was sufficiently studied. As is well known, a resting stage following the formation of the four megaspores is almost universal in plants. So, this phenomenon is in harmony with what would be expected.

(9) One of the strongest pieces of evidence favoring this view is the appearance of evanescent walls following the first and second divisions in the embryo sac of *Peperomia*—together with the fact that these walls have never been seen in the eight-nucleate embryo sac—that is, following the third division. These walls were first reported by Brown (4) in *Peperomia Sintenisii* and in *P. arifolia*. They have been seen by the writer in seven other



species of *Peperomia*, namely: *P. reflexa*, *P. verticillata*, *P. scandens*, *P. Fraseri* var. *resediflora*, *P. blanda*, *P. galioides*, and *P. Langsdorffii*(?). Similar evanescent separating walls occur in *Smilacina stellata* (McAllister, 45) and in *Epipactis* (Brown & Sharp, 5), in which cases it is plain that they are megaspore walls. Wiegand (79) reports an evanescent wall between the first two nuclei in the embryo sac of *Convallaria*, in which case there are no degenerating megaspores, but the definitive archesporial cell forms the embryo sac directly, and this wall very probably represents a megaspore wall. In this case, however, only the heterotypic division is followed by an evanescent wall.

The appearance of separating walls is, however, not absolutely essential in the formation of megaspores in cases where it is generally admitted that megaspores occur, *e. g.* the walls usually do not appear in *Crucianella* (Lloyd, 41), or in *Asperula* (Lloyd, 41), and sometimes not in *Eichhornia* (Smith, 68) or *Avena* (Cannon, 10). In each of these cases, however, the embryo sac develops from a single megaspore nucleus, while the others degenerate, regardless of the absence of walls. But, since separating walls do generally appear between the megaspore nuclei in other plants, their presence in *Peperomia* certainly strongly favors the homology.

Another explanation of the occurrence of these walls, in harmony with Campbell's (7) view, was suggested by Brown (4) and immediately rejected. He says: "If the walls corresponded to those of prothallial cells, we should expect to find them in the third division, but here not even a cell-plate was seen. Besides this, the nearest phylogenetic relatives in which the first divisions of a megaspore result in a cellular structure are found among the leptosporangiate Filicales, where the heterospory is supposed to be of rather late origin, and it does not seem probable that *Peperomia* has reverted to the characters of an ancestor as remote as one in which we would find the first divisions of the megaspore giving rise to a cellular structure."

Since the separating walls occur in *Peperomia* following the first and second divisions only, in the embryo sac, and not after the third division, it is difficult if not impossible to conceive of any satisfactory homology for them, except that with the mega-



spore walls of other Angiosperms, that is, if it be admitted, as it is so generally, that megaspores occur in Angiosperms.

From these significant relations—from the origin of the embryo sac from what seems clearly a megaspore mother-cell, from the occurrence of the reduction division of its nucleus, from the tetrahedral arrangement of the first four nuclei, from the complete number in the tetrad, from the resting period following the formation of the tetrad, from the increased number of nuclei in the sac, and from the appearance of evanescent walls—from all these facts in favor of our view, together with the fact that the germination of all four megaspores and the participation of all of them in the formation of one embryo sac do not constitute valid objections to the theory, we are very strongly inclined to the view that the first four nuclei in the embryo sac of *Peperomia* are the equivalents of megaspore nuclei.

This theory of homologies is in harmony with the classifications of embryo sacs by recent workers (Ernst, 20; Coulter, 13; Samuels, 59) with regard to the number of generations of nuclei from the beginning of the reduction division to the mature sac.

TEXT FIG. 1 illustrates diagrammatically the known types of derivation of the mature embryo sac from the definitive archesporial cell. The order in which these are arranged will suggest the phylogenetic sequence in which certain chief steps in the reduction of the number of cells or nuclear divisions between the definitive archesporial cell and the mature sac may have occurred. It also indicates the number of degenerating megaspores formed, where any occur.

In the type illustrated by TEXT FIG. 1a, there are *five* cell- and nuclear generations (the first two being cell-generations, and the last three being nuclear generations) in the development from the definitive archesporial cell to the mature embryo sac, which latter is of the common eight-nucleate type. The embryo sac is here indisputably the product of one megaspore, which divides three times.

In the type illustrated by TEXT FIG. 1b, the case is similar to that in TEXT FIG. 1a, but the upper cell formed by the first division of the definitive archesporial cell does not divide further. The embryo sac here contains eight nuclei, and is again clearly the product of but one megaspore, which divides three times.



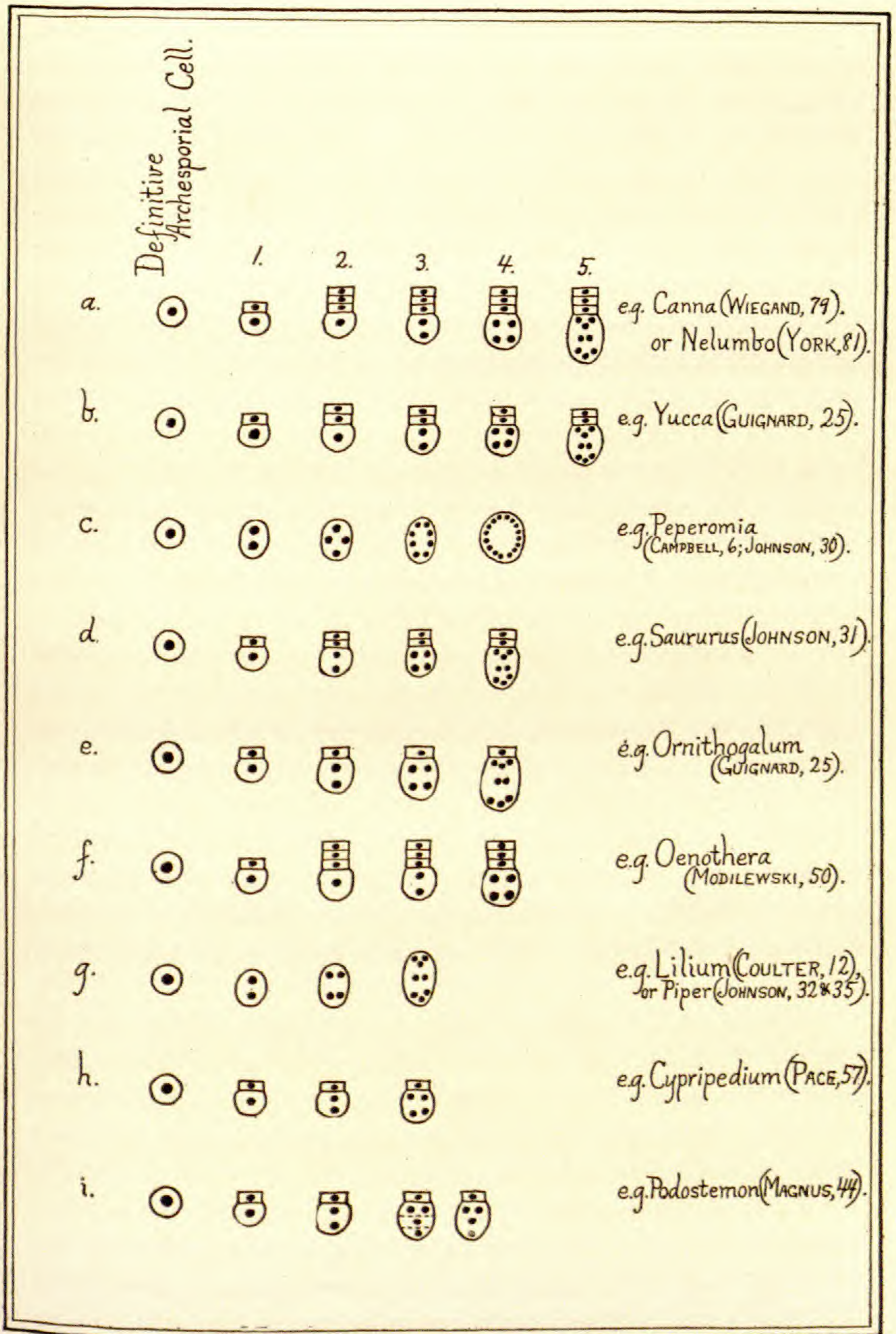


FIG. 1. Diagram illustrating the various types of embryo-sac development.



In the type illustrated by TEXT FIG. 1c, there are only *four* nuclear generations from the definitive archesporial cell to the mature sac. Since the first two of these nuclear divisions are followed by evanescent cell-walls, they may be regarded, as was pointed out above, as the equivalents of the first two cell-generations in TEXT FIG. 1a. That is, they are to be regarded as megaspore nuclei, and the mature embryo sac is the product of four megaspore nuclei, each megaspore nucleus dividing twice.

In the type illustrated by TEXT FIG. 1d, the definitive archesporial cell divides into an upper and a lower cell, of which the upper divides once more forming two potential megaspores, and the lower develops immediately, without the appearance of cell-walls, into an eight-nucleate embryo sac. Thus there are but *four* nuclear generations, from the definitive archesporial cell to the mature embryo sac, which is to be regarded as the product of the morphological equivalent of two megaspore nuclei.

In the type illustrated by TEXT FIG. 1e, there are *four* generations, one cell-generation and three nuclear generations, from the definitive archesporial cell to the mature embryo sac, which latter contains eight nuclei, and may be considered to be the product of the morphological equivalent of two megaspore nuclei, each dividing twice.

In the type illustrated by TEXT FIG. 1f, there are *four* generations, two cell-generations and two nuclear, from the definitive archesporial cell to the mature embryo sac. The sac here contains four nuclei and is clearly the product of one megaspore, which divides twice.

In the type illustrated by TEXT FIG. 1g, there are *three* nuclear generations, from the definitive archesporial cell to the mature embryo sac, which latter contains eight nuclei, and may be considered to be the product of the morphological equivalent of four megaspore nuclei, each dividing but once.

In the type illustrated by TEXT FIG. 1h, there are *three* generations, one cell-generation and two nuclear, between the definitive archesporial cell and the mature embryo sac, which latter contains four nuclei, and may be considered to be the product of the morphological equivalent of two megaspore nuclei, each dividing once.

In the type illustrated by TEXT FIG. 1i, the case is similar to



the preceding, the difference being that two evanescent cell-walls appear after the second division in the embryo sac, and that the lowest nucleus in the sac degenerates, so that the mature sac contains but three nuclei, which have arisen from the morphological equivalent of two megaspore nuclei.

If we accept this view of the phylogenetic sequence of the steps in the reduction of the development of sporogenous tissue, it is evident that *Peperomia*, as well as *Saururus*, *Ornithogalum*, and *Oenothera*, illustrates the first stage in the abbreviation of the development of megasporogenous tissue. The number of cell- or nuclear divisions from the definitive archesporial cell to the mature embryo sac has been reduced from five to four.

From the same point of view, *Piper*, as well as *Lilium*, *Cypripedium*, and *Podostemon*, illustrates the second stage in this reduction, where the number of cell or nuclear divisions from the definitive archesporial cell to the mature embryo sac has been reduced to three. This is the condition found by Yamanouchi (80) in *Fucus*, that is, the number of nuclear generations from the beginning of the reduction divisions to the mature egg is three.

As Miss Pace (57) has pointed out, if reduction should go one step further, we should have the condition present in the maturation of the animal egg. But no case showing reduction of the female sporogenous tissue to two cell-generations has been reported in plants.

It may be added that no unquestioned case of more than five cell and nuclear generations from definitive archesporial cell to mature embryo sac has been reported. Dessiatoff (16) reported a case of six cell-generations in *Euphorbia virgata*, but Modilewski (52) later got different results when working on the same species.

As has been frequently pointed out, there is much more variation in the development of embryo sacs than was formerly thought. Coulter & Chamberlain (14, p. 76, 77) call attention to the great variability in the family Liliaceae. The Podostemaceae, also, show considerable variation, as shown by Magnus (44). Sometimes the variability is very great in a single genus.

In the genus *Burmannia*, Ernst & Bernard (22, 23) found an interesting series of cases. In the species studied, the subepidermal primary archesporial cell becomes the definitive



archesporial cell without cutting off a parietal or tapetal cell. In *Burmannia Championii* this forms sometimes three, but usually four megaspores, and a typical eight-nucleate embryo sac develops from one of these, while the remaining two or three degenerate. In *B. candida* the definitive archesporial cell divides into two cells, the chalazal one giving rise to a typical eight-nucleate embryo sac, while the other degenerates. The division of the definitive archesporial cell is the heterotypic reduction division; therefore, the cell which gives rise to the embryo sac is the morphological equivalent of two megaspores. In *B. coelestis*, as a rule, the definitive archesporial cell develops directly into the embryo sac, without cutting off any non-functional megaspores. A typical eight-nucleate embryo sac is developed here from the morphological equivalent of four megaspores. It is interesting to note here that the end product in all three cases is a typical eight-nucleate sac, whether it is developed from one megaspore or from the morphological equivalent of two or of four megaspores.

In the genus *Euphorbia*, two species, *E. procera* and *E. palustris*, both investigated by Modilewski (49, 51, 52), have sixteen-nucleate embryo sacs, while at least thirteen other species of the same genus, investigated by the same author, have typical eight-nucleate embryo sacs. The latter condition was also found in *Ricinus*, *Phyllanthus*, *Securinega*, and *Croton*, four related genera belonging to the same family, the Euphorbiaceae.

Within a single species there is sometimes striking variation, as in *Epipactis pubescens* (Brown & Sharp, 5), where usually the embryo sac arises from the innermost one of three megaspores, but in other cases four megaspores take part in the formation of the sac. The authors further state that there is some evidence that the embryo sac may at times be derived from two megaspores. In *Salix glaucophylla* (Chamberlain, 11) there is even greater variation than in *Epipactis pubescens*.

That the origin of the embryo sac from the morphological equivalents of four megaspores as found in *Peperomia* is a derived condition rather than primitive, is further indicated by the following considerations:

(1) The vast majority of the embryo sacs of Angiosperms arise from a single megaspore, and the exceptions are not limited



to plants which for other reasons are known to be primitive. The sixteen-nucleate sacs, which have almost certainly arisen from four megaspores, are distributed among four families of dicotyledonous plants, the Piperaceae, the Haloragidaceae, the Penaeaceae, and the Euphorbiaceae, none of which except the first has been considered primitive.

The eight-nucleate embryo sacs, which have arisen from four megaspores or their morphological equivalents, are found in widely separated families of both monocotyledonous and dicotyledonous plants. They occur in *Typha* (Typhaceae) according to Schaffner (61), in *Lemna* (Lemnaceae) according to Caldwell (8), in *Lilium* (Liliaceae) according to Coulter (12), in *Epipactis* (Orchidaceae) according to Brown & Sharp (5), in *Piper* (Piperaceae) according to Johnson (32, 35), in *Salix* (Salicaceae) according to Chamberlain (11), in *Juglans* (Juglandaceae) according to Karsten (38), in *Avicennia* (Verbenaceae) according to Treub (77), and in *Aphyllon* (Orobanchaceae) according to Miss Smith (67).

While it may be doubted whether the embryo sac is the product of four megaspores or their morphological equivalents in all cases mentioned above, it certainly can not be doubted in cases like *Epipactis* (Brown & Sharp, 5) and *Smilacina* (McAllister, 45).

(2) In none of the heterosporous plants below the Angiosperms is the gametophyte known to be the product of the fusion of four germinating megaspores.

The endosperm nucleus of *Peperomia* in its origin from several nuclei shows a derived rather than a primitive condition, for nothing of this kind is found in other Angiosperms which are considered primitive, or in the heterosporous plants below the Angiosperms.

The endosperm of *Peperomia*, which is cellular from the start, exhibits in this condition a feature which is secondary rather than a characteristic that is primitive among Angiosperms.

The primary archesporial cell, which is single in *Peperomia*, represents a less primitive condition, according to Körnicke (40), than the multicellular archesporium which is found very much more commonly among the more primitive of the Dicotyledons than among the higher groups. The evidence for this view has also been briefly reviewed by Coulter & Chamberlain (14, p. 60).



Representatives of all four families of the order Piperales have been examined in an attempt to ascertain whether any species showed an intermediate stage between the embryo sac of *Peperomia* and that of the typical eight-nucleate embryo sac, and to see whether any feature of the development of the embryo sac confirmed the view that *Peperomia* is primitive.

Of the Piperaceae, besides the genus *Peperomia*, four species of *Piper* have been examined—three by Johnson (32, 35) and one by the writer and reported in this paper. All four have been shown to have eight-nucleate sacs, which develop directly from the definitive archesporial cell, no non-functional megaspores being formed. No other condition has been found in this genus. As was pointed out, the reduction in the number of generations, from the definitive archesporial cell to the mature embryo sac, has proceeded one step further in this genus than it has in the *Peperomia*.

Of the Saururaceae, species of *Saururus*, *Anemiopsis*, and *Houttuynia* have been examined by Johnson (31, 33), and *Houttuynia* by Shibata & Miyake (66), and it is found that one or more non-functional megaspores are cut off and that in all cases typical eight-nucleate embryo sacs are formed from single megaspores.

Of the Lacistemaceae, *Lacistema* (Johnson, 33) shows a typical eight-nucleate embryo sac derived from a single megaspore.

Of the Chloranthaceae, *Hedyosmum* (Johnson, 33) and *Chloranthus* (Armour, 1) have been examined, each of which shows a typical eight-nucleate embryo sac which arises from a single megaspore.

A mode of origin and development of the embryo sac, which would confirm the idea that *Peperomia* is primitive, has not yet been found in any other genus of the order Piperales.

Finally, when we consider, (1) that the primary archesporial cell of *Peperomia* is single—a condition probably derived; (2) that the first four nuclei of the embryo sac are probably homologous with megaspores, certainly not a primitive feature; (3) that the peculiar origin of the endosperm nucleus here probably represents a derived condition; (4) that an endosperm which is cellular from the start can not be regarded as primitive; and (5) that none of the close relatives of *Peperomia* furnishes any indication, from the



development of the embryo sac, that the genus is primitive, we are inclined to accept the view first advanced by Johnson (30) and since confirmed by other workers (Brown, 4; Samuels, 59) that the peculiarities in origin and development of the embryo sac of *Peperomia* have been secondarily acquired.

#### SUMMARY

The primary archesporial cell is single and subepidermal in all species of *Peperomia* examined.

The nucleus of the definitive archesporial cell, or embryo sac mother-cell, goes into synapsis before its first division.

Evanescent cell-walls occur following the first and second nuclear divisions in the embryo sac in all six of the species of which the material was most nearly complete.

The mature sac contains sixteen nuclei, one of which functions as the egg nucleus, one as that of the single synergid, from six to nine others fuse to form the endosperm nucleus, and the remainder are individually cut off by cell-walls about the periphery of the sac and afterwards degenerate.

The endosperm is cellular from the start.

The embryo is undifferentiated externally except for a slight flattening on the micropylar side.

In *Piper tuberculatum* we have a typical eight-nucleate embryo sac, developed directly from the definitive archesporial cell, no degenerating megaspores being formed.

That the first four nuclei in the embryo sac of *Peperomia* are homologous with megaspore nuclei, seems extremely probable from the following facts: (1) they arise from a cell which with very little doubt may be considered a megaspore mother-cell; (2) they are arranged tetrahedrally; (3) the tetrad is complete in number; (4) the larger than usual number of nuclei in the mature sac is in harmony with this view; (5) the reduction of chromosomes occurs in the divisions which give rise to these four nuclei; (6) a resting stage follows the formation of these four nuclei; and (7) evanescent cell-walls frequently follow the first and second divisions in the embryo sac, but not the third.

In view of the following considerations: (1) that the primary archesporial cell of *Peperomia* is single—a condition probably



derived; (2) that the first four nuclei of the embryo sac are probably homologous with megaspores—certainly not a primitive feature; (3) that the peculiar origin of the endosperm nucleus here probably represents a derived condition; (4) that an endosperm which is cellular from the start cannot be regarded as primitive; and (5) that none of the close relatives of *Peperomia* furnishes any indication, from the development of the embryo sac, that the genus is primitive, the writer is inclined to believe that the peculiarities in origin and development of the embryo sac of *Peperomia* have been secondarily acquired.

Finally, I wish to thank those who have helped make this study possible. I am under obligation to Dr. Charles B. Davenport, Director of the Biological Laboratory of the Brooklyn Institute of Arts and Sciences, Cold Spring Harbor, Long Island, New York, for the use of a room in the Research Laboratory of that Institution in 1911; to Captain John Donnell Smith for the use of certain books from his library; to Dr. Casimir de Candolle for determining specimens of the plants studied; to Mrs. Bessie Wiley Fisher who carefully made the majority of my slides; and to Professor D. S. Johnson who collected a large portion of the material and to whom I am also greatly indebted for helpful criticism throughout the work.

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### Explanation of plates 3-6

All figures are camera drawings except FIGS. 25 and 26, and all are from microtome sections except FIGS. 25, 26, and 36. The magnification given in the description of each figure is that actually shown by the figure as printed on the page.

#### FIGS. 1-18. *Peperomia reflexa*

- FIG. 1. Longitudinal section of nucellus showing primary archesporial cell.  $\times 670$ .
- FIG. 2. Longitudinal section of ovule, showing definitive archesporial or embryo sac mother-cell, and parietal or tapetal cell.  $\times 670$ .
- FIG. 3. Longitudinal section of nucellus containing mature embryo sac mother-cell and two-layered tapetum.  $\times 670$ .
- FIG. 4. Longitudinal section of carpel showing subtending bract, nucellus, embryo sac mother-cell, integument, micropyle, stylar canal, and immature stigma.  $\times 72$ .
- FIG. 5. Longitudinal section of definitive archesporial cell, or embryo sac mother-cell, the nucleus showing synapsis.  $\times 670$ .
- FIG. 6. Nearly longitudinal section of a two-nucleate embryo sac showing evanescent cell-wall.  $\times 670$ .
- FIG. 7. Longitudinal section of a four-nucleate embryo sac showing tetrahedral arrangement of the nuclei.  $\times 670$ .
- FIG. 8. Longitudinal section of a four-nucleate embryo sac showing evanescent cell-wall.  $\times 670$ .
- FIG. 9. Longitudinal section of an eight-nucleate embryo sac.  $\times 670$ .
- FIG. 10. Longitudinal section of an embryo sac containing sixteen free nuclei.  $\times 670$ .
- FIG. 11. Longitudinal section of a mature embryo sac showing group of endosperm nuclei.  $\times 670$ .
- FIG. 12. Group of eight nuclei almost completely fused to form the endosperm nucleus (from transverse section of spike).  $\times 670$ .
- FIG. 13. Longitudinal section of an embryo sac showing egg, two peripheral nuclei, and two-celled endosperm.  $\times 670$ .
- FIG. 14. Longitudinal section of an embryo sac showing male nucleus within the egg, but not yet fused with the egg-nucleus, also the single synergid and the several celled endosperm.  $\times 465$ .



FIG. 15. An embryo showing four cells in longitudinal section; endosperm several-celled.  $\times 465$ .

FIG. 16. Longitudinal section of mature embryo and endosperm.  $\times 300$ .

FIG. 17. Longitudinal section of a mature fruit showing how far it is sunk in the axis.  $\times 50$ .

FIG. 18. Hydathode and hair from a transverse section of peduncle of spike.  $\times 220$ .

FIGS. 19-27. *Peperomia verticillata*

FIG. 19. Transverse section of pollen-sac showing tapetum and tetrads of microspores.  $\times 670$ .

FIG. 20. Longitudinal section of ovule showing primary archesporial cell; the integument just started.  $\times 465$ .

FIG. 21. Longitudinal section of an embryo sac containing sixteen free nuclei.  $\times 670$ .

FIG. 22. Longitudinal section of young carpel containing a lobed ovule.  $\times 220$ .

FIG. 23. Longitudinal section of lobed ovule, older stage than preceding.  $\times 50$ .

FIG. 24. Lateral exterior view of a reconstruction of a lobed ovule.  $\times 80$ .

FIG. 25. Median longitudinal section of the preceding, showing integument and embryo sac of the fertile lobe.  $\times 80$ .

FIG. 26. Transverse section of a lobed ovule, showing position of embryo sac in small fertile lobe.  $\times 220$ .

FIG. 27. Longitudinal section of a deformed seed developed from a lobed ovule (somewhat diagrammatic).  $\times 50$ .

FIGS. 28-34. *Peperomia scandens*

FIG. 28. Nearly longitudinal section of a two-nucleate embryo sac, showing the cell-plate, which is the beginning of the evanescent cell-wall.  $\times 670$ .

FIG. 29. Transverse section of two-nucleate embryo sac showing evanescent cell-wall.  $\times 670$ .

FIGS. 30, 31. Longitudinal sections of two-nucleate embryo-sacs showing evanescent cell-walls.  $\times 670$ .

FIG. 32. Longitudinal section of a young carpel showing how far it is sunk in the axis.  $\times 50$ .

FIG. 33. Longitudinal section of a mature fruit, showing how far it is sunk in the axis.  $\times 50$ .

FIG. 34. Longitudinal section of the upper part of an embryo sac, showing the egg and the single synergid.  $\times 670$ .

FIG. 35. *Peperomia metallica*

FIG. 35. Lateral view of an interrupted flower-spike, showing zone of small vegetative leaves.  $\times 1$ .

FIG. 36. *Peperomia blanda*

FIG. 36. Longitudinal section of a four-nucleate embryo sac, showing evanescent cell-wall.  $\times 670$ .



FIGS. 37-43. *Piper tuberculatum*

FIG. 37. Longitudinal section of young ovule, showing primary archesporial cell; integuments not yet started.  $\times 670$ .

FIG. 38. Longitudinal section of a slightly older ovule, in which the primary archesporial cell has divided to the definitive archesporial cell and the parietal cell.  $\times 670$ .

FIG. 39. Longitudinal section of slightly older ovule, showing definitive archesporial cell or embryo sac mother-cell; the parietal cell has divided forming tapetum four cells thick.  $\times 670$ .

FIG. 40. Longitudinal section of nucellus, showing two-nucleate embryo sac.  $\times 670$ .

FIG. 41. Same as preceding in outline with addition of integuments.  $\times 220$ .

FIG. 42. Longitudinal section of four-nucleate embryo sac, showing the linear arrangement of the nuclei.  $\times 670$ .

FIG. 43. Longitudinal section of eight-nucleate embryo sac, the two polar nuclei fusing to form the endosperm nucleus.  $\times 670$ .







# On the relationship between the number of ovules formed and the number of seeds developing in *Cercis*

J. ARTHUR HARRIS

(WITH THREE TEXT FIGURES)

## I. INTRODUCTORY REMARKS

In an earlier paper\* I have stated certain problems concerning the relationship between the number of ovules laid down and the capacity of the ovary for maturing its ovules into seeds, and have illustrated the methods which seem suitable to me for their solution by a series of data drawn from experimental cultures of *Phaseolus vulgaris*. The results of this first analysis of extensive series of data seem to render desirable the like treatment of other similar but quite distinct materials. The present paper is, therefore, devoted to the analysis of numerous data from a wild small-seeded arborescent legume, *Cercis canadensis*.

The study has been in progress since the autumn of 1905, when the first large series of countings was made. The results given in this paper were made ready for the press in January 1910, but the manuscript was laid aside in the hope that it would be possible to secure data which would show the relationship between the correlations discussed and the then just discovered selective mortality of ovaries. In this hope I have met with only disappointment, and it seems best to withhold the materials no longer.

## II. MATERIALS

The materials here analyzed were collected in three series as follows:

A. A very large collection taken at Meramec Highlands, near St. Louis, Missouri; altogether 28,554 pods.

B. A collection from 22 trees in the neighborhood of Lawrence, Kansas; 2,200 pods.

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\* Harris, J. Arthur. On the relationship between the number of ovules formed and the capacity of the ovary for developing its ovules into seeds. Bull. Torrey Club 40: 447-455. Au 1913.



C. A collection from 26 trees near Sharpsburg, Athens County, Ohio; 3,900 pods.

The pods of *Cercis canadensis* are, like those of many other Leguminosae, somewhat unsatisfactory for investigations of fertility because of the difficulty of drawing a sharp line between ovules which fail to develop and those which form perfect seeds. It seems unfeasible, in the present state of our knowledge of these matters, to adopt more than the two categories, abortive ovules and matured seeds. In most cases, an observer will have little difficulty in determining to which class an individual ovule should be assigned. Nevertheless, we are dealing here with characters not perfectly discontinuous. This condition must always be borne in mind in considering the trustworthiness of our constants.

In counting, we considered as abortive ovules only those which had not developed at all, or only slightly, beyond the stage attained in the very young pod. Some of the seeds counted as matured were probably not well enough developed to be viable. Some of them were light and apparently blighted. The cause of this I do not know. The ovules failing to develop are not as easily made out in the mature pods of *Cercis* as they are in some other Leguminosae; this increased somewhat the labor of counting.

### III. DISCUSSION OF DATA

#### A. *The Meramec Highlands Collections*

The correlation between the number of ovules formed and the number of seeds developing in a first large sample of 6,000 pods, chiefly from a few (6 or 8) large trees growing closely together is shown in Table I. For comparison another 4,000 was gathered quite at random in the immediate neighborhood of the trees furnishing the first 6,000, but from a larger number (probably 25) of smaller trees: Table II gives the correlation surface.

The fundamental physical constants appear in Table III.

For the means the differences and probable errors of the difference of these two samples are

Ovules.....	+ .1536 ± .0137
Seeds.....	- .0261 ± .0166



The ovules are about fifteen one-hundredths more numerous in the sample collected from the few large trees. This is certainly not a difference which would have been detected by other than biometric methods, and some might consider it negligible, but it is slightly over eleven times its probable error and so unquestionably

TABLE I

## SEEDS

Ovules	1	2	3	4	5	6	7	
1	3	—	—	—	—	—	—	3
2	10	39	—	—	—	—	—	49
3	37	109	203	—	—	—	—	349
4	61	292	701	933	—	—	—	1,987
5	32	202	472	887	830	—	—	2,423
6	19	40	106	223	350	304	29	1,042
7	—	5	7	17	31	51	3	140
8	—	—	—	2	—	2	—	7
	162	687	1,489	2,062	1,211	357	32	6,000

TABLE II

## SEEDS

Ovules	1	2	3	4	5	6	7	
1	4	—	—	—	—	—	—	4
2	14	89	—	—	—	—	—	103
3	29	147	254	—	—	—	—	430
4	34	160	435	678	—	—	—	1,307
5	17	105	207	485	568	—	—	1,382
6	3	19	46	122	210	277	—	677
7	—	3	2	11	17	26	36	95
8	—	—	—	—	1	1	—	2
	101	523	944	1,296	796	304	36	4,000

TABLE III

## PHYSICAL CONSTANTS FOR RANDOM SAMPLES

Constants	6,000 Pods	4,000 Pods	10,000 Pods
Mean of ovules . . . . .	4.7498 ± .0080	4.5952 ± .0112	4.6880 ± .0062
Standard deviation of ovules . .	.9274 ± .0057	1.0532 ± .0079	.9826 ± .0046
Coefficient of variation of ovules . . . . .	19.5270	22.9215	20.9615
Mean of seeds . . . . .	3.7786 ± .0102	3.8047 ± .0131	3.7891 ± .0081
Standard deviation of seeds . . .	1.1781 ± .0072	1.2377 ± .0093	1.2024 ± .0057
Coefficient of variation of seeds	31.1792	32.5332	31.7337
Correlation, ovules and seeds .	.5763 ± .0059	.6782 ± .0057	.6133 ± .0042



significant. No importance need to be attached to the difference for seeds developing, which is not twice its probable error.

The difference for the standard deviations and coefficients of variation are:

Standard Deviation	Coefficient of Variation
Ovules..... $-.1258 \pm .0097$	$-3.395$
Seeds..... $-.0596 \pm .0117$	$-1.354$

The difference in S.D. for ovules is nearly 13 times its probable error and for seeds about 5 times its probable error. Both are clearly significant.

The difference for the coefficient of correlation is

$$r, \quad -.1199 \pm .0082,$$

a difference 13.5 times its probable error and undoubtedly significant.

It appears, therefore, that our samples are sensibly differentiated from each other in type, variability and correlation. This fact is sufficient ground for considering their correlations independently.

The significance of the coefficient of correlation depends upon linearity of regression. Using the familiar equation for the regression straight line

$$s = \left( \bar{s} - r \frac{\sigma_s}{\sigma_o} \bar{o} \right) r \frac{\sigma_s}{\sigma_o} o$$

I find

For first 6,000.....	$s = .3554 + .7207 o$
For additional 4,000.....	$s = .1423 + .7970 o$
For first 10,000.....	$s = .2712 + .7504 o$

The closeness of agreement of the observed means and those given by the equation is evident from Table IV where the two are compared. If the two extreme variates, where the numbers of observations are so small that little weight is to be attached to them, be omitted, there is only a single case out of the eighteen where the deviation of the observed from the theoretical mean reaches thirteen one-hundredths of a seed.

The average (weighted) deviations (disregarding signs) of the



TABLE IV

DEVIATION OF OBSERVED MEANS OF ARRAYS FROM THEORETICAL MEANS AS CALCULATED FROM THE REGRESSION STRAIGHT LINES

Ovules per Pod	First 6,000 Pods				Additional 4,000 Pods				First 10,000 Pods			
	<i>N</i>	Observed Mean Seeds	Calculated Mean Seeds	Difference	<i>N</i>	Observed Mean Seeds	Calculated Mean Seeds	Difference	<i>N</i>	Observed Mean Seeds	Calculated Mean Seeds	Difference
1	3	1.000	1.076	+ .076	4	1.000	.939	- .061	7	1.000	1.022	+ .023
2	49	1.796	1.797	+ .001	103	1.864	1.736	+ .128	152	1.842	1.772	- .070
3	349	2.476	2.517	+ .042	430	2.523	2.533	+ .010	779	2.502	2.522	+ .020
4	1,987	3.261	3.238	- .023	1,307	3.344	3.330	- .014	3,294	3.294	3.273	- .021
5	2,423	3.941	3.959	+ .018	1,382	4.072	4.127	+ .055	3,805	3.989	4.023	+ .034
6	1,042	4.686	4.680	- .006	677	4.991	4.924	- .067	1,719	4.806	4.774	- .033
7	140	5.450	5.400	- .050	95	5.779	5.721	- .058	235	5.583	5.524	+ .059
8	7	5.857	6.121	+ .264	2	5.550	6.518	+ 1.018	9	5.778	6.274	+ .497

empirical from the theoretical means is .0198 for the first 6,000, .0411 for the additional 4,000, and .0302 for the total 10,000 pods. The fit is also shown graphically for the 6,000 pod lot in FIG. 1.

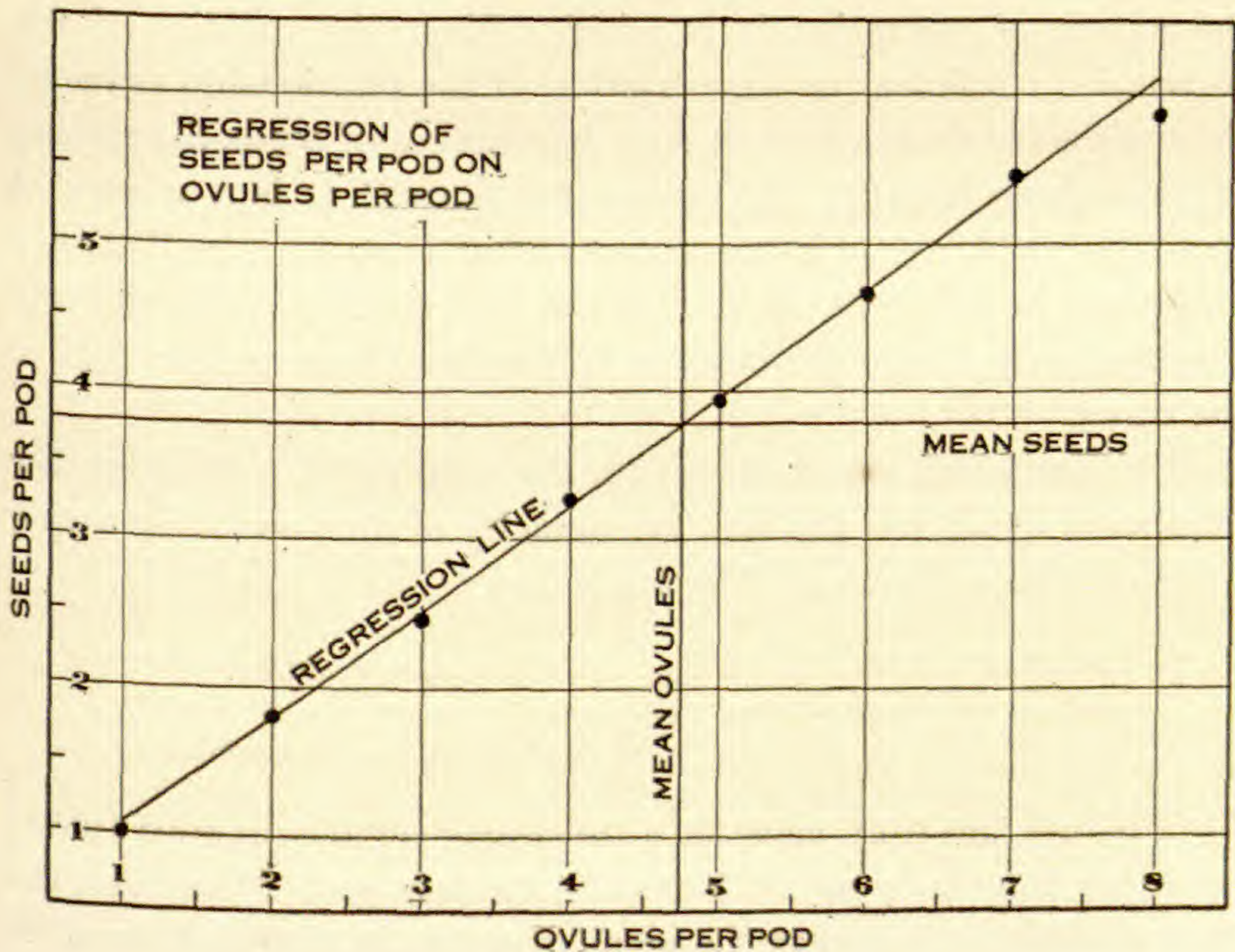


FIG. 1

For the 6,000 and the 10,000 lots, I have calculated  $\eta$  as well as  $r$ . I find



Constant	Series of 6,000 Pods	Series of 10,000 Pods
Coefficient of correlation, $r$ . . . . .	.5673 $\pm$ .0059	.6133 $\pm$ .0042
Correlation ratio, $\eta$ . . . . .	.5677 $\pm$ .0059	.6140 $\pm$ .0038
Difference, $\eta - r$ . . . . .	.00035	.00066
$\eta^2 - r^2 = \zeta$ . . . . .	.00040	.00081

Note the exceedingly small differences between  $r$  and  $\eta$ . For a scientific test of linearity, we have recourse to the constant  $\zeta$  as suggested by Blakeman,\* *i. e.*:

$$\frac{\sqrt{N}}{.67449} \cdot \frac{1}{2} \sqrt{\zeta} < 2.5$$

which gives

For 6,000 pods . . . . .	$\zeta/E\zeta = 1.144$
For 10,000 pods . . . . .	$\xi/E\xi = 2.110$

Hence regression may be considered linear within the limits of the probable errors of random sampling.

The reason so much stress has been laid upon the question of the nature of regression is two-fold. First, the validity of the correlation coefficient as a description of the relationship between the number of ovules formed and the number of seeds developing depends upon linearity of regression. Second, it is a matter of considerable biological importance to know that the rate of change in the number of seeds developing per pod remains constant from one end of the range of variation of number of ovules per pod to the other.

The coefficient which measures the relationships between the number of ovules per pod and the capacity of the pod for maturing its seeds is not  $r_{os}$  but  $r_{oz}$ . The results are:

For the first 6,000 . . . . .	$r_{oz} = - .0714 \pm .0087$
For the additional 4,000 . . . . .	$r_{oz} = - .0358 \pm .0106$
For the whole 10,000 . . . . .	$r_{oz} = - .0597 \pm .0067$

The first and third constants are clearly significant statistically deviating from 0 by about 8 or 9 times their probable errors: the second constant may also be significant but it differs from 0 by only about 3.5 times its probable error. They indicate that the pods with the larger number of ovules are not as capable of matur-

\* *Biometrika* 4: 332-350. 1905.



ing their ovules into seeds as those which do not produce so many, but that the relationship is a very slight one.

The differences between two random samples taken so closely together and the very low correlation makes one cautious in accepting our constants as biologically significant for *Cercis* as a species, or even for *Cercis* as a race growing at Meramec Highlands. Under the circumstances the only thing to be done is to collect wider series of data.

The collection of this additional material was carried out from two standpoints; first that of widening the sources of pods in number of trees and variety of habitats, second, that of securing greater homogeneity in the series of pods upon which individual constants are based by taking them all from individual trees. The discussion of the results of analysis of data for the individual trees must be reserved for a later contribution. In addition to the general samples just described from Meramec Highlands, smaller lots were taken from about 125 trees. These can be added to the 10,000 pods already discussed.

TABLE V

## SEEDS

Ovules	1	2	3	4	5	6	7	8	
1	7	—	—	—	—	—	—	—	7
2	67	281	—	—	—	—	—	—	348
3	190	837	1,407	—	—	—	—	—	2,434
4	236	1,264	3,536	4,582	—	—	—	—	9,618
5	100	620	1,691	3,630	3,955	—	—	—	9,996
6	46	142	444	1,064	1,787	1,806	—	—	5,289
7	2	21	42	88	180	261	232	—	826
8	—	1	—	4	10	6	10	5	36
	648	3,166	7,120	9,368	5,932	2,073	242	5	28,554

Consider now the total material, amounting to 28,554 pods, from Meramec Highlands. The data appear in Table V. The constants are:

$$\begin{aligned}
 A_o &= 4.7020 \pm .0040, & A_s &= 3.8399 \pm .0048, \\
 \sigma_o &= 1.0074 \pm .0028, & \sigma_s &= 1.2036 \pm .0034, \\
 V_o &= 21.425, & V_s &= 31.3452. \\
 r_{os} &= .6482 \pm .0023, & r_{oz} &= - .0463 \pm .0040.
 \end{aligned}$$



The equation to the regression straight line is

$$s = .1983 + .7745 o.$$

The means and the fitted line are seen in FIG. 2. Except for the final class, 8, the agreement of the predicted and the observed means is excellent, so close, indeed, that it is impossible to represent it graphically on a diagram of the size to be published on our page.

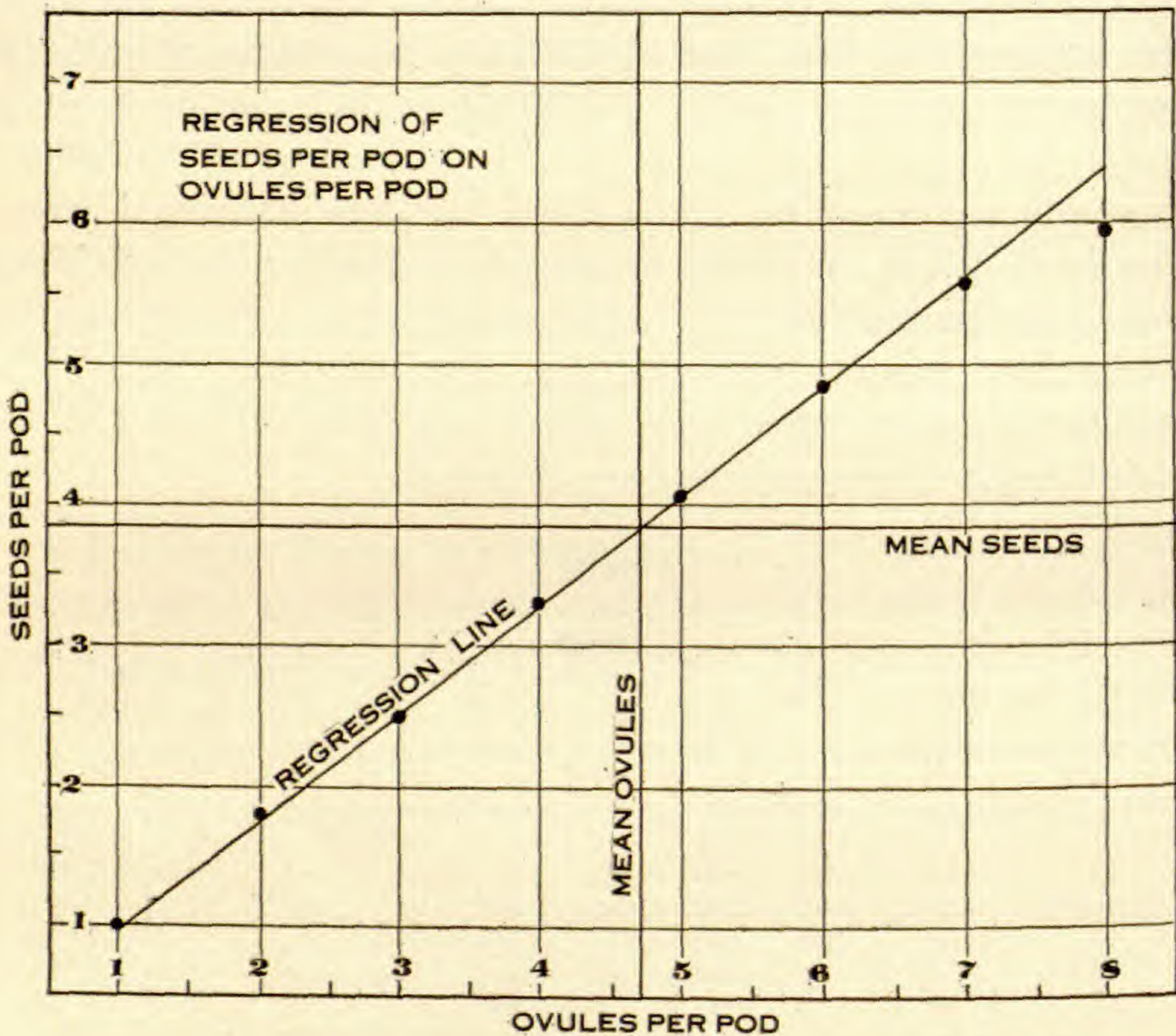


FIG. 2

To test more critically the linearity of regression, I determined the correlation ratio,  $\eta$ , and compared it with the coefficient of correlation  $r$ . I find

$$\begin{aligned}\eta &= .648443, \\ r &= .648226, \\ \eta - r &= .000217,\end{aligned}$$

a very close agreement indeed.



Applying Blakeman's test\* and using this time his more exact formula,

$$\frac{\zeta}{E_{\zeta}} = \frac{\sqrt{N}}{.67449} \cdot \frac{1}{2} \sqrt{\zeta} \cdot \frac{1}{\sqrt{1 + (1 - \eta^2)^2 - (1 - r^2)^2}}$$

I find

$$\eta^2 - r^2 = \zeta = .000281,$$

which gives

$$\zeta/E_{\zeta} = 2.101.$$

As far as one can state with certainty, therefore, the deviations of the observed means from the straight line due to the equation may be due to nothing more than the probable errors of random sampling. Comparing this diagram with those for other series of *Cercis*, I think it not unlikely that the falling off in the mean number of seeds for the pods with 8 ovules is biologically significant.

Here again, the sign of the correlation,  $r_{oz}$ , is negative and its value very small. However  $r_{oz}/Er_{oz} = 11.63$ , and perhaps it is a significant relationship.

It may have occurred to the reader that the negative relationship between the number of ovules per pod and the capacity of the pods for maturing their seeds may be due to some purely mathematical difficulty in dealing with the biological data—perhaps to some approximation in the formula.

To reassure those who may be skeptical on this ground, I have actually determined the deviation of each number of seeds per pod from the probable number which would have occurred if fecundity had been the same throughout all the population and have determined the correlation between these deviations and the number of ovules per pod.

In calculating the probable number of seeds for each pod the total seeds matured for all the pods was divided by the total ovules formed to get  $P$ , the probability of any ovule in the entire population—i. e., irrespective of the number of ovules in the pod in which it occurred—developing into a seed. This was

$$P = 109,644/134,261 = .816,648.$$

\* Biometrika 4: 350. 1905.



To obtain the probable number of seeds developing in any class of pods the number of ovules is multiplied by  $P$ .

In carrying out the arithmetic of the calculation of  $r_{oz}$  by the "brute force" method all the deviations were written down to six decimal places. The values of  $r_{oz}$  are:

Calculated by formula.....	-.046315
Calculated by "brute force".....	-.046311
Difference.....	.000004

Comments are superfluous.

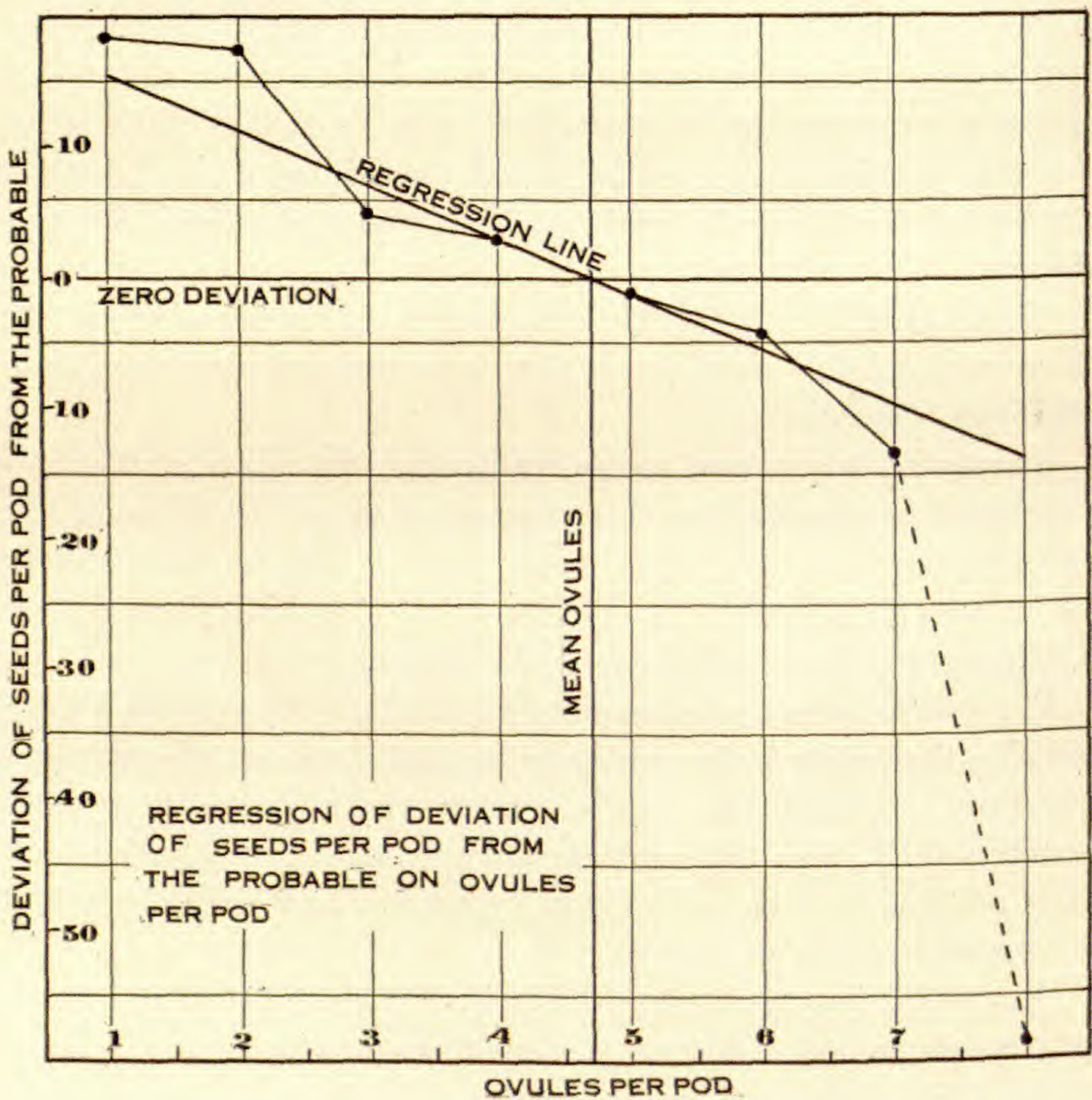


FIG. 3

Having actually obtained the deviations of the fertility of the individual pods from the probable fertility, it is easy to calculate the mean deviation for the arrays associated with different



numbers of ovules per pod. The standard deviation may also be computed for the entire material. The slope of the regression line is

$$z = .19833 - .04217 o.$$

The slope of this line and the empirical mean deviations are shown in FIG. 3.

It thus appears that while the relationship is an exceedingly slight one, in all the adequately large series of material from Meramec Highlands the capacity of the pods for maturing their seeds decreases as the number of ovules per pod increases.

*B. Analysis of The Data from the Vicinity of Lawrence, Kansas*

I have to thank my father, Mr. J. T. Harris, for the collection of a series of 100 pods each from 22 trees in the neighborhood of Lawrence, Kansas. All the trees grew in the same small field.

The correlation between the number of ovules per pod and the number of seeds developing per pod for the total material from the 22 individuals is set forth in Table VI. The results are:

$$\begin{array}{ll} A_o = 4.916 \pm .013, & A_s = 4.116 \pm .015, \\ \sigma_o = .925 \pm .009, & \sigma_s = 1.030 \pm .010, \\ V_o = 18.82, & V_s = 25.03, \\ r_{os} = .603 \pm .009, & r_{oz} = - .183 \pm .014. \end{array}$$

For the lumped conclusions, where  $N = 2,200$ , I find:

$$r_{oz}/Er_{oz} = 13.19.$$

*C. Analysis of the Data from the Vicinity of Sharpsburg, Ohio*

I am indebted to my grandfather, Mr. J. W. Harris, for the collection of 150 pods each from a series of 26 trees growing in the neighborhood of Sharpsburg, Athens Co., Ohio.

Calculating from the grand total of nearly 4,000 pods summarized in Table VII, I find:

$$\begin{array}{ll} A_o = 5.493 \pm .011, & A_s = 3.944 \pm .016, \\ \sigma_o = .983 \pm .008, & \sigma_s = 1.453 \pm .011, \\ V_o = 17.89, & V_s = 36.83, \\ r_{os} = .455 \pm .009, & r_{oz} = - .034 \pm .011. \end{array}$$



Here  $r_{oz}/Er_{oz} = 3.15$ . Possibly this value is statistically significant, but considering its extremely small magnitude I think one should be cautious in attaching any biological significance to it.

TABLE VI

## SEEDS

Ovules	1	2	3	4	5	6	7	
2	—	2	—	—	—	—	—	2
3	1	24	65	—	—	—	—	90
4	2	47	234	384	—	—	—	667
5	—	27	127	350	361	—	—	865
6	—	12	44	112	174	143	—	485
7	—	—	4	11	29	27	19	90
8	—	—	—	—	1	—	—	1
	3	112	474	857	565	170	19	2,200

TABLE VII

## SEEDS

Ovules	0	1	2	3	4	5	6	7	8	9	
3	1	2	23	23	—	—	—	—	—	—	49
4	18	27	106	194	162	—	—	—	—	—	507
5	36	41	182	320	504	381	—	—	—	—	1,464
6	26	17	86	212	295	420	265	—	—	—	1,321
7	5	4	25	41	95	110	120	74	—	—	474
8	1	1	2	8	9	12	24	18	6	—	81
9	—	—	—	—	1	—	1	—	1	1	4
	87	92	424	798	1,066	923	410	92	7	1	3,900

#### D. Comparison of Constants from Three Series of *Cercis*

A detailed comparison of the characters of red bud from various regions of the United States or from different habitats falls outside the scope of this paper. I will, however, lay the results from the total materials of the three side by side for a casual comparison in Table VIII.

It is clear without further arithmetic that many of these constants differ significantly from series to series, that is to say, the difference between them is several times as large as can be attributed to the errors of sampling from a homogeneous population. This fact does not, however, necessarily indicate that the three series are "genetically," "racially" or "genotypically" distinct. Each general collection is composed of a (relatively) small number of trees. These individuals are, as will be shown later, differenti-



ated in number of ovules and number of seeds per pod, and probably in the variability and correlation of these two characters. Since the general samples are made from a relatively small number of these individual trees some differences between collections might arise through the errors of sampling in the selection of individuals.

TABLE VIII  
COMPARISON OF THREE SERIES OF *Cercis*

	Missouri Series	Kansas Series	Ohio Series
Total individuals.....	More than 123	22	26
Total pods.....	28,554	2200	3900
OVULES			
Mean.....	4.702 $\pm$ .004	4.916 $\pm$ .013	5.493 $\pm$ .011
Standard deviation.....	1.007 $\pm$ .003	.925 $\pm$ .009	.983 $\pm$ .008
Coefficient of variation.....	21.43	18.82	17.89
SEEDS			
Mean.....	3.840 $\pm$ .005	4.116 $\pm$ .015	3.944 $\pm$ .016
Standard deviation.....	1.204 $\pm$ .003	1.030 $\pm$ .010	1.453 $\pm$ .011
Coefficient of variation.....	31.35	25.03	36.83
OVULES AND SEEDS			
Correlation, $r_{os}$ .....	.648 $\pm$ .002	.603 $\pm$ .009	.455 $\pm$ .009
Correlation, $r_{ox}$ .....	-.046 $\pm$ .004	-.183 $\pm$ .014	-.034 $\pm$ .011
Coefficient of fecundity.....	.8166	.8373	.7180

Again, no account whatever can be taken of environmental conditions, either edaphic or meteorological.

With two such factors, which may to some extent tend to bring about differences in the constants of the series dealt with, it has seemed to me rather surprising that the physical constants for ovules and seeds do not differ more widely than they do.

The coefficients of correlation,  $r$ , differ considerably; but two factors influencing this constant must not be forgotten. First, heterogeneity, due to the mixing of the pods from a large number of individuals, would tend to raise the value for the Missouri series. This appears very clearly in a comparison of the mean for the 60 individual constants from trees with 100 pods each and the constant for the 28,000 and more pods in the lumped sample. The former is .599, the latter .648. Second, the coefficients of fecundity show that the three series differ very materially in the percentage of ovules developing into seeds. The lowest value of the coefficient of correlation for ovules formed and seeds maturing (in the Ohio series) is associated with the lowest value of the coefficient of fecundity.

Finally, perhaps the most important point to be gathered from



this table is that in all three series  $r_{oz}$  is negative and of a very low order, but quite possibly significant even in the Ohio series.

### *E. Summary and Discussion*

The foregoing pages embody the results of an attempt to ascertain the relationship between the number of ovules per pod and the capacity of the pod for maturing its ovules into seeds in the leguminous plant *Cercis canadensis*. The methods of analysis are those of an earlier paper on *Phaseolus*. The data in hand lead to the following conclusions:

The correlations for number of ovules formed and number of seeds developing per pod,  $r_{os}$ , have always been found positive and of a moderate, considerable or even high intensity.

Regression of number of seeds on number of ovules per pod is sensibly linear in a population of pods from many individual trees. Possibly, however, there is a departure from linearity in the pods with eight ovules; in my largest series there are only 36 of these pods out of a total of 28,554, and this number is too small to be given great importance.

The significance of the linearity of regression is two-fold. Statistically, it justifies describing the interdependence between the number of ovules formed and the number of seeds maturing by the coefficient of correlation. Biologically, it shows that the rate of increase in number of seeds developing per pod remains the same as we pass from pods with the lowest to pods with the highest numbers of ovules.

Wherever large series of pod have been examined, the correlation between the number of ovules per pod and the capacity of the pods for maturing their seeds,  $r_{oz}$ , has a negative sign and a low, usually a very low, magnitude. For every large series examined the value of  $r_{oz}$  has been over 2.5 times its probable error. These evidences can leave little doubt of the existence of a slight negative relationship between the number of ovules formed and the capacity of the pod for maturing its ovules into seeds, the pods with the larger number of ovules producing relatively fewer seeds.

In a subsequent paper, these conclusions will be tested upon the more homogeneous collections of pods from individual trees. Until then further discussion may be reserved.



# INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1914

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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CONTENTS

Physical and chemical factors influencing the toxicity of inorganic salts to  
*Monilia sitophila* (Mont.) Sacc. . . . . LOUIS OTTO KUNKEL 265

Contributions to the Mesozoic flora of the Atlantic coastal plain, X.—Mary-  
land. . . . . EDWARD WILBER BERRY 295

The wild cotton plant (*Thurberia thespesioides*) in Arizona.  
VERNON BAILEY 301

Notes on two North American ferns. (Plate 7.) . . MARGARET SLOSSON 307

INDEX TO AMERICAN BOTANICAL LITERATURE. . . . . 311

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Physical and chemical factors influencing the toxicity of inorganic salts to *Monilia sitophila* (Mont.) Sacc.

LOUIS OTTO KUNKEL

(WITH TWO TEXT FIGURES)

The many researches of recent years on the relative value of various media for growing bacteria and fungi, and the almost equally extended studies of the toxicity of various mineral salts for these organisms have not so far led to any very careful analysis of the physiological relations of toxic salts as affected by the media in which they are tested. This is especially true of the commonly used organic constituents of culture media, such as the sugars, proteids, etc. The study of the toxic action of salts when mixed together in aqueous solutions as compared with their effects when used separately has led to the very fruitful conception of balanced solutions, which plays so large a role in modern studies of osmosis, penetrability, the making of media, etc. The chemical interrelations of the salts and organic constituents of ordinary media are doubtless of fundamental significance in determining their physiological effects. The chemical relation of a so-called toxic salt to the medium in which it is offered must be understood if the real nature of the toxic effect is to be correctly analyzed. The compounds formed when dilute solutions of salts are mixed with carbohydrates, proteids, etc., are as yet little understood. The study of the relative physiological effects of series of such combinations may indirectly throw light on the nature of the compounds themselves and indicate the conditions under which they

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are formed. Of still greater significance, however, is the bearing of such studies on the actual determination of the relative toxicity of different substances and the fundamental questions as to the nature of toxic effects in general.

In a former paper (15) I have already shown that the toxic action of various nitrates on *Monilia sitophila* (Mont.) Sacc. is greatly influenced by the medium in which the fungus is grown at the time it is being poisoned. For example, ferric nitrate and aluminum nitrate were found to be much less toxic in peptone media than in glucose, fructose, galactose or starch media. Barium nitrate, on the other hand, was more toxic in peptone media than in glucose, fructose or starch. Through further experiments which it is the purpose of this paper to report, I have studied the influence of carbohydrates and peptone on the toxicity of eleven different chlorides. Observations on the germination and growth of *Monilia* in slightly toxic media has led to the suggestion that an important effect of a toxic substance may be to diminish the rate of water absorption by the fungus. In the hope that this suggestion might throw light on the conditions that obtain in poisoned cultures, I have also studied the influence of the water supply on the rate and amount of growth which *Monilia* makes when growing in various media.

As already noted the discovery of the mutual antagonism which exists between inorganic salts as regards their toxicity to plants has led to the conception of balanced solutions. Boehm (3) was perhaps the first to observe this relation. He found that the poisonous action of magnesium salts on bean plants could be counteracted by calcium carbonate. He also noted that calcium nitrate and calcium sulphate had an ameliorating influence on the toxicity of sodium and potassium salts. Von Raumer (26) also observed the great toxicity of magnesium salts in the absence of calcium. The literature on this subject has recently been summarized by McCool (21) That such mutual antagonism exists between a rather large number of salts is one of the best established facts of plant physiology.

In 1902 Loeb (18) attacked the further problem as to whether or not the presence of non-electrolytes would effect the toxicity of inorganic salts. Using the eggs of *Fundulus*, he measured the



toxicity of sodium chloride and zinc sulphate in the presence of small amounts of urea, alcohol, glycerine and cane sugar and concluded that these non-electrolytes do not influence the toxicity of either salt. The toxicity of zinc sulphate, however, was greatly reduced by cane sugar. This result Loeb attributed to the formation of zinc saccharate. Judging from what we know of the conditions under which saccharates are produced, we can hardly accept this explanation for the case of a dilute solution of zinc sulphate and cane sugar. Saccharates are obtained in strongly alkaline solutions. Dilute solutions of zinc sulphate are quite acid in reaction. I shall discuss this point further in connection with my own observations.

Lidforss (16) had long before observed that the toxicity of calcium nitrate, sodium nitrate and sodium chloride for germinating pollen grains was much reduced by the addition of ten per cent. of cane sugar to the solution. Wassermann and Takaki (33) found that an infusion made from cells of the central nervous system of the guinea-pig has an inhibiting action on the toxin of *Bacillus Tetani*. Like infusions made from kidney or liver cells did not counteract the poison. Loew (19) was not able to lessen the toxicity of magnesium salts for *Spirogyra* by the addition of methyl alcohol or glycerine to his solutions. Kahlenberg and True (13) claim that cane sugar has no effect on the toxicity of boric acid for *Lupinus albus*, but that the addition of dextrine to a mercuric chloride solution greatly reduces its toxicity. They were unable to precipitate mercuric oxide from such a solution by means of caustic alkali and assume that the mercury and dextrine combine to form a complex ion which is less toxic than the mercuric ion. Winogradsky and Omeliansky (36) found that peptone and glucose had an inhibiting action on the growth of the nitrifying bacteria. Duggar (6) obtained better germination of the uredospores of *Puccinia Helianthi* in distilled water than in one per cent. peptone solution. Stockard (31) reports that when cane sugar is added to a solution of lithium chloride or ammonium chloride the toxic action of these salts on *Fundulus* eggs seems to be augmented by the presence of the sugar, although the osmotic pressure of the sugar-salt mixture is considerably below that of sea-water.



Quite recently Ritter (28) has made a study of the effects of acids on Mucors growing in several different media. He finds that the toxicity of citric, malic, tartaric, hydrochloric and nitric acids is much reduced by the presence of peptone in the medium. When the source of nitrogen is ammonium citrate, ammonium tartrate, ammonium malate, asparagin or peptone, the toxicity of the various acids is much less than when the nitrogen is offered in the form of ammonium chloride, ammonium sulphate or ammonium nitrate. Grape sugar was found to reduce the toxicity of tartaric acid to a less extent than peptone.

A review of the literature shows that the influence of the more complex organic compounds on toxic substances has generally been neglected by those who have studied the effects of poisons on fungi. In my further studies on this point I have tested the influence of carbohydrates and peptone on the toxicity of a number of different chlorides, and have obtained evidence which suggests that an important factor in toxicity is the influence of the poison on the ability of the protoplast to absorb water. I have used as before the fungus *Monilia sitophila* in all of my experiments. Went (34) found that this fungus was able to use as a partial source of its food supply a rather large variety of organic compounds. This, together with the fact that it is a rapid grower, makes it especially well suited to such investigations. In experiments on the effects of toxic substances on fungi the choice of a standard by which to judge the degree of the poisonous action is a matter of some difficulty. One method is to grow the fungus in media containing the poison in different concentrations and then to determine the weight of the mycelium produced in the several media in a given period of time. On account of the difficulty in getting all of the mycelium out of the culture vessels and freeing it from constituents of the medium this method was not used. In all of my experiments, I have taken as the standard for judging toxicity, *the highest concentration of the poison in which any of the spores germinate after three days of incubation*. The spores are considered to have germinated if they show any visible evidence of growth when magnified to about one thousand diameters. I find this method to be both reliable and convenient.

My cultures were grown in pint milk bottles or in two hundred



and fifty cubic centimeter Jena flasks. New bottles and flasks were obtained and a different set was used for each of the salts tested. Thus the same flask was never used for testing more than one salt. This prevents errors which might arise through small traces of one salt being taken up by the glass and carried into cultures of some other salt. All glassware used in the making of media or the growing of cultures was first treated for at least twelve hours with a chromic acid cleaning solution. It was then thoroughly rinsed with tap water and drained. After draining for a short time it was again rinsed, first in distilled water and then in triple distilled water. The water used in the making of culture media was triple distilled, once from acid potassium dichromate, once from alkaline potassium permanganate and then again redistilled. This water gave a resistance of approximately one hundred and twenty thousand ohms. All of the salts used were Baker's analyzed chemicals, except in the case of barium chloride, cobaltous chloride and cadmium chloride, which came from Kahlbaum. The glucose, saccharose, soluble starch and peptone were obtained from Kahlbaum; the lactose came from Merck. Five per cent. solutions of each of these substances gave the following resistances; glucose, fifty-six thousand ohms; saccharose, forty-nine thousand ohms; lactose, twenty-seven thousand ohms; soluble starch, three thousand, three hundred ohms; and peptone two thousand ohms. A comparison of these resistances gives a good idea of the relative purity of the organic substances used.

The concentration of the salts in the various media are expressed in terms of molar solutions; these concentrations were made by dissolving some multiple or some fraction of a gram molecular weight in one liter of solution. Twenty cubic centimeters of medium were placed in each flask, and the flask and medium were sterilized for approximately ten minutes at 100° C. As soon as the medium had thoroughly cooled it was inoculated with fresh ripe spores of *Monilia*. The spores used in inoculating any given series of media were taken from the same culture. They were shaken from the culture flask on to a piece of white paper and were thoroughly mixed by means of a sterile scalpel. Approximately equal quantities of spores were dusted over the



surface of each medium. The cultures were then incubated in a room which was kept at a temperature of about 26° C. Observations were always made after an incubation period of three days. For the purpose of making careful microscopic observations, each culture was poured out into a small Petri dish, which could be placed on the stage of the microscope. All cultures were first observed under a magnification of about two hundred diameters. If this observation showed no germination, they were then more carefully studied under a magnification of approximately one thousand diameters.

In the tables that follow the plus sign indicates that the spores had germinated while the minus sign means that there was no germination in the medium in question. The results thus given in the tables refer always to the presence or absence of germinated spores in the different cultures, after an incubation period of three days. The minus sign does not mean that the spores will not germinate in the given medium but only that they have not germinated after three days. If left in the medium for a longer time the spores might germinate. *The highest concentration of a salt that will allow germination of the spores within three days is termed the limit concentration for that medium and period of time.* The toxicity of eleven different chlorides has been tested. Chlorides were selected because they have been much studied by other investigators and because they are, on the whole, more soluble than nitrates, sulphates or other common salts. In order to determine the influence of saccharose, glucose, lactose, starch and peptone on the toxicity of the several chlorides, I have used each of these substances separately in testing the toxicity of each inorganic salt. In distilled water and tap water the spores of *Monilia* germinate but produce only a very small amount of mycelium. Any of the organic substances used, when added to distilled water, greatly increase the growth, and they also tend to shorten the time required for germination. Abundant mycelium is produced in five per cent. solutions of glucose, saccharose, lactose, starch or peptone. When chlorides in sufficient concentration are added to any of these media the germination of the spores is completely inhibited. The approximate value of the limit concentration of the different salts in each medium was



obtained through a number of preliminary experiments. It was impossible to predict what the limit concentration would be in any case. My method was to make a guess at this value and then test the accuracy of the guess through experiments. In some cases only one preliminary experiment was necessary in order to determine the approximate value of the limit concentration of a given salt in one of the media. In other cases, however, several preliminary experiments had to be made before this value was ascertained. The data given in the tables was obtained in the final set of experiments and shows the great influence of the organic part of the medium on the toxicity of the different chlorides. The tables are arranged in the order of the toxicity of the salts tested. The influence of the medium on the toxicity of potassium chloride is shown in Table I.

TABLE I

THE TOXICITY OF POTASSIUM CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. KCl	Growth After 3 Days	G.M. Conc. KCl	Growth After 3 Days	G.M. Conc. KCl	Growth After 3 Days	G.M. Conc. KCl	Growth After 3 Days	G.M. Conc. KCl	Growth After 3 Days
2.3	—	2.3	—	1.6	—	1.5	—	1.5	—
2.2	—	2.2	—	1.5	—	1.4	—	1.4	—
2.1	—	2.1	—	1.4	—	1.3	—	1.3	—
2.0	—	2.0	—	1.3	—	1.2	—	1.2	—
1.9	—	1.9	—	1.2	—	1.1	—	1.1	+
1.8	+	1.8	—	1.1	+	1.0	—	1.0	+
1.7	+	1.7	+	1.0	+	.9	—	.9	+
1.6	+	1.6	+	.9	+	.8	+	.8	+
1.5	+	1.5	+	.8	+	.7	+	.7	+
1.4	+	1.4	+	.7	+	.6	+	.6	+

A glance at the table shows that the toxicity of potassium chloride is decidedly influenced by the medium in which it is offered. It is more than twice as toxic in starch as in saccharose or glucose. It is also more toxic in starch than in lactose and peptone. Its toxicity in lactose is the same as in peptone, but is about thirty-five per cent. less than in saccharose. It is most toxic in starch and least toxic in saccharose. The average of the limit concentrations in the five media is 1.1 molar and shows that potassium chloride is less toxic than any of the other chlorides that I have tested; this may be associated with the high nutrient



value of potassium. The toxicity of potassium chloride in starch media is the same as was found for potassium nitrate in the same medium.

TABLE II

THE TOXICITY OF AMMONIUM CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. NH <sub>4</sub> Cl	Growth After 3 Days	G.M. Conc. NH <sub>4</sub> Cl	Growth After 3 Days	G.M. Conc. NH <sub>4</sub> Cl	Growth After 3 Days	G.M. Conc. NH <sub>4</sub> Cl	Growth After 3 Days	G.M. Conc. NH <sub>4</sub> Cl	Growth After 3 Days <sup>a</sup>
.80	—	1.30	—	1.0	—	1.2	—	.95	—
.75	—	1.25	—	.9	—	1.1	—	.90	—
.70	+	1.20	—	.8	—	1.0	—	.85	—
.65	+	1.15	—	.7	—	.9	—	.80	—
.60	+	1.10	—	.6	+	.8	—	.75	—
.55	+	1.05	—	.5	+	.7	+	.70	+
.50	+	1.00	+	.4	+	.6	+	.60	+
.45	+	.90	+	.3	+	.5	+	.50	+
.40	+	.80	+	.2	+	.4	+	.40	+
.35	+	.70	+	.1	+	.3	+	.30	+

Table II shows that the toxicity of ammonium chloride is not greatly different in the various media, though some differences are to be noted. It is least toxic in glucose and most toxic in lactose. The toxicity of potassium chloride in starch is approximately the same as the toxicity of ammonium chloride in peptone, glucose and starch. The average limit concentration of ammonium chloride is .72 molar. When all of the media are taken into consideration, we see that ammonium chloride is more toxic than potassium chloride but less toxic than sodium chloride. Ammonium chloride is a possible source of nitrogen for *Monilia* and it may be that for this reason it is less toxic than sodium chloride.

The toxicity of sodium chloride in the different media as shown by Table III stands in sharp contrast with that of potassium chloride. While potassium chloride is least toxic in saccharose, sodium chloride is most toxic in this medium. It is hard to understand how two salts that are so much alike chemically should be so different as regards their toxicity in saccharose media. It is very interesting to see that potassium chloride, ammonium chloride and sodium chloride show almost equal toxicity in starch media, while in saccharose, glucose, lactose and peptone they



TABLE III

THE TOXICITY OF SODIUM CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. NaCl	Growth After 3 Days	G.M. Conc. NaCl	Growth After 3 Days	G.M. Conc. NaCl	Growth After 3 Days	G.M. Conc. NaCl	Growth After 3 Days	G.M. Conc. NaCl	Growth After 3 Days
.56	—	1.30	—	.90	—	1.5	—	1.00	—
.40	—	1.20	—	.80	—	1.4	—	.95	—
.44	—	1.10	—	.70	—	1.3	—	.90	—
.38	—	1.00	—	.60	—	1.2	—	.85	—
.32	—	.90	—	.50	+	1.1	—	.80	—
.26	+	.80	+	.40	+	1.0	—	.75	+
.20	+	.70	+	.30	+	.9	—	.70	+
.14	+	.60	+	.20	+	.8	+	.65	+
.08	+	.56	+	.10	+	.7	+	.60	+
.02	+	.50	+	.05	+	.6	+	.55	+

differ widely. These differences may be due to the influence of the salts on the enzymes produced in the different media. Sodium chloride is least toxic in glucose, starch and peptone, the limit concentration being approximately the same in these three media. It is more toxic in saccharose than in lactose and more toxic in lactose than in glucose, starch or peptone. The average of the limit concentrations in the different media is .62 molar. When all of the media are thus taken into consideration we see that sodium chloride is much more toxic than potassium chloride.

TABLE IV

THE TOXICITY OF CALCIUM CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. CaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CaCl <sub>2</sub>	Growth After 3 Days
.80	—	1.2	—	.60	—	1.1	—	.80	—
.70	—	1.1	—	.50	—	1.0	—	.70	—
.60	—	1.0	—	.40	—	.9	—	.60	—
.50	+	.9	—	.30	—	.8	—	.50	—
.40	+	.8	—	.20	—	.7	—	.40	+
.30	+	.7	+	.12	+	.6	—	.30	+
.20	+	.6	+	.11	+	.5	+	.20	+
.10	+	.5	+	.10	+	.4	+	.10	+
.05	+	.4	+	.09	+	.3	+	.09	+
.01	+	.3	+	.08	+	.2	+	.08	+



Calcium is one of the most important plant nutrients. It also has great value for counteracting the toxicity of other salts. The above table shows how its toxicity varies in the different media. Its poisonous action in starch is the same as in saccharose and only slightly less than in peptone. It is most toxic in lactose and least toxic in glucose. The average limit concentration is .44 molar.

TABLE V

THE TOXICITY OF BARIUM CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. BaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. BaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. BaCl <sub>2</sub>	Growth After 3 Days.	G.M. Conc. BaCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. BaCl <sub>2</sub>	Growth After 3 Days
.70	—	.50	—	.55	—	.80	—	.50	—
.60	—	.40	—	.50	—	.70	—	.45	—
.50	—	.30	—	.45	—	.60	—	.40	—
.40	—	.20	+	.40	—	.50	—	.35	—
.30	—	.10	+	.35	+	.40	—	.30	—
.25	+	.09	+	.30	+	.30	—	.25	+
.20	+	.08	+	.25	+	.20	+	.20	+
.15	+	.07	+	.20	+	.10	+	.15	+
.10	+	.06	+	.15	+	.09	+	.10	+
.08	+	.05	+	.10	+	.08	+	.05	+

Table V gives the toxic values of barium chloride. Although barium is much like calcium chemically it is not a plant nutrient. Barium is on the whole much more toxic than calcium. It is less toxic in lactose media than in glucose. In this respect it is quite different from calcium chloride which is more than five times as toxic in lactose as in glucose. The average limit concentration is .26 molar. The toxicity of barium chloride is influenced less by the different media than that of any of the other chlorides which have been used. In saccharose, glucose, starch and peptone it is more toxic than calcium chloride. In lactose media, however, calcium chloride is more than three times as toxic as barium chloride. It is worth noting that the toxicity of the five chlorides as shown by the above tables is, on the average, as great in peptone as in the other media. Their toxicity is least in glucose and greatest in lactose. They are more toxic in peptone than in saccharose or glucose, although peptone is a much more favorable medium for the growth of the fungus. This shows that in some



cases at least, salts may be more toxic in a medium that is well suited to the growth of *Monilia* than in one which is less favorable.

TABLE VI

THE TOXICITY OF FERRIC CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. FeCl <sub>3</sub>	Growth After 3 Days	G M. Conc. FeCl <sub>3</sub>	Growth After 3 Days	G.M. Conc. FeCl <sub>3</sub>	Growth After 3 Days	G.M. Conc. FeCl <sub>3</sub>	Growth After 3 Days	G.M. Conc. FeCl <sub>3</sub>	Growth After 3 Days
.00050	—	.00050	—	.000400	—	.0013	—	.050	=
.00040	—	.00040	—	.000300	—	.0012	—	.045	—
.00030	—	.00030	—	.000200	—	.0011	—	.040	—
.00020	—	.00020	—	.000100	—	.0010	—	.035	+
.00010	+	.00010	+	.000080	—	.0009	—	.030	+
.00009	+	.00009	+	.000060	—	.0008	+	.025	+
.00008	+	.00008	+	.000040	—	.0007	+	.020	+
.00007	+	.00007	+	.000020	—	.0006	+	.015	+
.00006	+	.00006	+	.000010	+	.0005	+	.010	+
.00005	+	.00005	+	.000008	+	.0004	+	.005	+

Table VI shows that ferric chloride is far more toxic than the alkali and the alkali earth chlorides which have been tested. Although iron has a place among the nutrient elements it is nevertheless very poisonous. Of the alkali and alkali earth salts tested, potassium chloride is the least toxic. Iron chloride is least toxic of the salts of the heavy metals which have been used. It is very interesting to see that both potassium and iron are among the nutrient elements. This suggests that there may be some connection between toxicity and the nutrient relations of the elements. The effect of peptone on the poisonous action of ferric chloride is strikingly shown by the table. It is eight times more toxic in starch and ten times more toxic in lactose than in glucose and saccharose. In lactose it is more than three thousand times more toxic than in peptone. The average limit concentration in the different media is .007 molar.

Copper is known to be very poisonous to many algae and fungi, and is widely used in the making of fungicides. I find, however, that the chloride is, with the exception of iron, less toxic than any of the other chlorides of the heavy metals that have been tested. As shown by Table VII, cupric chloride, like ferric chloride, is more toxic in lactose than in saccharose, glucose, starch or peptone.



TABLE VII

THE TOXICITY OF CUPRIC CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. CuCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CuCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CuCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CuCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CuCl <sub>2</sub>	Growth After 3 Days
.00100	—	.00100	—	.000055	—	.00070	—	.050	—
.00095	—	.00095	—	.000050	—	.00065	—	.045	—
.00090	+	.00090	—	.000045	—	.00060	—	.040	—
.00085	+	.00085	—	.000040	—	.00055	—	.035	—
.00080	+	.00080	+	.000035	—	.00050	—	.030	—
.00075	+	.00075	+	.000030	+	.00045	+	.025	—
.00070	+	.00070	+	.000025	+	.00040	+	.020	+
.00065	+	.00065	+	.000020	+	.00035	+	.015	+
.00060	+	.00060	+	.000018	+	.00030	+	.010	+
.00055	+	.00055	+	.000015	+	.00025	+	.005	+

Its toxicity in glucose and saccharose is approximately the same. On the whole, cupric chloride is little more toxic than ferric chloride, its average limit concentration being .004 molar. The influence of the various media on the toxicity of copper is of special interest because the salts of this metal are so much used in the making of sprays. The action of lime on the copper in Bordeaux mixture is not thoroughly understood although this important subject has been given considerable attention (see Fairchild, 7).

TABLE VIII

THE TOXICITY OF ZINC CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. ZnCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. ZnCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. ZnCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. ZnCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. ZnCl <sub>2</sub>	Growth After 3 Days
.00050	—	.000300	—	.00080	—	.000300	—	.050	—
.00045	—	.000250	—	.00075	—	.000200	—	.045	—
.00040	+	.000200	—	.00070	+	.000100	—	.040	—
.00035	+	.000150	—	.00065	+	.000080	—	.035	—
.00030	+	.000100	+	.00060	+	.000060	+	.030	—
.00025	+	.000050	+	.00055	+	.000040	+	.025	—
.00020	+	.000010	+	.00050	+	.000020	+	.020	—
.00015	+	.000008	+	.00045	+	.000010	+	.015	—
.00010	+	.000006	+	.00040	+	.000008	+	.010	+
.00005	+	.000004	+	.00035	+	.000006	+	.005	+

Table VIII shows the toxicity of zinc chloride. It will be seen that it is most toxic in starch and least toxic in peptone. The



most striking point in this table is the high toxicity of zinc in starch. In this medium it is more toxic than any of the other salts tested except mercuric chloride. This observation suggests that the value of zinc chloride for preserving wood from decay is based on a similar relation between zinc and the cellulose of the wood. Starch and cellulose are much alike chemically and it is rather to be expected that a salt which is extremely toxic in starch media would also be very toxic in cellulose. The toxicity of zinc chloride in saccharose and glucose is practically the same and is greater than in lactose. In lactose, zinc is more than fifty times less toxic than either copper or iron. The average limit concentration is .0022 molar.

TABLE IX

THE TOXICITY OF COBALTOUS CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. CoCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CoCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CoCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CoCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CoCl <sub>2</sub>	Growth After 3 Days
.00050 <sup>1</sup>	—	.00050	—	.000080	—	.00080	—	.0400	—
.00040	—	.00040	—	.000070	—	.00070	—	.0350	—
.00030 <sup>1</sup>	+	.00030	—	.000060	—	.00060	+	.0300	—
.00020	—	.00020	—	.000050	—	.00050	+	.0250	—
.00010	—	.00010	—	.000040	—	.00040	+	.0200	—
.00009	+	.00009	+	.000030	—	.00030	+	.0150	—
.00008	+	.00008	+	.000020	+	.00020	+	.0100	+
.00007	+	.00007	+	.000015	+	.00020	+	.0050	+
.00006	+	.00006	+	.000010	+	.00009	+	.0010	+
.00005	+	.00005	+	.000008	+	.00008	+	.0008	+

The influence of the different media on cobaltous chloride is quite marked. It is five hundred times more toxic in lactose than in peptone. In starch it is less toxic than in glucose or saccharose but more toxic than in peptone. The average limit concentration is .0020 molar, which shows that, on the whole, it is only a little more toxic than zinc chloride. The poisoning of the fungus by cobalt, cadmium and mercury is different from that of calcium, iron, etc., in that *Monilia* in nature probably does not come in contact with any but minimal concentrations of the salts of these metals. Its resistance to cobaltous chloride, cadmium chloride

<sup>1</sup> The growth in this culture was quite limited; only a small per cent. of the spores had pushed out germ tubes.



and mercuric chloride is, therefore, not due to any acquired relation of immunity or susceptibility.

TABLE X

THE TOXICITY OF CADMIUM CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. CdCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CdCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CdCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CdCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. CdCl <sub>2</sub>	Growth After 3 Days
.00050	—	.00050	—	.00050	—	.00090	—	.0150	—
.00030	—	.00040	—	.00040	—	.00080	—	.0100	—
.00010	—	.00030	—	.00030	—	.00070	—	.0050	+
.00008	—	.00020	+	.00020	—	.00060	—	.0040	+
.00006	+	.00010	+	.00010	+	.00050	+	.0030	+
.00004	+	.00008	+	.00008	+	.00040	+	.0020	+
.00002	+	.00006	+	.00006	+	.00030	+	.0010	+
.00001	+	.00004	+	.00004	+	.00020	+	.0008	+
.000008	+	.00002	+	.00002	+	.00010	+	.0006	+
.000006	+	.00001	+	.00001	+	.00008	+	.0004	+

The toxicity of cadmium chloride is shown in Table X. It is most toxic in saccharose and least toxic in peptone. In glucose it is more toxic than in starch, but less toxic than in lactose. It is more than three times as toxic in saccharose as in glucose. Its average limit concentration in the different media is .001 molar. In saccharose, starch and peptone, cadmium chloride is more toxic than cobaltous chloride. In glucose and lactose, on the other hand, cobaltous chloride is more toxic than cadmium chloride.

TABLE XI

THE TOXICITY OF MERCURIC CHLORIDE IN SACCHAROSE, GLUCOSE, LACTOSE, STARCH, AND PEPTONE MEDIA

Saccharose 5%		Glucose 5%		Lactose 5%		Starch 5%		Peptone 5%	
G.M. Conc. HgCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. HgCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. HgCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. HgCl <sub>2</sub>	Growth After 3 Days	G.M. Conc. HgCl <sub>2</sub>	Growth After 3 Days
.000400	—	.00050	—	.000200	—	.000050	—	.0055	—
.000200	—	.00040	—	.000100	—	.000040	—	.0050	—
.000100	—	.00030	—	.000080	—	.000030	—	.0045	—
.000080	—	.00020	—	.000060	—	.000020	—	.0040	—
.000060	+	.00010	+	.000040	—	.000010	+	.0035	—
.000040	+	.00008	+	.000020	+	.000008	+	.0030	—
.000020	+	.00006	+	.000010	+	.000006	+	.0025	—
.000010	+	.00004	+	.000008	+	.000004	+	.0020	+
.000005	+	.00002	+	.000006	+	.000002	+	.0015	+
.000001	+	.00001	+	.000004	+	.000001	+	.0010	+



Overton (22) has pointed out that mercuric chloride, which differs from most salts in being more soluble in ether, lanolin, etc., exerts its poisonous action more quickly than the other salts of the heavy metals and thinks that this fact favors the view that the plasma membrane is a lipoid layer about the cell. The data in Table XI supports the evidence for the great toxicity of this salt in all of the different media used. It is, however, more toxic in starch and less toxic in peptone than in any of the other media. It is two hundred times more toxic in starch than in peptone. It is also more toxic in lactose than in glucose or saccharose. It is, as noted, the most toxic of all the chlorides used, its average limit concentration being .0004 molar. A comparison of the limit concentrations of the chlorides of zinc, cadmium and mercury shows that the toxicity of these salts is roughly proportional to the atomic weights of zinc, cadmium and mercury. Mercury is somewhat more toxic than would be expected from its atomic weight but the relation shown here suggests that a better knowledge of the toxicity of non-nutrient salts in different media may further support the view that toxicity is related to the periodic functions of the atomic weights of the elements.

TABLE XII

THE TOXICITY OF VARIOUS CHLORIDES IN FIVE DIFFERENT MEDIA

	KCl	NH <sub>4</sub> <sup>+</sup> Cl <sup>-</sup>	Na- Cl	Ca- Cl <sub>2</sub>	Ba- Cl <sub>2</sub>	FeCl <sub>3</sub>	CuCl <sub>2</sub>	ZnCl <sub>2</sub>	CoCl <sub>2</sub>	CdCl <sub>2</sub>	HgCl <sub>2</sub>
Saccharose . .	1.8	.7	.26	.50	.30	.00010	.00090	.00040	.00009	.00060	.00006
Glucose . . . .	1.7	1.0	.80	.70	.20	.00010	.00080	.00010	.00009	.00020	.00010
Lactose . . . .	1.1	.6	.50	.12	.35	.00001	.00003	.00070	.00002	.00010	.00002
Starch . . . . .	.8	.7	.80	.50	.20	.00080	.00045	.00006	.00060	.00050	.00001
Peptone . . . .	1.1	.7	.75	.40	.25	.03500	.02000	.01000	.01000	.00500	.00200

Table XII gives the limit concentration of each salt in each medium used. A comparison of these values brings out some interesting relations. Taking the average concentrations of the different chlorides in the various media, we see that the alkali and alkali earth salts which were tested are most toxic in saccharose and least toxic in glucose. The heavy metals are most toxic in lactose and least toxic in peptone. While potassium chloride is most toxic in starch and least toxic in saccharose, sodium chloride is least toxic in starch and glucose and most toxic in saccharose.



Ammonium chloride and calcium chloride are most toxic in lactose and least toxic in glucose. Barium chloride, however, is least toxic in lactose and most toxic in glucose and starch. Cupric chloride, ferric chloride and cobaltous chloride are most toxic in lactose. Zinc chloride and mercuric chloride are most toxic in starch. Cadmium chloride is most toxic in saccharose. None of the chlorides of the alkali or alkali earth metals, but all of the chlorides of the heavy metals are least toxic in peptone media. In lactose media, ferric chloride is more toxic than any of the other chlorides; in glucose media, cobaltous chloride is most toxic; in starch, peptone and saccharose media, mercuric chloride and cadmium chloride are most toxic. Potassium chloride in all of the media used is the least toxic of all of the salts tested, except sodium chloride in a starch medium. Potassium chloride in saccharose is less toxic, and mercuric chloride in starch is more toxic than any of the other salts in any of the other media. Reading from right to left in Table XII, one sees the increasing toxicity of the different salts. The arrangement of the salts in the order of their toxicity is different for each of the five different kinds of media.

In order to obtain evidence relative to the number of free ions in the various media containing limit concentrations of the same salt, a number of tests were made of the electrical resistances of the different media. The results of some of these tests are given in Table XIII.

TABLE XIII

THE ELECTRICAL RESISTANCE OF SOME OF THE MEDIA

Medium	G.M. Conc. of FeCl <sub>3</sub>	Resist-ance in Ohms	G.M. Conc. of CuCl <sub>2</sub>	Resist-ance in Ohms	G.M. Conc. of CdCl <sub>2</sub>	Resist-ance in Ohms	G.M. Conc. of HgCl <sub>2</sub>	Resist-ance in Ohms
Saccharose . . . .	.00010	3,700	.00090	8,900	.00006	6,500	.00006	14,400
Glucose . . . . .	.00010	4,900	.00080	10,100	.00020	5,000	.00010	6,900
Lactose . . . . .	.00001	5,600	.00003	—	.00010	7,100	.00002	12,500
Starch . . . . .	.00080	4,200	.00045	1,600	.00050	1,200		
Peptone . . . . .	.03500	10	.02000	97	.00500	160	.00200	200

The tests of electrical resistance were made by means of the Wheatstone bridge method, a Freas electrolytic cell being used. The resistances shown by five per cent. solutions of the organic substances used have already been given. Table XIII shows in a



striking way the low resistance of peptone media and indicates that *Monilia* is actually able to endure higher concentrations of these poisonous substances when it is growing in peptone media than when it is in any of the other media which have been used. The table also suggests the probability that the susceptibility of the fungus to the same kind of ions varies according to the medium in which it is growing.

In an attempt to further elucidate the nature of the toxic action of the various salts on *Monilia*, I have also attacked the problem from the standpoint of the hypothesis that failure of the spores to germinate in a medium containing less than the lethal dose of a toxic substance is due to the inability of the protoplast to absorb sufficient water. Careful observation of the appearance and behavior of spores in toxic media has led to the belief that the retarding action of a toxic salt on germination and growth is the result of its influence on the ability of the cells to take up water. As has already been stated, the highest concentration of a salt in which *Monilia* spores show germination after three days, has been designated the limit concentration for that medium. It is recognized that this is an arbitrary standard. The limit concentrations given in the above tables hold only in the case of an incubation period of three days. Germination will take place in concentrations which are greater than this limit concentration, provided the spores are left in the medium for a longer period of time.

Spores placed in a medium in which the toxic substance is slightly more dilute than the limit concentration, germinate and produce mycelia. The rate of growth in such a medium is much slower than in a non-toxic medium. The most obvious characteristic of a poisoned culture is the long incubation period and the slow rate of growth. The effect of potassium chloride on the time of germination of spores of *Monilia* on a potato medium (thirty-five per cent. potato cubes) is shown by Table XIV.

While growth becomes visible in twenty-one hours in a medium containing potassium chloride at a concentration of .62 molar, it takes thirty-four hours when the concentration is 1.26 molar and fifty-five hours when the concentration is 1.9 molar. This experiment illustrates the behavior of the fungus in media which are toxic but which do not entirely inhibit growth.



TABLE XIV

THE EFFECT OF POTASSIUM CHLORIDE ON RATE OF GROWTH

Concentrations of KCl	Incubation Period	Concentrations of KCl	Incubation Period
0.62 molar.	21 hours.	1.42 molar.	36 hours.
0.70 "	22 "	1.50 "	37 "
0.78 "	23 "	1.58 "	38 "
0.86 "	25 "	1.66 "	40 "
0.94 "	27 "	1.74 "	42 "
1.02 "	29 "	1.82 "	44 "
1.10 "	31 "	1.90 "	55 "
1.18 "	32.5 "	1.98 "	59 "
1.26 "	34 "	2.06 "	63 "
1.34 "	35 "	2.14 "	No germination after 20 days.

If now we study the condition of the spores in media that entirely inhibit germination, we obtain some interesting data. The spores will remain viable for two weeks or longer in the presence of so toxic a substance as mercuric chloride, provided the concentration is slightly below that which causes plasmolysis. Some spores which had been kept for two weeks on a starch medium containing mercuric chloride at a concentration of .00005 molar germinated when transferred to potato agar. This shows that although the spores do not germinate in such a toxic medium, they are not much injured by it. The toxic substances which I have used cause serious injury to the spores, only when they are concentrated enough to bring about plasmolysis. At concentrations less than this, the spores do not germinate but they remain alive for a long time. At still lower concentrations they not only remain alive but germinate and make a slow growth.

This slow growth in media containing approximately limit concentrations of toxic substances seems to me strong evidence that although the poison is not present in sufficient quantities to cause plasmolysis, it nevertheless hinders the absorption of water by the spores and in this way inhibits their growth. This assumption seems fully in accord with the facts above noted. As the concentration of the toxic substance is increased, the ability of the protoplasm to absorb water becomes less and less and the time required for germination longer and longer. A concentration is finally reached at which the spores are no longer able to absorb any water from the surrounding medium. Although this con-



centration inhibits germination, it does not kill the spores, even after considerable periods of time. When the concentration is still further increased the water holding power of the spores becomes less and plasmolysis results.

If as is here assumed the rate of growth of the fungus in a toxic medium depends on its rate of water absorption, then any means by which the water content of the mycelium could be lessened should also decrease the rate of growth. If, for example, *Monilia* be placed in a dry atmosphere where the loss of water by the aerial part of the mycelium would be great, the rate of growth should be correspondingly decreased. The following experiments show the effect of a dry atmosphere on the rate of growth of the fungus mycelium.

The media used in this work consisted of cubes of potato to which was added enough water to fill the bottom of the culture vessel to depth of about one half of a centimeter. On such a substratum *Monilia* makes very abundant growth. The cultures were incubated at a temperature of 29° C. This is one degree below the temperature most favorable for its growth (see Went, 34). Since the effect of drying the atmosphere over cultures of *Monilia* varies somewhat with the age of the culture at the time the drying agent is used, a few remarks regarding the appearance of the fungus at different stages in its development seem desirable at this point.

Under the conditions outlined above, growth first becomes visible to the naked eye after an incubation period of from nine to ten hours. During the next fifteen hours the mycelium grows so rapidly that it almost hides the surface of the potato cubes. In the next seven hours the fungus makes still more rapid growth, rising from five to ten centimeters above the culture medium. This is followed by a period of about six hours, during which there is little visible change. When the cultures are approximately forty hours old they begin to take on a beautiful pink color and during the next hour spore formation begins.

If the vapor pressure above cultures that are more than thirty hours old is unduly lowered, the mycelium withers and fails to produce spores. An entirely different result is obtained in the case of young cultures. If five cubic centimeters of a four molar



potassium chloride solution be suspended in an oiled paper bag above a young culture, it checks the growth of the mycelium to a remarkable extent. The less concentrated the solution in the paper bag, the greater will be the mycelial growth in the culture above which it is suspended. Drying the air by placing small amounts of calcium chloride over the cultures gives still more striking results. The mycelium can be kept from rising more than a few millimeters above the surface of the medium. Table XV shows the effect of suspending potassium chloride solutions of different concentrations over cultures kept under conditions that were otherwise identical. The bags containing the solutions were placed in the bottles at the time the inoculations were made.

TABLE XV

INFLUENCE OF HUMIDITY ON THE GROWTH OF *Monilia*

Solution Suspended Above Culture	Height of Mycelium After 32 Hours
5 c.c. of 4.0 molar KCl solution.	1.0 cm.
5 c.c. " 3.2 " KCl "	1.5 "
5 c.c. " 2.4 " KCl "	3.0 "
5 c.c. " 1.6 " KCl "	3.5 "
5 c.c. " .8 " KCl "	3.2 "
5 c.c. " distilled water	4.0 "

FIG. 1 shows the six cultures referred to in Table XV. The photograph was taken several hours after obtaining the measurements used in the table. The culture that made the least growth is the one above which was suspended five cubic centimeters of four molar potassium chloride solution. Distilled water was suspended over the culture that made the greatest amount of growth. As the rate of loss of water by the mycelium is increased the rate of growth is correspondingly decreased. By suspending one gram of anhydrous calcium chloride over alternate cultures (FIG. 2) the influence of vapor pressure on rate of growth is still more strikingly shown. The amount of water taken up by the calcium chloride, however, is very small.

In order to determine the amount of water taken up by calcium chloride suspended over cultures of *Monilia* when it causes such variations in growth as are to be noted in FIG. 2, bags were weighed before and after being suspended over cultures. The difference in weight gives the amount of water taken up by the



drying agent. This amount was found to be in ten instances respectively: 1.32g; 1.45g; 1.40g; 1.32g; 1.38g; 1.43g; 1.39g; 1.36g; 1.30g; 1.37g or an average of 1.33 grams. A similar calcium

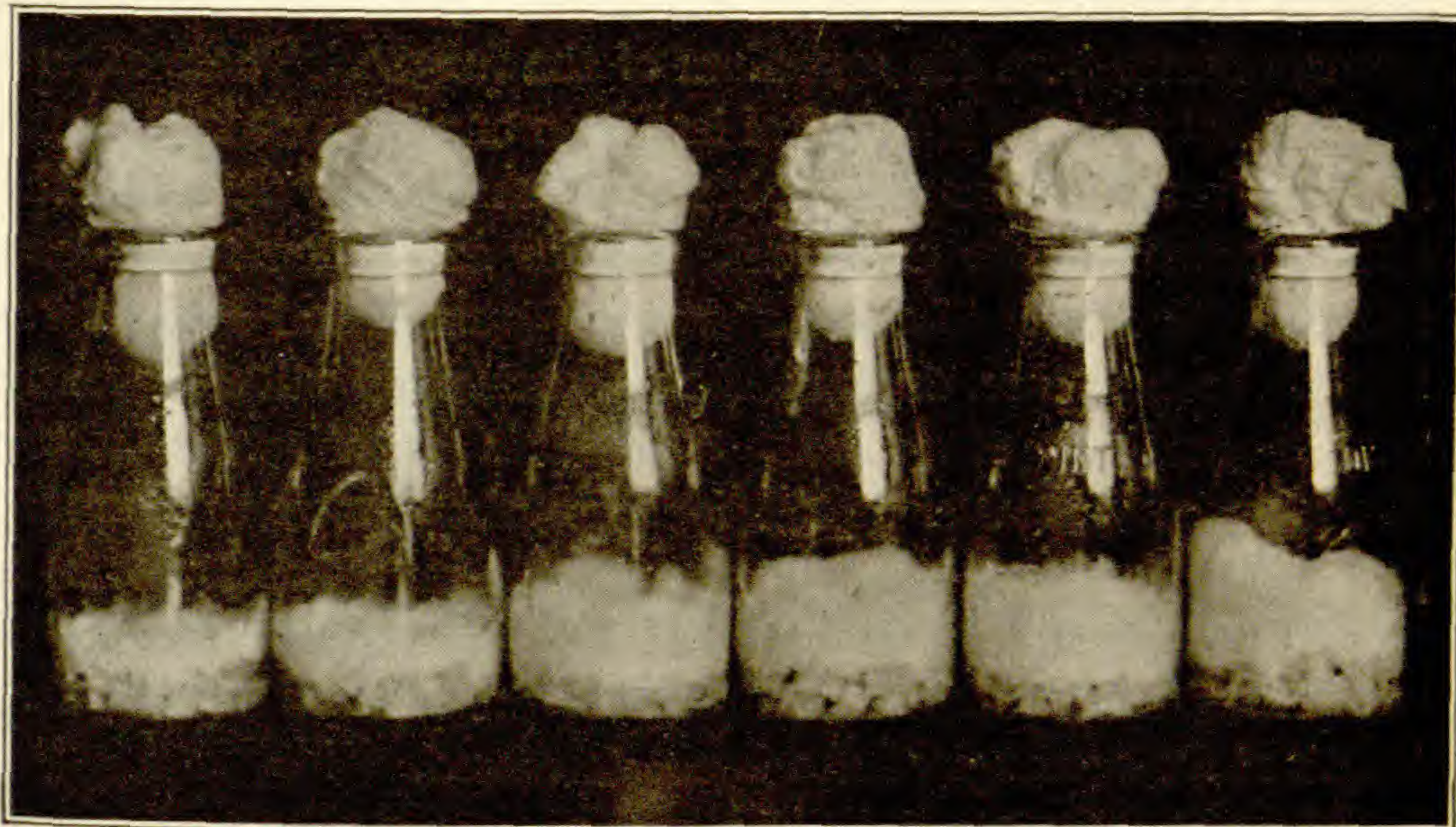


FIG. 1. Cultures of *Monilia sitophila*. This photograph shows the influence of humidity of the atmosphere on the rate of growth of *Monilia*. An oiled paper bag, containing a 4 molar potassium chloride solution, was suspended over the culture that shows the least growth, while distilled water was suspended over the culture that made the greatest growth. The series of six cultures shows the effect of drying the air over the mycelium to different degrees.

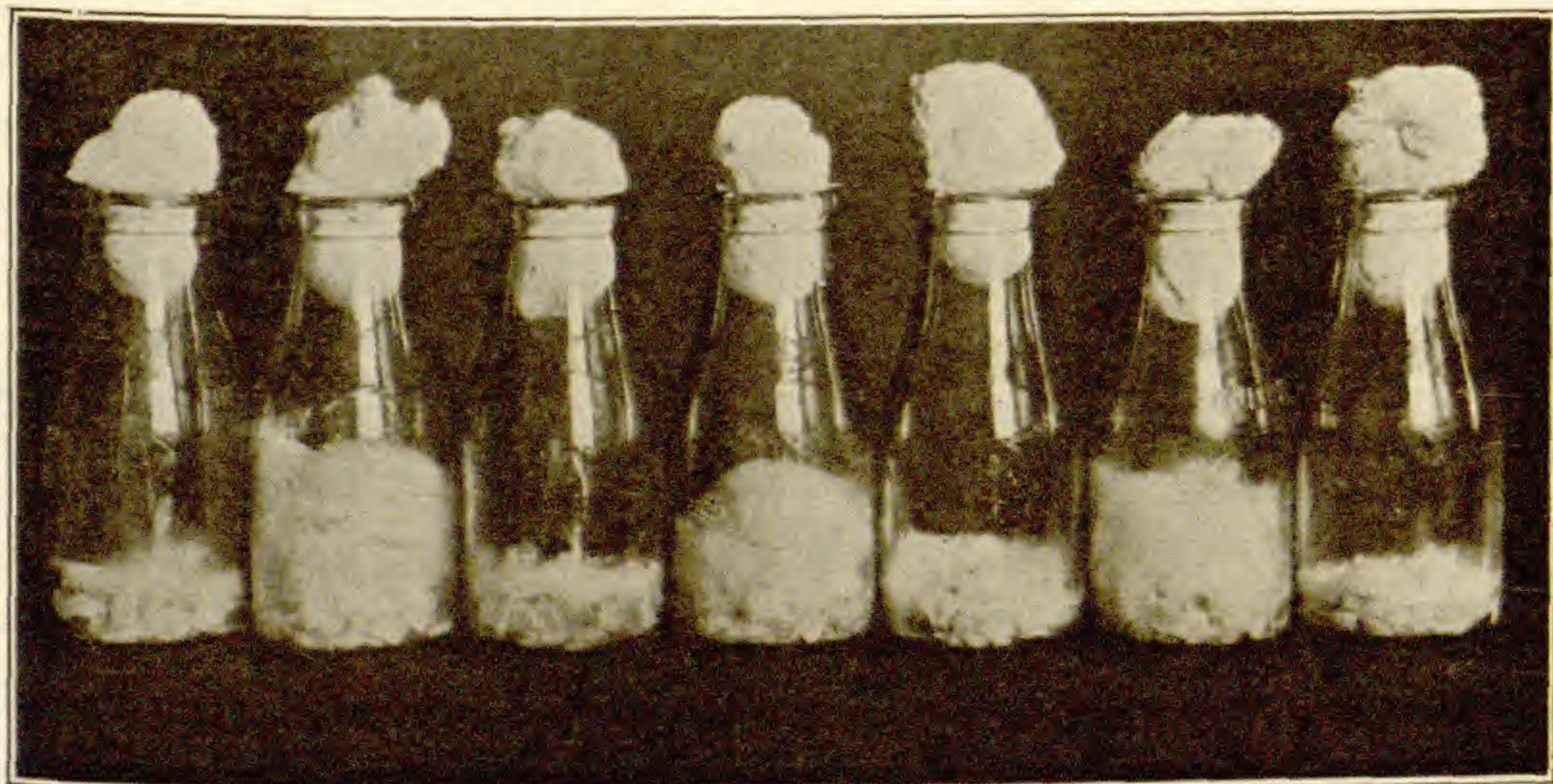


FIG. 2. Cultures of *Monilia sitophila*. This photograph shows the influence of drying the air over young cultures of *Monilia*. One gram of anhydrous calcium chloride was suspended above the cultures in alternate bottles; the small amount of growth made by the fungus in these bottles is shown.



chloride bag was suspended for the same length of time over a sterile medium exactly like that on which the *Monilia* was being grown. This bag took up only .39 gram of water, showing that most of the water taken up by the drying agent suspended over cultures comes from the mycelium of the fungus. These experiments show that the removal of less than one and one half grams of water from the atmosphere above cultures greatly decreases the rate of growth of the mycelium. Similar experiments were performed with *Mucor Mucedo*, *Sporodinia grandis* and *Phycomyces nitens*. In each case, drying the air above young cultures greatly reduces the rate of growth. *Sporodinia grandis* and *Mucor Mucedo* produce shorter sporangiophores when grown in a culture over which a drying agent is suspended than when grown in a moist atmosphere. In the case of *Phycomyces nitens* the rate of growth is greatly checked by drying the atmosphere but the final length of the sporangiophores is not decreased.

These experiments show in a striking manner the well known importance of water to growth. They also suggest that the slow germination and the slow rate of growth in toxic solutions of potassium chloride may be largely due to the lowering of the vapor pressure above the medium. The same thing is probably true of all other salts that must be used in considerable concentrations in order to inhibit growth. But it is quite different with more toxic substances such as the salts of the heavy metals which inhibit growth when present in very small quantities. Their effect on the vapor tension of the medium is, of course, insignificant. This difference between toxic and relatively non-toxic substances has not been sufficiently emphasized. It seems to me that the above experiments offer strong evidence in support of the assumption that an important factor in many cases of toxicity is the effect of the poison on the ability of the protoplast to absorb water. They, at least, show that this factor is sufficient to account for a large part of the decrease in growth which is to be observed in toxic media containing relatively large amounts of dissolved salts.

A salt like potassium chloride when added to a medium in sufficient quantities to check growth, increases the affinity of the medium for moisture and in this way makes it difficult for the



mycelium to take up sufficient water. By lowering the vapor tension of the medium it also increases the rate at which water is lost by the fungus. If instead of adding the salt to the medium it is dissolved in a small amount of water and suspended above a young culture the strong solution takes up water from the air. In this case the salt does not retard the rate at which water is taken up by the mycelium but does increase the rate at which water is given off. It is very interesting to see that when the salt is suspended above the growing culture it causes a decrease in the rate of growth which is similar to that to be observed when it is added directly to the medium. There can be little doubt that in media containing toxic concentrations of potassium chloride, the retardation in growth is largely the result of the inability of the fungus to absorb and to retain sufficient water. Though toxic concentrations of the salts of the heavy metals do not appreciably lower the vapor pressure above the medium, it is possible that these salts also act by decreasing the power of the cells to absorb water.

A consideration of the factors which may be involved in bringing about the variations in toxicity in the different media leads to the suggestion of several possibilities. In the first place it is known that certain salts react with sugars, starch and proteids. The resulting compounds if formed in a given medium would be expected to show properties different from the salt and different from other compounds that might be formed in still other media. Relatively little is known of these substances, but some of them have been studied and the conditions that favor their formation have been determined.

In a solution of sodium hydroxide, cane sugar is converted into sodium saccharate (see Thomsen, 32). Saccharates of calcium, potassium and barium are also known (see Peligot, 24). All of these saccharates are formed by the action of the hydroxides of the different metals on cane sugar. The addition of ammonia to a solution of cane sugar increases the rotatory power of the solution and has been taken as evidence that a compound is formed between the sugar and ammonia (see Wilcox, 35). Copper and iron saccharates have also been reported (see Graham, 10). They are made by adding the chlorides to alkaline solutions of cane sugar. We can not, however, in the cases before us, attribute the variations in



toxicity of different salts in cane sugar media to the production of saccharates, since the addition of chlorides to a neutral solution of cane sugar does not furnish the conditions necessary for their formation. In order to obtain saccharates it would be necessary to add alkalies to these solutions. There seems to be good evidence, however, that some of the chlorides do form loose combinations with cane sugar (see Peligot, 24). A compound represented by the formula  $2C_{12}H_{22}O_{11}.BaCl_2$  has been prepared in crystalline form (Gauthier, 8). It may be that such addition compounds are factors in determining the relative toxicity of the chlorides in saccharose media. Barium chloride is less toxic in saccharose than in starch, glucose or peptone. It may be that this rather low toxicity in saccharose is due to the formation of the compound referred to above.

Compounds of glucose and lactose, analogous to the saccharates, are also known (Hönig & Rosenfeld, 11, 12). They are formed by the action of alkalies on these sugars. With glucose, sodium chloride and potassium chloride form compounds which are represented by the formulae  $C_6H_{12}O_6.NaCl$  and  $C_6H_{12}O_6.KCl$  respectively (Gladstone, 9). It may be that the rather low toxicity of sodium chloride and potassium chloride in glucose media is due to the formation of these compounds. Starch has been shown to have the properties of a very weak acid and to be able to react with small quantities of neutral salts (see Demoussy, 5). Sodium chloride is less toxic in starch than in any of the other media except glucose. It may be that some of the salt has combined with starch to give a compound that is less toxic than sodium chloride. Potassium chloride, on the other hand, is more toxic in starch than in any of the other media. It is possible that this is due to the formation of a complex compound which is more toxic than the chloride.

The addition of any of the chlorides to a five per cent. peptone solution always causes a certain amount of precipitation. That the salts are to some extent carried down by this precipitate seems highly probable. Pauli (23) has shown that neutral proteids adsorb electrolytes. The antitoxic action of peptone on the salts of the heavy metals may be in part due to this adsorption. Table XII shows that the toxicity of all of the chlorides of the heavy metals is less in peptone than in any of the other media.



Although some of the variations in the toxicity of the chlorides in the different media may be the result of reactions between the salts and organic substances, there is good evidence that this can not account for all of the variations brought out in Table XII. A study of some of the media from the standpoint of their resistance to the passage of the electric current has shown that there is considerable variation in the ionic concentration of different media that contain limit concentrations of the same salt, indicating that some media do influence the concentration of the ions but that these differences are not correlated directly with the observed differences in toxicity. Limit concentrations of ferric chloride, cupric chloride, cadmium chloride and mercuric chloride in peptone show in each case a much lower resistance than limit concentrations of these same salts in saccharose, glucose, lactose or starch. This seems to be strong evidence in support of the view that the fungus is actually able to resist higher ionic concentrations of these salts when it is growing in peptone than when it is in any of the other media tested, thus showing an effect of the peptone other than that due to its precipitation of a portion of the toxic salt.

Another factor of probable importance in this connection is the influence of the different media on the production of enzymes. Went (34) has shown that *Monilia sitophila* produces a number of different enzymes and that the organic part of the medium determines which enzyme will be produced in any given case. The effect of the various chlorides on trypsin, which the fungus produces in peptone media, may be quite different from their influence on diastase produced in starch media. The rather high toxicity of potassium chloride and barium chloride in starch media may be due to the influence of these salts on diastase. Similar variations may be brought about by the actions of the poisons on lactase, lipase and invertase.

My observations show clearly that the organic part of the medium must be taken into account in studies on toxicity. This important factor, however, has generally been disregarded by those who have tested the resistance of fungi and bacteria to poisons. Stevens (30) tested the toxic action of mercuric chloride and other poisons on *Penicillium crustaceum* growing in bread media. In a study of the toxicity of a whole series of substances for *Aspergillus*



*flavus*, *Sterigmatocystis nigra*, *Oedocephalum albidum*, *Penicillium glaucum* and *Botrytis vulgaris*, Clark (4) used a sugar beet infusion. Klebs (14) determined the poisonous influence of various substances on *Saprolegnia mixta* growing in a pea infusion. Bessey (2) tested the resistance of fungi to copper sulphate, mercuric chloride and other poisons without taking into account the possible influence of organic materials in the synthetic media which he used.

Pulst (25) measured the toxicity of copper sulphate, zinc sulphate and nickel sulphate. He tested the action of these salts on *Mucor Mucedo*, *Aspergillus niger*, *Botrytis cinerea* and *Penicillium glaucum* in a medium containing sugar and peptone, without regard to the effect of sugar or peptone on the toxicity of the salts.

Loew (20) has studied the poisonous action of sodium fluoride on *Bacillus mycoides*, *B. pyocyaneus*, *B. subtilis* and *B. prodigiosus*. Using a bouillon medium, he found that these bacteria could endure approximately one per cent. of sodium fluoride. He, therefore, disagrees with Arthus and Huber (1) who held that a one per cent. solution of this salt is deadly to all cells. He also compares the toxic action of sodium fluoride on *Spirogyra communis* in an aqueous solution with its effect on bacteria in a bouillon medium and notes that the bacteria have a much higher resistance than the alga.

Ssadikow (29) studied the resistance of *Bacillus subtilis* to strychnin salts in bouillon, nutrient agar and nutrient gelatin. My observations suggest that the high concentrations which this organism was able to endure might have been fatal to it in a medium containing no peptone. Renard (27) has tested the antitoxic action of different concentrations of each of twelve nutrient salts on the poisonous effects of eleven different toxic substances, mostly chlorides and nitrates of the heavy metals. He finds that in general, the antitoxic action increases with the concentration of the inhibiting salt. Except in a few cases where the antagonistic substance is a salt of an organic acid, he has made his tests in glucose media. The antitoxic coefficients by which he attempts to express the relations between the several poisons and their antidotes would undoubtedly have been found to be different for each medium tested if he had tried other common organic sub-



stances. He has not taken into account the influence of the glucose on the toxicity of the poisons used although in an experiment in which he studies the action of copper salts in the presence of potassium acetate both with and without glucose, he obtains evidence that the glucose lessens the toxicity of the copper. Although Lipman (17) makes mention of the fact that sodium carbonate is much less toxic to ammonifying organisms in certain soils than in pure peptone solutions, he has, nevertheless, drawn conclusions as to the toxicity of various salts after testing them in a medium consisting of soil and dried blood, without taking into account the effect of the organic substances on the salts which the soil must have contained.

My results show that toxicity measurements which are made without regard to the organic substances in the medium are of little value as indicating the relative resistance of different organisms. The bearing of the facts here brought out on a number of practical problems is evident. They must be reckoned with in considering the influence of the decomposition products of humus in the soil, on soil toxins, in the preparation of antidotes, in the chemical sterilization of water and in the preservation of milk and other food materials by chemical means.

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Contributions to the Mesozoic flora of the Atlantic coastal plain,  
X.—Maryland

EDWARD WILBER BERRY

One of the first attempts to correlate the strata of the Atlantic coastal plain with those of Europe, that by John Finch<sup>1</sup> in 1824, was based on the amber-bearing lignites of the Magothy formation found at Cape Sable in Anne Arundel County, Maryland, while only a few years later Richard Harlan<sup>2</sup> mentions "dicotyledonous lignite" from the deep cut of the Chesapeake & Delaware canal. These are among the earliest references to the remains of former vegetation preserved in the Upper Cretaceous deposits of Maryland. Two incidental references by Ward<sup>3</sup> show that the important plant-localities at Grove Point, Bodkin Point, Round Bay, and Brightseat were discovered between 1887 and 1893 and collections made from them. These, however, remained unstudied in the National Museum collections until the writer took up the study of these floras in 1904. Meanwhile but a single paper had appeared which was devoted to Maryland Upper Cretaceous paleobotany. This was a short paper by Knowlton<sup>4</sup> describing the structure of the amber bearing lignite at Cape Sable.

The writer has published several preliminary papers<sup>5</sup> containing descriptions of Upper Cretaceous plants from the Maryland area. The last of these, published in 1911, brought the known Magothy

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<sup>1</sup> Finch, J. Am. Jour. Sci. I. 7: 31-43. 1824.

<sup>2</sup> Harlan, R. Trans. Geol. Soc. Penna. 1: 46-112; 256-262. 1834, 1835.

<sup>3</sup> Ward, L. F. 8th Ann. Rep. U. S. Geol. Surv. 1886-87: 871. 1889; 15th Ann. Rep. U. S. Geol. Surv. 1893-94, pt. 2: 371-372. 1895.

<sup>4</sup> Knowlton, F. H. American amber-producing trees. Science II. 3: 582-584. f. 1-4. 1896.

<sup>5</sup> Berry, E. W. Fossil plants along the Chesapeake & Delaware Canal. Jour. N. Y. Bot. Gard. 7: 5-7. 1906. Contributions to the Mesozoic flora of the Atlantic coastal plain I. Bull. Torrey Club 33: 163-182. pl. 7-9. 1906. New species of plants from the Magothy formation. Johns Hopkins Univ. Circ. N. S. 1907 7: 82-89. f. 1-5. A new Cretaceous *Bauhinia*. Torreyia 8: 218-219. 1908. Contributions to the Mesozoic flora of the Atlantic coastal plain, IV and VII. Bull. Torrey Club 37: 19-29. pl. 8. 1910; 38: 399-424. pl. 18, 19. 1911.



flora up to 88 species and recorded for the first time a species from the Matawan formation and fifteen species from the Raritan formation. During the last few years the manuscript for the Maryland Geological Survey monograph on the Upper Cretaceous has been completed so that it is now possible to present a brief summary of these floras, together with certain deductions regarding the age of the deposits.

#### THE RARITAN FLORA

The oldest of these Upper Cretaceous floras is that found in the Raritan formation, of the same age as the Amboy clays in New Jersey, whose flora occupied the late Professor Newberry for so many years. The Raritan formation in the vicinity of Raritan Bay in New Jersey carries several heavy beds of clay which have furnished a flora of 166 species.<sup>1</sup> In Maryland, however, the Raritan is not only thinner but it is predominantly sandy and has thus only yielded fragments of the varied flora found in its New Jersey extension. The Maryland Raritan flora is of especial interest nevertheless since it contains several characteristic forms of the Dakota sandstone of Kansas and Nebraska, such as *Aspidiophyllum*, *Protophyllum*, and *Araliopsis*, which have never before been found except in the type area of the West. There are nine localities in the Maryland Raritan where identifiable fossil plants have been found. These are, from northeast to southwest: Bull Mountain and Shannon Hill in Cecil County; Cedar Point in Baltimore County; Forked Creek and Drum Point RR. in Anne Arundel County; Brightseat and Glymont in Prince George's County; and East Washington Heights and Overlook Inn Road in the District of Columbia. Combining the identifications from these several localities gives the following list of species as comprising the known Raritan flora in Maryland:

<i>Cladophlebis socialis</i>	<i>Cinnamomum Newberryi</i>
<i>Asplenium Dicksonianum</i>	<i>Sassafras acutilobum</i>
<i>Podozamites lanceolatus</i>	<i>Aralia washingtoniana</i>
<i>Podozamites marginatus</i>	<i>Araliopsis breviloba</i>
<i>Czekanowskia capillaris</i>	<i>Araliopsis cretacea</i>
<i>Salix Lesquereuxii</i>	<i>Araliopsis cretacea dentata</i>

<sup>1</sup> Berry, E. W. Bull. Geol. Surv. New Jersey 3. 1911.



<i>Ficus ovatifolia</i>	<i>Araliopsis cretacea salisburiaefolia</i>
<i>Platanus Heerii</i>	<i>Diospyros primaeva</i>
<i>Aspidiophyllum trilobatum</i>	<i>Diospyros vera</i>
<i>Protophyllum Sternbergii</i>	<i>Fontainea grandifolia</i>
<i>Protophyllum multinerve</i>	

The foregoing 21 forms include two ferns, two cycad-like species, one conifer, no monocotyledons and sixteen dicotyledons. The most abundant forms, due in a measure to their maceration-resisting character, are *Aspidiophyllum*, *Protophyllum*, *Platanus*, and *Araliopsis*.

#### THE MAGOTHY FLORA

The Magothy formation which overlies the Raritan formation unconformably is much richer in plant remains. In the Maryland region the following six localities have furnished identifiable fossil plants: Deep Cut of the Chesapeake & Delaware Canal, just east of the Maryland state line in Delaware; Grove Point in Cecil County; and Bodkin Point, Round Bay, Little Round Bay, and Cape Sable in Anne Arundel County. Combining the identifications from these six localities results in the following list:

<i>Sphaerites raritanensis</i>	<i>Carpites liriophylli</i>
<i>Algites americana</i>	<i>Nelumbites primaeva</i>
<i>Gleichenia Zipppei</i>	<i>Cinnamomum Newberryi</i>
<i>Gleichenia delawarensis</i>	<i>Laurus proteaefolia</i>
<i>Gleichenia Saundersii</i>	<i>Laurus plutonia</i>
<i>Osmunda delawarensis</i>	<i>Laurus Hollickii</i>
<i>Onoclea inquirenda</i>	<i>Laurophyllum elegans</i>
<i>Asplenium cecilensis</i>	<i>Laurophyllum angustifolium</i>
<i>Williamsonia delawarensis</i>	<i>Sassafras acutilobum</i>
<i>Williamsonia marylandica</i>	<i>Leguminosites canavalioides</i>
<i>Podozamites Knowltoni</i>	<i>Leguminosites coronilloides</i>
<i>Araucaria bladenensis</i>	<i>Leguminosites omphalobioides</i>
<i>Araucaria marylandica</i>	<i>Liriodendropsis constricta</i>
<i>Brachyphyllum macrocarpum</i>	<i>Colutea obovata</i>
<i>Brachyphyllum macrocarpum for-</i>	<i>Colutea primordialis</i>
<i>mosum</i>	<i>Bauhinia marylandica</i>
<i>Protophylocladus lobatus</i>	<i>Dalbergia severnensis</i>
<i>Protophylocladus subintegrifolius</i>	<i>Crotonophyllum cretaceum</i>



<i>Sequoia heterophylla</i>	<i>Ilex severnensis</i>
<i>Sequoia ambigua</i>	<i>Elaeodendron marylandicum</i>
<i>Sequoia Reichenbachii</i>	<i>Celastrus arctica</i>
<i>Cupressinoxylon (?) Bibbinsi</i>	<i>Celastrophyllum crenatum</i>
<i>Thuja cretacea</i>	<i>Celastrophyllum undulatum</i>
<i>Juniperus hypnoides</i>	<i>Rhamnites apiculatus</i>
<i>Widdringtonites Reichii</i>	<i>Cissites Newberryi</i>
<i>Raritania gracilis</i>	<i>Cissites formosus magothiensis</i>
<i>Geinitzia formosa</i>	<i>Hedera cretacea</i>
<i>Moriconia americana</i>	<i>Hedera cecilensis</i>
<i>Carex Clarkii</i>	<i>Sterculia minima</i>
<i>Doryanthites cretacea</i>	<i>Sterculia cliffwoodensis</i>
<i>Pistia Nordenskioldi</i>	<i>Eucalyptus attenuata</i> <sup>1</sup>
<i>Sabalites magothiensis</i>	<i>Eucalyptus latifolia</i>
<i>Myrica longa</i>	<i>Eucalyptus Geinitzi</i>
<i>Salix flexuosa</i>	<i>Eucalyptus Wardiana</i>
<i>Salix Lesquereuxii</i>	<i>Cornus cecilensis</i>
<i>Populus stygia</i>	<i>Cornus Forchhammeri</i>
<i>Quercus Morrisoniana</i>	<i>Aralia groenlandica</i>
<i>Quercus severnensis</i>	<i>Aralia Ravniana</i>
<i>Ficus daphnogenoides</i>	<i>Andromeda Cooki</i>
<i>Ficus Cecilensis</i>	<i>Andromeda Parlatorii</i>
<i>Ficus crassipes</i>	<i>Andromeda Novae-Caesareae</i>
<i>Ficus Krausiana</i>	<i>Andromeda grandifolia</i>
<i>Coccolobites cretaceus</i>	<i>Myrsine borealis</i>
<i>Magnolia Hollicki</i>	<i>Myrsine Gaudini</i>
<i>Magnolia Lacoearia</i>	<i>Sapotacites Knowltoni</i>
<i>Magnolia longipes</i>	<i>Bumelia praenuntia</i>
<i>Magnolia obtusata</i>	<i>Diospyros primaeva</i>
<i>Magnolia Boulayana</i>	<i>Diospyros rotundifolia</i>
<i>Magnolia tenuifolia</i>	<i>Cordia apiculata</i>
<i>Magnolia Capellinii</i>	<i>Carpolithus septloculus</i>
<i>Illicium deletoides</i>	

The foregoing list includes exactly one hundred species, of which six are ferns; 19 are gymnosperms; 4 are monocotyledons,

<sup>1</sup> Although no changes in nomenclature are made the writer does not regard these forms as true species of *Eucalyptus* but as representing the ancestral stock of the early Tertiary species of *Myrcia*.



including well marked leaves of a fan-palm; and 69 are dicotyledons, well distributed among the natural orders and in many cases foreshadowing the wonderful display in the rich subtropical floras of the Eocene of our southern states.

It is not worth while in the present brief abstract to present an analysis of the botanical character of this flora or the indicated ecological conditions, or to trace its members in detail beyond the confines of Maryland. A hint of the problems suggested by its study is given when it is stated that many of its elements are found northward as far as west Greenland in latitude 70°, re-appearing on Marthas Vineyard and Block Island and extending from Staten Island to the valley of the Potomac, again reappearing in North and South Carolina, in western Alabama and again in northeastern Texas.

#### THE MATAWAN FLORA

The Matawan formation, a typically marine series of glauconitic sands with marine mollusca, is a unit which has been traced from Raritan Bay in New Jersey to the Potomac River. Its deposits often show evidence of shallow water origin in their lithologic character and in the contained lignite but they have yielded practically no fossil plants—a *Ficus* from New Jersey, fragments of undeterminable dicotyledons from Pennsylvania, and the following Araucarian cone-scale in Maryland, *i. e.* *Dammara cliffwoodensis*. This is a species described originally from the Magothy formation of New Jersey, one very close to the widespread *Dammara borealis* of Heer. It was found near Millersville in Anne Arundel County and is of importance since it would seem to indicate that the Magothy flora survived with but little change into at least the lower part of the Matawan formation. This fact, while of slight interest to the botanist, has this significance, that it helps to explain the association of a Magothy-like flora with a Matawan-like invertebrate fauna in the coastal plain of the South Atlantic states.

#### CONCLUSIONS

The present contribution is no place for a detailed discussion of correlation, nevertheless a statement of the general results of the writer's studies in terms of the standard European section can be given in a few words.



*Age of the Raritan.*—In a paper published in 1910 after a detailed study of the Raritan flora as typically developed in New Jersey the writer<sup>1</sup> showed that in terms of the European section it was unquestionably of Cenomanian age. The present study has only confirmed this conclusion, which is emphasized here since the late Professor Ward as well as some European paleobotanists have considered the Raritan as of Albian age while on the other hand certain American invertebrate paleontologists have held that it was even younger than Cenomanian.

*Age of the Magothy.*—The Magothy flora from its resemblance to that of the underlying Raritan has also been considered to be of Cenomanian age although the writer<sup>2</sup> has more than once suggested that it represented the Turonian stage. The paleobotanical studies carried on by the writer during the past eight years and covering the coastal plain from New York to Texas completely confirm this supposition. In preparation for the Maryland report the Upper Cretaceous floras of Europe were all restudied in the light of the most recent stratigraphic and paleontologic work in France, Germany, Bohemia, etc. Detailed comparisons have shown that no less than six of the Magothy species are known from the European Turonian, while several additional are represented in the two areas by closely related forms, so that the Turonian age of the Magothy may be regarded as established. With regard to the overlying Matawan formation, since it has an abundant fauna any statements regarding its age may be postponed for the present, although it is interesting to know that several invertebrate paleontologists have correlated it also with the Turonian, a correlation that receives some measure of support from a study of the floras.

All of the forms mentioned on the preceding pages will be fully described and figured in the forthcoming volume of the Maryland Geological Survey, in which will also be found the results of detailed studies by various authors of the genesis of the sediments, the faunas, ecology, correlation and local geology.

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<sup>1</sup> Berry, E. W. *Journ. Geol.* 18: 252-258. 1910.

<sup>2</sup> E.g. in 1912 in *The Coastal Plain of North Carolina*, pp. 309-312.



## The wild cotton plant (*Thurberia thespesioides*) in Arizona

VERNON BAILEY

(WITH TWO TEXT FIGURES)

The wild cotton plant, which harbors a native cotton boll weevil *Anthonomus grandis Thurberiae*,\* is common in certain localities in the mountains of southern Arizona. To determine the vertical, or zonal, range of the plant and weevil I visited, from October 19 to November 15, many of the mountain ranges where the plant was known to occur and others where it might occur, and gathered such data on its distribution, abundance and habits as the limited time would admit. Additional information was obtained from Professor J. J. Thornber, of the State University at Tucson.

### DISTRIBUTION

The plant was studied mainly in the Santa Catalina and Santa Rita Mountains, and in the mountains about Globe and Roosevelt. The Dragoon, Graham, Pinal, Tortilla, Salt River, and Date Creek Mountains were visited without finding it.

In Sabino Canyon, on the south side of the Santa Catalina Mountains, where both *Thurberia* and the weevil are abundant, the limits of range on various slopes were worked out with great care. These limits are given in some detail as the subsequent localities showed little or no extension of zonal range. The lowest *Thurberia* plants found were at 3,600 feet on a west slope, 600 feet above the bottom of the canyon, and they were common at 3,800 feet on other west slopes. On open southwest slopes in the upper part of Sabino Canyon they began at 4,000 feet and extended up to 5,000 feet in the upper division of Lower Sonoran zone. That is they range from the upper limits of giant cactus and paloverde to the lower limits of juniper, nut pine, and Emory oak. This range seems to hold true except that *Thurberia* occurs, so far as I can learn, only on south, west or east slopes and consequently does not go so low as do most of the plants of its zonal

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\*Pierce, Jour. Agr. Research 1: 90. 10 N 1913.



subdivision which range over the colder slopes. It does not usually occur near the bottoms of canyons but prefers the hottest, driest open slopes or open side gulches in rocky situations. Its range, however, is not continuous even in the most favorable parts of its own belt, as it occurs only in interrupted areas on each of many isolated and widely separated mountain ranges. It is therefore especially important to know the more abundant plants with continuous ranges which mark its subdivision, so as to know where to look for it.



FIG. 1

FIG. 1. *Dasyilirion Wheeleri*; near Globe, Arizona. November, 1913.



FIG. 2

FIG. 2. *Thurberia thespesioides*; in Sabino Canyon, Santa Catalina Mountains, Arizona. October, 1913.

The most conspicuous plant with which *Thurberia* seems always to be associated, is the sotol (*Dasyilirion Wheeleri*). This has the same lower limit but runs a little higher and overlaps the lower edge of Upper Sonoran zone. The sotol is a very abundant and conspicuous plant, fully encircling most of the mountain ranges that reach above Lower Sonoran zone.

Other plants generally associated with *Thurberia* and marking



its belt are given in the following list. Still others from the upper and lower zones overlap and mix with it or extend below or above it on colder or warmer nearby slopes. The presence of several of the following species is a good indication that *Thurberia* may also occur in the same locality:

<i>Dasyilirion Wheeleri</i>	<i>Crossosma Bigelovii</i>
<i>Quercus oblongifolia</i>	<i>Tecoma stans</i>
<i>Vauquelinia californica</i>	<i>Rhus mollis</i>
<i>Anisacanthus Thurberi</i>	<i>Atriplex angustifolia</i>
<i>Acacia suffrutescens</i>	<i>Aesclepias linearis</i>
<i>Calliandra erophylla</i>	<i>Chrysoma laricifolia</i>
<i>Erythrina flabelliformis</i>	<i>Brickellia californica</i>
<i>Dodonaea angustifolia</i>	<i>Abutilon Lemmoni</i>

In the Santa Rita Mountains *Thurberia* is abundant on side slopes of Stone Cabin Canyon, mainly on east and west exposures, from 4,000 to 4,500 feet. A few scattered plants were found on banks along the stony-sided dry wash, but they were most abundant on steep, open, very stony, east and west slopes. None were found on north slopes which otherwise seemed just as suitable for it, and there were no real south slopes at this end of the range. The almost level plain at the northwest base of the mountains comes up to 4,000 feet, which prevents the plant from going lower, as it might otherwise do. The plants with which it is most closely associated here are mainly the same as in the Santa Catalina Mountains. Sotol and the blue oak are invariably with it, but also range higher. It is found side by side also with *Prosopis velutina* of Lower Sonoran and *Mimosa biuncifera* of Upper Sonoran, both of which overlap along the edges of the zones.

Near Globe, north of the Gila Valley, *Thurberia* is abundant with the sotol among big granite boulders on a steep west exposure a mile north of the town. It begins near the railroad at the bottom of the slope at 3,500 feet and extends up to 3,800 feet. Giant cactus grows on adjoining southwest exposures and junipers on an adjoining northeast exposure close by at the same level.

Near Fish Creek Canyon, on the stage road from Roosevelt to Phoenix, there is an extensive area of *Thurberia* which O. F. Cook and E. W. Hudson have carefully examined. I went through this in the evening when it was too dark to identify many of the



plants, but giant cactus and sotol occupy slightly different exposures in such close proximity as to appear all mixed up. Mr. Hudson marked the range of *Thurberia* along this section on the contour map, bringing it down to about 2,500 feet in places on the canyon sides but showing most of the range to be on dry slopes and mesa tops at about 3,000 feet. This region is so exceedingly rough and broken that the zones are hopelessly mixed and run abnormally high and low.

The plant has been collected in several other mountain ranges but many of the records are so indefinite as to be of little use in defining its zonal range. Professor Thornber showed me specimens from the Rincon Mountains (Manning Trail), the Mule Mountains, Dragoon Summit and Fort Bowie. In the National Herbarium there are specimens from the Rincon Mountains at 4,500 feet altitude, Davidson Spring, Arizona (collected by Dr. Rothrock in 1874), and from the Mexican Boundary Line south of Bisbee (collected by Dr. Mearns in 1892), and from some of the localities previously mentioned. There are also specimens labeled "Arizona" and one labeled Mexico.

Localities where *Thurberia* has been found in Arizona have been indicated on maps and colored belts drawn to show where it has been, or is likely to be, found at irregular intervals. These belts represent sections of the upper division of Lower Sonoran zone but are carried out only where it occurs on mountain slopes with south, west or east exposures. The plant has not been found, so far as I am aware, on the northern, or cold, slopes of mountains nor in open valleys or plains country.

#### THE PLANT

The plant is a shrub, usually four to ten feet in height, with a woody stem often two inches in diameter. It has an open, spreading top, deeply cut three-lobed leaves, large pink flowers and small naked capsules, which resemble little cotton bolls without enveloping squares. The capsules are full of naked black seeds and a little fuzzy cotton fiber clinging to the inner walls. The plant blossoms late in summer and on October 19, in Sabino Canyon of the Santa Catalina Mountains, the flowers were gone. The bolls were practically all full grown with ripe



seeds and a few had ripened sufficiently to open. By October 26 in the Santa Rita Mountains many of the bolls had ripened and opened, and on November 5, near Globe, they were about half opened. The uninjured bolls do not drop off when ripe but stand erect and open so that the seeds are gradually scattered by the wind. Many plants carry old and empty last year's bolls. The young branches of the plant are herbaceous in appearance and the woody stems are rather soft and brittle. One trunk an inch in diameter has seven or eight annual rings.

In places some old plants show evidence of having been grazed down by stock during previous seasons. New sprouts have come up from the old stumps and the plants are thriving, but the evidence that stock eat the plant, even down to the woody stems, suggests a cause for the present absence of *Thurberia* from open land, and its restricted habitat on steep and usually very rocky slopes. In most of the places where I have seen the plant in any abundance it was growing among big rocks where cattle could not get at it. In this extremely arid region an edible and unarmed shrub does not stand much chance where cattle are driven to eating many rank tasting and thorny bushes and even the spiniest cactus plants.

From the great abundance of seeds ripened and scattered abroad each season it would seem that the plant should reproduce itself profusely. That it does not may be due in part to the abundance of sparrows which winter in the foothills and are eagerly searching for such good sized and edible seeds as *Thurberia* yields, and in part to the numerous mice which probably get most of the seeds that the sparrows do not find.

#### THE BOLL WEEVIL

The weevil was abundant throughout the vertical range of *Thurberia* in Sabino Canyon in the Santa Catalina Mountains and in Stone Cabin Canyon in the Santa Rita Mountains. The bolls occupied by weevils do not open when they ripen, or dry up, and each of these unopened bolls almost invariably contains a weevil.

Many were gathered and brought back in tin cans. No weevils were found outside of the bolls which were ripening when



I first saw them October 19, and were mostly ripe when last seen November 6. Weevils have been found also in other canyons of the Santa Catalina, Rincon, and Santa Rita Mountains, but have not been found north of the Gila. At Globe I spent nearly a whole day examining thousands of bolls without finding a trace of weevils. Cook and Hudson did not find them in the Fish Creek region.

BIOLOGICAL SURVEY

UNITED STATES DEPARTMENT OF AGRICULTURE



## Notes on two North American ferns

MARGARET SLOSSON

(WITH PLATE 7)

The smallest species of the ferns found in the United States, the minute filmy fern *Trichomanes Petersii*, has been supposed not to occur elsewhere. Originally discovered in Hancock county, Alabama, not far from the Sipsev River, its range is cited in Christensen's *Index Filicum* as Alabama, Mississippi and Georgia. Specimens from these states are in the Underwood Herbarium at the New York Botanical Garden. Chapman, in all three editions of his *Flora*, reports it as having been sent him among mosses from Pensacola, Florida, but apparently no specimens can be found to substantiate this statement. A letter in the Underwood Herbarium, written in reference to this by Mr. C. D. Beadle in 1902, states that on examining the material of *T. Petersii* in the Biltmore collection in North Carolina, which contains the Chapman Herbarium, he finds it is all from the counties of Winston and Etowah in Alabama, with the exception of a single specimen collected by M. A. Curtis, without locality or date cited. Mr. Curtis is not living and it is not likely that any information about his specimen is to be had. It is possible that young specimens of the West Indian *Trichomanes punctatum*, which does occur in Florida,<sup>1</sup> may have been mistaken by Chapman for *T. Petersii*. However that may be, it would be interesting to know the facts of the case, for many species known to the West Indies find a foothold in Florida, and *T. Petersii* must now be credited to Santo Domingo! A small specimen is in the Underwood Herbarium, consisting of a rhizome with four fertile fronds, found tangled in a mat of *T. hymenoides*, collected in woods near Constanza, Santo Domingo, at an altitude of 1,260 meters, March, 1910, by H. von

<sup>1</sup> Specimens of this species from Florida are in the Underwood Herbarium, collected in hammocks near the Homestead Road, between Cutler and Longview Camp, *Small & Carter 1478*, and there are also specimens of another West Indian *Trichomanes*, *T. Krausii*, collected partly in the same locality, *Small & Carter 1479*, and partly in hammocks near the Hempstead Trail, near Camp Longview, *Small & Carter 1500*.



Türckheim (*no.* 3066). This specimen is figured on PLATE 7, FIGS. 2 and 4. It agrees exactly in character with the United States plant (FIG. 3). No differences are to be found in the venation, size of the cells and thickness of the cell-walls of the laminae and of the lips of the involucre, size and character of the spores, trichomes of the margins of the laminae, etc.

This is not the first instance of species known to the United States occurring on the high mountains of Santo Domingo. Dr. I. Urban<sup>1</sup> has recently cited some six or seven species, at least three of which, *Chimaphila umbellata* (L.) Nutt., *Sphenopholis obtusata* (Michx.) Scrib., and *Agrostis perennans* (Walt.) Tuckerm., are to be found in the vicinity of New York City! One is a fern, *Pellaea ternifolia* (Cav.) Link, which, however, ranges from Chile to Texas.

A new fern species has been unexpectedly added to the flora of the United States lately by the discovery of Dr. Rydberg and Professor Garrett, while collecting plants in Utah in the summer of 1911, of two small colonies of maidenhair, fast in the cracks of the wall of the Armstrong Cañon. The plants were found on the north side of a small branch of the cañon, near the Edwin Bridge. The two colonies grew in partial shade, less than a hundred yards apart, both imbedded in horizontal crevices of sandstone, under overhanging rocks.

These plants represent an undescribed species, and I am indebted to Dr. Rydberg for the privilege of describing it. It is related to *Adiantum Capillus-Veneris*, but differs in several particulars, noticeably in the flexuose rachises, peculiarly tapering bases of the fertile pinnules, and long heavy indusia. It may be described as follows:

***Adiantum rimicola* Slosson sp. nov.**

Rhizome creeping but often closely branched, thus making the fronds appear tufted, about 2 mm. in diameter, thickly chaffy; scales 4 mm. or less long, dark brown, linear or lanceolate, acuminate, entire or with one or more sharp lobes, long-celled; similar scales on the lower parts of the stipes; plant otherwise glabrous; stipes up to 15.3 cm. long, dark reddish-brown, flattened or somewhat grooved on face, otherwise rounded; laminae up to 17.5 cm. long, up to 12 cm. broad, ovate-deltoid or the smaller ovate-oblong,

<sup>1</sup> *Symbolae Antillarum* 6: 289. 1909.



broadest at base, bipinnate or rarely tripinnate; pinnae and pinnules alternate, not articulated at base, conspicuously stalked, diverging from the flexuose rachises at an angle of  $45^{\circ}$ – $90^{\circ}$ : basal pinnae with 2–5 divisions, uppermost pinnae often simple; ultimate divisions (pinnules) rather bright often bluish-green, mostly flabelliform from a narrowly cuneate base, the basal sides entire and often unequal, flaring and often recurving, the upper margin broadly rounded or rarely subdeltoid, cleft  $\frac{1}{8}$ – $\frac{1}{3}$  of their depth into 1 or 2 lobes; lobes sometimes entire, usually once or more times slightly notched, between the notches usually completely recurved to form the indusia but when sterile sharply denticulate; sterile pinnules flatter at base, often scarcely cuneate, otherwise similar to the fertile; apical pinnules the largest, up to 2.5 cm. broad and 2 cm. long; veins flabellate-dichotomous, about 5–7 times forked, the basal fork and the outer branches of the second fork often dark brown like the rachis and edging the leaflet's base; texture firm; indusia heavy, up to 8.3 mm. long, subentire or erose; spores verrucose.

Type in the Underwood Herbarium at the New York Botanical Garden, collected in the Armstrong Cañon, in southeastern Utah, altitude 1,600–1,800 meters, August 4–6, 1911, *Rydberg & Garrett 9423*. Represented also by *Rydberg & Garrett 9422*. A fertile frond is shown on PLATE 7, FIG. 1.

#### Explanation of plate 7

FIG. 1. *Adiantum rimicola*; fertile frond, natural size, *Rydberg & Garrett, 9423*.

FIGS. 2–4. *Trichomanes Petersii*; 2, plant from Santo Domingo,  $\times 3\frac{1}{4}$ , *H. von Türckheim 3066* in part; 3, fronds collected near Gadsden, Alabama,  $\times 3\frac{1}{4}$ , *Pollard & Maxon 353*; 4, part of plant from Santo Domingo, much enlarged, *H. von Türckheim 3066* in part.







# INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1914

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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**Bates, J. M.** Some new Nebraska plants. Am. Bot. 20: 16-18. F 1914.

Includes *Helianthus Besseyi* sp. nov.

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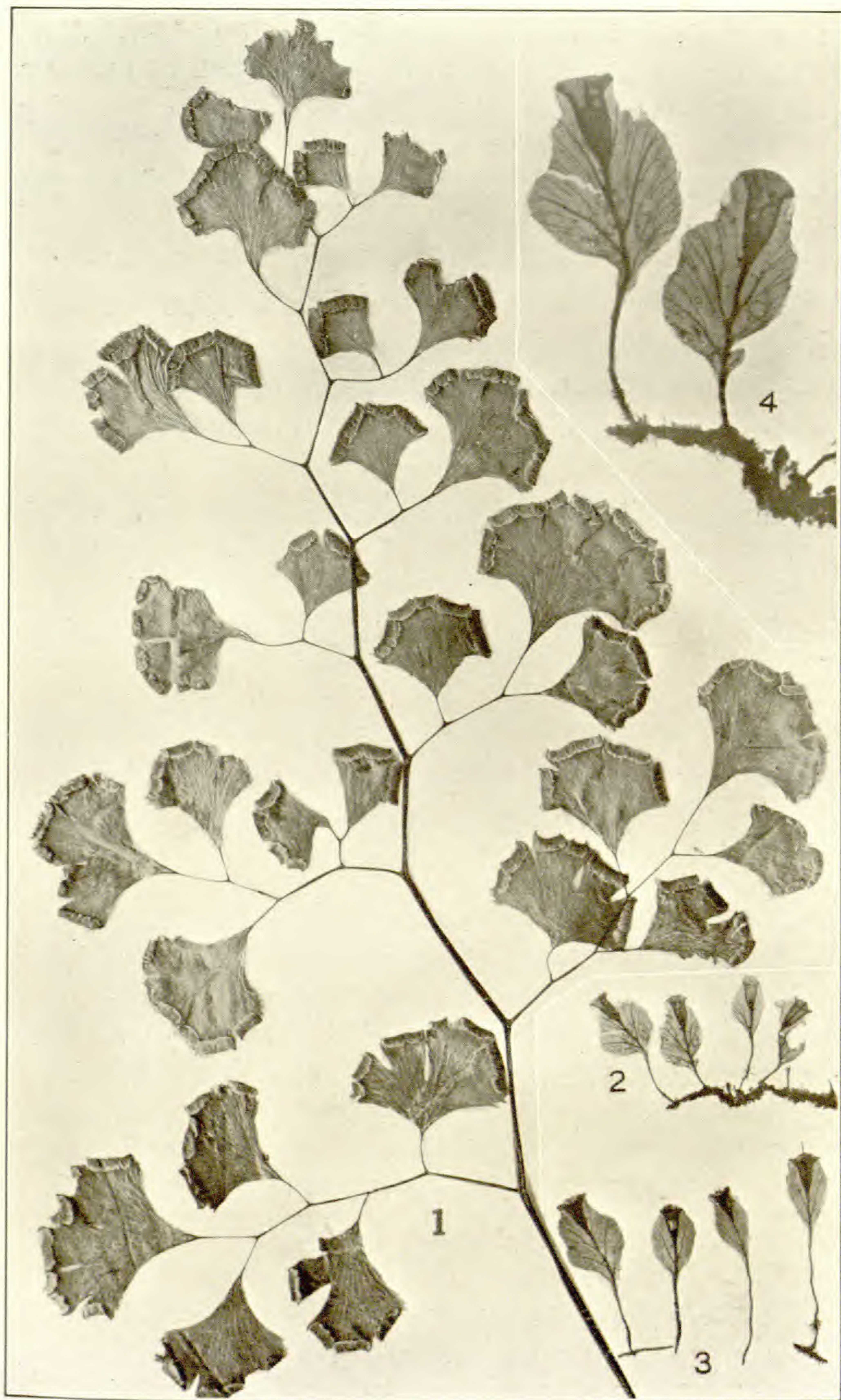


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A plant from Brazil.





1. ADIANTUM RIMICOLA SLOSSON  
2-4. TRICHOMANES PETERSII A. GRAY



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OF THE

# TORREY BOTANICAL CLUB

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### CONTENTS

Notes on Rosaceae—VII . . . . . P. A. RYDBERG 319

The appearance of polar bodies in the spermogenous tissue of *Ricciocarpus natans* (L.) Corda. (Plate 8.) . . . . . RUTH S. ATWELL 333

Slope exposure as a factor in the distribution of *Pseudotsuga taxifolia* in arid Parts of Washington . . . . . GÖTE TURESSON 337

INDEX TO AMERICAN BOTANICAL LITERATURE. . . . . 347

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BULLETIN  
OF THE  
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JUNE, 1914

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Notes on Rosaceae—VII\*

PER AXEL RYDBERG

ALCHEMILLA

In the North American Flora this genus is taken in a narrow sense, *i. e.*, as Linnaeus originally understood it. The genus *Aphanes* L., which was merged in *Alchemilla* by Scopoli, differs not only in the habit, being leafy-stemmed annuals, instead of scapose perennials with rootstocks, but the stamens are usually solitary, rarely more numerous, and opposite to one or more of the sepals, instead of being 4 and alternate with the sepals. The disk in the throat of the hypanthium, so characteristic of the typical *Alchemillas*, is almost obsolete in *Aphanes*.

The so-called *Alchemillas* of America are perennials, some of them in habit not so unlike the Old World species; but in all the stamens are only 2 and inserted on the inside of the disk instead of the outside, and the anthers extrorse instead of introrse. For these the subgeneric name *Lachemilla* of Focke was adopted, except for one species of exceptional habit, which was made into a distinct genus *Zygalchemilla*.

All the species of true *Alchemilla* have their home in Europe. Only five of them are either adventive or naturalized on this side of the Atlantic and all are confined to the northeastern corner of North America.

*Alchemilla alpina* L. ranges in America from Greenland to the island of Miquelon and the White Mountains of New Hampshire.

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\* These notes, continued from Bull. Torrey Club 38: 367 (1911), are supplementary to the monograph in volume 22 of the North American Flora.

[The BULLETIN for May (41: 265-318. pl. 7) was issued 29 My 1914.]



*Alchemilla pratensis* F. W. Smith and the three succeeding species are segregated from *A. vulgaris* L. *A. pratensis* has usually been known here under the name *A. vulgaris* and has become naturalized from Nova Scotia to Massachusetts.

*Alchemilla Wichurae* Buser has been collected only in East Greenland.

*Alchemilla glomerulans* Buser and *A. filicaulis* Buser range on this side of the Atlantic from Greenland to Labrador, and the latter has been collected also on Newfoundland.

### APHANES

See remarks under *Alchemilla*. The true *Aphanes arvensis* L. has been collected in America in Nova Scotia, evidently there an introduced plant. The American plants, included in it or confused with it, have much smaller flowers, the hypanthium being only 1 mm. instead of nearly 2 mm. long. They were distinguished in the North American Flora as four species, differing in minor characters.

*Aphanes australis* Rydb. includes all specimens collected in the southeastern United States. It differs from those on the Pacific coast in the short ovate sepals, connivent in fruit. In the western species the sepals are lanceolate to ovate-lanceolate and ascending in fruit.

*Aphanes macrosepala* Rydb. differs in the elongated sepals, nearly as long as the densely pilose hypanthium.

*Aphanes occidentalis* (Nutt.) Rydb. and *A. cuneifolia* (Nutt.) Rydb. have short sepals and puberulent or glabrous hypanthium. They differ from each other in the form of the leaves.

### LACHEMILLA

See remarks under *Alchemilla*.

*Lachemilla orbiculata* (R. & P.) Rydb. and *L. venusta* (Cham. & Schlecht.) Rydb. belong to a group in habit and leaf-form approaching the genus *Alchemilla*, but the plants are sarmentose. Both *Alchemilla orbiculata* R. & P. and *A. pectinata* HBK. have been recorded for Mexico and Central America. It is evident that the specimens labeled as either of the two constitute but one species. A closer examination of literature and specimens has revealed



that the two supposed species are identical, and that *Lachemilla orbiculata* ranges from Central Mexico to Bolivia.

The rest of the North American species except *L. ocreata* resemble *Aphanes* more strongly in habit and leaves, but they are all perennials.

*Lachemilla procumbens* (Rose) Rydb. is perhaps the most common of the Mexican species. Specimens of it are usually labeled *Alchemilla sibbaldiaefolia* HBK. Humboldt, Bonpland & Kunth's figure\* shows that the original *A. sibbaldiaefolia* has different hypanthium, inflorescence and leaves, the latter in fact less like those of *Sibbaldia procumbens* than those of *L. procumbens* are.

*Lachemilla domingensis* (Urb.) Rydb. was based wholly on the description of *Alchemilla domingensis* Urb., no specimens of any *Lachemilla* having been seen from the West Indies at that time. Long after the publication of that part of the North American Flora containing *Lachemilla*, the first specimens were seen, but both the place in the key and the description were found to be correct and nothing needs to be added.

The following species were proposed as new: *Lachemilla Schiedeana* Rydb., *L. Pringlei* Rydb., *L. orizabensis* Rydb., and *L. Bourgeaui* Rydb. The first two were based in part on *Alchemilla hirsuta campestris* Cham. & Schlecht., which was described from a mixture.

*Lachemilla ocreata* (Donn. Smith) Rydb. is a very peculiar plant, apparently leafless, the leaves being reduced to connate imbricate sheaths, cleft into linear divisions. It is closely related to the South American *Alchemilla nivalis*.

### ZYGALCHEMILLA

This genus was based on *Alchemilla pinnata* R. & P., which has pinnate instead of palmately lobed leaves, as all the other species of the tribe have. This character, as well as the 3-nerved sepals and bractlets, constitutes the basis for the generic segregation. A rather interesting fact in its history may be recorded. Remy† described a supposed new species as *Alchemilla pinnata*, but finding that the name was preoccupied by *A. pinnata* R. & P.,

\* Nov. Gen. & Sp. 6: pl. 561.

† Ann. Sci. Nat. Bot. III. 6: 354. 1846.



he changed it to *A. achilleaefolia* Remy.\* Remy's species was based on Dombey's plant from Peru, he overlooking the fact that this plant belonged to the original *A. pinnata* R. & P. He, therefore, originally described the same plant under the same name, and consequently the second synonym was superfluous.

### SANGUISORBA

In the North American Flora, the genus *Sanguisorba* was taken in its original narrower sense, *i. e.*, the perennial species with only 2-4 stamens, and 1 pistil with muricate papillose stigmas. Of this genus, four native North American and one introduced species, *S. officinalis* L., were recognized.

*Sanguisorba canadensis* L. is limited to the northeastern part of this continent. The plants referred to it from the northwest belong to the following two species.

*Sanguisorba sitchensis* C. A. Meyer [*S. latifolia* (Hook.) Coville] has white flowers. Piper in his Flora of Washington,† makes the following remark: "The red-flowered form of this species is referred by Howell to *S. officinalis* L. The white-flowered ordinary form was referred to *S. media* L. in Hooker's Flora." This statement is not correct. Hooker's *S. media* is described as having red flowers and is the same as *S. Menziesii* Rydb., described in the North American Flora. Howell's *S. officinalis* has, as stated, red flowers, but the filaments are but slightly exerted and filiform, not twice as long as the sepals nor dilated. It is the same as *S. microcephala* Presl.

### POTERIDIUM

I believe that the genus *Poteridium* Spach should be reëstablished for the annual species of *Sanguisorba* with brush-like stigmas. The first species of this genus was originally described as *Poterium annuum* Nutt. in Hooker's Flora Boreali-Americana. Hooker adopted Nuttall's manuscript name, which the author had applied to the species growing in Arkansas and neighboring states, but the specimens treated in that flora belong to the Pacific coast species. Hooker's *Poterium annuum* is, therefore, a composite. The

\* *L. c.* III. 8: 224. 1847.

† *Contr. U. S. Nat. Herb.* 11: 336. 1906.



question then arises, which of the two species should be called *Poteridium annuum*. As Nuttall himself afterwards in Torrey & Gray's Flora separated the two, and applied *Poterium annuum* to the eastern plant and *P. occidentale* to the western one, it is best to apply the names in that way.

### POTERIUM

This genus resembles *Sanguisorba* in habit, but the stamens in the staminate flowers are numerous and declined; the pistils are usually 2, and the stigmas brush-like. Linnaeus originally had two species in this genus, of which the first, *P. Sanguisorba*, for several reasons must be regarded as the type. To use *Poterium* for the second species, *P. spinosum* L., as Focke has done,\* is not correct. For that genus the name *Sarcopoterium* Spach should be used.

### ACAENA

This genus has been taken in its narrower sense, excluding the genus *Ancistrum*.

*Acaena agrimonioides* HBK. I have seen no specimens agreeing with the original description of this species. All specimens seen and so named belong to *A. elongata*. Bitter, in Bibliotheca Botanica,† cited it as a synonym and on page 324 he stated that it is "to be regarded as synonymous with *A. elongata*," but nowhere does he give any reason for so doing. In the original diagnosis of *A. agrimonioides*, the leaflets are described as being 8-10 lines (*i. e.*, 16-20 mm.) long, and the lower gradually smaller. In all specimens of *A. elongata* I have seen from Mexico the leaflets are rarely 15 mm. long and the lower pairs scarcely smaller than the upper. Although *A. agrimonioides* is unknown to me and my description in the North American Flora was drawn from the original Latin diagnosis, I can but regard it as distinct from *A. elongata*.

*Acaena elongata* L. Hemsley in his Biologia Centrali-Americana‡ admitted four species of *Acaena* to Mexico, viz. *A. agrimonioides* HBK., *A. elongata* L., *A. lappacea* R. & P. and *A.*

\* Engl. & Prantl, Nat. Pflanzenfam. 3<sup>3</sup>: 45.

† 74: 28.

‡ 1: 378.



*laevigata* Vahl. Under *A. agrimonoides* HBK., he cited only Humboldt & Bonpland's specimens and hence held the same opinion of this species as I do.

In the North American Flora I have given my reasons for excluding *A. lappacea* and *A. laevigata* from the Mexican flora. There is no question regarding *A. laevigata* not being found there, neither is there in regard to *A. lappacea*, unless Bitter is correct in regarding it as a synonym of *A. elongata*. Against this speaks the fact that the typical *A. elongata* has not been found in Peru. In giving the distribution of *A. elongata*, Bitter gave "perhaps also in Peru," which shows that he had seen no specimens from that country. The typical *A. elongata* he described under the name *A. elongata gracilis* n. var. (an altogether unnecessary name), and this is limited by him to Mexico. It extends, however, through Central America to Colombia, but is not found as far south as Ecuador. Here it is represented by *A. elongata robusta* Bitter. If any form extends into Peru, it is this, which may be *A. lappacea*. My sincere opinion, however, is that *A. lappacea* was redescribed by Bitter under the name *A. torilicarpa* n. sp.

*Acaena californica* Bitter. The Californian species of *Acaena* has had a rather varied history. It was first treated by Hooker and Arnott in the Botany of Beechey's Voyage under the name *A. pinnatifida*, the authors supposing that it was the same as *A. pinnatifida* R. & P. of Peru. Torrey saw that it was not, but rather closer to *A. trifida* R. & P. and even listed it as such,\* although it was not described under that name until twenty years later, in the Botany of California. For some years I have known that even this identification was erroneous, but have regarded it as the lost *Acaena tridactyla* Presl.† That author gives as the type locality "Mexico occidentale." As California at the time Haenke visited it was a part of Mexico, this interpretation does not seem out of place, and I still think it possible that it is not far from the truth. Bitter,‡ however, claimed that he had seen the type at Prague and identified it as the South American *A. trifida* R. & P. It is possible that Haenke, who also

\* Pac. R. Rep. 4: 84. 1856.

† Epim. Bot. 201. 1849.

‡ Bibl. Bot. 74: 294.



collected in Chili and Peru, might have mislabeled the specimens. On the strength of this claim of Bitter's, I have reluctantly adopted his name *A. californica*. Bitter distinguishes not less than five varieties of this species. Anyone who knows the variability of the plant can see only individual variation in these varieties.

### AGRIMONIA

Mr. Bicknell\* in his paper on *Agrimonia* states: "Perhaps no one of our long-known plants has more effectually escaped a right understanding by botanists than the familiar Agrimony of the Eastern States, current in local floras and text-books as *Agrimonia Eupatoria* L." In fact, the genus as a whole was poorly understood here in America, before Mr. Bicknell took up the work on the same, and from the publication of his paper dates really our true conception of the species. It is strange, however, that this should have been the case, when Dr. Wallroth had presented a very good paper on the genus in 1842. It is true that most monographic work done in Europe on North American plants is rather poor and unreliable, and therefore we are liable to ignore such work done abroad. This might have been the reason why Wallroth's species have not been adopted. The writer took up most of Wallroth's names in the North American Flora. That Mr. Bicknell did not do so was unfortunate, as he will now not get the full credit for what his paper really was worth to us. The main reasons for his not taking up Wallroth's names were the following: (1) at that time the unfortunate Madison amendments to the Rochester Code were in force making older varietal names supplant specific names; (2) at that time the names proposed in Muhlenberg's Catalogue were generally regarded as properly published. In fact, most of them should be regarded as *nomina nuda*, for the adjectives added to these names evidently were not intended as descriptions, but as a part of the trivial or common name. If these two causes had not influenced Mr. Bicknell, I should not have had occasion to change his nomenclature except in one case, viz. *Agrimonia striata* Michx., which he had misunderstood. Even in this case, he was really not to blame. See below under that species.

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\* Bull. Torrey Club 23: 508. 1896.



*Agrimonia gryposepala* Wallr. This has gone under the name of *A. Eupatoria* L. ever since Pursh's time or perhaps even since Walter's time. In general habit and in the size of the fruit it approaches more the European *A. Eupatoria* than any other of our North American species; but the structure of the fruit and the flowers are different. See the key. It was first distinguished by Muhlenberg, who gave it the name *A. Eupatoria hirsuta* in his Catalogue in 1813, but, as stated before, without proper description. It was subsequently published under Muhlenberg's name by Torrey in his Flora, in 1824. The first specific name, however, is that of Wallroth in 1842. His is also the first really good and extensive description. He was the first one to point out the peculiar sepals and characteristic arrangement of the bristles of the fruit, which distinguish it from any other of the species of the United States. It is therefore very appropriate that his specific name is now restored. The specimens from California, Arizona, New Mexico, and Mexico are usually somewhat different, but no constant characters have been found on which to base a separation.

*Agrimonia macrocarpa* (Focke) Rydb. This is the only North American species which approaches *A. gryposepala* in the structure of the sepals and of the fruit. It differs, however, in the elongated hypanthium and the more copious pubescence. Focke made it a variety of *A. parviflora*, to which it has little relationship. The only characters in which it approaches that species are the form (not the number) of the leaflets and the coarse pubescence. The structure of the fruit and the flower and the number of the leaflets are not at all the same. Its range is limited to Guatemala, from where the following specimens have been seen:

GUATEMALA: Coban, 1907, *von Tuerckheim 1377*; Dept. Huchuetenango, 1896, *Seler 2594*.

*Agrimonia rostellata* Wallr. Muhlenberg was also the first one to distinguish this species and gave it in his Catalogue the name *A. Eupatoria glabra*, but without a proper description. De Candolle mistook it for *A. parviflora* Ait., probably because it has the smallest flowers of all our North American species. It has also the smallest fruit, which is different from the rest in that it is more rounded at the base and less grooved. Mr. Bicknell



adopted for this species the name *A. striata* Michx. See under that species, where the case is discussed in full.

*Agrimonia microcarpa* Wallroth. The first name for this species was *A. pumila* Muhl., printed in his Catalogue. The only thing said about this species beside the name is: "Small, Miss.," which means that the trivial name is small agrimony and that it grows in Mississippi. Now the only small agrimony growing in Mississippi is the present species and Mr. Bicknell evidently identified *Agrimonia pumila* Muhl. correctly. It had never been published under that name however, before Bicknell adopted it in his paper. There is no question that the species that Bicknell had in mind and that I now discuss is *A. pumila* Muhl. There is even more doubt that *A. microcarpa* Wallr. belongs to this plant. Wallroth cites three specimens: Pennsylvania (*Moser*), southern Georgia (*Beyrich*), and Jalapa (*Schiede*). As there is no indication of type, the first specimen should be regarded as such. I have seen no specimen of it from Pennsylvania, the nearest being from Maryland. In the former state it is represented by *A. platycarpa* Wallr. It is not likely that Wallroth should have confused the two species, as he is the author of both. Beyrich's plant undoubtedly belongs to *A. microcarpa* as here understood, but Schiede's plant from Jalapa, Mexico, belongs to *A. Pringlei*. The latter is glandular-granuliferous and must, therefore, be placed near *A. striata*. No one before Bicknell seems to have noticed the tuberous character of *A. microcarpa* and the other non-glandular species. This is not found in *A. Pringlei*.

*Agrimonia platycarpa* Wallr. This has not been recognized since Wallroth's time. It is closely related to *A. microcarpa*. In the latter the leaves are situated near the base of the stem, having either 3 leaflets of nearly the same size, or else also an additional much smaller pair below. In *A. platycarpa* the leaflets are 5 or 7 and the lower only slightly reduced. The fruit in *A. platycarpa* is broader than in *A. microcarpa*, usually broader than long, and with a more prominent flange or rim. Its range is more northern than that of *A. microcarpa*.

*Agrimonia pubescens* Wallr. This was first distinguished by Torrey & Gray under the name *Agrimonia Eupatoria mollis*. It was raised to specific rank by Britton,\* following the Madison

\* Bull. Torrey Club 19: 221. 1894.



amendment and well knowing the publication of *A. pubescens* Wallr., which he gives as a synonym.

*Agrimonia Bicknellii* (Kearney) Rydb. This was well described by Mr. Bicknell\* as a variety of *A. mollis*, but without a varietal name. This was supplied a year later by Mr. Kearney. It is true that the characters separating *A. pubescens* (= *A. mollis*) and this species are not absolute and that intermediate forms are not lacking. *A. pubescens* is at home in the central states west of the Alleghenies, but extends east thereof into Virginia and Georgia. The home of *A. Bicknellii* is the Atlantic coast, but it is found as far west as Pennsylvania and Tennessee. In the Mississippi valley only *A. pubescens* is found and on the Atlantic border only typical *A. Bicknellii*. The intermediate forms are found in the Alleghenian region, where the ranges of the two overlap. These two species are the nearest American representatives of the European *A. Eupatoria*, but have much smaller fruit. Especially is *A. Bicknellii* sometimes hard to distinguish from *A. Eupatoria* without the fruit. Two western specimens in the United States National Herbarium I have determined doubtfully as *A. Bicknellii*, viz. one collected at Fort Snelling, Minnesota, by Mearns, and the other at Naperville, Illinois, by Umbach. They may belong to *A. Eupatoria* L.

*Agrimonia Eupatoria* L. Britton and Bicknell believed that this species was not found at all in America. No specimen has been seen from the East, where the species is most likely to be found introduced. There are, however, two specimens, one in the National Herbarium and one in the herbarium of the Missouri Botanical Garden, which without any doubt belong to the species. Holzinger's specimen, especially, has the fruit so well developed that there is no question of the identity. The specimens are:

MINNESOTA: Winona, 1889, Holzinger.

WISCONSIN: Mirror Lake, 1903, Eggert.

*Agrimonia striata* Michx. This species has been badly misunderstood. Probably the real cause of this is that in Michaux's herbarium there are two specimens on the sheet of *A. striata*. The left-hand specimen represents the plant, here treated under that name, and the right-hand specimen is one of *A. rostellata*.

\* Bull. Torrey Club 23: 517. 1896.



One of the authors of Torrey & Gray's Flora, probably Dr. Gray, had seen this sheet, for they cite *A. striata* Michx. and appendage an exclamation point (!) after the same. They gave this as a synonym of their *A. Eupatoria parviflora*, which was based on *A. parviflora* DC., the same as *A. rostellata* Wallr. They also cite under this a specimen collected by Dr. Pitcher. This specimen is in the Torrey herbarium and belongs also to *A. rostellata*. This shows that Torrey and Gray regarded *A. striata* Michx. the same as what we now call *A. rostellata*. It was, therefore, not strange that Mr. Bicknell followed them, especially as one of the specimens in Michaux's herbarium belonged to that species. He, therefore, proposed a new name, *A. Brittoniana*, for the plant represented by the left-hand specimen in Michaux's herbarium and here treated under the name *A. striata*. By the courtesy of the Gray Herbarium we have received a print of a photograph of the type of *A. striata*, and this shows that the left-hand specimen is to be regarded as the type, not only bearing the name *Agrimonia striata* Michx., but also the word Canada on the labels. This is also the only species of the two which agrees with the description: "*fructibus . . . sulcato-striatis.*"

*Agrimonia Pringlei* Rydb. One specimen of this, as said before, was included in *A. microcarpa* by Wallroth. It is true that it resembles that species, *A. platycarpa*, and *A. rostellata* in habit and leaf-form, but not in pubescence nor in the roots. The leaves are glandular-granuliferous and more or less pubescent as they are in *A. striata*, and the roots are not tuberous-thickened. It is represented by the following specimens:

MEXICO, STATE OF VERA CRUZ: near Jalapa, 1903, C. G. Pringle 11876; Huatusco, 1841, Liebmann 1637; State of Vera Cruz, Pringle 11830.

*Agrimonia parviflora* Ait. This species has been the best understood of the North American species except *A. incisa*. It is true that in the beginning two additional names were given to it, *A. suaveolens* by Pursh, and *A. serrifolia* by Wallroth. The latter was probably led astray by De Candolle who had used the name *A. parviflora* for another species, viz. *A. rostellata*. Lately, Professor Urban\* has proposed a new species, *A. polyphylla*. To me

\* Symb. Ant. 7: 227. 1912.



this seems only a slender form of *A. parviflora*, grown under somewhat abnormal conditions. The specimens on which this new species were based extend the range of *A. parviflora* to Santo Domingo.

*Agrimonia incisa* T. & G. No new facts were added in regard to this species in the North American Flora.

### ADENOSTOMA

This genus has often been included in the Dryadeae, Sanguisorbeae, or Cercocarpeae. It could not very well be included in either the Dryadeae or the Cercocarpeae, as the ovules and seeds are inserted in the distal end of the ovary. It was placed in Cercocarpeae on account of its solitary achenes, but there are several other genera with solitary achenes that could not be placed in that tribe. In the characters of the fruit and hypanthium, it agrees best with the Sanguisorbeae, but the ovary is covered with a cushion, under the margin of which the style is inserted on one side and doubly bent; the species are shrubs of a peculiar habit with small entire linear leaves. It is, therefore, best to regard the genus as representing a distinct tribe.

*Adenostoma fasciculatum* H. & A. This species is very variable, and it is hard to decide if the next species should be merged in it or not. The leaves are either short or long, but usually distinctly petioled. The branches are glabrous or minutely puberulent, and in such cases approach the next species. *Adenostoma fasciculatum densifolium* Eastw. is in my opinion only a mere form of this species with more crowded leaves and inflorescence.

*Adenostoma brevifolium* Nutt. It was with some reluctance that I took up Nuttall's view regarding this plant. Usually, however, Nuttall had good reasons for his segregates, even if Torrey and Gray reduced many of them. Whatever value this plant may have as a species, the form is usually well marked by its short obtuse, subsessile leaves, and pubescent branches. S. Watson regarded it a variety of *A. fasciculatum*, and described it as var. *obtusifolium*. C. K. Schneider reduces the latter to a mere form, but describes a new variety under the name var. *hirsuta*. Whatever Schneider might have had in mind when he made the reduction, the fact is that his var. *hirsuta* is the same as the original *A. brevifolia* of Nuttall.



*Adenostoma sparsifolium* Torrey. This was originally described under the form "*A. sparsifolia*." The name *Adenostoma* is, however, neuter. The species may perhaps represent a distinct genus as the throat of the hypanthium lacks the fleshy glands, characteristic of the type species.

### COLEOGYNE

This genus was included in Cercocarpeae by Focke in Engler and Prantl's *Pflanzenfamilien*, but evidently erroneously so. The tribe Cercocarpeae in that work was a very unnatural one, composed of five genera. *Purshia* and *Chamaebatia* evidently belong to Dryadeae, notwithstanding their solitary carpels. *Adenostoma* and *Coleogyne* represent distinct tribes, which leaves *Cercocarpus* alone in the tribe. In *Coleogyne* the ovule and seeds are inserted at the distal end of the ovary and pendent, in Dryadeae and Cercocarpeae at the proximal end and erect or ascending. Furthermore, the pistil and the stamens in *Coleogyne* are separated by a tube equalling the stamens. The filaments are adnate to the base on the outside of this tube. Whether this tube represents a prolonged hypanthium or a set of abortive and united filaments, is hard to tell. The fact is that no such structure is found anywhere else in Rosaceae, but something similar is found in Capparidaceae. The fruit itself, however, is an achene, and hence very unlike the capparidaceous fruits. Another character abnormal to the Rosaceae is the opposite leaves and branches. The only other rosaceous genus, that I can remember, having opposite leaves is *Rhodotypos*.\* The latter is so closely related to *Kerria* and in other respects typical, that no doubt can be entertained regarding its belonging to the family. It is not so with *Coleogyne*. Its peculiar flowers, its peculiar habit, more resembling Rhamnaceae, and opposite leaves and branches, etc., give rise to the question, may it not properly represent a new family?

### WALDSTEINIA

*Waldsteinia Doniana* Tratt. Fifteen years ago Dr. Small distinguished from *W. fragarioides* a new species which he published

\* Since the above was written Captain John Donnell Smith has described (*Bot. Gaz.* 57: 420. 1914) another abnormal genus with opposite leaves, viz. *Guamatela*.



under the name *W. parviflora*, the main difference being the smaller flowers. In looking up the illustrations of *W. fragarioides*, I found two plates that evidently illustrate *W. parviflora* instead of *W. fragarioides*. These were *plate 1567* in the Botanical Magazine and *plate 408* in the Botanical Cabinet. I also found that Trattinick had based his *Waldsteinia Doniana* on the former of these plates, which name therefore should supersede the later *W. parviflora* Small.

*Waldsteinia lobata* (Baldw.) T. & G. This species must be very local, for in the herbaria I have seen specimens from scarcely half a dozen localities, all in the mountains of Georgia and North Carolina. The achenes in this species are but 1 or 2.

*Waldsteinia idahoensis* Piper. This, like its eastern relative, is very local; in fact, it has been collected only at the type station, but may have a wider distribution, that region having been rather little botanized. The achenes are usually 2.

NEW YORK BOTANICAL GARDEN



The appearance of polar bodies in the spermogenous tissue of  
*Ricciocarpus natans* (L.) Corda

RUTH S. ATWELL

(WITH PLATE 8)

The presence of polar or centrosome-like bodies in spermogenous cells and their possible function and origin in the cell continues to be the subject of much discussion and interest among the cytologists working with Bryophyta. Such bodies have been noted by Ikeno (2) and Mottier (4) in *Marchantia* and regarded by them as true centrosomes. Lewis (3) observes them in *Riccia natans* L. (*Ricciocarpus natans* Corda) and in *Riccia crystallina* L. but does not regard them as true centrosomes since they arise *de novo* with each division. Miss Black (1) observes that the last division in the spermogenous tissue of *Riccia Frostii* Aust., the diagonal division, is accompanied sometimes by granules at the poles.

For this preliminary study of spermatogenesis in certain Hepaticae, *Ricciocarpus natans* (L.) Corda furnished the material from which slides were prepared and certain facts noted. These may be of interest by way of comparison or confirmation of the conclusions formed by workers in other related species. Material of *Ricciocarpus natans* was gathered near the Skokie Marsh, Cook County, Illinois, during June and July, 1913, and was fixed in chromic-osmic-acetic solution. The sections were stained with analin safranin and gentian violet. Occasionally orange G was also used. Deep staining followed by washing was necessary as it was difficult otherwise to differentiate the cytoplasmic structures.

As has been observed by others, it was noted that nearly all the stages of karyokinesis could be found in different segments of one of the nearly mature antheridia. All the cells of each segment, as marked off by the first divisions of the antheridium, contained nuclei in the same stage of development. Thus in large antheridia many successive stages of division were found. Fig. 2 shows such an antheridium.



In the earliest prophase of division noted, the chromatin seems to be arranged in a mass of irregular lumps, surrounded by a homogenous material which seems denser next to the nuclear membrane and which has a staining reaction quite similar to the surrounding cytoplasm; no nucleolus is distinguishable; the nuclear membrane is pronounced, the cytoplasm finely and evenly granular. FIG. 3 shows cells typical of this condition. Centrosome-like bodies appear in cells of younger antheridia as well as in older ones. They are also present in cells of both old and young antheridia during the earlier as well as the diagonal division. FIG. 1 shows a young antheridium in one of the segments of which these bodies were observed in connection with the three nuclei of that segment. One of these cells is drawn under higher magnification in FIG. 4. FIG. 6 represents these bodies in a cell of a much older antheridium when the spindle and nucleus are in a more advanced stage than in FIG. 4. The bodies are distinct and cannot be explained as granules appearing accidentally for they appeared quite constantly. They do not seem to be permanent organs as they arise and disappear with each new division.

The origin of these bodies was not taken up. However, their position at the poles and their direct connection with the spindle suggest that they may represent an important factor in the formation of the spindle. Lewis describes these bodies as first appearing at a little distance from the nuclear membrane which elongates as it approaches them. FIGS. 4 and 5 are typical, and show the bodies as entirely outside and free from the nuclear membrane. Kinoplasm is collected about and extending away from them in cap- or cone-like form outlining the spindle, which is apparently produced from the kinoplasm and consists of a few thick fibers converging at the poles. The bodies lie in the position of true centrosomes.

The chromosomes are formed from the central mass of nuclear material and become arranged in the nuclear plate. FIGS. 6 and 7 show them in this position during the diagonal division. They split and pass to the poles. The polar bodies are always present in this last division. No stages of anaphase were observed, probably due to the rapid change of the position of the chromosomes from the plate to the poles. FIG. 7 shows the chro-



mosomes splitting. Occasionally granules other than those appearing at the poles are observed in the cytoplasm, as shown in FIG. 5.

Mottier and Ikeno, who observed true centrosomes in plants, report that they are formed from a single body dividing in two. In these observations on *Ricciocarpus natans* the bodies seem to appear at once in the polar position with each new division. Whether or not they persist in the spermatid after the diagonal division and may later become blepharoplasts has been discussed by Black (1), Lewis (3), Wilson (5), Woodburn (6), and others. This study was not carried far enough to observe these late stages in *Ricciocarpus natans*.

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#### Explanation of plate 8

All drawings were made with the aid of a camera lucida. A Spencer microscope was used with apochromatic objectives, 1.5 mm. oil immersion, 3 mm., 16 mm., and compensating oculars 6 X and 12 X. FIGS. 1 and 2 were drawn at stage level and all others at table level.

FIG. 1. Young antheridium. One segment showing three nuclei with polar bodies. X 1,600.

FIG. 2. Older antheridium. X 150.

FIG. 3. Two cells in early prophase. The chromatin of the nucleus is seen in an irregular mass. X 3,200.



FIG. 4. Cell from segment in FIG. 1, the chromatin in a central mass, the bodies at the poles with kinoplasm extending from them outlining the spindle.  $\times 3,200$ .

FIG. 5. Cell from an older antheridium. The chromatin is in an early spireme form and the spindle is more fully developed.  $\times 3,200$ .

FIG. 6. The oblique spindle with chromosomes in equatorial plate, the spindle fibers terminating in the polar bodies.  $\times 3,200$ .

FIG. 7. Similar to FIG. 6, the chromosomes splitting.  $\times 3,200$ .



## Slope exposure as a factor in the distribution of *Pseudotsuga taxifolia* in arid parts of Washington

GÖTE TURESSON

It is a well-known fact that the vegetation on hills and mountain slopes differs according to the exposure of the locality to different quarters of the compass. A flora of mainly xerophytic character inhabits the south-facing slope, while the northern declivity, less exposed to insolation, is covered with a more or less mesophytic vegetation. Also the southwest and southeast slopes are generally occupied by a xerophytic flora, the northeast and northwest by a mesophytic.

The great differences in the distribution of plant-communities as well as individuals due to variations in insolation may be seen in every part of the world. Warming (10, 11) tells us how in Greenland the southern slopes of a mountain chain may have an open xerophytic vegetation "appearing as if burnt up," while the northern slopes are at the same time covered by a dense, green, mossy carpet, with many flowering plants. The same may be observed in the Mediterranean countries, and even in the proximity of the equator we find a marked distinction between the flora of the northern and southern slopes.

But slope exposure is an important factor not only in the determining of different types of vegetation over wide areas; it also affects the vegetation within a very limited area. Giltay (3) has shown how a great difference may exist between the temperature and atmospheric humidity on the northern and southern slopes respectively of the sand-dunes in Holland, even when only a few paces apart. More recently Stenström (4) investigated the difference in the flora of the embankments of railways, showing how some plants occupy the southern embankment, others the northern, etc.

While studying the influence of slope exposure upon the distribution of the various plants on the banks of Spokane River in eastern Washington the writer's attention was particularly directed



to the behavior of *Pseudotsuga taxifolia*, popularly known as Douglas spruce. The range of this conifer is extensive. It is found most luxuriant in the Vancouver strip, reaching perhaps its highest development in the Puget Sound region (see also Sudworth, 9). This region, falling within the limits of Merriam's Humid Transition area (5), is notable for its moist climate favoring a luxuriant growth of dense forests, almost exclusively composed of Douglas spruce, which here assumes gigantic dimensions. Less conspicuous and never attaining the development it reaches in the Vancouver strip, it reappears in the extreme eastern part of Washington and in northern Idaho where the climatic conditions approach those of the coast region. The main distribution of the tree in this region seems to coincide with the Canadian Zone of Merriam.

Abundance of moisture in atmosphere and soil seems to be of vital importance to the growth of Douglas spruce. It is therefore surprising to find this conifer occupying the drier parts of eastern Washington, Merriam's Arid Transition area. Realizing the scanty rainfall—about 18 inches in Spokane—it may well be questioned how the tree is able to endure the extremities to which Humid Transition plants are submitted in this arid region. The problem loses some of its complexity when it is found that Douglas spruce in this region always occupies the shady northern slope of hills and ridges, and is entirely absent on the southern, thus affording a most notable example of the effect of slope exposure. Nowhere is this more beautifully shown than on the banks of Spokane River in the vicinity of Spokane. The banks, composed of glacial detritus, sometimes attain a height of 50 meters, and the vegetation of the sunny south-facing bank is in striking contrast with that of the more shady north-facing bank. This latter is occupied by a pure growth of *Pseudotsuga taxifolia*. A small belt of *Populus trichocarpa*, *Alnus tenuifolia*, *Cornus stolonifera* and *Salix Scouleri-ana* fringes the edge of the river. The following herbs are common in this belt:

*Artemisia ludoviciana*\*

*Aster Douglasii*

*Aster foliaceus frondeus*

*Aster laevis Geyeri*

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\* In questions of nomenclature Piper's Flora of the State of Washington (6) is followed.



<i>Aster oreganus</i>	<i>Scutellaria lateriflora</i>
<i>Heracleum lanatum</i>	<i>Senecio hydrophilus</i>
<i>Impatiens biflora</i>	<i>Solanum Dulcamara</i>
<i>Mentha canadensis borealis</i>	<i>Stachys palustris</i>
<i>Roripa Nasturtium</i>	<i>Steironema ciliatum</i>

Higher up on the steep slope, where *Pseudotsuga* becomes dominant, the vegetation shows the following composition:

## TREES

*Pseudotsuga taxifolia*

## SHRUBS

<i>Ceanothus sanguineus</i>	<i>Schizonotus discolor</i>
<i>Opulaster pauciflorus</i>	<i>Spiraea corymbosa</i>
<i>Sambucus glauca</i>	

## HERBS

<i>Antennaria rosea</i>	<i>Geranium viscosissimum</i>
<i>Arnica cordifolia</i>	<i>Heuchera cylindrica</i>
<i>Campanula rotundifolia</i>	<i>Hieracium albiflorum</i>
<i>Castilleja miniata</i>	<i>Hieracium Scouleri</i>
<i>Claytonia linearis</i>	<i>Mertensia olbongifolia</i>
<i>Claytonia perfoliata</i>	<i>Pentstemon confertus</i>
<i>Claytonia sibirica</i>	<i>Ranunculus glaberrimus</i>
<i>Collinsia tenella</i>	<i>Sedum stenopetalum</i>
<i>Crepis barbiger</i>	<i>Sieversia ciliata</i>
<i>Crepis gracilis</i>	<i>Silene Douglasii multicaulis</i>
<i>Disporum majus</i>	<i>Synthyris rubra</i>
<i>Dodecatheon puberulum</i>	<i>Tellima parviflora</i>
<i>Drymocallis Convallaria</i>	<i>Tellima tenella</i>
<i>Erigeron speciosus</i>	<i>Trillium petiolatum</i>
<i>Erythronium grandiflorum</i>	<i>Vagnera amplexicaulis</i>
<i>Fragaria platypetala</i>	<i>Valerianella macrocera</i>
<i>Galium Aparine</i>	<i>Vicia americana</i>
<i>Galium boreale</i>	<i>Viola adunca</i>
<i>Gentiana oregana</i>	<i>Viola retroscabra</i>

As easily seen, the herbaceous vegetation is made up of truly Transition or Arid Transition plants with one exception, *Claytonia*



*perfoliata*, a Humid Transition plant here having an isolated station. The formation is of a somewhat open character, but in deeper shade the ground is generally covered by a continuous mat of mosses. Epiphytic lichens are common. On the steep declivity no humus has been able to accumulate, and it is only on the lower part of the bank that a rather thick layer of humus is to be found, owing its existence to the mass of dead matter which is in continuous downward motion.

The opposite south-facing bank has a very different flora; in fact, the contrast is so striking as to make it seem almost unnatural. The heavily *Pseudotsuga*-forested north-facing slope faces a vegetation on the opposite bank, which in xerophily rivals the desert flora! The greater part of the bank is devoid of trees. *Populus trichocarpa* fringes the edge of the river, but *Alnus tenuifolia* has disappeared. Shrubs of quite different kind from those in the corresponding belt of the northern bank form the undergrowth. The shrubs are:

<i>Amelanchier florida</i>	<i>Prunus demissa</i>
<i>Clematis hirsutissima</i>	<i>Ribes aureum</i>

The dominant herbs at the water-edge are:

<i>Artemisia ludoviciana</i>	<i>Coleosanthus grandiflorus</i>
<i>Asclepias mexicana</i>	<i>Euthamia grandiflora</i>
<i>Aster laevis Geyeri</i>	<i>Steironema ciliatum</i>
<i>Aster oregana</i>	

The declivity proper has two very marked belts, a lower closed formation, and an upper and open formation, the difference being largely due to the obvious fact that the lower zone is more sheltered against insolation and drying winds than is the upper. A continuous turf of various grasses covers the lower belt, and many of the plants recorded in the list from the northern slope reappear in this relatively sheltered zone. More or less dominant are the following additional:

<i>Apocynum androsaemifolium</i>	<i>Erysimum asperum</i>
<i>Astragalus Purshii</i>	<i>Lomatium triternatum</i>
<i>Delphinium Menziesii</i>	<i>Sphaeralcea rivularis</i>

The most remarkable feature of this zone, however, is the



abundance of shrubs. They do not form thickets, but are scattered widely apart over the area. In some cases, however, one of them, *Berberis repens*, may form a pure growth of some extent. The stratum of shrubs is composed of:

- |                             |                             |
|-----------------------------|-----------------------------|
| <i>Amelanchier Cusickii</i> | <i>Philadelphus Lewisii</i> |
| <i>Berberis repens</i>      | <i>Rhus Toxicodendron</i>   |
| <i>Crataegus brevispina</i> |                             |

The remaining part of the bank, the upper zone, is by far the most interesting one. As said before, no continuous turf of vegetation is found, only scattered individuals often several feet apart. The intense insolation and the exceedingly dry winds which are so common in eastern Washington in the summer months must be considered as the chief causes for this scanty xerophytic vegetation. Another factor, which may play some part in the difficulty of establishing a closed formation, is the mobility of the substratum. Owing to the steepness of the bank, gravel is rapidly moving downward. Many plants which probably are able to withstand the strong insolation are unable to get a foothold, thus giving room to other plants more adapted to the moving substratum, but poor in the formation of a continuous turf. That many of these plants show a high degree of adaptation to the habitat is evident from the fact that they do not occur outside of these south-exposed banks. The formation, which includes many of the most decorative and at the same time the rarest plants in Spokane Valley, shows a composition of the following nature:

SHRUBS

- |                      |                                 |
|----------------------|---------------------------------|
| <i>Ramona incana</i> | <i>Rhus glabra occidentalis</i> |
|----------------------|---------------------------------|

HERBS

- |                               |                              |
|-------------------------------|------------------------------|
| <i>Allocarya hispidula</i>    | <i>Eriogonum niveum</i>      |
| <i>Carduus undulatus</i>      | <i>Eriophyllum lanatum</i>   |
| <i>Chaenactis Douglasii</i>   | <i>Cilia aggregata</i>       |
| <i>Collomia grandiflora</i>   | <i>Lappula ciliata</i>       |
| <i>Cuscuta californica*</i>   | <i>Lithospermum ruderale</i> |
| <i>Eriogonum compositum</i>   | <i>Lomatium Grayi</i>        |
| <i>Eriogonum heracleoides</i> | <i>Lupinus Piperi</i>        |

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\* Infesting *Scutellaria grandiflora*.



*Machaeranthera canescens**Phacelia heterophylla**Mentzelia laevicaulis**Physaria Geyeri**Mentzelia integrifolia**Ptiloria exigua**Oreocarya sericea**Scutellaria grandiflora*

The vegetation of the upper belt of the south-exposed bank, as recorded in the above list, corresponds closely to the Upper Sonoran flora, to follow Merriam's terminology. In Washington the Upper Sonoran life area is confined to the interior southern part of the State with a rainfall less than 10 inches. However, many of the Upper Sonoran plants follow the valley of Columbia River and its tributaries, and extend far up in the Arid Transition Area. Through the valley of Okanogan River they even reach British Columbia. The warm and sunny south-facing slope of the river banks is well fitted to support this vegetation of a more southern character. They all exhibit xerophily, protecting them from desiccation. A well-developed coating of hair is the most common means of protection, reaching an extreme development in such forms as *Eriogonum niveum* and *Eriophyllum lanatum*, which have a thick felt on leaves as well as stem. One of the forms included in the above list is of more than common interest, namely, *Physaria Geyeri*. This beautiful crucifer is known to occur only in the upper region of Spokane Valley, here usually occupying the southern river banks. The dense coating of hair is apparently a very effective means for depressing transpiration, but it also constitutes, in connection with the cushion-like and tufted character of the plant, a method of protection against the low winter temperature. Flowering in the latter part of April and the whole month of May, reflorescence very often takes place in August, and this reflorescence lasts often through all winter. A few hours of sunshine even in the most severe winter months, December and January, is enough to induce it to open its yellow flowers.

Where the slope terminates upwards and level ground commences this characteristic flora ceases abruptly, and the dry *Pinus ponderosa* forest with its scanty undergrowth takes its place. In some places where the slope is gentle it merges into the flora of the gravelly prairie dominated by *Balsamorhiza sagittata* and *Gaillardia aristata*.

From the above we find how profoundly slope exposure in-



fluences, and how it determines, the kind of vegetation present. Coming back to *Pseudotsuga taxifolia* the evidences have showed that exposure is the regulating factor in the distribution of the tree in this region, the northern slopes and ridges being the only localities which offer the needed humidity in soil and atmosphere. Not only around Spokane but in all more or less arid regions can this be observed. Piper (6) cites the example of Kamiak Butte, a granitic cone in the arid region of eastern Washington projecting about 500 meters above the surrounding basalt, having its entire south exposure covered by a bunchgrass flora, while the northern slope is densely timbered with yellow pine and other coniferous trees (including *Pseudotsuga taxifolia*). Even in regions with a higher amount of annual precipitation, as in the extreme eastern part of the State and in northern Idaho, we find *Pseudotsuga* by far better developed on the northern exposure, though lacking in the more moist situations, not being able to compete successfully with *Thuja plicata*, which here becomes dominant. At a higher altitude, mainly in the Canadian zone, it again becomes the dominant tree on the northern slopes, while *Pinus contorta* often becomes the most conspicuous on the southern exposure. Watson (12) describes a similar case from north central New Mexico, in which region *Pseudotsuga taxifolia* covers the north-facing slopes above 8,000 feet (the Canadian Zone) and extends down in the narrow canyons to about 7000 feet.

Turning now our attention to the distribution of *Pseudotsuga taxifolia* in the dry regions of western Washington, we find it growing in the San Juan Islands. These islands, situated between the Strait of Juan de Fuca and the Strait of Georgia, are remarkable for their dry climate and for the many Arid Transition plants which there have been able to get a foothold, since the climatic conditions resemble those in eastern Washington. The nature of the climatic conditions may best be illustrated by mentioning that the only cactus which occurs in the Vancouver strip, *Opuntia polyacantha borealis*, is confined to one of these islands. Other truly Arid Transition plants are also found, for instance *Sieversia ciliata*, *Polemonium micranthum*, *Lupinus microcarpus* and *Juniperus scopulorum*. The problem is a somewhat puzzling one, and Piper (6, p. 44) remarks: "Only one physical factor



presents itself which may explain these strange cases, namely, the fact that these islands lie in the lee of the Olympic Mountains and therefore have a lesser rainfall. The conditions, therefore, more nearly approximate those of the Arid Transition area than any other portion of Washington west of the Cascade Mountains." It is not surprising to find *Pseudotsuga taxifolia* confined to the northern slopes of the hills in these islands; in fact, a different behavior would be hard to understand, since it is here submitted to practically the same climatic conditions as in other arid regions of its range, where it, as has been shown, always occupies the northern declivity as a result of the effect of slope exposure.

Rigg (7) has in an interesting paper, dealing with the forest distribution in these islands, pointed out the seemingly peculiar distribution of *Pseudotsuga taxifolia* as limited to the north-facing slopes of the hills. He is inclined to attribute to the soil the difference in the forest distribution. Upon investigation of the soil on the barren south-facing slope and on the forested north-facing, it was shown that the soil on the barren portion was black and powdery, containing a good deal of gravel, while the forested portion was everywhere covered with two feet or more of yellow clay, containing occasional irregular fragments of rock.

It is hard to believe that the chemical nature of the different soils should cause the difference in the forest distribution, but as darker soil is more readily and strongly heated than is that of lighter color, this character may in a subordinate way have some influence (see Falk, 2; Schimper, 8; Warming, 11). When we on the other hand know how profoundly slope exposure affects the distribution of *Pseudotsuga taxifolia* in regions with similar climatic conditions to those in the San Juan Islands, the determining factor is presumably the same.

Cowles (1) no doubt is right when stating that a species in general can grow in a large number of formations at its center of distribution, since there the climatic condition favors it most highly. In other regions, especially near its areal limits, it can grow only in those formations which resemble most closely in an edaphic way the climatic feature at the distribution center. We have found how *Pseudotsuga taxifolia* when growing under conditions not favorable to its development always establishes itself



on north-facing slopes and banks, and thus secures the greatest possible amount of atmospheric and telluric moisture.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1912-1914

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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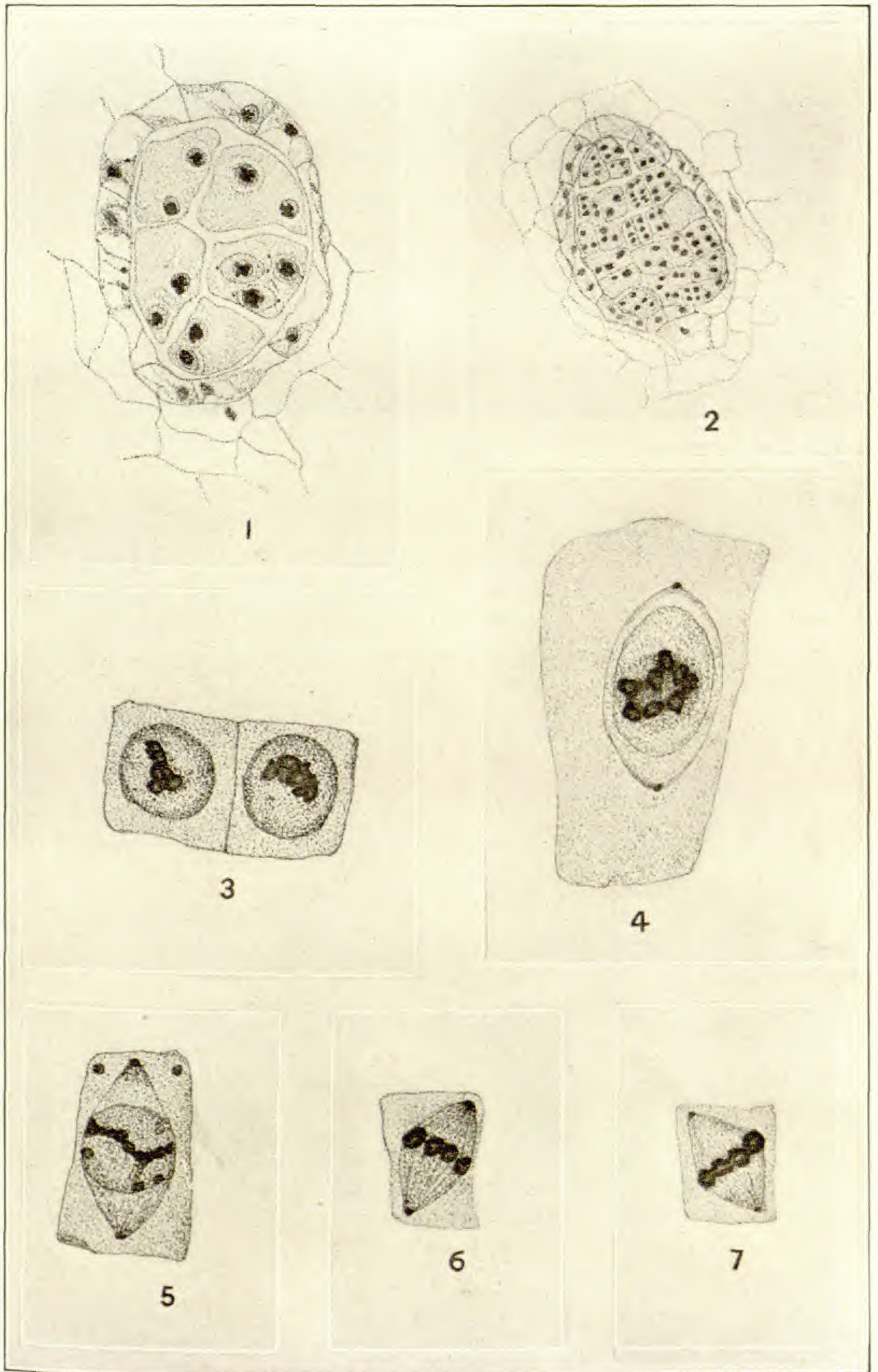


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*Delphinium abietorum* sp. nov.





ATWELL: POLAR BODIES IN RICCIOCARPUS NATANS



# BULLETIN

OF THE

# TORREY BOTANICAL CLUB

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### CONTENTS

A black-soil prairie station in northeastern Illinois . . . ARTHUR G. VESTAL 351

Mechanical tissue development in certain North American vines  
HOWARD H. M. BOWMAN 365

The nomenclature of the genus *Usnea*. (Plates 9-14.) R. HEBER HOWE, JR. 373

Observations on the edge of the forest in the Kodiak region of Alaska  
ROBERT F. GRIGGS 381

INDEX TO AMERICAN BOTANICAL LITERATURE . . . . . 387

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BULLETIN  
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TORREY BOTANICAL CLUB

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JULY, 1914

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A black-soil prairie station in northeastern Illinois

ARTHUR G. VESTAL

(WITH SEVEN TEXT FIGURES)

The prairie station described in this account is an example of perhaps the most luxuriant type of prairie, the mesophytic prairie-grass of the eastern border of the prairie region. This type is particularly well developed in the upper Wisconsin glaciation of northeastern Illinois, and until recently small and scattered areas of this type of prairie were still abundant west of Chicago as far as the Fox River and beyond. In the last ten years, however, the extension and development of suburban areas, and disturbance of relic colonies of prairie along railroad rights-of-way, have diminished the areas of original prairie to a small fraction of their recent extent. The particular area described possibly owes its survival to the fact that it is not large, and that it is nearly surrounded by forest and by prairie sloughs.

The station lies immediately north of the tracks of the Chicago Great Western railroad, very near the stopping-place of the Aurora, Elgin, and Chicago electric road known as Stratford Hills. It is one mile east of Elmhurst, and lies at the summit of a morainal ridge. The boundary separating Cook and Du Page counties passes through the area, which may conveniently be known as the county line prairie. The forest adjoining is also of interest to botanists, and the border zone between prairie and forest is still in good condition. The writer first visited the locality in 1905, and has made observations there and near by during four summers since that time. He wishes to express obligation to

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[The BULLETIN for June (41: 319-350. pl. 8) was issued 22 J1 1914.]



Dr. H. A. Gleason, who has accompanied him to the area, for the use of some of his notes. The accompanying sketch map shows very well the local distribution of the plant associations of the immediate vicinity. The length of the area mapped is about 600 feet. Just south of it is the Great Western railroad; to the east lies a blue-grass pasture and a picnic ground, with many of the original trees, but with the ground cover replaced by blue-grass; on the west the clover field continues; on the north the clover field, with its line of prairie sloughs, and the forest, continue also.

Local distribution of the plant associations of the county line station would be of little significance of itself, but there is one condition which this area has in common with others in northern and central Illinois: the forest is to the east of a line of sloughs, which may have served to protect it from the inroads of prairie fires. In this region forest areas are much more frequent and more extensive just east of streams and sloughs than just on the western side. Prairie fires, in former times very prevalent, traveled generally from west to east, in the direction of the prevailing winds. The bearing of these facts on vegetational history in the transition area between interior prairie and eastern forest regions has been developed by Gleason.\* At the county line station, the narrow strip of prairie which separates the forest area mapped into a woodland on the north and several small groves on the south, may have invaded the formerly more extensive forest by the aid of prairie fires which were not stopped by the line of sloughs. It is seen on the map that the tongue of prairie extending into the forest is in line with the conspicuous gap in the series of prairie sloughs.

Established black-soil prairie of the eastern part of the prairie region, in its original condition, may be thought of as a luxuriant grassland with a large number of plant species and with very many local appearances, caused by local dominance or abundance of one or several species. The surface is usually slightly undulating, and in the recently glaciated areas stream development is poor, so that depressions have very wet or submerged soil, and elevations may at times be very dry. The local variation in soil

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\* Gleason, H. A. An isolated prairie grove and its phytogeographical significance. *Bot. Gaz.* 53: 38-49. *f. 1, 2.* 1912.



moisire therefore is rapid, though gradual. The species composition of the prairie growth changes with the soil moisture, and a complete transitional series of prairie growths can be recognized.

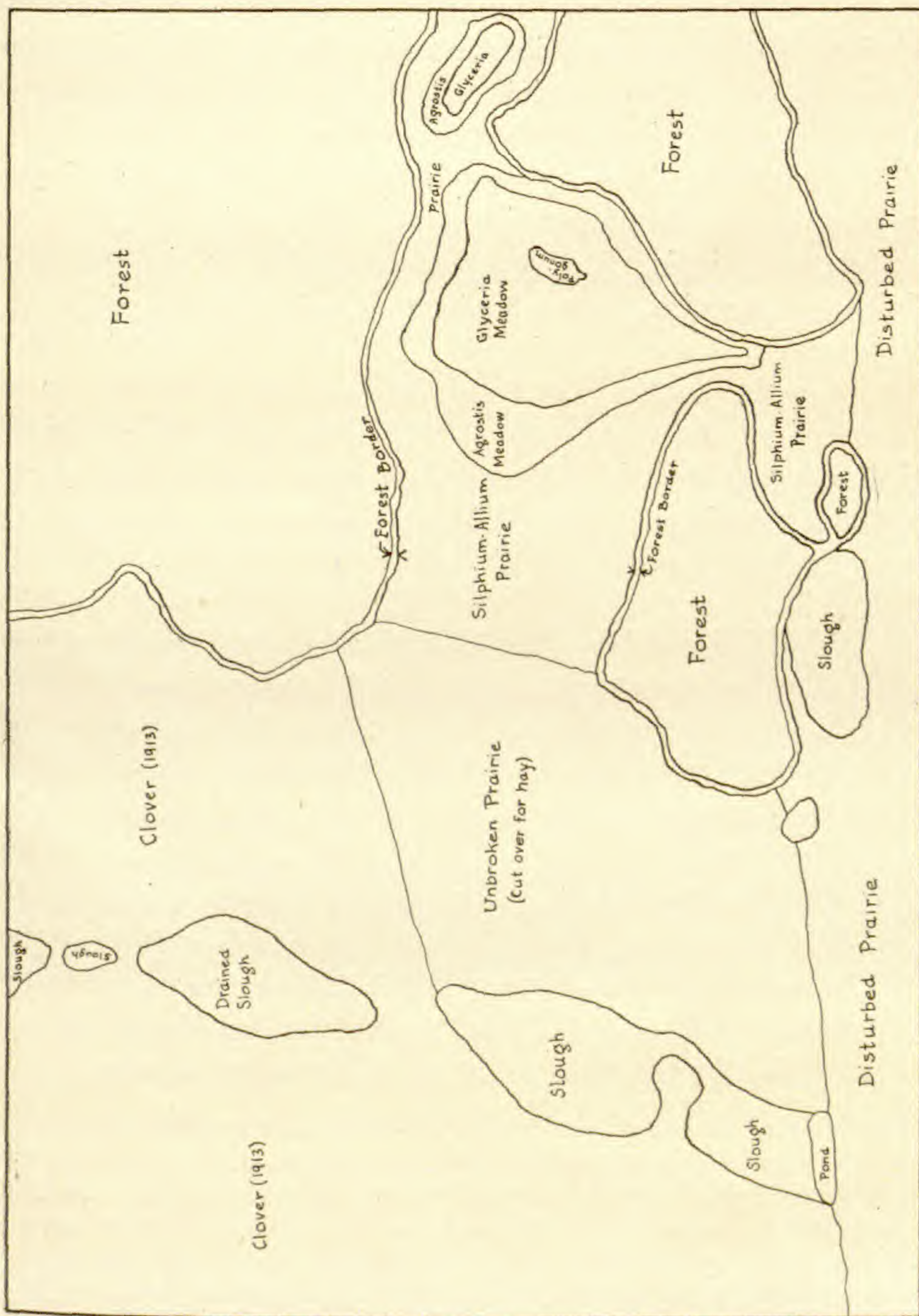


FIG. 1. Map of the county line station.

It will perhaps be helpful to regard the mean and the two extreme conditions of this series as constituting distinct plant associations, which may be called (1) xerophytic prairie-grass, (2) mesophytic



prairie-grass, and (3) hydrophytic or swamp prairie, or fen. It should be noted that these intergrade, passing into one another gradually, instead of alternating sharply, and that many species tolerate a wide range of soil moisture and of other environmental conditions, so that some species are found abundantly in more than one association. Some species, too, reach greatest abundance in transitional growths intermediate between two associations.

*The xerophytic prairie-grass association.*—This growth is not very extensively developed in upper Wisconsin glaciation of northeastern Illinois. Its best representative is the *Silphium laciniatum* consociation. The dominant species, often called the compass-plant, is very conspicuous. This type of prairie is rather locally seen in eastern Du Page County, and is hardly at all represented at the county line. Following is a list of species typical not only of the *Silphium laciniatum* prairie, but of the xerophytic prairie-grass association in general, as represented in eastern Du Page County.

\*SPECIES TYPICAL OF XEROPHYTIC PRAIRIE-GRASS

d or ld <i>Andropogon scoparius</i> , ch	i <i>Verbena stricta</i>
l <i>Andropogon furcatus</i> , m	l <i>Physalis virginiana</i>
l <i>Sorghastrum nutans</i> , m	l <i>Liatris scariosa</i>
l <i>Panicum virgatum</i>	lf <i>Solidago nemoralis</i>
l <i>Stipa spartea</i>	f <i>Solidago canadensis</i>
l <i>Sporobolus heterolepis</i> , m	lf <i>Solidago serotina</i>
f <i>Koeleria cristata</i>	lf <i>Solidago rigida</i> , ch
l <i>Comandra umbellata</i>	i <i>Aster sericeus</i>
f <i>Rosa humilis</i>	f <i>Aster multiflorus</i> , ch
l <i>Cassia Chamaecrista</i>	i <i>Erigeron ramosus</i>

\* Notation as used in the above table of species, and in other tables of this article, is as follows: symbols to the left of the species name have to do with frequency or abundance of the species in the station or in the association; d = dominant, a = abundant, f = frequent, i = infrequent, l = local, of scattered distribution, or prefixed = locally; symbols to the right of the name have to do with the degree to which the species is characteristic of this or of other associations and habitats; ch = a character species for the association or habitat; m = rather more typical of, or frequent in, comparatively mesophytic situations; x = rather more typical of comparatively xerophytic situations, or a relic from xerophytic prairie; h = rather more typical of, or a relic from, comparatively hydrophytic communities, or in very local depressions within mesophytic prairie growths.



1 <i>Baptisia bracteata</i>	f, ld <i>Silphium laciniatum</i> , ch
f <i>Amorpha canescens</i> , ch	lf <i>Silphium integrifolium</i> , ch
f <i>Petalostemum purpureum</i>	i, la <i>Heliopsis scabra</i> , ch
1 <i>Tephrosia virginiana</i>	f <i>Rudbeckia hirta</i> , m
i <i>Desmodium illinoense</i>	i, la <i>Brauneria pallida</i> (seldom seen in e. Du Page Co.)
lf <i>Lespedeza capitata</i>	
f, la <i>Euphorbia corollata</i> , ch	f, la <i>Lepachys pinnata</i> , ch
i <i>Oenothera biennis</i>	lf <i>Helianthus scaberrimus</i> , ch
i <i>Asclepias tuberosa</i>	i <i>Helianthus occidentalis</i>
1 <i>Asclepias verticillata</i> , ch	i <i>Helianthus Maximiliani</i>
1 <i>Convolvulus sepium</i>	lf <i>Achillea Millefolium</i>
i <i>Lithospermum canescens</i> , ch	i <i>Cirsium discolor</i>

*The mesophytic prairie-grass association.*—This type of prairie is more generally distributed within the area of study than is the

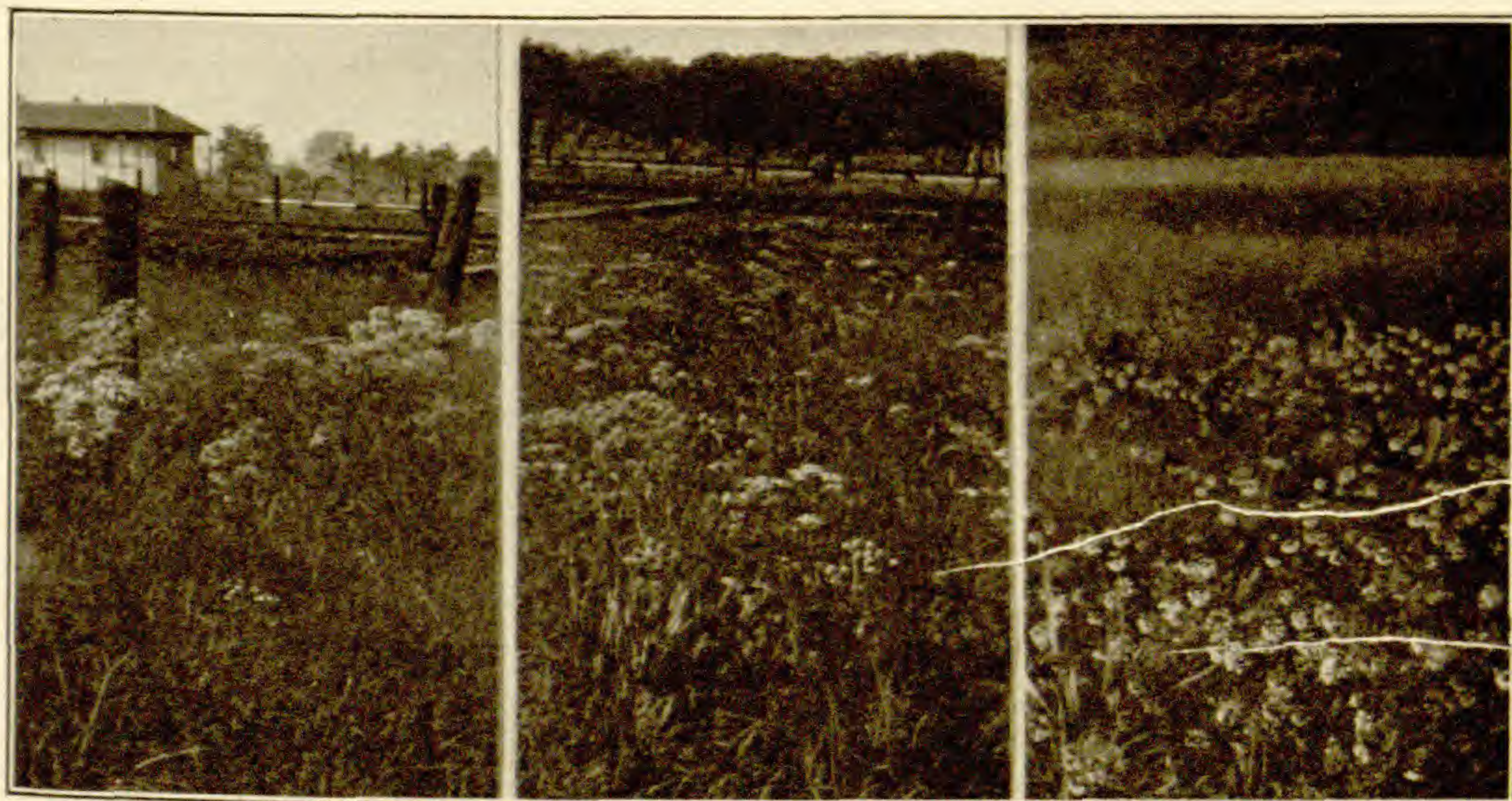


FIG. 2

FIG. 3

FIG. 4

FIG. 2. A fragment in the mesophytic prairie-grass association, mixed grass consociates; a rather dry spot, *Euphorbia corollata* locally conspicuous; west of Elmhurst.

FIG. 3. A moister spot close to the first, with *Eryngium* and *Parthenium* in flower.

FIG. 4. At the county line; mesophytic prairie-grass, with *Eryngium* and *Silphium terebinthinaceum*; *Allium* abundant and conspicuous; behind is lower ground with *Agrostis* and *Glyceria*.

xerophytic prairie-grass. There are several well-defined representatives of the mesophytic association. One is dominated by the tall grass *Andropogon furcatus*, often with hardly any other



species present; one is dominated by a number of grass species (the mixed consociates of mesophytic prairie-grass); and one is dominated by the large rosin-plant *Silphium terebinthinaceum* and by grasses. All of these three consociates are well developed in and near the county line prairie. The best area of the association seen is the mixed grass growth shown on the map near the left, adjoining the clover field; this has been mowed for hay each summer. The following species, mostly those of early summer, have been observed here:

MIXED CONSOCIATES OF MESOPHYTIC PRAIRIE-GRASS, COUNTY LINE

l <i>Equisetum arvense</i>	i <i>Dodecatheon Meadia</i> , h, ch
f, ld <i>Panicum Scribnerianum</i> , ch	li <i>Asclepias tuberosa</i> , x
li <i>Stipa spartea</i> , x	i <i>Asclepias Sullivantii</i> , h
f, ld <i>Sporobolus heterolepis</i> , ch	f <i>Phlox glaberrima</i> , ch
i, ld <i>Koeleria cristata</i>	lf <i>Phlox pilosa</i> , h
i, ld <i>Poa compressa</i> , ruderal ?	lf <i>Monarda mollis</i>
l <i>Bromus Kalmii</i> , ch	lf <i>Pycnanthemum virginianum</i> , ch
l <i>Elymus canadense</i>	i <i>Castilleja coccinea</i> , ch
li <i>Tradescantia reflexa</i>	lf <i>Pedicularis canadensis</i>
f <i>Allium cernuum</i> , ch	f <i>Lobelia spicata</i> , ch
li <i>Lilium canadense</i>	li <i>Solidago rigida</i> , x
li <i>Spiranthes cernua</i> ?	li <i>Erigeron ramosus</i>
li <i>Polygonum</i> sp.	i, la <i>Antennaria plantaginifolia</i>
li <i>Heuchera hispida</i>	f, ld <i>Silphium terebinthinaceum</i> , ch
la <i>Fragaria virginiana</i>	li <i>Silphium integrifolium</i> , x
i <i>Amorpha canescens</i> , x	lf <i>Parthenium integrifolium</i> , ch
f <i>Lathyrus palustris</i>	f <i>Rudbeckia hirta</i> , ch
f <i>Viola pedatifida</i> , ch	i <i>Cirsium Hillii</i> , h, ch
la <i>Eryngium yuccifolium</i> , h, ch	i <i>Krigia amplexicaulis</i> , h, ch
i <i>Oxypolis rigidior</i> , h	

Another very representative station of practically the same kind of prairie is seen in a fenced-in triangular area at the intersection of the Illinois Central and Aurora, Elgin, and Chicago rights-of-way somewhat less than a third of a mile west of the Elmhurst station of the latter railroad. A tabulation of the plant population of an area about thirty feet square is here given. It was made August 18, 1913.



MIXED CONSOCIES OF MESOPHYTIC PRAIRIE-GRASS, WEST OF  
ELMHURST

- |  |   |
|--|---|
| i, ld <i>Andropogon scoparius</i> , x            | lf <i>Eryngium yuccifolium</i> , h, ch      |
| a, ld <i>Andropogon furcatus</i> , ch            | i <i>Dodecatheon Meadia</i> , h, ch         |
| f, ld <i>Sorghastrum nutans</i> , ch             | i <i>Galium</i> sp.                         |
| f, ld <i>Panicum</i> sp., near <i>P. nitidum</i> | i <i>Solidago canadensis</i>                |
| li <i>Stipa spartea</i>                          | lf <i>Solidago rigida</i> , x               |
| f, ld <i>Sporobolus heterolepis</i> , ch         | lf <i>Aster Novae-Angliae</i> , ch          |
| i, ld <i>Poa compressa</i> , ruderal ?           | lf <i>Antennaria plantaginifolia</i>        |
| lf <i>Carex</i> sp.                              | f, ld <i>Silphium terebinthinaceum</i> , ch |
| lf <i>Juncus</i> sp.                             | lf <i>Parthenium integrifolium</i> , ch     |
| li <i>Sisyrinchium</i> sp.                       | i <i>Ambrosia artemisiifolia</i>            |
| lf <i>Rosa humilis</i>                           | i <i>Rudbeckia hirta</i> , ch               |
| la <i>Euphorbia corollata</i> , x                | i <i>Lepachys pinnata</i>                   |
| i <i>Viola pedatifida</i> , ch                   |   |



FIG. 5

FIG. 6

FIG. 5. Mesophytic prairie-grass at the county line station. The boundary is seen between the area regularly cut over for hay, and the undisturbed *Silphium terebinthinaceum* consociates, in which *Allium cernuum* is abundant and conspicuous.

FIG. 6. The *Liatris spicata* consociates of the swamp prairie or fen association.

The *Silphium terebinthinaceum* consociates is very distinctive in appearance, as the principal dominant is so conspicuous. Grasses



and most of the species of the mixed consocieties occur here also, and no separate list is accordingly given for the *Silphium* growth. The areas labeled *Silphium-Allium* prairie in the map belong to this consociety. Local abundance of *Allium cernuum* is frequently seen in mesophytic prairie-grass of very rich, moist soil. This may be called the *Allium* society. *Allium canadense* sometimes replaces *Allium cernuum*. Certain species not listed from the two stations above mentioned appear in the following table:

ADDITIONAL SPECIES OF MESOPHYTIC PRAIRIE-GRASS

lf <i>Hypoxis hirsuta</i> , h	lf <i>Stachys palustris</i> , h
lf <i>Oxalis stricta</i>	lf <i>Eupatorium perfoliatum</i>
la <i>Viola papilionacea</i>	la <i>Helianthus grosse-serratus</i>
l <i>Asclepias syriaca</i>	f <i>Achillea Millefolium</i>
la <i>Convolvulus sepium</i>	i <i>Senecio Balsamitae</i>
i <i>Physostegia virginiana</i> , h	

*The swamp-prairie or fen association.*—The hydrophytic extreme of prairie-grass passes insensibly, in places, into marsh associations; in other places there is conspicuous zonation, the boundaries following contour lines about depressions. One of the most distinctive appearances of swamp prairie is the *Liatris spicata* consociety, which has been rather fully described by Gates.\* Scattered representatives of the blazing-star prairie are found in eastern Du Page County, though formerly they were more abundant. There is also a mixed consociety, variable in composition, in which umbellifers are frequently prominent. The meadow rue, *Thalictrum dasycarpum*, sometimes marks a well-defined zone. The species typical of the hydrophytic prairie are here listed. Many of them persist as relics in mesophytic growths.

SPECIES TYPICAL OF SWAMP PRAIRIE OR FEN

l <i>Calamagrostis canadensis</i>	f <i>Asclepias incarnata</i> , ch
l <i>Spartina Michauxiana</i>	i <i>Asclepias Sullivantii</i>
l <i>Glyceria nervata</i>	f <i>Phlox pilosa</i>
l <i>Cyperus</i> sp.	l <i>Veronica virginica</i>

\* Gates, F. C. The vegetation of the beach area in northeastern Illinois and southeastern Wisconsin. Bull. Ill. State Lab. Nat. Hist. 9: 255-372. (*Liatris spicata* prairie, pp. 301-303.) 1912.



l <i>Iris versicolor</i> , ch	l, i <i>Valeriana edulis</i>
f <i>Thalictrum dasycarpum</i> , ch	l, i <i>Lobelia syphilitica</i>
i <i>Hypericum</i> sp.	l, f <i>Eupatorium perfoliatum</i> , m
f, ld <i>Eryngium yuccifolium</i> , ch	ld <i>Liatris spicata</i> , ch
f <i>Cicuta maculata</i> , ch	l <i>Solidago Riddellii</i> , m
i <i>Thaspium aureum</i>	l <i>Solidago ohioensis</i>
f <i>Oxypolis rigidior</i> , ch	i <i>Aster paniculatus?</i>
l, i <i>Gentiana Andrewsii?</i>	lf <i>Parthenium integrifolium</i> , m
l <i>Apocynum cannabinum</i>	i <i>Senecio Balsamitae</i>

What may be called the *Eryngium* consocieties of swamp prairie is characterized by dominance of this peculiar umbellifer, and corresponds fairly well with the *low prairie* of Cowles.\* This growth shades into the *Silphium terebinthinaceum* consocieties of the mesophytic prairie-grass association, *Silphium* and *Eryngium* frequently being seen together in about equal abundance. This is then the transitional growth between hydrophytic and mesophytic prairie. The plants conspicuous in this intermediate prairie are marked "h, ch" in the list of mesophytic prairie-grass species.

*The marsh associations.*—Areas of marsh vegetation are usually scattered and not large. There are now few areas of open water, since many of the ponds and swamps west of Chicago have been artificially drained. Marsh growths are commonly dominated by a single or by very few plant species. Prominent among these are *Spartina Michauxiana*, *Calamagrostis canadensis*, *Phragmites communis*, *Glyceria nervata*, *Scirpus lineatus*, and *Typha latifolia*. Willows (*Salix longifolia*) and cottonwoods (*Populus deltoides*) are able to establish themselves on the margins of some of these swamps, particularly in mud flats left by summer shrinking of ponds. A small pond near the southwest corner of the area mapped, and the slough directly east of this pond, are thus margined with good-sized trees.

The zone marked "*Agrostis*" in the map is probably disturbed swamp prairie. It is now dominated by the single grass species *Agrostis alba* (red-top), and there are also a few swamp prairie plants, as *Cicuta maculata*. Lower ground is occupied by a vir-

\* Cowles, H. C. The physiographic ecology of Chicago and vicinity. Bot. Gaz. 31: 73-108, 145-182. 1901. (Low prairie, p. 156.)



tually pure growth of *Glyceria nervata*, which thus forms an inner zone. The large depression in the map has a deeper region occupied by a smartweed with large hairy leaves (*Polygonum amphibium* var. *Hartwrightii*).

*Disturbed prairie.*—Ruderal and primitive prairie growths which come up in broken or otherwise modified prairie ground are often dominated by single plant species. The native prairie plants include the following: *Lepachys pinnata*, forming conspicuous pure growths, usually in rather dry soil; *Asclepias verticillata*, and *Lespedeza capitata*, locally abundant (rather infrequently in eastern Du Page County) in disturbed prairie along rights-of-way; *Helianthus grosse-serratus*, forming tall growths in rather moist soil; *Cassia Chamaecrista*, *Erigeron annuus*, and *Ambrosia artemisiifolia*, not very frequent; *Erigeron canadensis*, and *Lactuca canadensis*, acting quite like successful introduced weeds; *Aster multiflorus*, persisting as a prairie relic even in city lots; and *Convolvulus sepium*, an insidious creeping dominant which replaces prairie plants under changed conditions.

The prominent introduced plants are *Agrostis alba* and *Trifolium repens* in moist soil, especially with grazing; *Phleum pratense* and *Trifolium pratense*, hay plants common in rights-of-way, and in prairie which is occasionally cut for hay; *Melilotus alba*, a serious pest which has replaced extensive areas of prairie (once the prairie is broken, the sweet clover may assume complete dominance); *Poa pratensis*, very generally distributed, perhaps succeeding sweet clover after some years, in many stations; *Daucus Carota* and a number of other plants, infrequent.

*Development of the prairie.*—Mesophytic black-soil prairie may develop from either of two extreme types of vegetation, hydrophytic or xerophytic. The developmental series beginning in shallow water or marshy situations has been discussed by Cowles (l. c., pp. 155–156). Gates has described succession from marsh associations to the *Liatris spicata* type of prairie (l. c., p. 335, pl. 39). The development from grassland of pronounced xerophytic type has hardly been mentioned, with exception of that which takes place in prairie of dry sandy soil (sand prairie). The development of open xerophytic bunch-grass of sand prairie into less xerophytic types such as the *Sporobolus heterolepis*-*Sorghas-*



*trum* and *Liatris scariosa* prairie consociates has also been treated by Gates (l. c., pp. 300-303, *pl.* 39). The convergence of sand prairie and xerophytic prairie of other soils into less xerophytic prairie-grass has been described by the writer.\* The more markedly xerophytic prairie-grass types are no longer present in eastern Du Page County, but may be seen in areas of older drift, as in Ogle County (Illinoian glaciation), or in still drier situations, as loess-capped bluffs of the Mississippi River (seen at Savanna, Illinois) and other prairie-grass stations farther west. Development of mesophytic prairie, from both xerophytic and hydrophytic



FIG. 7

FIG. 7. A forest border at the county line station. *Andropogon furcatus* prominent in foreground; sunflower and dogwood zones at the edge of the forest; grapevines on some of the shrubs.

extremes, may be due to action of the vegetation itself or to physical changes of environment. Retrogressive successions occur locally. Relic species from the former condition are perhaps more

\* Vestal, A. G. An associational study of Illinois sand prairie. Bull. Ill. State Lab. Nat. Hist. 10: 1-96. 1913. (The black-soil transition association, p. 80.) The status of prairie associations in the southern beach areas of Lake Michigan. Jour. of Ecology. In press. (The dry prairie-grass association.)



abundant than invading species: it is probable that change in floristic composition lags behind changes in ecological conditions, due to greater or less plasticity of environmental relations in most of the plant species.

*The forest border.*—The forest of the area mapped is not in itself part of the subject-matter of the present discussion. Much of it is a mixed tree growth, in which basswood is very prominent. Other trees are elm, walnut, oaks (several species), hackberry, wild crabapple, choke-cherry, and wild plum. The undergrowth is made up of characteristic species of mesophytic forest, with blackberry and raspberry shrubs in more open spots.

Parts of the forest border are in apparently original condition. The undisturbed growth is of two types, first that of exposed sunny borders, best seen on south and west edges of wooded areas, and second that of shaded borders, on north edges. No east-facing borders in good condition are to be seen at the county line.

The *exposed borders* show very distinct zonation. In some places a *low-tree zone* is seen at the edge of the forest proper. This is composed of wild crab (*Pyrus coronaria*) or of plum (*Prunus americana*) or of thorn-apple (*Crataegus* sp.). These trees are usually from nine to fourteen feet in height, and form a zone of varying width. A *shrub zone* is seen just outside the trees. A dogwood (*Cornus Amomum*) dominates; hazel (*Corylus americana*) and elder (*Sambucus canadensis*) are locally abundant. The dogwood is usually three and a half feet high, the hazel is about seven feet high; the shrub zone is four to ten feet wide. Grapevines (*Vitis vulpina*) cover some of the outer shrubs and trees. The *outermost zone* is almost a pure growth of sunflowers (*Helianthus decapetalus* and *H. divaricatus*), locally replaced by a species of *Verbesina*.\* The height of the sunflowers is two to four feet; the zone is two to eight feet in width. The prairie just outside the sunflower zone is strikingly uniform with that farther from the forest.

The *shaded forest borders* are less regular in composition and structure. The border of one grove, which abuts at its northern edge on a moist grassland (*Agrostis* zone, see map), was observed

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\* Dr. T. D. A. Cockerell has examined the specimens, which are alternate-leaved, resembling *Verbesina helianthoides*, but differing from the description of that species in that the leaves are not sessile.



to contain the following plants: thorn-apple, occasional at the edge of the forest; dogwood, in a narrow and interrupted zone next the trees; occasional shrubs of black raspberry (*Rubus occidentalis*); lianes (*Rhus Toxicodendron*, *Vitis vulpina*, and *Psedera quinquefolia*), climbing on some of the outer shrubs and trees; tall herbs (*Veronica virginica*, *Campanula americana*, *Geum strictum*); other herbaceous plants, some being prairie plants common near forest areas (*Monarda mollis*, *Pycnanthemum virginianum*), some common in swamp prairie (*Thalictrum dasycarpum*, *Oxypolis rigidior*). Less mesophytic borders, particularly at northwest-facing forest edges, are transitional between shaded and very exposed borders, the *Cornus* and *Helianthus* zones usually being present, but often very narrow. Additional secondary species of infrequent occurrence are seen.

A disturbed south-facing border near the railroad track has the sunflower zone partially replaced by Canada blue-grass (*Poa compressa*). Scattered shrubs of *Rosa humilis*, *Rhus glabra*, and blackberry (*Rubus* sp.) are invading the grassland at some little distance from the woods.

*Summary.*—The county line station, a half-hour's ride west of Chicago, contains areas of prairie, forest, and forest border in still fairly good condition. Preservation of the forest from former prairie fires is suggested by its location on the east side of a line of prairie sloughs. The prairie, like that of other stations in this part of Illinois, is largely mesophytic; this type is of three appearances: (1) the *Andropogon furcatus* prairie, (2) the mixed grass prairie, and (3) the *Silphium terebinthinaceum* prairie. Mesophytic prairie-grass may be derived either from marsh growths and swamp prairie or fen, small areas of which are still abundant near by, or from xerophytic prairie-grass, represented in the area chiefly by *Silphium laciniatum* prairie. The markedly xerophytic types of prairie-grass no longer persist in upper Wisconsin glaciation of northeastern Illinois, but are well represented in central and western parts of the state. Sunny forest borders show an outer zone of sunflowers, a shrub zone of dogwood, occasionally with hazel or alder, and sometimes a low-tree zone, in which plum, thorn-apple, or wild crab may be seen. Shaded borders show less definite and narrower zones, with tall mesophytic herbs, climbers, and usually dogwood.







## Mechanical tissue development in certain North American vines\*

HOWARD H. M. BOWMAN

During the year 1912, a study was made of various woody vines growing in temperate North America, with the idea that there might be some relation between them and intermediate forms bearing on the origin of the liana habit in these temperate regions. This paper refers more particularly to the mechanical tissues of these plants.

The liana habit of course shows no phylogenetic connections and in this respect is analogous to parasitism, saprophytism, etc. The habit evidently did not arise early in the temperate zone since among the plants indigenous to this zone it is developed to a very slight extent among the lower orders, Liliales perhaps being one of the first, that is, on the arbitrary basis of the coördination of structure with time of origin. In the tropics, however, the monocotyledonous families having the liana habit are much more numerous, e. g., some bamboos and various members of the Palmaceae, Pandanaceae, and Araceae, etc. But if, as some recent investigators (see Henslow, 5) conclude, the monocotyls arose from the dicotyls, this theory of chronological origin may be discredited altogether. At any rate, it is fair to suppose that the habit did not arise until there was such dense vegetation as to make the habit an advantage to the plant. Most of the lianas, according to Schenck's estimate (see Schimper, 7, p. 197) ten elevenths, are tropical because the conditions in the tropical rain forests are the causative factors, i. e., deficiency of light and abundance of moisture.

However, the simplest internal physiological reason for the origin of this vine habit seems to be the lack of adequate mechanical tissues. A secondary factor is the lengthening of the internodes but this is due to the evident physiological process of elongation by diffuse light reaction. This can easily be accounted for by an

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\* Contribution from the Wolff Biological Laboratory, Franklin and Marshall College, Lancaster, Pennsylvania.



adaptive line of reasoning since the vine habit is most prevalent in habitats of diffuse light and plenty of water. As Schimper (7, p. 309) says, the origin of both lianas and epiphytes is to be traced to a low intensity of light and an abundance of moisture. But the lack of adequate mechanical tissue is not well accounted for. To attempt to explain this it seems to be necessary to look at the plant characters from a genetic point of view. Clearly the amount of mechanical tissue is a unit character in a plant and any variation in this direction affects this character. In the course of the formation of the ancestral germs of plants showing this habit there must have occurred a dissociation of characters and this segregation of characters associated together in the normal ancestor gave rise to their present form; since Bateson (2) says segregation thus defines the units concerned in the constitutions of organisms and provides the clue by which an analysis of the complex heterogeneity of living forms may be begun. Right in the line of this investigation is the peculiar phenomenon observed by de Vries in his *Oenothera* cultures in the specific example of *Oenothera rubrinervis*, which has among other characters bast fibers with thin walls. According to de Vries's observations *O. rubrinervis* arose once in every thousand seedlings and twelve times in cultures not in the direct line of descent, i. e., from the pure *O. Lamarckiana* family. In this instance de Vries thinks that if the group of *rubrinervis* characters could be dissociated, then its compound nature would be disclosed. How the unit can cause the bast walls to become thin cannot be explained, but he insists that the habit of a species can be so much altered by mutation that during its whole life and in every organ it differs from its parent species (8). Now, just as this could happen in *Oenothera rubrinervis*, could there not be a similar segregation and recombination of different characters so as to cause a decrease in the mechanical tissue of any plant in a period of mutation?

With this question in mind an examination of the stems of various plants in diverse families found in the temperate zone was made to see if there was a warrantable deficiency in mechanical tissue development to account for the inability of these plants to stand erect. This group of plants was composed of the following: *Rhus Toxicodendron*, var. *radicans* (L.) Torr., *Psedera quinque-*



*folia* (L.) Greene, *Vitis vinifera* L., *Hedera Helix* L., *Akebia quinata* L., *Rosa polyantha* L., *Lycium halimifolium* Mill., *Wisteria frutescens* (L.) Poir., *Lonicera japonica* Thunb., *Tecoma radicans* (L.) DC., *Rubus occidentalis* L., and *Kerria japonica* L.

The *Lonicera* was first examined and, as de Bary (1, p. 532) observed, this plant has a simple arrangement of its tissues, producing one zone of bast fibers and one of soft bast each year. This inner zone is just on the inner boundary of the bast and the wood fibers are disseminated in the xylem in single radial rows. The arrangement of fibrous strands gives sufficient tensile strength but is not enough to permit the plant to stand upright. These bast strands are not close enough together to give adequate support in an upright position. Under the epidermis the cortical parenchyma is somewhat thickened but as a source of mechanical support this is almost negligible. The wood cambium consists of ordinary parenchyma. Inside the soft bast zone between it and the pith there is a parenchymatous tissue called by Strasburger *vascular parenchyma*. This may give some support, particularly under a tension. The vascular elements occupy the remaining space. In older stems of the *Lonicera* of course the secondary tissues give considerable stability to the stem, but the primary xylem of a first year stem is not nearly enough to enable the stem to maintain a perpendicular position.

The stem of the *Akebia* is angled and for each ridge there is a large vascular bundle, oval in cross section. The bundles fill most of the space in transverse section. The most important mechanical tissue is the bast, which forms a small cushion, four or five cells in thickness, on the outer edge of each bundle. The bast fibers are heavy and have very small lumina but they are deficient in number. The cortical parenchyma is assimilative in the *Akebia* and therefore has very thin walls. The primary xylem is not important from a mechanical standpoint in this plant; the conductive elements occupy 58.3 per cent, while the mechanical tissue occupies only 8.3 per cent of the transverse area, i. e., a ratio of 7 to 1. The bast cells in the *Akebia* are thicker than those of the *Lonicera* but the numerical proportion is smaller.

In *Hedera Helix* the most noticeable feature is the narrowness of the medullary rays, which are only one cell thick. The mechan-



ical tissues are represented only by the xylem and the small amount of bast next to the outer cortex parenchyma. A peculiar feature of this latter is that under certain conditions it is greatly increased and bush forms of the *Hedera* can be noted in many gardens. The occurrence of this form as a variety is frequently noted in botanical literature (see de Vries, 8, vol. 1, p. 44). This would go to show that in the ivy, if it grows as a bush, i. e., if it is well fertilized and pruned, the bast elements will develop to such a degree that it can maintain an erect position. The shock of pruning seems to cause this undue development of bast. This plasticity of the stereome development offers ground for the theory that the liana habit arose from erect plants.

In the *Rhus* there are almost no medullary rays to be clearly distinguished, the primary xylem is well developed and in the phloem the resin ducts are seen, as mentioned by de Bary (1, p. 452). The mechanical tissues are poorly developed in primary growth except the collenchyma, of which there are approximately three layers of cells. In the secondary growth the bast fibers are parallel in development with the secondary wood. In the *Rhus* the estimate is 39.51 per cent for the vascular elements.

The *Wisteria* shows the greatest development of sclerenchymatous fibers with very heavy walls, so that they appear almost solid. In the wood cambium and the cortical parenchyma there are a great many calcium oxalate crystals and in the latter region are also many irregularly shaped stone cells. These give the plant considerable strength, but there are not enough of the long fibers to produce a solid cylinder. A young plant with this amount of mechanical tissue can keep an erect position until it is a half meter high, when the weight of the increasing growth becomes too great for these tissues and it assumes a recumbent position. This was observed in young plants grown under various conditions and in different situations. The leaning position is assumed much earlier in diffuse light.

There are peculiar conditions in the mechanical development of the *Lycium*. This plant is half shrub and half vine. Its manner of growth is most interestingly discussed by Kerner von Marilaun (6, vol. 1, p. 672). The xylem occupies a very large space and the bast is developed so as to fill 18 per cent of the transverse area.



The pith and the parenchyma of the cortex also occupy relatively large spaces and contribute nothing to support. In this plant the characteristics of the ivy are again reviewed. If the *Lycium* is grown in open situations, such as fields, the plants can make a growth of several meters before becoming entirely prostrate, and if pruned will form a dense, shiny shrub. If it grows in diffuse light near a support, however, the characteristic "leaner" habit or, as Kerner von Marilaun calls it, the "weaving" habit, is developed.

The *Psedera* has a very definite arrangement of the mechanical tissues. The xylem occupies almost a continuous cylinder outside the pith, the rays separating the bundles being very narrow. In the wood cambium the bast fibers conform to the type called by de Bary branched sclerenchymatous fibers, forming a continuous cylinder with a thickness of six cells. This makes the stems very tough and by experiment in the laboratory it was found that a stem of one season's growth, 70 cm. long and 0.3 cm. in diameter, bore a strain of 8845.2 grams before breaking but could not support an erect position in a stem of the same dimensions more than 70 cm. in length. These sclerenchymatous fibers in transverse section measured 0.06–0.08 mm. in their greater dimension and 0.01–0.02 mm. in the shorter, the sections being irregularly oblong; the lumina were about 7  $\mu$  wide, thus showing the walls to be comparatively heavy. According to the above experiment, however, the fibers do not suffice to maintain the stem in an upright position.

The arrangement in the *Vitis* is similar to the preceding in a great many respects. The xylem is here developed to a greater extent and this gives a considerable support. The medullary rays are clearly defined and also the cambium ring. In the *Tecoma* there is very good reason for the toughness of the stem. In transverse section, by measurement it was seen that in a belt of the cortical parenchyma 0.9 mm. wide there were thickly scattered groups of short sclerenchymatous fibers and also a heavy reinforcement in the external layer of collenchyma. The stem, too, occupies a large area. In fact, in the *Tecoma* the vascular elements occupy  $33\frac{1}{3}$  per cent of the stem and the secondary thickening is, of course, very interesting. Haberlandt (4, p. 629) remarks that Sanio first observed that the wood and bark formation took place in the reverse order from most plants.



However, as the secondary thickening is not considered in this study, its details will not be mentioned. A peculiar though common phenomenon is seen in the *Tecoma* in that there is a great increase in the parenchymatous tissues on the side from which adventitious roots or holdfasts are put out, so that there is a great differential growth seen in transverse section.

In the *Rosa*, which is a "leaner" or "weaver" according to Kerner von Marilaun's terminology, the vine habit is almost lost. This is like the *Hedera* inasmuch as it has so much plasticity that by proper culture it can be made to assume a tree-like or shrub-like form. The mechanical tissues are well represented, the large, thick-walled fibers form an interrupted sheath in the transverse section and there are also many large crystals of calcium oxalate in the peripheral region; the collenchyma is very thick-walled and the xylem is arranged in numerous narrow bundles separated by frequent, though attenuated medullary rays. The *Rubus* shows very similar characters. This genus is also included in Kerner von Marilaun's weaving category, but it has various species in southern Asia and Australia which are typical lianas. In both *Rosa* and *Rubus*, of course, the pith area is very large in cross section. In the *Rubus* the bast fibers form a heavy belt and the collenchyma too is developed to six layers of cells. The last species studied, *Kerria japonica*, is a weak shrub and never develops any vine habit. In this plant, however, the mechanical support does not seem to come so much from the bast fibers, etc., as from the principle of construction, i. e., a very firm outer cylinder filled with pith. The bast fibers are large but few in number and scattered in small groups, the perennial epidermis doubtless also contributing to the stability of the stem as also the lignified tissues of the very broad, flattish vascular bundles.

Now in looking over the anatomy of this group of plants it would seem that the variation in stereome elements in stems would naturally be a factor of great importance in the evolution of the vine habit. Of course the first and most important agent is light, since light by its action on the chloroplast tends to change the shape of the cell. Diffuse light is known to cause an elongation of parenchymatous cells and this of course produces elongation in an organ. This then partially accounts for the elongated habit of



vines but why there should be also a decrease in the mechanical tissues or at least an inefficiency in support for the stem can not be explained on this basis. The fact that reduced photosynthesis due to shade can bring about a decrease in constructive tissues might seem of some importance, but plants that have the habit develop characteristically in full light as well as shade so this argument is negligible.

So it would seem that there must be some basis for argument in support of the position taken before, viz., that in the light of de Vries's classic experiment on *Oenothera* the mechanical tissue development has its origin in the unit characters of the plant. As these are partially dependent on nutriment in the ancestors it follows that there must have been considerable variation in the premutation stages of the vines studied. As de Vries says all mutations are not progressive, i. e., visibly differentiated, we may speculate and suppose the plant to have undergone a retrogressive mutation which produces a change, a decrease in the bast fibers, etc. These characters then of the normal type have become latent or suppressed and may be retained as internal units, e. g., in the *Hedera* and at a future time under proper conditions may become activated. When once the plant has become a "leaner" by deficiency in mechanical support the secondary result of diffuse light can produce its effects towards elongation. However, this is speculation and mere argument based on *a posteriori* grounds. As stated above, all mutations need not be advantageous, and the first stages in the vine habit may have been distinctly disadvantageous. It may be said that the primary variation in mechanical tissues is due to recombination of the characters of certain plants and that plants with vine habits arise as mutations due to the preceding causes. In conclusion a quotation from the Chicago Textbook (3, p. 656) may give the general idea of this line of evolution: "It is assumed, and probably correctly, that lianas have come from erect ancestors, and that their evolution was subsequent to that of trees. . . . Probably the first lianas were leaners, the twiners and tendril climbers developing later."

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## The nomenclature of the genus *Usnea*

R. HEBER HOWE, Jr.

(WITH PLATES 9-14)

In my first paper on the genus *Usnea* (Bull. Torrey Club 36: 309-327. *pl.* 21-23. 1909) I made no attempt to solve the nomenclatural questions presented in this genus. In my second paper (Bull. Torrey Club 37: 1-18. *pl.* 1-7. 1910) I located the types of the species concerned and attempted to use determinations made of the Dillenian types by Crombie to elucidate the problem of the Linnean species. In a still later paper (Bull. Torrey Club 37: 605-609. 1910) I made further notes based on Dr. Wainio's report on the Linnean types. These three papers presented the nomenclature of the Linnean species as follows, as compared with Tuckerman's and Dr. Zahlbruckner's treatments.

Tuckerman, based on E. Fries:

*Usnea barbata* (L.) Fr.

*barbata a. florida* Fr.

*barbata a. florida \*hirta* Fr.

*barbata a. florida \*\*rubiginea* Michx.

*barbata b. ceratina* Schaer.

*barbata c. dasypoga* Fr.

*barbata d. plicata* Fr.

*barbata e. articulata* Ach.

Author's 1909 paper:

*Usnea barbata* (L.) Fr.

*barbata florida* (L.) Fr.

Contingent phases: *Usnea barbata hirta*

*barbata rubiginea*

*barbata florida f. strigosa* Ach.

*barbata ceratina* (Ach.) Schaer.

*barbata dasypoga* Fr.

*barbata plicata* Fr.

*barbata articulata* Ach.

Author's 1910 paper, based on Crombie:



*Usnea florida* (L.) Web.

Cont. phase: *Lichen hirtus* L.

*Usnea florida* Michx.

*Usnea plicata* (L.) Web. = *Usnea ceratina* Ach.

*plicata* var. *barbata* (L.) R. H. Howe = *Usnea dasypoga*  
(Ach.) Nyl.

*articulata* (L.) Hoffm.

Author's 1910 paper, based on Dr. Wainio:

*Usnea florida* (L.) Web.

Syn. *Lichen hirtus* L.

*plicata* (L.) Web. = *Usnea ceratina* Ach.

*barbata* (L.) Web. or *U. plicata* var. *barbata* (L.) R. H.  
Howe = *Usnea dasypoga* (Ach.) Nyl.

*articulata* (L.) Hoffm.

Dr. Zahlbruckner; Engler & Prantl, Nat. Pflanzenfam.:

*Usnea florida* (L.) Hoffm.

*ceratina* Ach.

*dasypoga* (Ach.) Nyl.

*dasypoga* var. *plicata* (Hoffm.) Hue

*articulata* (L.) Hoffm.

The only correction made by me,\* which has had general adoption, is the acceptance of Weber as the first author responsible for the combination *Usnea florida* as a binomial.

During the year 1912, through the kindness of Dr. S. H. Vines and Dr. B. Daydon Jackson, I had the opportunity to study both the Dillenian and Linnean herbariums and also authentic Fries and Acharian material. I here present photographs of the types and trust that the problem may now be considered settled beyond all doubt.

#### Series: *Mesinae*

Chondroid axis one third the diameter of thalline filament.

*Usnea florida* (L.) Web. I find two type specimens preserved in the Linnean herbarium in the apartments of the Linnean Society, Burlington House, London. They are mounted on one sheet labeled *Lichen floridus* in Linné's handwriting, with the Flora Suecica (1745) number 991 written below the specimens. These are typical (as long understood) and are well described in the original description.

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\* Brought to my notice by Dr. J. H. Barnhart.



*Usnea florida* f. *hirta* (L.) Ach. I find three types of this sorediate and generally sterile form of *U. florida* preserved in the Linnean herbarium. One of these bears the Flora Suecica number of *Lichen plicatus*; the other two are atypical (as now understood). The original description is diagnostic.

*Usnea plicata* (L.) Web. I find no true type specimen in the Linnean herbarium. A specimen, probably only a portion of the original plant, answering poorly to Linné's description, is in his herbarium labeled *Lichen hirtus*, but with number 984 (the number of *L. plicatus* in Flora Suecica) written below the specimen. Thus with no definite type, I have endeavored to interpret the Linnean description, and the Dillenian plate (and his type) to which Linné refers and on which Linné based his *Lichen plicatus*. The Dillenian plate and specimen answer perfectly to the Linnean description and must be considered the only sound evidence available, by means of which the status of *Lichen plicatus* L. can be settled. The Acharian *plicata*\* represents the same plant and is not the plant often referred to as var. *plicata* (Hoffm.) Hue. There seems no doubt whatever that though *plicatus* L. and *U. ceratina* Ach. are synonymous (as commonly understood of late in this country and in Europe), we must not consider them identical, no matter with what plants we have since associated the names. The error has arisen through a misunderstanding of *ceratina* of Schaerer and *ceratina* of Acharius, the latter author having priority for the name. The Dillenian type was not determined by Acharius *ceratina* as it was by Schaerer, and as we find Crombie labeled it, and as the Acharian synonymy and material here figured goes to show.† Acharius's *plicata* is the same plant that Linné called *Lichen plicatus*; in other words the *coarse, pendulous* (partially papilloso-orediate but *not* "asperrimo") species of the middle Atlantic States from where the American Dillenian type came (Pennsylvania), and a type locality cited by Linné as directly taken from Dillenius. I cannot see that we are in need of any further data. *Usnea plicata* Hoffm. is therefore also preoccupied, and in Hoffman's own herbarium, moreover, is represented, Dr. Wainio tells us, by a plant referable to *florida* of Fries.

\* Based on Linné and Dillenius, see Lich. Meth. 310. 1803.

† See remarkable plate by Westring, Sven. Lafv. Faerghist 69. 1805, showing complete structure.



*Usnea ceratina* Ach. Through the kindness of Dr. Elfving I am reproducing a photograph of the type of this species. It does not occur in temperate North America and appears to be as Acharius made it a *prostrate* and entirely *asperate* species, perhaps as Dr. Jatta calls it synonymous with *U. coralloides, aspera* Eschw.,\* and certainly *totally* unlike the papillate or partially sorediate and *pendulous* species recognized as *ceratina* (No. 95 Decades No. Amer. Lich., Cummings) or as the especially luxuriant specimens *U. californica* Herre, which may deserve subspecific rank.

*Usnea barbata* (L.) Web. In my former paper I adopted the name *barbatus* L. as synonymous with *dasy-poga* Ach. and pointed out that I believed it to be the proper name for this variety, but my argument was based on Crombie's partially inaccurate statement in regard to the Dillenian type, and also on account of the ("Europae & Americae septentrionalis") type localities. My reasons heretofore stated were that the Dillenian type was said by Crombie to be *Usnea dasy-poga* (Ach.), and also the ruling of early post Linnean authors Westring, Hoffmann, and Fries (see author's Class. *Usneaceae* 14. 1912). An examination of the Dillenian type, a figure of which is here published, shows it to be composite, *Usnea articulata* and *Usnea dasy-poga* mounted on the same sheet. In an examination of the plate of these plants a few semi-inflated articulations (explaining Linné's "subarticulatus") are to be found,† as appears to have been the case in the plant, and Dillenius seems to have ignored the other specimen as he figures it in another and entirely typical plate illustrating his *Usnea capillacea et nodosa*, = *Lichen articulatus* L. It would seem therefore so far as Dillenius is concerned that his type is composite, though not his plate, and by his plate he himself contradicts the duplicity of his type. In the Linnean herbarium, however, we find no type of *articulata*, but a single and perfect specimen of *barbata* which answers exactly to our modern conception of *articulata*. According to Dr. B. Daydon Jackson, however, Linné must have based his *Lichen barbatus* entirely on Dillenius, for he did not have a specimen of it in his own herbarium until 1767 (Index Linn. Herb., Supp. Proc. Soc. 96. 1912). One is therefore left with

\* A caespitose, erect, not prostrate species.

† A condition not infrequently met.



two alternatives, the first plainly defying Linné's intention, i. e., to use *articulata* as a synonym of *barbata*, turning to Acharius's name for the present plant, either exactly as he proposed it or as combined by Nylander. The other, to accept Linné's descriptions of both *Lichen barbatus* and *L. articulatus*, which are diagnostic and (except for the composite type conditions referred to) as Dillenius figured and understood them, for the two descriptions leave no doubt that Linné intended to indicate two different plants. This latter procedure is it seems clearly the proper one, soundly based and entirely satisfactory.

#### Series: *Leptinae*

Chondroid axis one fifth diameter of thalline filament (internodal section).

*Usnea articulata* (L.) Hoffm. I find in the Linnean herbarium one sheet labeled 72 *barbatus* by Linné, which represents the typical plant generally recognized as *articulata* (L.) Hoffm. As already shown Linné was describing another species, based entirely on Dillenius, when he named *Lichen barbatus*, as this specimen was not acquired until 1767, twenty-two years after he first described it. Linné's description is diagnostic, and his type locality an added argument.

Our North American Linnean species therefore stand as follows:

*Usnea florida* (L.) Web.

*plicata* (L.) Web. = *U. ceratina* Schaer. non Ach.

*barbata* (L.) Web. = *U. plicata* var. *dasy-poga* Ach.

*Usnea articulata* (L.) Hoffm.

One cannot emend and adopt the Acharian name *implexa* for the plant known as *U. dasy-poga* var. *plicata* (Hoffm.) Hue, a name absolutely untenable as preoccupied by a recognizable plant, as Acharius himself finally made it a synonym of his own *plicata*. Again, as I have said, Hoffmann referred to the same Dillenian plate (*pl. II, f. I*) as Linné did, and the plant so named in the Hoffmann herbarium is curiously enough *florida* of Fries. One must therefore turn to Schaerer and adopt his variety *stricta*\*

\* Orig. desc. "ramis simplicissimis, stricta" Spicil. 507. 1840; "straminea, subdichotoma, flaccida, pendula, tenera, ramis simplicibus, strictis, efibrillosis." Type loc. "sylv. alpin. Helvetiae." Enum. crit. Lich. Europ. 4. 1850. Latin *strictus* = straight.



as he seems to be the first author to recognize this simple, naked variety of *barbata*,—which plants can be hailed as *Usnea barbata* var. **stricta** (Schaer.) comb. nov., a name that antedates *Usnea barbata* var. *intermedia* Mass., given seemingly to the same plant.\* The question now presents itself, shall botanists consider these actual specimens in the light of types. Whether they do or not seems of little importance. The investigation of them has led to an understanding of really what plants Linné named, and this I take it is what we most desire to know if we are ever to place our nomenclature on a sound basis. My view taken in 1910 is therefore unchanged, except in the realization that *Usnea ceratina* Ach. is not synonymous with the plant (Linné's *plicatus*) Crombie, Tuckerman and many other recent authors (based on Schaerer) supposed, but is a distinct and very different species. Dr. Zahlbruckner's work fails to take account at all of the coarse, pendulous plants, i. e., *ceratina* of Schaerer or *plicatus* of Linné, as he cites only *ceratina* of Acharius.

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#### EXPLANATION OF PLATES 9-14

##### PLATE 9

UPPER FIGURE. The Linnean type of *Lichen floridus* in the Linnean herbarium (reduced one half).

LOWER FIGURE. The Acharian specimen of *Lichen comosus* in the Linnean Society herbarium (reduced to two fifths actual size).

##### PLATE 10

The Dillenian type of *Usnea vulgaris*, etc., incorrectly referred by Crombie to *U. ceratina* Ach. (reduced one half). It also represents Linné's conception of his *L. plicatus*.

##### PLATE 11

UPPER FIGURE. The specimen in the Linnean herbarium bearing the Flora Suecica number 984 of *Lichen plicatus*; labeled *hirtus*, and representing one of the types of the latter species (slightly reduced).

LOWER FIGURE. The Acharian type of *Usnea ceratina* (slightly reduced).

##### PLATE 12

The Acharian specimen of *Usnea plicata* in the herbarium of the Linnean Society in London (reduced one half).

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\* See *U. barbata*, f. *Schraderi* Dalla Torre & Sarn. Flecht. Tirol., etc. 4. 1902.



PLATE 13

The Dillenian types of *Usnea barbata*, etc. (reduced one half).

PLATE 14

LEFT-HAND FIGURE. The Linnean specimen of *Lichen barbatus* in the Linnean herbarium (slightly reduced). This specimen has little claim to be considered a type because of its acquisition twenty-two years after the species was originally described.

RIGHT-HAND FIGURE. The Acharian material of *Usnea barbata*, var. *articulata* (L.) Ach., in the Linnean Society herbarium (reduced one half).







## Observations on the edge of the forest in the Kodiak region of Alaska\*

ROBERT F. GRIGGS

(WITH ONE TEXT FIGURE)

As is well known, the western limit of the Alaskan spruce forest, composed of *Picea sitchensis*, crosses Kodiak Island. The forest on the northeastern portion of the Kodiak group of islands consists of fairly large trees forming a dense stand but further westward the trees are much smaller and grow only in the more sheltered situations, finally failing altogether. The last of them that we saw as we went down the outside coast were on Ugak Island while the furthest extension on the opposite inside coast is at Cape Uganik.

The edge of the coniferous forest is generally spoken of as the edge of the forest but it is by no means the limit of arborescent growth. For both the paper birch, *Betula papyrifera alaskana*, and the cottonwood, *Populus balsamifera*, though mapped by Harshberger† as terminating at the head of Cook Inlet, reach Kodiak Island and extend for many miles beyond the last spruce, growing abundantly in suitable habitats. In our trip around the island we saw the last of them on Two-headed Island, beyond which the country was a treeless grassland or tundra. Coming back on the opposite side we met them again at the entrance to Uyak Bay.

Our nearest stopping place to their limits was at Three Saints Bay. Here the birches occurred singly on the edges of the bogs, reaching a height of about fifteen feet. The poplars grew in clumps on the better drained land. They were about twenty feet tall and somewhat deformed but the deformation was somewhat less marked than in the outermost spruces. The largest plants

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\* Contribution from the Botanical Department of the Ohio State University, No. 81. The writer's opportunity to visit this interesting region came with his employment during the summer of 1913 as scientist in kelp investigations by the Bureau of Soils of the United States Department of Agriculture.

† Harshberger, J. W. Phytogeographic survey of North America. *Veg. der Erde* 13. 1911.



were less than a foot in diameter. These small plants contrasted strongly with those seen later at Kalsin Bay about 55 miles northwestward, which were large trees 60–80 feet tall and 2 feet in diameter. Very much to our regret in view of the conditions later found on the edge of the spruce forest we did not obtain data as to the comparative ages of these trees.

As opportunity presented, observations were made on the fruiting habits of the spruce and the birch; the poplar was not seen in fruit. Most of the trees of both species bore little fruit but some few of them were fruiting copiously. This matter varies much,



FIG. 1. Stunted Alaskan spruce (*Picea sitchensis*) on Afognak Island, near the edge of its range.

however, from season to season. Fernow\* reports that the year 1898 was a heavy seed year for the spruces, which bore an enormous crop of cones, which, turning brown and persisting on the branches through the summer of 1899, "gave the trees at a distance the appearance of having been killed by fire."

Near the edge of the spruce forest it appeared very evident

\* Fernow, B. E. The forests of Alaska. Harriman Alaska Exped. 2: 245. 1910.



that conditions were unfavorable for growth, and that the trees were barely able to maintain themselves. When growing alone their shape contrasted strikingly with the familiar slender spires seen further east. They were squatty and broad with thick stocky trunks (FIG. 1) and evidently grew very slowly. They did better when growing in clumps but the dependence of the individuals on the protection of the clump as a whole was very striking. Regardless of the age of the trees there was a very definite clump-contour beyond which no single branch projected. The growth of the individual members was evidently conditioned on that of the clump. Each tree was kept in exact proportion to its neighbors. The trees in the center were the tallest while those near the edges were progressively shorter and shorter until those on the edges were nearly as much dwarfed as those standing alone.

Apparently here was what I had looked for in vain in studying species on the edges of their ranges in the Sugar Grove area of Ohio,\* namely a species which had reached the limits imposed by climatic conditions so that it could go no further. The climatic extreme in this case would appear to be Merriam's "Effective Temperature Factor" which has been positively assigned as the cause by Piper,† who says "Undoubtedly this effective temperature factor is the principal cause of the sharp demarkation between the timbered and timberless regions on the Alaska coast."

As far as observation could determine, then, here was a clear-cut case of a species which had reached the limits imposed on its extension by its adaptability to climatic conditions. But as a matter of fact this is not at all the case for *the edge of the range of the spruce is not held stationary but is advancing rapidly.*

The advance is so rapid that it is evident to persons who have lived in Kodiak only a few years. According to Mr. M. D. Snodgrass of the Experiment Station all of the old men of Kodiak remember when there were but a few trees on Woody Island which is now heavily forested. On Near Island there are large numbers of young trees coming in on land that was never forested before.

---

\* Griggs, R. F. Observations on the behavior of some species on the edges of their ranges. Bull. Torrey Club 41: 25-49. f. 1-6. 1914.

† Piper, C. V. The grasslands of the South Alaska coast. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 82: 27. 1905.



Mr. Snodgrass himself has observed the advance of the spruce on the station lands at the head of Kalsin Bay, which is within a few miles of the extreme edge of the range. Land which was prairie pasture six years ago when he came to Kodiak is now growing up in spruce.

This unstable condition of the edge of the forest has already been reported by Fernow\* who says:

“There is some evidence that this western limit is not, or may not remain, stable—that the spruce has wandered in recent times and may still wander. There is also evidence that the treeless country beyond, made up of the Alaska peninsula and the Aleutian Islands, is not incapable of growing trees.

“An interesting evidence of the progress of the spruce may be seen on Long Island, a few miles east of Kadiak, where an extensive spruce grove has established itself within the last century. Many trees had been freshly cut and a count of the rings showed none older than ninety or a hundred years. While on Kadiak and Wood Islands the oldest growth was found to be between 125 and 150 years with some few rotten stumps possibly older. This difference in age of entire groves so near together allows the inference that the older has furnished seed for the younger and that the spruce has wandered from Kadiak to Long Island.”

It might seem a simple matter of arithmetic to determine from the data at hand the rate of advance of the spruce forest. This however is not the case. The probability is that the advance goes by long jumps at considerable intervals of time. Fernow (*l. c.*) pointed out that it is conditioned on the conjunction of a good seed-year and a favorable wind, the prevailing winds being adverse. The limits of the spruce which he reports are exactly the same as those we observed after an interval of fourteen years. It must be clear also that after one step forward, further advance is delayed until the trees along the newly established boundary begin to fruit and in their turn supply seed for further invasion. Thus while it may be that there was no actual advance during this fourteen-year period, it is clear from Mr. Snodgrass's experience that the vanguard has been spreading over the newly acquired territory and strengthening itself, so to speak, for another move forward.

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\* Fernow, B. E., *l. c.* 244.



The advancing forest at Kodiak is peculiarly significant because it is a typical example of the kind of evidence upon which most of the assumptions of static plant ranges have been based. The edges of the forests more than any other vegetational lines have been used to show the correlation of plant ranges with climatic factors. Such work is all based on an assumption of complete adjustment of plants to climate and loses its significance wherever such adjustment does not exist, i. e., wherever the ranges are not fixed but changing. Our knowledge of the conditions obtaining at the limits of forests except in a few cases has all been derived from reports by travelers of stunting and apparent struggle against climatic extremes has seemed conclusive just as similar observations appeared conclusive to the writer at Kodiak. In few cases has the history of the regions been examined to find the actual facts.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1913-1914

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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**Bicknell, E. P.** *Viola emarginata* in Massachusetts. *Rhodora* 16: 76, 77. 27 Ap 1914.

**Blakeslee, A. F., & Schulze, A. F.** A possible mutant in the bellwort (*Oakesia sessilifolia*), which prevents seed formation. *Science* II. 39: 621, 622. f. 1, 2. 24 Ap 1914.

**Bödeker, F.** *Mamillaria Gürkeana* Bödeker, sp. nov. *Monats. Kakteenk.* 24: 52-55. 15 Ap 1914. [Illust.]

**Börjesen, F.** The species of *Sargassum*, found along the coasts of the Danish West Indies, with remarks upon the floating forms of the Sargasso sea. 1-20. f. 1-8. Köbenhavn, 1914.

Reprinted from vol. 32 of "Mindeskift" for Japetus Steenstrup.

**Bolley, H. L.** Wheat: Soil troubles and seed deterioration. Causes of soil sickness in wheat lands. Possible methods of control. Cropping methods with wheat. *N. Dakota Agr. Exp. Sta. Bull.* 107: 9-94. f. 1-45. D 1913.

**Boyer, C. S.** A new diatom. *Proc. Acad. Nat. Sci. Philadelphia* 66: 219-221. pl. 10. Mr 1914.  
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Thirty-five new species are described.



- Collins, F. S.** The marine algae of Vancouver Island. Canada Geol. Surv. Victoria Memorial Museum Bull. **1**: 99-137. 23 O 1913.
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- Cook, O. F.** Terms relating to generic types. Am. Nat. **48**: 308-314. My 1914.
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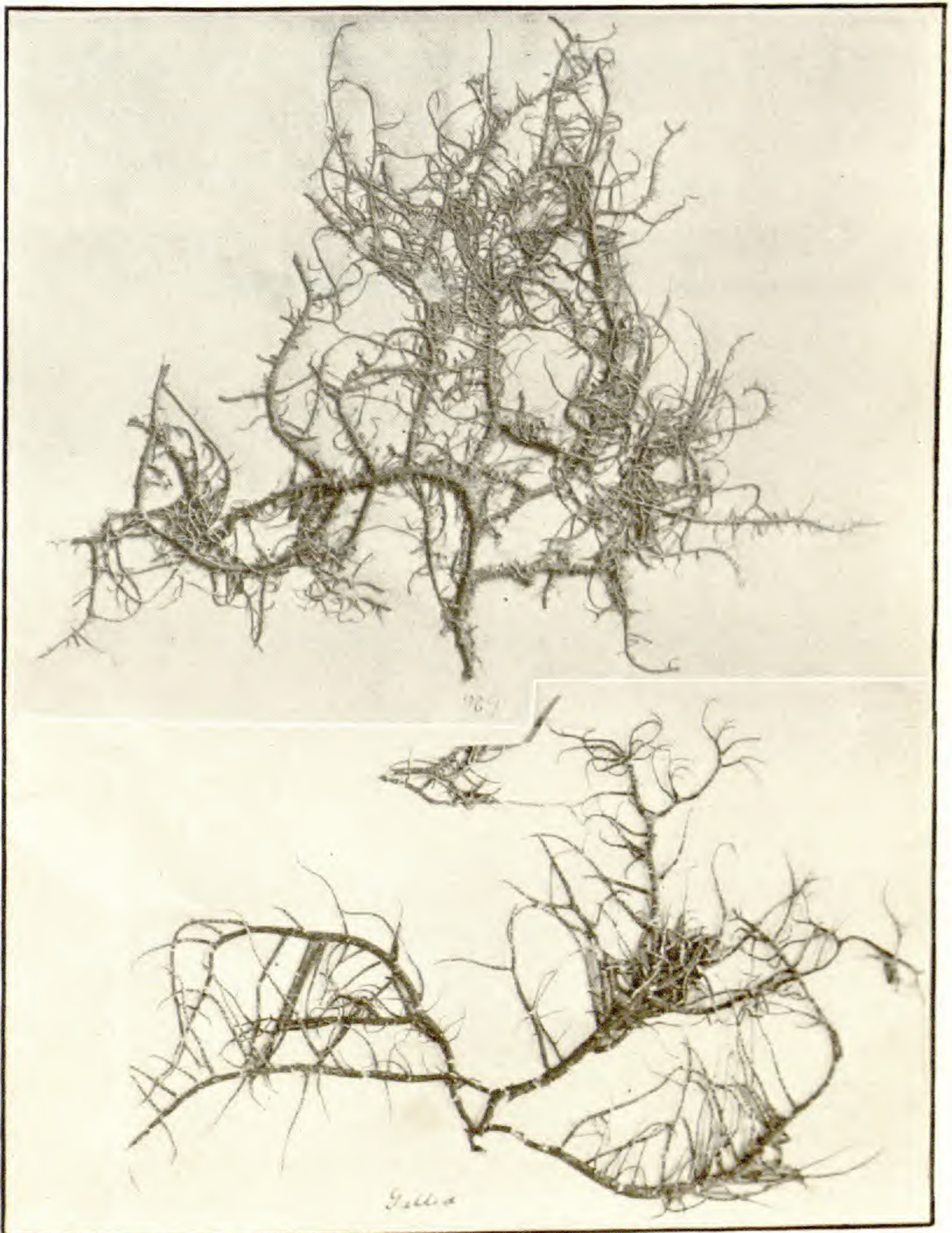
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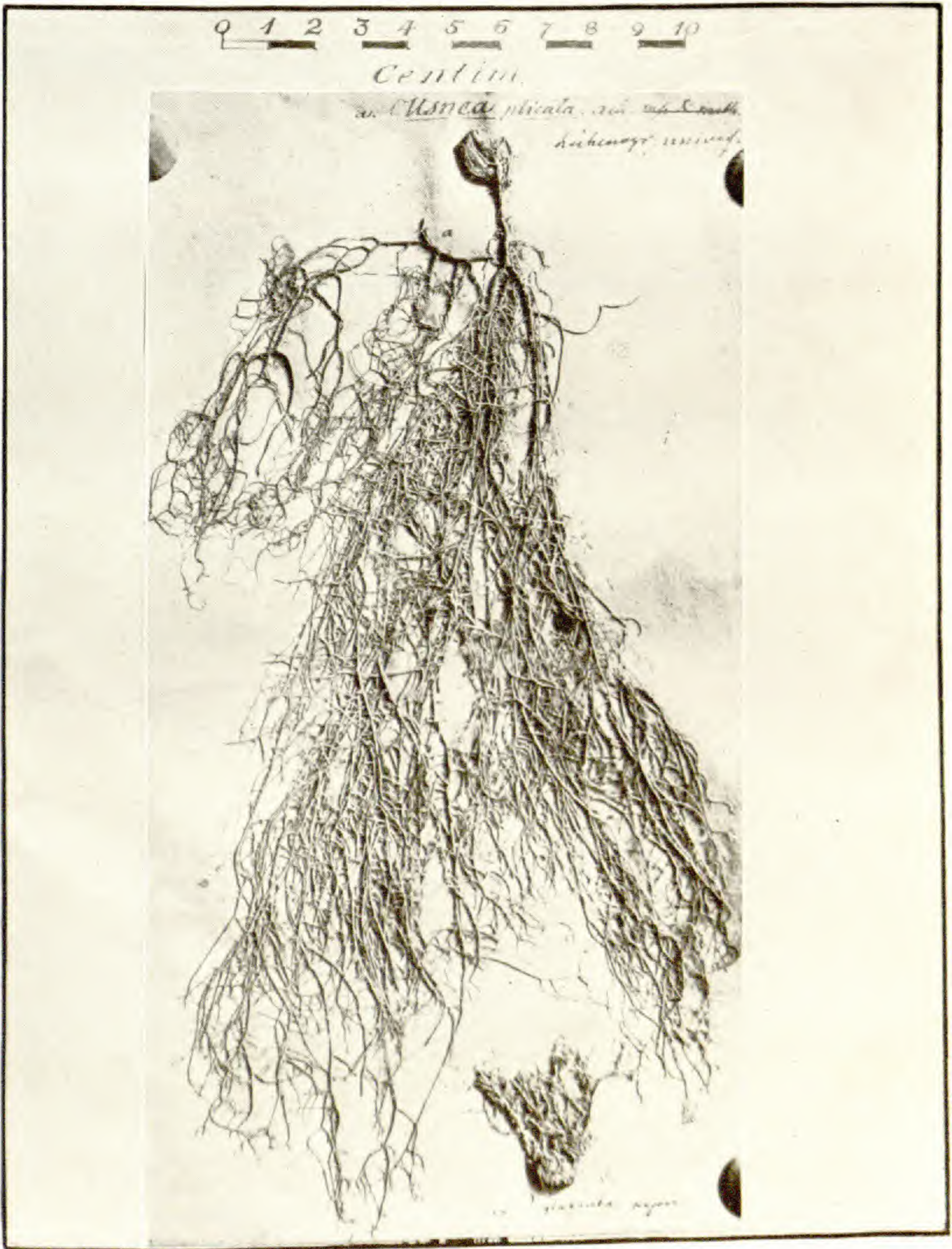
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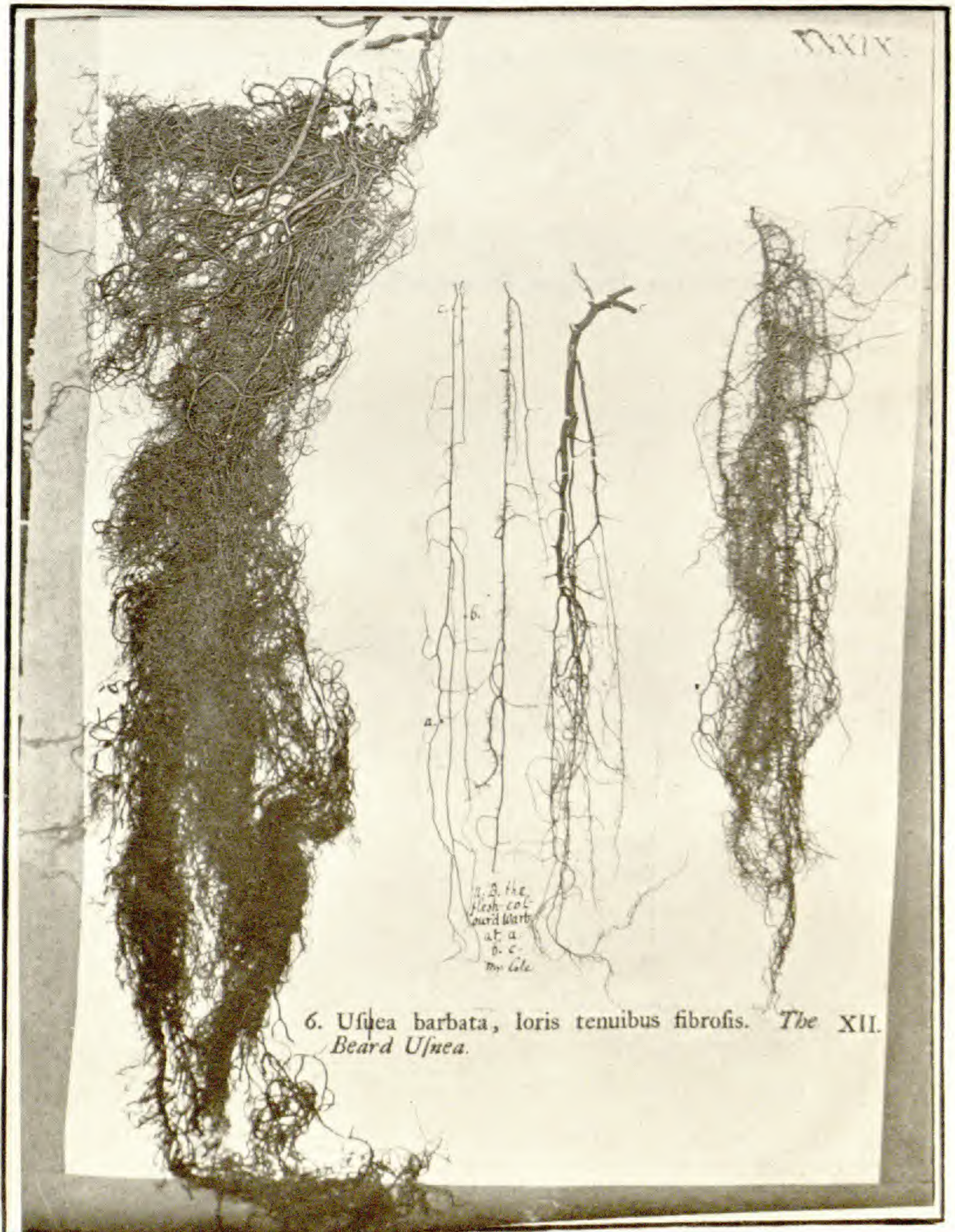
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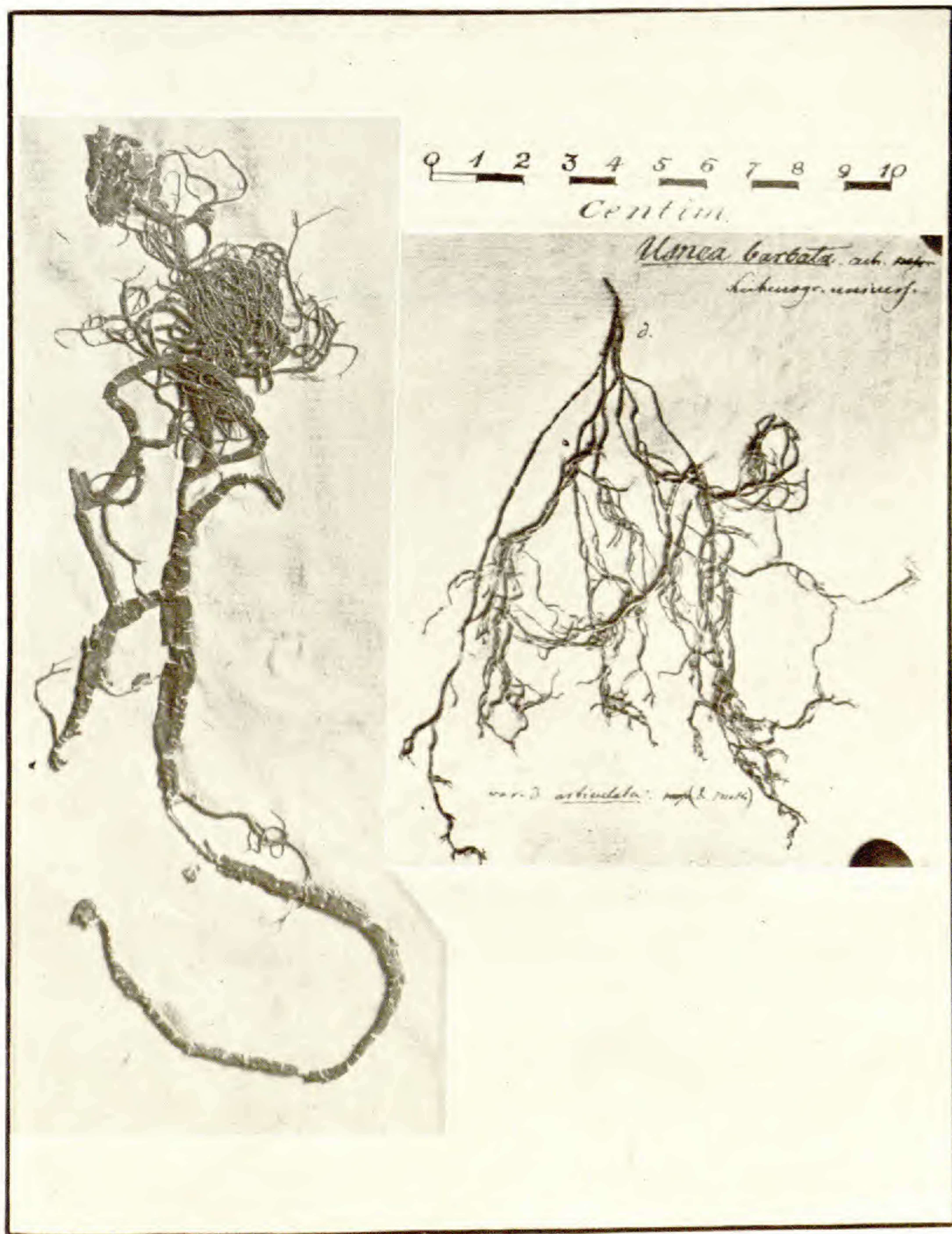


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### CONTENTS

A revision of the genus *Vittaria* J. E. Smith. (Plates 15-20.)  
RALPH C. BENEDICT 391

The ferns and flowering plants of Nantucket . . . EUGENE P. BICKNELL 411

INDEX TO AMERICAN BOTANICAL LITERATURE . . . . . 431

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AUGUST, 1914

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A revision of the genus *Vittaria* J. E. Smith

I. THE SPECIES OF THE SUBGENUS RADIOVITTARIA

(WITH PLATES 15-20 AND SEVEN TEXT FIGURES)

RALPH C. BENEDICT

In an earlier paper on the genera of the fern tribe Vittarieae\* the writer endeavored to point out the natural generic and subgeneric groups of the tribe, to discuss as well some of the interesting morphological features, and to indicate also the probable relationships of the genera. The present paper deals with the species of one of the subgenera of *Vittaria* indicated in the earlier paper. Most of the work of which the results are presented here was done before the paper on the genera was published, but completion was delayed until the present. As indicated by the title of this article, it is intended to continue the study of the species of *Vittaria*, and it may be added, most of the necessary work has been accomplished.

The genus *Vittaria* as delimited in the writer's paper already cited includes all those species of the tribe Vittarieae which have a midvein with uniseriate lateral areolae along each side formed by the pinnate interlocking simple veinlets. (See FIGS. 1-3; also the illustrations of venation under each plate.) As it appears, this type of venation is practically unique among ferns, the only possible exceptions being two or three species in the genus *Polypodium* L., as used in a broad sense. From such species as these the species of *Vittaria* differ largely not only in general aspect,

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\* Bull. Torrey Club 38: 153-190. pl. 2-8. 1911.

[The BULLETIN for July (41: 351-390. pl. 9-14) was issued 28 J1 1914.]



but in more critical characters of the scales, texture, and tissues, and especially in the uniform arrangement of the sporangia in indeterminate lines along the outer portions of the veinlets. (See FIGS. 1-7, and the plates.)

The taxonomic revision of *Vittaria* presents unusual difficulties as compared with other ferns, owing to the fact that although there appear to be a fairly large number of valid species—about forty—the very simple venation pattern allows only a small range of variation in the more evident characters of gross outline and venation, so that these, the characters ordinarily used in differentiating fern species, are not available. Nearly all the species are grass-like in the outline of the leaves, and the problem is thus about the same as would be offered by a genus of grasses if no flowers and fruit were obtainable. In the case of some few species, the differences in size, outline or coloration of the leaves, or in the venation, are sufficiently marked to allow of specific determination, but in general it is necessary to study the plants microscopically and by sectioning the stems and leaves, to arrive at any understanding of the real specific characters. It has been found by this method of study that there are very considerable differences in the outline of the leaf petioles and blades as best shown in cross-section, in the arrangement of the vascular tissues in the stem and petioles, and in the kind of cortical tissue developed. The scales which cover the stems and leaf-bases, although of one pattern, often show well-marked differences in cell structure. There may also be important differences in the shape of the spores and paraphyses.

Some of the differences in these characters have been indicated by one writer or another during the last sixty years or so, but no one has used them consistently or accurately over any number of species. The last and only monographic treatment of the whole genus was that by Fée\* who attempted to figure the scales, spores, and paraphyses, as well as the general appearance of the species he recognized. Unfortunately he seems to have been inaccurate. Müller† discovered differences in the scales which seemed to him to justify the description of several new species, but he appears unfortunately to have missed the really important

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\* Mém. Foug. 3: 1852.

† Bot. Zeit. 537. pl. 13. 1854.



features of scale differences and to have made several species from what should properly be included in only one. Mettenius\* and Luerssen† described and figured accurately some of the important differential characters of leaf outline as seen in section, but neither writer covered many species. More recently Jeffrey‡ and Mrs. Britton and Miss Taylor§ have described and figured carefully the morphology of one or two species each. The present paper represents an attempt to describe and figure as thoroughly as necessary the differential characters of the seven species included in the subgenus *Radiovittaria*, as I have recently described it. As has been noted, these seven species are all American.

The work of which this paper, as also the earlier paper on the genera of the tribe Vittarieae, is a partial report, has been carried on intermittently during the last six years at the New York Botanical Garden. The present article was brought nearly to completion during a month's residence as research scholar during parts of November and December, 1911, also at the N. Y. Botanical Garden, and I am glad to acknowledge my indebtedness to Dr. N. L. Britton for the opportunities of study thus afforded. In general the material studied has been sufficiently cited in my earlier paper on the genera of the tribe, but important additional material has been received from the collections of Mr. W. R. Maxon in Panama, and I have also been greatly aided by Mr. Maxon's descriptions of the field conditions under which his material grew.

The present paper deals with less than one fifth of the total species of *Vittaria*, but in order that the problems of the characters and nomenclature may be clear at the start, a description of the genus and its synonymy are included and also a discussion of its division into subgenera.

VITTARIA J. E. Smith, Mem. Acad. Turin 5: 413. pl. 9. 1793

(Type species *Pteris lineata* L.)

*Haplopteris* Presl, Tent. Pterid. 141. 1836.

\* Fil. Hort. Bot. Lips. 25-27. pl. 27, f. 21, 22. 1856.

† Schenk & Luerssen, Mittheil. Bot. 1: 57. pl. 11-19. 1871.

‡ Phil. Trans. Roy. Soc. London 195 B: 119-146. pls. 1-6. 11 Je 1902.

§ Mem. Torrey Club 8: 185-211. pl. 28. 1902.



(Type species *Pteris scolopendrina* Bory)

*Taeniopteris* Hooker, Gen. Fil. *pl.* 76 B. 1842.

[Type species *Vittaria Forbsei* Fée = *V. scolopendrina* (Bory)  
Thwaites]

*Taeniopsis* J. Smith, Jour. Bot. 4: 67. 1841.

(Type species *V. lineata* [L.] J. E. Smith)

Ferns usually of epiphytic habit and of comparatively small dimensions, of herbaceous texture and entirely without sclerenchymatous tissue; stem slender, creeping, clothed with clathrate scales, the vascular tissue in the form of a tube (siphonostele) or a simple net (dictyostele); the phyllotaxy distichous or radial; leaves usually few, linear to linear-elliptic, usually grass-like in outline, the epidermis with scattered linear cystoliths, the leaf-trace single or double, the venation consisting of a midvein with pinnate branches which anastomose anteriorly to form a row of simple areolae along each side of the midvein; sporangia in two indeterminate submarginal or sometimes practically marginal lines along two continuous receptacles formed by the outer portions of the veinlets, the receptacle usually in a groove often of considerable depth and sometimes with the edges produced so as to serve as an indusium; a true indusium wanting; spores diplanate or triplanate; paraphyses usually present, consisting of large reddish or yellowish cells borne on simple or branching pedicels.

The generic name *Vittaria* is fortunately well established. It was based originally on a single species, *Pteris lineata* L., so that there is no difficulty as to its typification, notwithstanding the fact that by several writers another species has been recognized as type. *Pteris lineata* has even been made the type of another genus, *Taeniopsis* J. Smith. Smith based his division of *Vittaria* on the position of the sporangial line, including in *Euvittaria* the species of the type of *V. elongata* Sw., in which the fruiting line is practically marginal, the leaf margin being double and including the sporangia between the two lips. This type, however, as Luerksen has shown, is not generically different from that of *V. lineata*, in which the lines of sporangia are clearly submarginal and dorsal. The extremes of the two types are connected by all possible intermediate forms among the various species.

*Haplopteris* Presl was based on the largest species in the genus,



*V. scolopendrina* (Bory) Thwaites. Superficially this is very different from species like *V. lineata* and *V. sikkimensis* Kuhn, but in its essential characters it does not appear to have even subgeneric differences from *Euvittaria*. *Taeniopteris* Hooker is a straight synonym of *Haplopteris*, as its original species seems to be identical with *V. scolopendrina*.

The only other possible nomenclatorial difficulty in connection with *Vittaria* concerns the name *Oetosis* Necker,\* published in 1790. Of course if this name were to be found valid, its seniority of three years would give it precedence of *Vittaria*. It is, however, like most of Necker's names, quite without definite typification, and if recognized as originally described, would comprise in its six Linnaean species five widely separated genera. I make this statement with entire assurance notwithstanding the fact that Dr. E. L. Greene has concluded from the same evidence that Necker intended *Oetosis* to include only one Linnaean species, *Pteris lineata*, the type of *Vittaria*. Since Christensen also is not certain that *Oetosis* might not properly replace *Vittaria*, it may be worth while to give in some detail the evidence which needs to be considered, particularly as it bears on questions relating to other Neckerian names.

To begin with, it may be stated that Dr. Greene's error springs from two incorrect premises. These are: first, that Necker intended his description of *Oetosis* to be applied only to one Linnaean species of *Pteris*, instead of to several; and second, that when Necker referred to Linnaean plants, he had reference to the first edition of *Species Plantarum* and to no other work of Linnaeus. I am indebted to Dr. J. H. Barnhart for the discovery of both these inadvertencies.

In correcting the second of these mistakes, it is almost sufficient to suggest that it is scarcely probable that Necker would have used such an out-of-date work as the first edition of the *Species Plantarum* when there were two later editions of the same book, as well as several later editions of Linnaeus's *Systema Naturae*, the latest of these having appeared in 1784, six years before Necker's *Elementa Botanica* appeared. The case is about the same as at present with the various editions of the floras of the

\* *Elementa Botanica* 3: 318. 1790.



United States. Only the latest editions are of any general interest or use.

For incontrovertible evidence, however, that Necker used later texts than the 1753 *Species Plantarum*, I am able to cite two distinct references which I owe to Dr. P. A. Rydberg and which definitely identify the Linnaean work to which Necker is referring as the fourteenth edition of the *Systema Naturae*, the work of John Murray and not of Linnaeus. These references are Necker, *Elementa Botanica* 2: 94, and 3: 12.

The other of Dr. Greene's misconceptions has to do with the wording of Necker's original description of *Oetosis*, which is as follows:

1726. CHAR. DIAGN. *Lineae*, parallelae, ad periphaeriam frondium, in aversa pagina.

*Fronde*s simplices.

CHAR. PEC. *Fructific.* lineae parallelae, ad periphaeriam in aversa pagina frondium sitae.

*Globuli*, coacervati; singuli, annulo elastico cinguntur.

*Besimina* in globulis inclusa, exigua, fertilia.

*Individa* neutra in hac specie, stipitata.

*Fronde*s simplices. Quaed. Pterid. Linn.

In the first place, it seems to me *a priori* improbable that Necker could have intended this description to apply to only a single Linnaean species of *Pteris*. "Quaed." is of uncertain number as far as its form is concerned, but I believe in this case it is certainly plural. A general examination of Necker's text will show that the generic names used are either Linnaean names or else they are new; that is, apparently he has either retained the Linnaean genera exactly, or he has divided them, retaining the old name for part of the species and proposing a new name for the others. Often in such a case, it is evident that Necker's new genus corresponds exactly to some species-group recognized by Linnaeus. The present case furnishes a good illustration of this point.

The genus *Pteris* as delimited in the first edition of *Species Plantarum* (and later texts) is divided into three groups as follows:

"Frondeb<sup>us</sup> simplicissimis

"Frondeb<sup>us</sup> simpliciter pinnatis

"Frondeb<sup>us</sup> sub-compositae"



Necker retains *Pteris* to include, as he writes, "*frondes compositae*." In *Oetosis*, however, the leaves are "simplices," and it is reasonable to suppose that he meant to include under this name all the Linnaean species of *Pteris* with simple leaves. In the 1753 *Species Plantarum* there are four of these, but by 1767 two others had been added, and this is also the number in Murray's edition of the *Systema Naturae* of 1784. This fact seems to have been overlooked by Dr. Greene, but it was noted by Kuntze, who in attempting to validate *Oetosis*, selected as type of the genus the first species named in the later Linnaean works, i. e. *Pteris piloselloides* L., which, however, was not among the four known to Linnaeus in 1753. This would identify the genus with a group of the tribe Polypodieae, now known either as *Drymoglossum* Presl, or perhaps more properly as *Pteropsis* Desvaux.

It is probably unnecessary to pursue further the *ignis fatuus* of a type for *Oetosis*, but it may be stated with certainty as additional confirmation of the invalidity of this name that Necker's description does not, as was Dr. Greene's main contention, fit *Pteris lineata* better than any other of the simple *Pterides* known to Linnaeus. The specific phrase which he cited as diagnostic, "lineae parallelae," may be applied as well to the *Pteris piloselloides* of Linnaeus, but it is scarcely probable that Necker had any thought of distinguishing generically between one species which has sporangial lines exactly parallel as in *Vittaria lineata*, and another in which the lines diverge from the parallel one or two degrees as in Linnaeus's *Pteris lanceolata* and others.

Subgenus RADIOVITTARIA Benedict, Bull. Torrey Club 38: 166.

#### 191

Stem radial, phyllotaxy polystichous, leaf-trace always single, stem and petioles brown, owing to the highly developed collenchyma. Spores diplanate, paraphyses with cupuliform terminal cells.

The radial stem structure and leaf arrangement as well as the specialized collenchyma (see FIG. 6) serve to separate the species included from the other species of the genus, which also show a much wider range of characters.

In the key which follows, the species are arranged as nearly as



possible according to natural relationships. *V. minima*, the simplest of the species treated, belongs at the bottom of the series, and is probably like the primitive form from which the others have been derived. The remaining six species fall naturally into two groups as indicated.

In connection with the species-descriptions, complete citations of the specimens examined are given. The letters following the individual citations refer to the herbarium in which the specimen is located. "U" represents the Underwood Fern Herbarium of the New York Botanical Garden; "N" the National Herbarium at Washington; "E" the Eaton Herbarium at Yale; "C" the Herbarium of the Botanisk Museum of Copenhagen.

- |  |                            |
|--|----------------------------|
| Leaves 3-6 <sup>c</sup> mm. long.  | 1. <i>V. minima</i> .      |
| Leaves more than 6 <sup>c</sup> mm. long.  |                            |
| Petioles 2-angled from near the base, lamina with a ventral ridge along the midvein                            |                            |
| Sporangial line 0.5-1 mm. from the margin, lamina linear.  |                            |
| Lamina less than 1 cm. broad (4-7 mm.), the areolae longitudinal.  | 2. <i>V. Gardneriana</i> . |
| Lamina usually more than 1 cm. broad, the areolae oblique.   | 3. <i>V. remota</i> .      |
| Sporangial line 2-3 mm. from the margin, lamina elliptic to lanceolate.  | 4. <i>V. latifolia</i> .   |
| Petioles terete or oval in section except near the top, lamina without a ventral ridge.                        |                            |
| Scales unicostate (rarely 2-3 costate), sporangia in two narrow deep grooves about 0.5 mm. from the margin.    | 5. <i>V. stipitata</i> .   |
| Scales always pluricostate, sporangia in a shallow groove 1-1.5 mm. from the margin.                           |                            |
| Lamina 4-10 mm. broad, the margins parallel, scales of the petiole longer and narrower than those of the stem. | 6. <i>V. Ruiziana</i> .    |
| Lamina 8-14 mm. broad, narrowed both ways from the middle, scales all alike, with heavy costae.                | 7. <i>V. Williamsii</i> .  |

1. VITTARIA MINIMA (Baker) Benedict, Bull. Torrey Club 38: 164.

5 My 191

*Antrophyum minimum* Baker, Ann. Bot. 5: 448. 1841.

*Hecistopteris minima* Benedict, Bull. Torrey Club 34: 457. 19 O  
1907.

*Antrophyum Werckleanum* Christ, Bull. Herb. Boiss. II. 5: 11.  
1905.



*Hecistopteris Werckleana* Christ, Bull. Herb. Boiss. II. 7: 265.  
1907.

Stem slender, 4-5 cm. long, the scales small, often contorted, 4-6 cells wide at the base, the costae rather heavy; leaves few, spreading, 3-6 cm. long, the petiole brownish, the lamina oblong or lanceolate, broadest about the middle, 4-7 mm. broad, long-acute or sometimes blunter and forked, the margins plane, the leaf-trace single, dividing to form 2-8 veinlets, the areolae parallel to the midvein; sporangial line nearly straight, 1.5-2 mm. from the margin, superficial, the paraphyses as in the other species of the subgenus. (TEXT FIGS. 1-5.)

TYPE from COSTA RICA: *Endres, 1869, 5,000 ft. altitude.*

SPECIMENS EXAMINED. COSTA RICA: (without definite localities), *Endres, type; Wercklé, 1903 (= Hecistopteris Werckleana Christ).*



FIGS. 1-5. *Vittaria minima* (Baker) Benedict. Figures 1-3 show general habit of species, soriation, and venation. (All natural size.) Figures 4 and 5 illustrate a small and a large scale from the stem (enlarged about 60 times). All the drawings are from material of the original collection of Endres.

To *Vittaria minima* may be accorded the distinction of being the simplest species in the genus, and it is also one of the few species of *Vittaria* which can be adequately differentiated by a knowledge of its more evident characters of size and venation. There is no other American species with which it need be confused, and the smallest Old World species, *V. sikkimensis* Kuhn, has a different outline and texture and bears the sporangia in distinct



grooves, to say nothing of other marked differences. The material illustrated (*Endres*) does not show the narrowed apices believed to be characteristic of the species, but the blunting appeared to be abnormal. In the *Wercklé* material, of which two plants and a photograph of a series of plants were seen, the narrowed almost acuminate tip was an evident character.

*Vittaria minima*, in spite of its obvious differences from the other species, falls naturally into the genus and into the subgenus *Radiovittaria*. There was so little material that no attempt was made to section the stem or petiole, but the brown coloration of the petiole probably indicates the presence of the kind of collenchyma found in this subgenus. The fact that the spores and paraphyses are indistinguishable throughout the seven species is further evidence of close relationship.

It is also worthy of note that there appear to be good grounds for believing that *V. minima* is a real connecting species between *Vittaria* and *Hecistopteris* J. Smith, as has already been indicated in the synonymy. The occurrence of identically the same type of paraphysis and spore in *Hecistopteris*, as well as the suggestively similar leaves sometimes developed in this genus, lead to the suspicion that *Hecistopteris* is probably more a genus of taxonomic convenience than one of generically different evolution.

2. VITTARIA GARDNERIANA Fée, *Mém. Foug.* 3: 15. *pl.* 3. 1851

*Vittaria Karsteniana* Mett. *Ann. Sci. Nat. Bot.* V. 2: 207. 1864.

(Type from Colombia.)

*Vittaria gracilis* Kuhn; in *Moritz, Linnaea* 36: 67. 1869. (Type from Colombia.)

Rhizome erect, unbranched, 1.5–2.5 cm. long, with the persistent petiole bases about 0.05 cm. thick (about 2 mm. thick in section), radially symmetrical, the scales brown, iridescent, soft, lanceolate, 5–8 cells wide at the base. Leaves several, erect or spreading, 20–40 cm. long, usually very thin, the petiole solid, about 1 mm. thick (less when dry), terete at first, but soon becoming flattened and angled laterally, dull brown or greenish brown, or becoming polished, 1–3 cm. long, the lamina broadest (3.5–7 mm.) near or just above the middle, narrowed very gradually above and below, with or without a median brown stripe extending a few centimeters along the surface from the petiole, either thin, and with all the veins prominent, or thicker, and with



the veins immersed, but with a strong convexity over the midrib along the ventral surface, the margins acute, plane, the leaf-trace single, thick-reniform in section, branching in the very base of the petiole to form the midrib and secondary veinlets, the veinlets intersecting, 1.5 cm. apart along the margin, the marginal portions forming a nearly straight line, the areolae with their axes parallel to the midrib; soral line nearly straight, about 0.5 mm. from the margin, sunken in a shallow open groove, the paraphyses numerous, pyriform, becoming collapsed and wrinkled, the spores diplanate. (PLATE 15.)

TYPE from BRAZIL: Organ Mts., *Gardner 147*, 1837.

SPECIMENS EXAMINED. BRAZIL: Organ Mts., *Gardner 147* (scraps of type, U); *Glaziou 3553* (C). COLOMBIA: Santa Marta, 6000 ft., *H. H. Smith 1112 in part* (several plants, U, N); Bogota, *Lindig 176, vide V. Karsteniana* (U). VENEZUELA: Tovar, *Fendler 259 b* (U, E). ECUADOR: "crescit in silv. trop. et suband.," *Sodiolo* (U); *Jameson 1116* (E); Quitensian Andes, *J. P. Couthouy 25*, 1885 (E). BRITISH GUIANA: Mt. Roraima, *Mt. Roraima Expedition 212*, 12 Nov. 1884 (N).

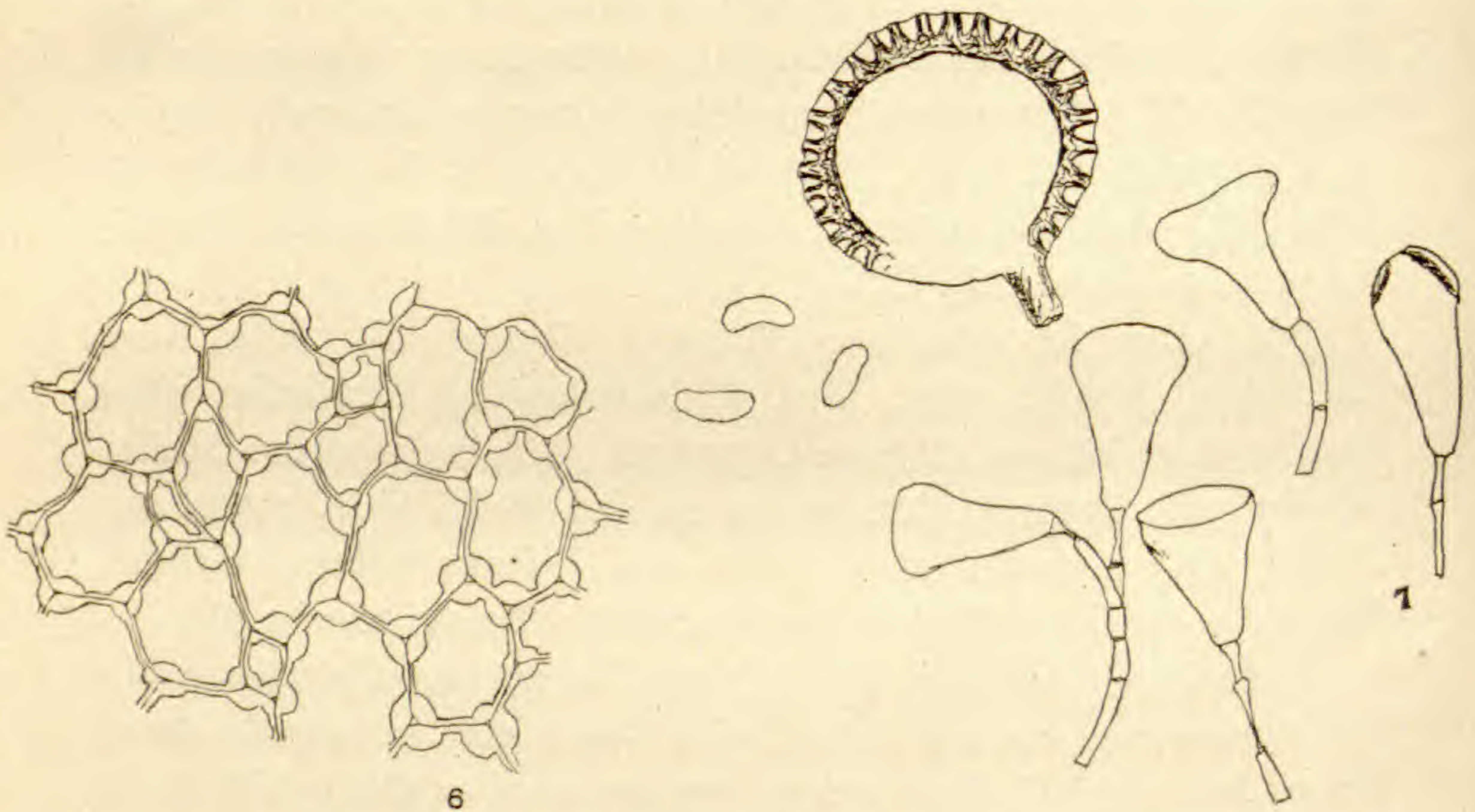
Fée cites in addition: MEXICO, *Goudot, Pl. Mex.* and Colombia, *Moritz 1226*. For *V. Karsteniana* Mettenius cites specimens as follows, all from COLOMBIA: San Pedro, prov. Ocaña, *Schlim 318*; Bogota, altit. 2,800 m., La Peña, altit. 2,900 m., *Lindig 176*; Quindio, altit. 3,000 m., *Triana*; Tolima, *Goudot*. The type of *V. gracilis* is from COLOMBIA: Tovar, *Moritz 464*.

*Vittaria Gardneriana* and *V. remota* are species of similar habit and appearance and are undoubtedly closely related to each other. Broad leaves of *V. Gardneriana* are not easy to distinguish from narrow leaves of *V. remota*, but in general, taking whole plants, the differences in breadth of leaves, etc., appear sufficiently constant to warrant the recognition of two species, especially as these differences seem to accompany partly separated geographic ranges. The material from Central America, where both species occur, offers no special difficulties in differentiation, even in the herbarium, and it is not unlikely that field study will discover additional differences. *V. Bommeri* Christ, referred to later in the present article as a species of uncertain identity, is apparently of the same general size and shape as *V. Gardneriana*.



3. *VITTARIA REMOTA* Fée, Mém. Foug. 7: 26. *pl.* 20, *f.* 1. 1857

Rhizomes erect, often associated in clumps of 5 or 6, 0.5–2 cm. long, about 2 mm. thick in section, radially symmetrical, the scales lanceolate, brown, 7–11-costate at the base, the median costae considerably thickened; leaves 2–10, cespitose, 15–42 cm. long, the petioles purplish-brown, sparsely verrucose, solid, 1–5 cm. long, about 2 mm. thick, nearly terete at first but soon flattened and angled, the laminae linear-lanceolate, broadest (6–18 mm.), about the middle, somewhat acuminate, below very gradually narrowed and marked with a dark brown stripe both ventrally and dorsally, the margin plane, thin and sharp, the leaf-trace single, branching in the base of the petiole, the midrib marked ventrally by a distinct angled ridge, whitish on the dorsal surface, veinlets 4–9 per cm.,



FIGS. 6 and 7. *Vittaria remota* Fée. FIG. 6. Well-developed collenchyma from the stem. (Material collected by *P. Wilson 81*, Porto Rico. Enlarged about 300 times.) FIG. 7. Showing spores, paraphyses, and a sporangium. (Enlarged about 60 times.) Two of the paraphyses, the lower two, are shown partly collapsed, their usual condition when dry. (From material collected by *R. S. Williams 889*, Panama.)

intersecting 0.5–1.5 cm. apart along the margin, the areolae linear, with the long axes usually divergent from the midrib; soral lines slightly crenate, 0.5–1 mm. from the margin, in an open shallow groove. (PLATE 16 and TEXT FIGS. 6, 7.)

TYPE from COLOMBIA: province of Ocaña, altit. 2,400 m., on trees in forest, *L. Schlim 611*, 1846–52.



SPECIMENS EXAMINED. VENEZUELA: Tovar, *Moritz 143 in part* (U); Tovar, altit. 2,300 m., *Fendler 260* (U, E). PANAMA: Cana, 2,000 m., *R. S. Williams 889* (U). COSTA RICA: La Palma, altit. 1,450–1,550 m., *Maxon 397* (U, N); La Palma, *C. Brade, 26 Mr 1908* (N); *L. C. Wercklé, 1901–05* (U, N). JAMAICA: numerous collections by *Jenman* (U), *Underwood* (U, N); *Maxon* (U, N), *Harris* (U), and *Clute* (U, N). PORTO RICO: Sierra de Luquillo, *P. Wilson 81* (U, N); *Sintenis 1139* (U, N); Sierra de Naguabo, *Sintenis 5451* (U, N); El Yunque Mts., *Everman 674* (N); *Blauner 307* (U).

*Vittaria remota* seems to be the commonest West Indian species of this subgenus, at least as far as representation in herbaria is concerned. It is most easily distinguishable from the preceding species, as has been noted, by the greater breadth of the leaves. In scales and rhizome, it is generally similar.

#### 4. *Vittaria latifolia* sp. nov.

Rhizome erect, unbranched, 1–2 cm. long, with the persistent petiole bases and roots about 5 mm. thick, 2–3 mm. thick in section, radially symmetrical, the leaves and roots arising from all sides, the scales ciliate, dull brown, very soft, lanceolate, 7–10-costate at the base, the costae uniformly slender; leaves 3–6, erect or spreading, 12–22 cm. long, the petioles solid, about 2 mm. thick, flattened and laterally angled except at the very base, dull brown or greenish, 1–4 cm. long, the scales like those of the rhizome but smaller, the lamina herbaceous, thin, narrowly lanceolate, broadest (1.5–2.2 cm.) near, usually somewhat above, the middle, acute with a blunt apex, narrowed very gradually below into the petiole, the margins thin, sharp, often reflexed, the leaf-trace simple, branching in the base of the petiole, the midrib evident along the ventral surface of the lamina as a slight but distinctly angled ridge, and marked below by a whitish line, the veinlets alternate, rather prominent when dry, whitish below, divergent from the midrib at an angle of 20°, bent forward near the margin and connivent with the anterior veinlet, the areolae thus formed simple, 3–4 mm. broad, elongate-rhomboid, the oblique sides about 20 mm. long, the marginal and costal sides about 10 mm. long; sporangia and paraphyses borne along the intersected portions of the veinlets, forming a continuous shallowly crenate soral line, 2–3 mm. distant from the margin, superficial or scarcely immersed, the spores diplanate, the paraphyses pyriform or cyathiform, rounded at first, but soon collapsing and becoming angular and ribbed. (PLATE 17.)



TYPE collected at Santa Barbara, BOLIVIA, altitude 5,500 feet, R. S. Williams 1337, 30 August 1902.

*Vittaria latifolia* is interesting as having the broadest laminae in proportion to their length of any species of the genus. It is so different from the ordinary type of *Vittaria* as represented by *V. lineata* that one might well be excused for regarding it as a different genus until the vittarioid venation is discovered. It represents an extreme development of the type seen already in *V. remota* and *V. Gardneriana*, but is well differentiated from these not only by its greater width, but by scale characters as well.

5. VITTARIA STIPITATA Kunze, *Linnaea* 9: 77. 1835.

Rhizome erect, 1–2 cm. long, usually branching several times, the branches fasciculate, forming a close cluster 0.5–2 cm. thick, radially symmetrical, the scales linear, unicostate, or sometimes with 2–3 costae at the base, thick and bent.

Leaves pendent, one or two on each rhizome branch, 12–100 cm. long, the lamina linear, parallel-sided through much of its length, gradually narrowed above and below (about 0.75 mm. thick), the surfaces usually smooth and plane, or sometimes with a low median ridge along the ventral surface, the margins thick, usually blunt, the petiole 3–9 cm. long, about 1 mm. thick, brown or purplish-brown, hard, partly hollow, terete below becoming flattened dorsiventrally and angled in the upper part, the leaf-trace single, dividing to form the midvein and two lateral veinlets in the base of the petiole, the veins not evident on either surface of the lamina, the veinlets intersecting 2.5–4 cm. apart, along the margin, the areolae with the long axes longitudinal; soral lines straight, 0.5 mm. from the margin, in deep narrow grooves inclined to the margin. (PLATE 18.)

TYPE from PERU: (definite locality not given), *Poeppig* 176.

SPECIMENS EXAMINED, UNDERWOOD FERN HERBARIUM. BOLIVIA: Tigre Pata, 2,000 m., R. S. Williams 1338, 10 F 1902; Yungas, H. H. Rusby 340, 1885; Yungas, M. Bang 353, 1890. BRAZIL: prope Rheos, *Martius* 386, Herb. Flora Brazil, 1839. COLOMBIA: H. H. Smith 1112 in part, 20 Au 1898 or 1899; Sierra de Onaca, Sta. Marta, "moderately common on trees in forest," 2538; Minca Estate, near stream, Sta. Marta, 800 m. (2 sheets); Atrato and Truando, *Schott* 61, D 1857. COSTA RICA: L. C. Wercklé, 1901–1905; *Tonduz* 12782 (scraps), N 1898. CUBA: C.



*Wright 865*, "Cuba orientali, prope villam Monte Verde; in arboribus," Ja-Ju 1859; forested slopes of the Finca las Gracias, Yaleras, Oriente, about 500 m.; on trunk of dead (lodged) tree, *W. R. Maxon 4476*, 5 My 1907. JAMAICA: vicinity of Troy, 600-660 m., *W. R. Maxon 2972*, 30 Je 1904; on trees over Ginger and Ugly Rivers, St. Mary's Parish. *G. S. Jenman*, 1874-79. PANAMA: above Penonome, 650-1,000 m., *R. S. Williams 456*, Mr 1908; Cana and vicinity, 1,900 m., *R. S. Williams 890*, Ap-Je 1908. PERU: Cumbassauma Mts. (scrap); *Poeppig 176* (scraps of type).

SPECIMENS EXAMINED, U. S. NATIONAL HERBARIUM. BOLIVIA: Yungas, *Bang 353*. BRAZIL: *Riedel*; San Paulo, Rais da Serra, "ad arbores," *L. Wackett*, 1907; COLOMBIA: *H. H. Smith*, 2568, 800 m.; COSTA RICA: *Wercklé (2)*; Las Vueltas, Tucurrique, 630 m., *A. Tonduz 12782*, N 1898. CUBA: *C. Wright 865*; *W. R. Maxon 4476*. ECUADOR: Rio Talesa, 1,400 m., *J. Rimhart 72*.

SPECIMENS EXAMINED, EATON HERBARIUM. COLOMBIA: Atrato and Truando *A. Schott 61*, D 1857. CUBA: Cuba orientali, *C. Wright*, Ja-Je 1859. (2). VENEZUELA: Tovar, 2,000-2,300 m., *A. Fendler 259*.

SPECIMENS EXAMINED, HERBARIUM OF THE BOTANISK MUSEUM. BRAZIL: San Paulo, Santos, *Riedel*. *H. Mosen 3526*. CENTRAL AMERICA: *Oersted*. COLOMBIA: *Moritz 143* in part.

The great variation in length of specimens included under this species is one of the most notable facts. There can, however, be no doubt as to the identification of all the material as this species. The unicostate scales give a simple and very easily applicable test by which it can be separated from the following species or any other of this group. It seems to grow under a wide range of conditions, this presumably accounting for the variation in size, the small specimens being probably only physiological forms. In the West Indies it rarely reaches as full development as in South America, but even the smallest specimens measured were usually fertile.

6. VITTARIA RUIZIANA Fée, *Mém. Foug.* 3: 16. *pl. f. 3*. 1852
- Vittaria Moritziana* Mett. *Ann. Sci. Nat. Bot.* V. 2: 207. 1864.
- Vittaria Orbignyana* Mett. in *Kuhn, Linnaea* 36: 66. 1869.
- Vittaria longipes* Sodiro, *Crypt. Vasc. Quitenses* 417. 1893.



Rhizome erect, 1–2 cm. long, unbranched or branching to form a close cluster of shoots, each radially symmetrical, the scales 6–10-costate at the base, the median costa much thickened in the upper portion of the scale. Leaves pendent, 1–5 to each shoot, 40–70 cm. long, the petiole 5–15 cm. long, atropurpureous, hard, partly hollow, flattened to the base, becoming 2-angled toward the lamina, the scales very narrow and elongate, 1–4-costate, the lamina linear, parallel-sided through most of its length, 4–10 mm. broad, narrowed gradually above and below, the dorsal surface plane or nearly so, the ventral surface with a broad low median ridge, the margins usually thin and sharp, often reflexed in old leaves, the leaf-trace single, dividing in the base of the petiole, the veins not evident on either surface of the lamina, the veinlets intersecting about 3.5 cm. apart along the margin, the areolae linear-rhomboid, the longitudinal sides about 3.5–4 cm. long, the oblique sides 2.5–3 cm. long. Soral lines straight, about 1–1.25 mm. from the margin, in a shallow open groove. (PLATE 19.)

TYPE from PERU: (definite locality not given), *Ruiz*.

SPECIMENS EXAMINED. COLOMBIA: Tablazo, Tuluá, *I. F. Holton 60*, 26 O 1853, "*V. stipitata*," "et in Ibaque" (U); Santa Marta, *H. H. Smith III 2* in part (N); *Lindig* (scrap, U). ECUADOR: S. Domingo, *Sodirol*, "*V. stipitata*." VENEZUELA: Tovar, *Moritz 143*, *143b* (scraps, U); Tovar, *Fendler 259*, 1854–5, "*V. stipitata*" (E).

For *V. Moritziana*, Mettenius cites as type: Canoas, COLOMBIA, *Lindig 319*; for *V. Orbignyana*: Yungas, BOLIVIA, *d'Orbigny 229*. For *V. longipes*, Sodirol cites as type-locality: subandine woods of western range in the valley of Nanegal, near Anca (translated).

As may be seen from the synonymy this species has been recognized as distinct by several writers. The material of it is rather scanty, indicating that it must be rare. It furnishes an especially good illustration of the habit of writers of describing species of *Vittaria* on very insufficient data. It is possible of course that there may be more than one species represented under this name, but there are not now sufficient data for such differentiation, even on the basis of the most careful microscopic study, although much less than that was counted sufficient for the original descriptions.

The species is easily distinguishable from *V. stipitata* on the basis of the scales, which are broad, many-costate, and of two sorts.



The margins are also usually sharper than those of *V. stipitata*, and the sporangia are borne in shallower grooves.

7. *Vittaria Williamsii* sp. nov.

Rhizome erect, 0.5–1 cm. long, 2–2.5 mm. thick, unbranched, radially symmetrical, the scales small, lanceolate, blackish-costate at the base. Leaves 1–3, 25–70 cm. long, rather thick and rigid when dry, the petiole 10–15 cm. long, hard, terete or nearly so at the base, soon becoming flat and angled, hollow above the base, atropurpureous or green along the anterior ventral portion of the stipe, the lamina linear-lanceolate, 8–14 mm. broad, narrowed gradually both ways from the middle, plane or somewhat recurved, the apex somewhat acuminate, the margin thin, sharp, plane, the lower dorsal surface marked with a median purplish stripe extending up from the petiole: leaf-trace one, dividing in the base of the petiole, the midvein not evident on the surface, the veinlets not evident on the surface, intersecting 1.5–2 mm. apart, the areolae about 2 mm. broad, linear-rhomboid with the long axes at an angle of about  $15^\circ$  to the midvein; sporangia in a straight or slightly sinuate line, about 1 mm. from the margin, in an open very shallow groove. (PLATE 20.)

TYPE from BOLIVIA, Santa Ana, altitude 1,800 meters, *R. S. Williams* 1349, 29 J1 1902.

Also collected at Yungas, BOLIVIA, altit. 1,300 m., *H. H. Rusby* 339. 1885.

It is always a pleasure to work with Mr. Williams's specimens owing to the excellence of their preparation. The present species is no exception. It is as well distinguished from the other species of this subgenus as is *V. latifolia* also collected by him. Its association is, however, clearly with the species of the *stipitata* alliance of which it is the broadest example.

SPECIES INQUIRENDA

*Vittaria Bommeri* Christ, Bull. Herb. Boiss. II. 5: 11.

I have seen a fragment of the original specimen of this species through the kindness of His Highness, Prince Roland Bonaparte, in whose herbarium it is deposited. I have not, however, enough to determine certainly the specific characters, although it appears to be close to *V. Gardneriana* Fée.



**Explanation of plates 15-20**

Unless otherwise noted, the reductions and magnifications are as follows: tracings of whole plants and leaves reduced one-half; leaf and stem sections enlarged twelve times; scales enlarged about thirty-five times. The sections and scales were drawn by means of a camera lucida.

## PLATE 15. VITTARIA GARDNERIANA Fée

- FIG. 1. Whole plant, showing general habit and soriation.  
 FIG. 2. Cross-section through leaf in fertile part.  
 FIG. 3. Cross-section through petiole, showing 2-angled character.  
 FIG. 4. Single broad leaf from another plant, showing venation.  
 FIG. 5. Cross-section same leaf, showing similarity to *V. remota* Fée.  
 FIG. 6. Cross-section of petiole of same leaf.  
 FIG. 7. Cross-section of another leaf through fertile portion.  
 FIG. 8. Cross-section of petiole of same leaf.  
 FIG. 9. Typical scale.

Specimens figured: figures 1-6, *H. H. Smith 1112*, Santa Marta, Colombia (this number includes also *V. Moritziana* Mett.—see *plate V*, and *V. stipitata* Kunze—see *plate IV*, *fig. 20*); 7-9, Gardner, Organ Mts., Brazil 1837, probably part of type collection.

## PLATE 16. VITTARIA REMOTA Fée

- FIG. 1. Whole plant, showing general habit, venation, and soriation.  
 FIG. 2. Cross-section through fertile part of leaf.  
 FIG. 3. Cross-section of leaf just below fertile part.  
 FIG. 4. Cross-section of leaf still lower down than preceding.  
 FIG. 5. Cross-section through petiole more than 2 mm. above stem, to show angled character.  
 FIG. 6. Cross-section through petiole just after it leaves the stem. The angles are not developed at this point, but the single leaf-trace has already given off the lateral veinlets.  
 FIG. 7. Cross-section through stem, showing origin of petiole—at left—and a still younger leaf-trace—at right. A root is shown just leaving the stem at the lower side.  
 FIG. 8. Cross-section of a broader leaf through the fertile part, showing that the sporangia are borne in a slight depression.  
 FIGS. 9-12. Cross-sections of same leaf, comparable to those in figs. 4-6, but each respectively lower than the corresponding one in the first series.  
 FIGS. 13-15. Tracings from leaves showing abnormal modifications in the venation.

Specimens figured: figure 1, *P. Wilson 81*, Porto Rico; 2-7, *L. M. Underwood*, Jamaica, 1903; 8-12, *R. S. Williams 889*, Panama; 13-15, from a plant grown at the N. Y. Botanical Garden, probably self-sown from Jamaica spores.

## PLATE 17. VITTARIA LATIFOLIA Benedict

- FIG. 1. Whole plant, showing general habit, venation, and soriation.  
 FIG. 2. Cross-section of leaf through fertile part, showing very slight depression in which sporangia are borne.  
 FIG. 3. Cross-section of leaf below fertile part.



- FIG. 4. Cross-section of petiole about 2 mm. above stem.  
 FIGS. 5-8. Successive cross-sections of petiole less than 2 mm. from stem, showing single leaf-trace and its division.  
 FIG. 9. Cross-section of stem, showing origin of a petiole and a leaf-trace.  
 FIG. 10. Stem scale, showing cilia, most of which have been broken off.  
 All the figures were drawn from type material, *R. S. Williams 1337*, Bolivia.

## PLATE 18. VITTARIA STIPITATA Kunze

- FIG. 1. Whole plant, showing general habit and soriation.  
 FIG. 2. Cross-section of leaf in fertile part.  
 FIG. 3. Cross-section of leaf below fertile part.  
 FIGS. 4 and 5. Cross-sections of petiole more than 2 mm. above stem.  
 FIG. 6. Cross-section of stem showing origin of a petiole with a leaf-trace not yet divided.  
 FIG. 7. Whole plant, about the smallest seen.  
 FIG. 8. Cross-section of leaf of larger plant of same collection number.  
 FIG. 9. Single leaf attached to stem; the leaf was about the longest and broadest observed.  
 FIG. 10. Cross-section through fertile part of same leaf shown in fig. 9.  
 FIG. 11. Cross-section through fertile part of another somewhat different leaf.  
 FIGS. 12-14. Cross-sections of same leaf about where the blade narrows into the petiole. The shaded strip below represents the band of collenchyma which runs part way up the blade.  
 FIGS. 15 and 16. Scales with an unusual amount of cell development.  
 FIGS. 17-19. Scales of the usual type.  
 FIG. 20. An old scale from which the softer parts of the cells have been lost.  
 Specimens figured: figures 1-6, *W. R. Maxon 4476*, Cuba; 7 and 8, *R. S. Williams 1338*, Bolivia; 9 and 10, *H. H. Smith 2568*, Colombia; 11-14, 17-19, *R. S. Williams 890*, Panama; 15 and 16, *Wercklé*, Costa Rica; 20, *H. H. Smith 1112*, Colombia.

## PLATE 19. VITTARIA RUIZIANA Fée

- FIG. 1. Whole plant, showing general habit, venation, and soriation. The petioles are unusually short in this plant.  
 FIGS. 2 and 3. Cross-sections through fertile part of a leaf, showing pointed margin, and the sporangial groove, which is much shallower than in *V. stipitata* Kunze.  
 FIG. 4. Cross-section through petiole more than 2 mm. above stem, showing heavy collenchymatous development with aerated central portion. The leaf-trace has divided into the midvein and two lateral veinlets.  
 FIG. 5. Cross-section through fertile part of leaf of type collection.  
 FIG. 6. Cross-section through fertile part of an unusually narrow leaf.  
 FIGS. 7 and 8. Cross-sections through petiole more than 2 mm. above stem.  
 FIG. 9. Cross-section through petiole very close to stem, and before simple leaf-trace has divided.  
 FIG. 10. Stem scale.  
 FIG. 11. Petiole scale.  
 Specimens figured: figures 1-4, *H. H. Smith 1112* (in National Herbarium), Colombia; 5, 11, *Moritz 143*, Tovar, Venezuela (type 6-10, *Sodi*, Ecuador).



## PLATE 20. VITTARIA WILLIAMSII Benedict

- FIG. 1. Single leaf, showing sori and the extreme of length noted.
- FIG. 2. Whole plant (*type*), showing general habit, venation, and sori.
- FIG. 3. Cross-section of half of leaf in fertile part, showing very slight depression where sporangia are borne.
- FIG. 4. Cross-section through leaf below fertile part.
- FIG. 5. Cross-section through petiole more than 2 mm. above stem.
- FIG. 6. Scale showing the very heavily thickened apical portion.
- Specimens figured: figure 1, *Rusby 339*, Yungas, Bolivia; 2-6, all from type material.



## The ferns and flowering plants of Nantucket—XIII

EUGENE P. BICKNELL

### CLETHRACEAE

#### CLETHRA ALNIFOLIA L.

Abundant in low thickets and about the borders of ponds and pools. Flower buds in close green spikes July 14, 1912; some flowers remaining Sept. 14, 1907.

### PYROLACEAE

#### PYROLA AMERICANA Sweet.

Not common, but widely scattered on the island in dry thickets, less often in open ground. Racemes of close buds June 15, 1911; precocious flowers in an open sunny spot June 23, 1910; first flowers July 2, 1912.

#### PYROLA CHLORANTHA Sw.

Found here and there in scattered colonies through the pine woods near the County Fair grounds and in open ground beyond towards the north, also still farther on among pines along the Wauwinet road; a few stunted plants among bearberry in open ground on Saul's Hills. Flower buds June 5, 1911; in full flower June 17, 1908, June 18, 1910; past flowering July 9, 1912.

#### CHIMAPHILA MACULATA (L.) Pursh.

In pine woodland; common and of large size east of Hummock Pond and found locally eastward to the County Fair grounds. Flower buds ready to open July 9, 1912.

#### CHIMAPHILA UMBELLATA (L.) Nutt.

Not more common than the preceding and often growing with it but of freer range and occasionally met with on the open commons, as in the North Pasture and above the "Cliff" near "Mon-salvat." Just in flower July 9, 1912.



## MONOTROPACEAE

## MONOTROPA UNIFLORA L.

Frequent in pine woodland; under beeches in Quaise; occasional on the open commons pushing up through the thick carpeting of bearberry. Not seen farther east than Quaise, nor west of Hummock Pond; observed in full flower from early August until late in September. On Marthas Vineyard I have seen it in flower as early as June 28. Plant often tinged with clear pink.

## \* HYPOPITYS AMERICANA (DC.) Small.

Pine woods towards Surfside, Sept. 8, 1904, passing out of bloom. Determined by Doctor Small. Plant pale and yellowish throughout, thinly short-pubescent, the stigma not bearded. I do not myself well understand this species, never having met with it in perfect flowering condition, but the characters adduced by Doctor Small appear to be distinctive.

## HYPOPITYS LANUGINOSA (Michx.) Nutt.

Common locally among the pines east of Hummock Pond; Miacomet Pines; pine grove on Surfside road. Pale yellowish throughout, or the stems, especially basally, tinged with light yellowish pink; lanate-pubescent, the stigma retrorse-bearded. In full flower Aug. 9, 1906, the largest plants 4 dm. high; mostly past flowering Sept. 16, 1907. Inflorescence occasionally compound. The flowering period appears to be considerably earlier than that of *H. americana*.

Both of these plants occur in pine woods on Marthas Vineyard where, also, in deciduous woodland, there is yet a third species, smaller and later-flowering, and conspicuous by reason of its vivid red color, the shade varying from clear pink to carmine and almost scarlet. Other characters combine with size and color to mark it a distinct species. Its pubescence is short and close and the stigma densely white-bearded; its capsule is small, 4-5 mm. long, and ovoid to nearly globose. Its late flowering period is noteworthy. On Chappaquiddick Island, as late in the season as October 5, 1912, it was only just coming into bloom. On Long Island, where *H. lanuginosa* blooms in July and early in August, this red species is not seen at all until about the middle of September. I have not met with it on Nantucket, but it would



seem to be altogether probable that it is to be found there late in the season.

Specimens from Chappaquiddick Island, Marthas Vineyard, Oct. 5, 1912, have been deposited as the type in the herbarium of the New York Botanical Garden named *Hypopitys insignata* sp. nov.

## ERICACEAE

## AZALEA VISCOSA L.

Everywhere in swamps and bogs. First flowers June 17, 1910, June 18, 1908; mostly not yet in bloom June 17, 1912, generally in bloom July 10; some flowers in mid-September, 1907.

In a number of instances it was observed that corollas with long tube and short limb were pure white and that those with shorter tube and broad limb were often deeply tinged with pink. The pink-flowered shrubs seemed to be, as a rule, earlier flowering and, at least in the most pronounced examples, had rather coarsely bristly-ciliate pedicels, and acute leaves, somewhat pale beneath, thus corresponding with Pursh's description of his *Azalea hispida*.

## AZALEA NITIDA Pursh.

Occasional or frequent in bogs and wet thickets; Polpis, Quaise, Tom Never's swamp, below the "Cliff." In full flower Aug. 4, 1906. Leaves numerous and crowded, small, 2-2.5 cm. long and 5-10 mm. wide, coriaceous and very acute, dark green and shining on both sides, especially above. A very different shrub in conformation and aspect from the more openly branched and larger leaved *A. viscosa*, yet quite obviously intergrading with it.

\* AZALEA GLAUCA Lam. Encyc. I: 340. 1783.

Frequent; Quaise, Polpis, Tom Never's Swamp, Millbrook Swamp, Trot's Swamp. A beautiful and always strikingly individualized shrub. Neither on Nantucket nor on Long Island have I seen any convincing evidence that it blends with *A. viscosa*, although it may well be true that interbreeding tends to keep it within the organic influence of that species.

## KALMIA LATIFOLIA L.

Mrs. Owen's catalogue preserves the record of "a single dwarf specimen not more than a foot high" found by Mr. Dame on the plains opposite Bloomingdale.



## KALMIA ANGUSTIFOLIA L.

Common in moist levels about sphagnum bogs and also entering freely into the low woody growth of dry level tracts in low grounds or on the moorland. First flowers June 7, 1908; June 10, 1911, and generally coming into bloom June 15; June 12, 1909; still in flower July 13, 1912. Not rarely a few flowers open in the autumn, even late in September.

## XOLISMA LIGUSTRINA (L.) Britton.

Abundant in low grounds either in moist or in drier soils. First flowers July 1, 1912, in full flower generally by July 4.

This is one of the strong and rigidly branched shrubs that especially combine with the high bush blueberry to give resistance and impenetrability to the Nantucket swampy thickets. It mixes also with the Azaleas, Aronias and Amelanchiers, *Clethra alnifolia*, *Ilex fastigiata*, and other less abundant species that make up the dense thickety growths that invest many of the ponds and pools.

## CHAMAEDAPHNE CALYCVLATA (L.) Moench.

Locally common in very wet bogs. Still in flower May 31, 1909; only dried corollas remaining June 3, 1911.

## EPIGAEA REPENS L.

On Nantucket, contrary to its usual habits, the trailing arbutus favors less the seclusion of woodland or pine groves than the exposure of open barrens where the sun beats upon it all through the season contracting its growth into little compact mats flattened upon the sandy soil. It even grows tenaciously on the bare tops of the rolling hills, and is common over the plains on the south side of the island, in some places extending quite to the edge of the low bank along the ocean shore.

I have never been on Nantucket early enough in the spring to see it in bloom, but in the deep shade of the Miacomet pines, on June 3, 1909, the dried corollas were not yet all fallen away.

## GAULTHERIA PROCUMBENS L.

Locally very common on heaths and dry level tracts among low trees and shrubbery, sometimes in moister soil at the borders of sphagnum bogs. Ripe fruit in September, 1899, and fruit still persistent June 1, 1909.



## ARCTOSTAPHYLOS UVA-URSI (L.) Spreng.

The bearberry is probably the most abundant flowering plant on Nantucket, where it spreads a thick evergreen carpet over unnumbered acres of the rolling commons and of hill and plain. Throughout wide tracts not a point of ground is left uncovered by its even mantle of firm shining foliage, which makes a clean and springy footway, and on slopes and hillsides a very slippery one. The long trailing stems and branches weave so strong in interlacement that many kinds of plants that would thrive well upon the same soil are either choked away or find no spot whereon to begin their growth. Nevertheless the close abundance of the bearberry often gives good protection to many another plant in a most unexpected way. Beneath its low covering the soil is ever in shade and remains cool and damp under the hottest sun. By this are some woodland species afforded conditions which enable them to exist far out on the dry barrens, and growing up out of the bearberry comes many an unexpected thing. The Indian pipe is occasionally to be seen pushing up through its close fretwork as well as *Pyrola americana*, *Pyrola chlorantha*, *Chimaphila umbellata*, *Cypripedium acaule*, probably all plants of acid soils, and *Vagnera stellata*, *Linum intercursum*, *Grossularia hirtella*, and other species, including some of the grasses natural to the damp soil of low grounds.

The bearberry was everywhere in full flower June 1, 1909. In other years it had passed out of bloom either before or soon after the middle of the month; green fruit June 7, 1908, and some becoming red June 18; in 1912 the fruit had only begun to redden June 30; abundant fruit in September, 1899.

## CALLUNA VULGARIS (L.) Salisb.

The late lamented Mrs. Owen\* in a most interesting paper, one of the latest from her always agreeable pen, on "The Adventive Heaths of Nantucket" (*Rhodora*, 10: 173-179. O 1908) has given us a history of the three heaths that are found growing wild on the island. We are told that the *Calluna*, or ling, was first found on Nantucket in 1880 by Mr. Lawrence Coffin, a single plant on the open commons, which persisted for many years and

\* Maria Louisa (Tallant) Owen. Born on Nantucket in 1825. Died June 8, 1913.



finally disappeared. This is the only plant of *Calluna* ever found on the island whose presence there remained to Mrs. Owen altogether unexplained. At the place where in this day the heather principally grows it came in with trees imported from Europe by Mr. Henry Coffin in 1877 and subsequent years, and was first found by Mr. Lawrence Coffin in 1886, then well established. Since that time it has been sought to naturalize the heather on the island by several persons who have scattered the imported seed and even set out young plants.

The earliest record known to me of *Calluna vulgaris* on Nantucket, as well as of the cross-leaved heath, *Erica Tetralix*, was published by Mr. O. R. Willis in the Bulletin of the Torrey Botanical Club for December, 1886; the plants had been found the same year by Mrs. Charlotte E. Pearson in a tract planted with larches imported from Europe.

Mrs. Owen has mentioned half a dozen localities other than this now well-known one, where this heather has been found, at three of which, two of them far out on the commons, it is not known to have been planted. I, myself, have met with it at five localities, all of them mentioned by Mrs. Owen except perhaps one on the plains in the direction of the old Kimball farm where, on June 3, 1909, a solitary cluster was growing which measured 28 inches in greatest diameter.

At the place where this heather was first introduced I came upon it quite accidentally on Aug. 9, 1906, when, with the cross-leaved heath, it was in full flower. Since that time it has continued to spread, and of late years has become well naturalized in scattered growth among the pines. In 1908 the main growth covered a general area of 17 by 14 paces, made up of straggling groups, small separate clusters, and several masses of considerable size. In 1911 it seemed to be more abundant than I had seen it at any time before, but in July of the following year, after the intervening cold but not snowy winter, much of it had been winter-killed, at least its upper parts. It showed no signs of flowering on July 3, 1909, nor on July 17, 1908; on July 26, 1910, no buds could be found on the wild plant but one in cultivation in a garden in the town bore long racemes of pink buds. The wild plant was in full flower August 9, 1906, August 10, 1895 (F. G. F), and bore some fresh flowers September 18, 1897.



I have elsewhere reported\* that the common heather, so well established on Nantucket at the locality where it was first introduced, is not the typical glabrate form of the species but is the pubescent form, var. *pubescens* Koch. As I have observed it, this is a neater appearing and more attractive plant than the glabrous type and by contrast of appearance a very different one. The heather found on Marthas Vineyard is, on the contrary, the typical glabrate plant. It is an interesting fact that this form occurs on Nantucket also, but at a locality remote from that where the pubescent form is found. The single cluster already referred to as growing not very far from the Kimball farm was of the glabrate form, and an old specimen in the Columbia University herbarium bearing no other record than "Nantucket" is the same. Another old specimen in this herbarium, presumably of the same period, is of the pubescent form. It was collected by Mrs. Pearson twenty-seven years ago, in 1886, and was from the same locality where the pubescent plant is found today. The occurrence of both forms on Nantucket at the period of its early discovery there would appear to indicate that the island had received this addition to its flora not alone from its chance introduction with trees imported from Europe but also through some other channel which remains quite unknown.

#### ERICA TETRALIX L.

It is related of the cross-leaved heath by Mrs. Owen (loc. cit.) that it, also, was introduced with the imported pines that brought the *Calluna* and was first observed on Nantucket in 1884 by Miss Susan Coffin. Mr. Willis, in his note already cited, has recorded that, in 1886, Mr. Henry Coffin made a thorough search of the tract where this heath had been found the same year by Mrs. Pearson and discovered twenty patches of the *Erica*, which "was as abundant among the firs [pines] brought from Illinois as among the larches from England." The cross-leaved heath appears to have been found on Nantucket nowhere else than at this locality. In 1911 it was fairly common there, well scattered among the clusters of *Calluna* and evidently perfectly naturalized. The following season, like the *Calluna*, much of it had been winter-killed and no flowers were to be found as late as July 12. In 1909

\* *Rhodora*, 15: 189-192. N 1913.



no flower buds had appeared by June 12, but some of the stem tips bore little terminal rosettes showing where the buds were coming; buds visible June 11, 1911; first flowers June 17, 1908; in full flower August 9, 1906, August 10, 1895 (F. G. F.); a single cluster of pink buds September 18, 1907.

#### ERICA CINERA L.

In Alphonso Woods's "Botanist and Florist," edition of 1871, it is recorded that this heath, the bell heather, was discovered on Nantucket in June 1868, by Mrs. E. E. Atwater. Mrs. Owen's paper, already cited, tells us that only a solitary plant was found, that it was found again in 1871, and was rediscovered independently by Mrs. William A. Spinney in 1878. It lived until 1902 or 1903. Shortly before this a second plant was found not far off, and a year or two after, yet a third plant was discovered nearby. These facts, taken by themselves, would seem to make it perfectly obvious that the two later plants had been derived from the older one by self-sown seed. But the evidence gathered by Mrs. Owen puts this in some doubt, for it is known that heather plants of some kind were at one time set out somewhere in the same part of the island where these plants were found.

Mr. Willis in his note, published in 1886\* reported that Mrs. Charlotte C. Pearson in September of that year sent him a specimen of *Erica cinerea* from a new locality and stated that the plant had been found in four different places on the island far apart, and that she had found it when a child in a locality far from dwellings and where trees had never been known to grow.

On June 23, 1911, Mr. John Appleton took me to the locality where this heath is said to have grown since 1868. There we found one bushy plant covered with flower buds, some of them pink and on the point of opening. The spot was among an open growth of pines, part of an extensive and much denser tract, and the plant was well concealed from every side a few yards away. Many a time I had passed close to it without making the discovery. The year after this it had disappeared, and I was told that, in order to protect it from extermination by visitors it had been transplanted to private grounds where, at the middle of July, it was beginning to show signs of life. I have to thank Mrs. Albertson for a

\* Loc. cit.



fragment of this heather collected July 6, 1909, then just in flower. In flower September 3, 1902, F. G. Floyd.

## VACCINIACEAE

GAYLUSSACIA BACCATA (Wang.) C. Koch.

Abundant in dry thickets and open ground. In full flower May 30, 1909, June 15, 1911; green fruit June 18, 1910; first ripe fruit July 14, 1912.

Although a low and inconspicuous shrub this huckleberry has much to do with giving character to parts of the Nantucket landscape. Here it is less a plant of woods and thickets than of open ground, where its habit is to mass itself into extensive growths, for the most part unmixed with any other species. Thus outspread along the hills in distant view its foliage blends into breadths of brassy or golden green in effective contrast with the more sombre tones of color spread in broad patchwork about it. The gray green of scrub-oak thickets, the dark olive of the widespread bearberry, the varied neutral shades of other low-growing vegetation all go to make up a composition in which the livelier green of this huckleberry gives the stronger contrasts and dominating note.

GAYLUSSACIA FRONDOSA (L.) T. & G.

Locally common, mainly on the eastern side of the island, keeping in and about thickets and never straying into the open like the preceding. Not yet in flower June 12, 1909; first flowers June 10, 1911; in full bloom June 20, 1910; some flowers remaining July 4, 1912. On Chappaquiddick Island I have found it bearing abundant fruit in the second week of October.

GAYLUSSACIA DUMOSA (Andr.) T. & G.

Locally common in low grounds on the eastern side of the island; cranberry bogs about Long Pond on the western side. In full flower June 11, 1908, in Quaise; just in flower June 22, 1910, Long Pond; July 2, 1912, Tom Never's Swamp; abundant fruit Sept. 15, 1907.

The Nantucket plant, or much of it, is typical of the form called by Doctor Fernald var. *Bigeloviana*.



## VACCINIUM VACILLANS Kalm.

Common among the low woody growth of hillsides and dry open places. In full flower June 5, 1911; still some flowers June 29, 1908, June 30, 1910; ripe fruit July 11, 1912.

The common form has the leaves either entire or serrulate, and nearly or quite glabrous, varying from pale and glaucous to merely glaucescent, the branches often slightly puberulent. A taller form with larger and somewhat pubescent, pointed leaves, and soft pubescent branchlets, may be a cross with *Vaccinium corymbosum*. It was found only in a bushy tract on the plains west of the railroad at about the third milestone.

## VACCINIUM ANGUSTIFOLIUM Ait.

*V. pennsylvanicum* Lam., not Mill.

Abundant in dry open places and among open growths of low shrubbery. In full flower May 30, 1909, June 3, 1911; not many flowers left June 7, 1908; first ripe fruit June 7, 1912.

Diminutive forms, sometimes only a few inches high, have very small and crowded oblong-lanceolate leaves narrowly tapering to the base and the very acute apex. Other forms have larger oval or elliptic less pointed leaves. The Nantucket plant seems to be never strictly glabrous, the branchlets and the midvein of the leaf, at least on its upper side, showing more or less pubescence.

Growing with the common form near Tom Never's Head and west of the railroad at about the third milestone occurs var. *nigrum* Wood, having dark green shining leaves and large black fruit either wholly without glaucescence or with the bloom so faint as to be barely perceptible.

\* *Vaccinium Brittonii* Porter, sp. nov.

*Vaccinium nigrum* Britton, Man. 710. 1901. Not *V. nigrum* (Wood) Britton, Mem. Torrey Club 5: 252. 1894.

Low, 1-4 dm. high, from stout horizontal or ascending rootstocks; stems clustered, the branches often fastigate; bark pale green or violaceous, the shoots white glaucous; branchlets usually with traces of puberulence; leaves numerous, often crowded, oval to elliptic, obtuse or pointed, 1.5-3 cm. long, 7-12 mm. wide, or larger on the season's shoots, pale bluish green and glaucous



or glaucescent, often whitened beneath, firm and cartilaginous-serrulate, the venation prominent, especially on the lower surface, glabrous, or puberulent on the midvein on the upper side; corolla cylindric-urceolate, about 6 mm. long; calyx lobes commonly larger and more venose than those of *V. angustifolium*; fruit glaucous at least when young, becoming dark.

Type from Nantucket, Tom Never's swamp, June 13, 1908.

The *Vaccinium pennsylvanicum* var. *nigrum* Wood was described as "Dark green, berries black and shining without bloom" (Bot. and Fl. 199. 1873). The reference is unmistakably to the black-fruited form of *V. angustifolium*, which is not a very uncommon plant and, when in mature fruit, is at sharp contrast with the common blue-fruited form with which it grows. *Vaccinium Brittonii*, which is characteristically pale green and glaucescent, is altogether a different plant. This was seen long ago by the late Doctor Thomas C. Porter, and the name here adopted for it was proposed by him in a letter to Doctor Britton dated Feb. 25, 1891, now preserved in the herbarium of Columbia University. This letter is attached to a sheet bearing two separate collections of the plant, one by Doctor Britton from High Point, Sussex County, New Jersey, May 30, 1891, the other, by Mr. O. A. Farwell, from sand dunes along the shore of Lake Superior in Keweenaw County, Michigan, Aug., 1890. There appears to be no specimen collected by Doctor Porter or designated by him, but his letter is perfectly clear in pointing out the characters that distinguish this blueberry from *V. angustifolium*, which he discusses under the then current name of *V. pennsylvanicum*. On Nantucket *Vaccinium Brittonii* was met with only in Tom Never's swamp where it grows in several places in association with *Cassandra*, *Gaylussacia dumosa*, *Aronia nigra*, and also *Vaccinium angustifolium*. Last flowers June 13, 1908; green glaucous fruit July 2, 1912.

At the Thousand Islands, in 1905, I found it a representative species, particularly on La Rue Island, where it was in fruit late in August. The pale green color of the firm oval leaves and the white glaucous leafy shoots distinguished it strikingly from *V. angustifolium* and *V. canadense*, also common there. The mature fruit although very dark was covered with a faint glaucous bloom.

It seems appropriate here to report an evident hybrid between



*V. angustifolium* and *V. vacillans* that might readily be mistaken for *V. Brittonii*. It was collected on Long Island, east of Smithtown, Aug. 1, 1908, a single plant growing with an abundance of both the others, and appearing quite intermediate between them except in respect of the fruit, which was very dark, having only the faintest glaucescence. In other respects it differs from *V. Brittonii* in larger and relatively broader leaves of thinner texture, which are elliptic to obovate, mostly 3-3.5 cm. long and 1.5 cm. wide, distinctly pointed, not obviously paler beneath, and closely ciliate-serrulate.

Since this was written I have seen in the herbarium of the New York Botanical Garden a specimen of *Vaccinium Dobbini* Burnham from Jackson, Washington County, New York, (Am. Bot. 12: 8. 1907). It is in all respects the same as the Long Island hybrid and, like the latter, was found growing with both the parent species.

\* *Vaccinium atlanticum* sp. nov.

A compact, often rounded shrub, commonly 6-9 dm. high, often close branched and leafy from the base; branches greenish, verrucose-punctulate, glabrous or minutely crisp-puberulent in lines, branchlets more or less pubescent when young; leaves rather close and numerous, small for a high bush blueberry, 3-5 cm. long, 1-2 cm. wide, or larger on the shoots, oblong- to elliptic-lanceolate, gradually narrowed to base and apex, acute, often attenuate, ciliolate-serrulate, dark green and more or less shining above, paler beneath, the midvein pubescent with spreading hairs, at least towards the base on the lower side, rarely quite glabrous; flowers opening with the unfolding leaves; inflorescence of short racemes clustered towards the ends of the branches or lateral; pedicels slender; corolla broadly cylindraceous to openly urceolate, the widest part often above the middle or towards the throat, angulate, 6-8 mm. long, 4-5 mm. wide, white or pink-tinged, calyx lobes round to triangular and subacute; fruit dark blue, glaucous, becoming 9 mm. in diameter, sweet.

Rather common on Nantucket about the borders of low thickets or in open low grounds. Type, flowering, Millbrook Swamp, May 31, 1909; fruiting, Pocomo, July 11, 1912, deposited in the herbarium of the New York Botanical Garden. Also collected on Chappaquiddick Island, Marthas Vineyard, and at Lake Ronkonkoma, Long Island.



This is perhaps the blueberry reported by Mr. Kenneth K. Mackenzie from New Jersey and Staten Island as *Vaccinium virgatum* Ait. (Torreya 7: 144-145. 1909). Certain New Jersey specimens so named in the herbarium of the New York Botanical Garden agree closely with the Nantucket plant. They do, indeed, convey a suggestion of *V. virgatum*, but I have seen no northern *Vaccinium* that I could deem as at all referable to the plant of the Southern States taken up under Aiton's name, none, for instance that showed the same naked and virgate inflorescence, or the cylindric-conic corolla, or the characteristic brown stipitate glands on the lower surface of the leaf. *Vaccinium atlanticum* is evidently in closer relationship with *V. corymbosum*, differing obviously however by lower stature, more compact habit, and smaller and narrower leaves dark shining green above and ciliolate-serrulate on the margins. In the aspect of this blueberry there is something both of *V. corymbosum* and *V. angustifolium*, and were only a single example known it might well be supposed to be a hybrid of these species. It appears to have, however, a perfectly natural coastwise range of considerable extent, and I have observed nothing in the manner of its occurrence on Nantucket to lead me to believe that it is not in itself a valid species.

It is scarcely probable that this blueberry has not been frequently collected and, if so, it has perhaps been referred to the *V. corymbosum* var. *amoenum* of Gray (*V. amoenum* Ait.), which is described as differing from *V. corymbosum* by bristly ciliate leaves bright green on both sides. I have never met with any high bush blueberry having just such leaves except one herein presently to be described as a possible hybrid between *V. corymbosum* and *V. angustifolium*. But I find no warrant in Aiton's description of his *V. amoenum* for thus understanding the shrub he sought to define, which he denominated the broad-leaved whortleberry and characterized as having leaves pubescent on the veins beneath and only subserrulate. A blueberry having just such leaves is not uncommon. It is an openly branched shrub, mainly of low shaded woodland, the leaves of which are more or less obscurely serrulate or some of them entire and which has claims to recognition, although perhaps passing into the ordinary *V. corymbosum* of more open grounds.



## VACCINIUM CORYMBOSUM L.

An abundant shrub, mainly of low grounds, where it mixes with other shrubbery or groups itself into close thickets that form impassable barriers about pools and swampy spots. In full flower May 31, 1909; no flowers left June 5, 1910; first ripe fruit July 4, 1912.

\* VACCINIUM ANGUSTIFOLIUM  $\times$  CORYMBOSUM?

A very distinct appearing blueberry midway in size between the high bush and the low bush series, having bright green serrulate leaves, broadened like those of *V. corymbosum*, with the membranous and lucid character of those of *V. angustifolium*, and further noteworthy by reason of puberulent pedicels and ciliolate calyx lobes.

From 5 to 9 dm. high; leaves ovate to elliptic, acute, mostly 4 cm. long by 2 cm. wide, the largest 5.3  $\times$  2.7 cm., firm and membranous, ciliolate, and bristly serrulate, on both sides bright green and shining, strictly glabrous beneath, the upper face puberulent along the principal veins; branches green, verrucose, puberulent; inflorescence mostly compound, consisting of short racemes or corymbiform clusters along naked terminal branchlets; fruit large, becoming 1 cm. in diameter, depressed-globose, deep blackish blue with a bloom; pedicels mostly curved, about 5 mm. long, crisp-puberulent; calyx lobes tomentulose-ciliolate.

On Coatue, near Third Point, July 13, 1912, a single colony. Specimens deposited in the herbarium of the New York Botanical Garden.

If not a hybrid I do not see how this plant is to be accounted for except as a hitherto unrecognized species. Its membranous leaves bright shining green on both surfaces keep it sharply apart from all of the *corymbosum* series and seem to place it in relationship with *V. angustifolium*, but in size and habit and in breadth of leaf it is more of a high bush blueberry, appearing, indeed, quite intermediate between *V. angustifolium* and *V. corymbosum*. The puberulence of the pedicels is a character not shared with any northern species of the *corymbosum* group, although more or less evident on many examples of *V. angustifolium*; in the latter, also, obscurely ciliolate calyx lobes are sometimes seen.

## \* VACCINIUM AUSTRALE Small.

*V. corymbosum* var. *glabrum* A. Gray, Man. ed. 5, 292. 1867.

*V. caesariense* Mackenzie, Torreya 10: 230. 1910.



Common in low thickets. In full flower June 1, 1909; June 8, 1910; corolla broadly cylindric, variable in size, becoming 8-9 mm. long and 5-7 mm. wide, sometimes considerably smaller; ripe fruit Aug. 6, 1906, Aug. 9, 1908; berry blue and very glaucous, becoming as large as a half inch in diameter.

The handsomest of our high bush blueberries. In its typical form the thick entire leaves, bright green above and often glaucous, are whitened on the lower surface, and are wholly glabrous even in veneration, except sometimes for a minute pubescence along the midvein on the upper face. Quite possibly intergrades or hybridizes with *V. corymbosum*.

VACCINIUM ATROCOCCUM (A. Gray) Heller.

Common in the dense thickets of low grounds, often associating with *V. corymbosum*. Last flowers, and young fruit, June 10, 1908; some ripe fruit July 11, 1912.

At Coskaty on Aug. 14, 1906, a form was collected bearing the characteristic dark shining fruit, but with the leaves very acute and more or less serrulate, or some of them entire, thus answering to Michaux's description of his *V. disomorphum*. Bigelow, long ago (Fl. Bost. ed. 2, 151. 1824) correlated this name with the shrub we now call *V. atrococcum*, and it comes out pretty clearly that his judgment was correct, unless a distinction is to be discovered between those shrubs having strictly entire leaves and those with the leaves subserrulate or sometimes entire as Michaux described them. His Latin, "*folia . . . subtus pubentia, interdum integriscula . . . corolla albido-purpurascens, oblonga, ovoideo-urceolata*" quite definitely excludes *V. corymbosum* as well as all other northern species at present recognized, except *V. atrococcum*.

\* *Vaccinium vicinum* sp. nov.

Characterized by a close soft pubescence, similar to that of *V. atrococcum*, and large flowers as well as glaucous fruit, more like that of *V. corymbosum*; the leaves, more or less serrulate, but often entire, are commonly narrower than in either of those species and of marked oblanceolate or obovate-oblong tendency.

An openly branched shrub 1-2 m. or more high; branchlets and young leaves beneath tomentulose-canescens or villous-



tomentulose with a white pubescence; mature leaves thick; villous-pubescent on the pale lower surface, becoming tawny in age, bright green and shining and usually thinly pubescent on the upper surface, entire or serrulate even on the same branch, firm, oblanceolate, long-tapering to the base and tapering-acute at apex to obovate-oblong or elliptic and acuminate, often 5-6 cm. long by 1.5-2 cm. wide, sometimes oblong-ovate and 2.5 cm. wide; flowers appearing with the leaves, disposed in numerous close clusters along the leafless or leafy terminations of the branches or scattered on lateral branchlets; corolla white, broadly cylindrical, 8-10 mm. long, 4-5.5 mm. wide; fruit blue-glaucous, dark beneath the bloom.

Frequent on Nantucket and on Long Island in low grounds. Type from Nantucket, Trot's Swamp, July 3, 1912, young fruit; in flower, near Maxcy's Pond, May 30, 1909; deposited in the herbarium New York Botanical Garden.

It might be thought that this blueberry was a cross between *V. atrococcum* and *V. corymbosum* were it not that the flowers do not show any intermediate character and that the leaves are commonly narrower and more tapering towards base and apex than in either. It is evidently closely related to *V. corymbosum* and approaches *V. fuscatum* Ait. of the Southern States, described as fuscous-pubescent and with entire leaves.

#### CHIOGENES HISPIDULA (L.) T. & G.

Very local, on the eastern side of the island. Abundant in a sphagnum bog east of Almanac Pond, growing with the small cranberry and the pitcher plant. I have not myself seen it at any other station, but it is said to grow in other sphagnum bogs in the same neighborhood. Berries half grown June 11, 1909.

#### OXYCOCCUS OXYCOCCOS (L.) MacM.

Locally abundant in cold sphagnum bogs: Long Pond; Hummock Pond; Abrams Point bog; Quaise; Pocomo; Sachacha Pond. Blooms rather earlier than the common cranberry. Just in flower June 2, 1909; June 9, 1911; June 11, 1908; in full flower July 6, 1912.

#### OXYCOCCUS MACROCARPUS (Ait.) Pers.

One of the abundant native plants of Nantucket, thriving in sandy bogs and on the level shores of fresh water ponds. Now also



extensively cultivated, many sandy swamps and acres of low ground having been transformed into cranberry bogs. Just in flower June 17, 1908; in full flower June 15, 1910; July 5, 1912.

A smaller and more delicate form occurs, having narrower linear-oblong leaves, only 5-10 mm. long by 2-3 mm. wide, the inflorescence frequently terminal, and the corolla segments only 5.9 mm. long.







# INDEX TO AMERICAN BOTANICAL LITERATURE

1914

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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**Ames, O.** The orchids of Guam. *Philip. Jour. Sci.* 9: (Bot.) 11-16.  
F 1914.

Includes eight new species.

**Atwood, W. M.** A physiological study of the germination of *Avena fatua*. *Bot. Gaz.* 57: 386-414. f. 1-13. 16 My 1914.

**Bicknell, E. P.** Some grasses noteworthy in Massachusetts. *Rhodora* 16: 81-83. 11 My 1914.

**Brand, A.** Symplocaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* 6: 172. 4 Ap 1914.

Includes *Symplocos Ulei* sp. nov.

**Brause, G.** Polypodiaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* 6: 109-111. 20 Mr 1914.

Includes *Polypodium roraimense* and *Dryopteris roraimensis*, spp. nov.

**Clements, F. E., & Clements, E. S.** Rocky Mountain flowers. i-xxxii + 1-392. pl. 1-47. White Plains, 1914.

**Cook, M. T.** Crown gall and hairy root. *New Jersey Agr. Exp. Sta. Circ.* 34: 1-14. [1914.] [Illust.]

**Cook, M. T.** Potato diseases in New Jersey. *New Jersey Agr. Exp. Sta. Circ.* 33: 1-24. f. 1-14. [1914.]



- Cook, M. T.** Some diseases of nursery stock. New Jersey Agr. Exp. Sta. Circ. 35: 1-24. *f.* 1-15. [1914.]
- Copeland, E. B.** New Papuan ferns. Philip. Jour. Sci. 9: (Bot.) 1-9. F 1914.  
Includes new species in *Cyathea* (2), *Dryopteris* (4), *Tectaria* (2), *Athyrium* (1), *Adiantum* (1), *Polypodium* (6), and *Aglaomorpha* (1).
- Cotton, A. D.** The genus *Atichia*. Kew Bull. Misc. Inf. 1914: 54-63. *f.* 1. Mr 1914.
- Cross, E. R.** *Viola Selkirkii* in Colorado. Rhodora 16: 94, 95. 11 My 1914.
- Dachnowski, A., & Gormley, R.** The physiological water requirement and the growth of plants in glycocoll solutions. Am. Jour. Bot. 1: 174-185. 23 My 1914.
- Diels, L.** Droseraceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. Notizbl. Königl. Bot. Gard. Berlin 6: 136. 20 Mr 1914.
- Diels, L.** Menispermaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. Notizbl. Königl. Bot. Gard. Berlin 6: 132-134. 20 Mr 1914.  
Includes *Anomospermum chloranthum* and *Odontocarya floribunda*, spp. nov.
- Engler, A., & Krause, K.** Araceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. Notizbl. Königl. Bot. Gard. Berlin 6: 113-117. 20 Mr 1914.  
Includes *Anthurium micranthum* Krause, *Stenospermatium Ulei* Krause, *Monstera acreana* Krause, *Dracontium Ulei* Krause, *Xanthosoma Hylaeae* Engl. et Krause, and *Taccarum Ulei* Engl. et Krause.
- Evans, A. W.** Hepaticae: Yale Peruvian Expedition of 1911. Trans. Connecticut Acad. Arts & Sci. 18: 295-345. Ap 1914.  
Includes *Metzgeria scyphigera*, *Plagiochila Binghamiae*, *P. Footei*, *P. pauciramea*, *P. striolata*, and *Dicranolejeunea rotundata*, spp. nov.
- Farrell, M. E.** The ovary and embryo of *Cyrtanthus sanguineus*. Bot. Gaz. 57: 428-436. *pl.* 24 + *f.* 1-3. 16 My 1914.
- Fernald, M. L.** Three lupines naturalized in eastern Canada and Newfoundland. Rhodora 16: 92-94. 11 My 1914.
- Graves, A. H.** The future of the chestnut tree in North America. Pop. Sci. Mo. 84: 551-566. *f.* 1-4. Je 1914.
- Harms, H.** Araliaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. Notizbl. Königl. Bot. Gard. Berlin 6: 167, 168. 4 Ap 1914.  
Includes *Didymopanax psilophyllum* sp. nov.



- Harper, R. M.** The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession. *Bull. Torrey Club* **41**: 209-220. *f.* 1-4. 13 My 1914.
- Harris, J. A.** On the relationship between the number of ovules formed and the number of seeds developing in *Cercis*. *Bull. Torrey Club* **41**: 243-256. *f.* 1-3. 13 My 1914.
- Heimerl, A.** Nyctaginaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* **6**: 126-132. 20 Mr 1914.  
Includes four new species in *Neea*.
- Higgins, B. B.** Contribution to the life history and physiology of *Cylindrosporium* on stone fruits. *Am. Jour. Bot.* **1**: 145-173. *pl.* 13-16. 23 My 1914.  
Includes *Coccomyces prunophorae* and *C. lutescens*, spp. nov.
- Howe, M. A.** The marine algae of Peru. *Science* II. **39**: 254. 13 F 1914.
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- Knowlton, C. H.** *Spiraea salicifolia* in Alburg, Vermont. *Rhodora* **16**: 96. 11 My 1914.
- Krause, K.** Rutaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* **6**: 143-149. 4 Ap 1914.  
Includes one new species each in *Fagara*, *Galipea*, *Rauia*, *Erythrochiton*, and *Metrodorea*, and *Sohnreyia excelsa* gen. et sp. nov.
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Includes one new species each in *Lucuma*, *Bumelia*, *Vitellaria*, and *Chrysophyllum*.
- Lipman, C. B.** The poor nitrifying power of soils a possible cause of "die-back" (exanthema) in lemons. *Science* II. **39**: 728-730. 15 My 1914.
- MacDougal, D. T.** The measurement of environic factors and their biologic effects. *Pop. Sci. Mo.* **84**: 417-433. *f.* 1-8. My 1914.
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Includes *Siparuna dasyantha* and *S. heteropoda*, spp. nov.
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Includes *Pariana Ulei* sp. nov. from Brazil.
- Pilger, R.** *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* 6: 109-142. 20 Mr 1914; 143-179. 4 Ap 1914.  
Includes articles by Brause, Engler & Krause, Malme, Schlechter, Heimerl, Diels, Perkins, Schulz, Brand, Krause, Radlkofer, Ulbrich, Harms, and Pilger, here indexed separately.
- Pilger, R.** Rapateaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* 6: 119, 120. 20 Mr 1914.  
Includes *Rapatea Ulei* Pilger.
- Pilger, R.** Rosaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. *Notizbl. Königl. Bot. Gard. Berlin* 6: 136-142. 20 Mr 1914.  
Includes eleven new species in *Moquilea* (1), *Licania* (2), and *Hirtella* (8).
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Includes new species in *Blepharodon* (4), *Metastelma* (1), *Ditassa* (3), *Orthosia* (1), *Oxypetalum* (1), *Gonolobus* (1), and *Fimbristemma* (1).
- Schlechter, R.** Orchidaceae. In Pilger, R. *Plantae Uleanae novae vel minus cognitae*. Notizbl. Königl. Bot. Gard. Berlin **6**: 120-126. 20 Mr 1914.  
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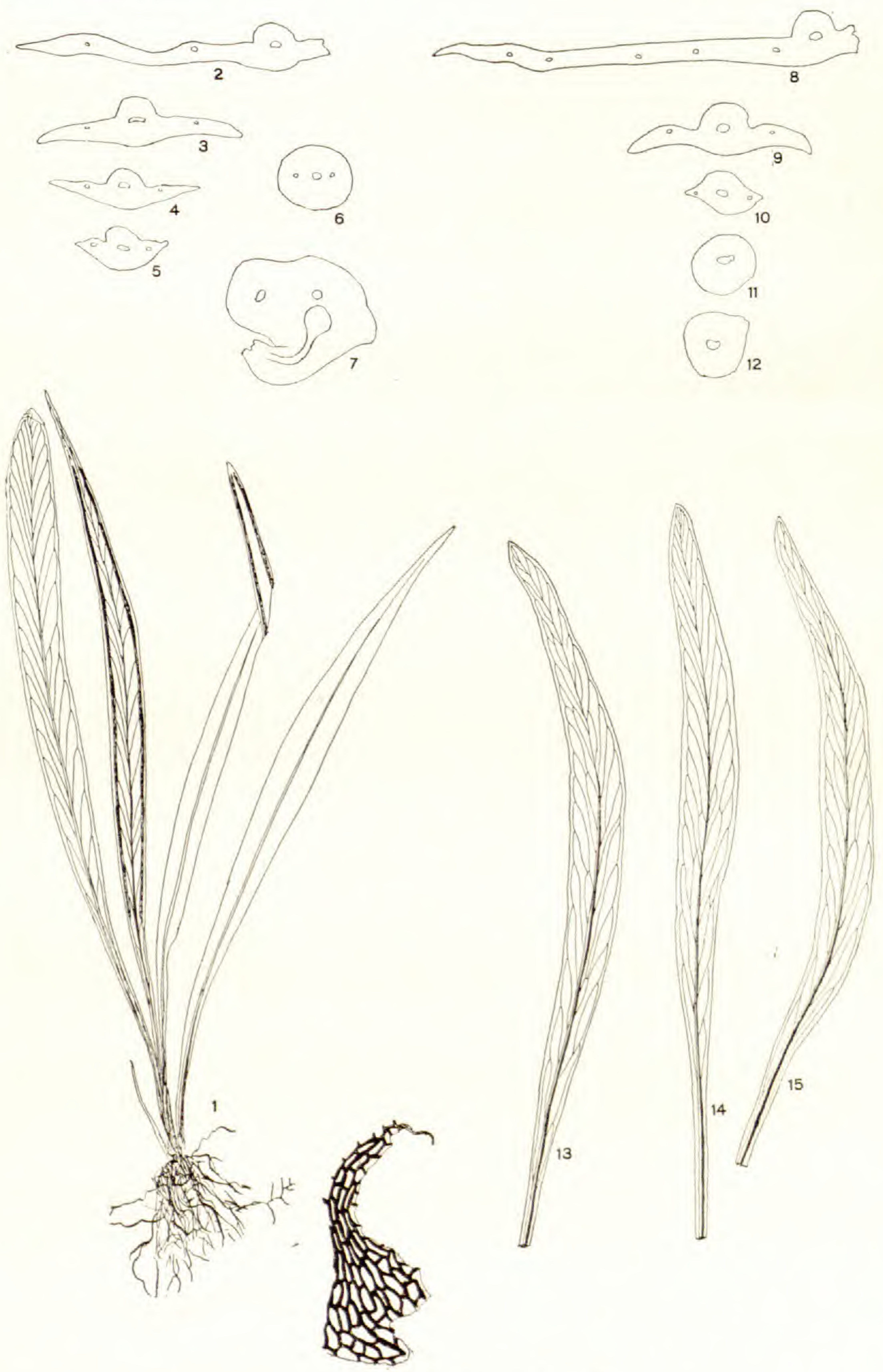
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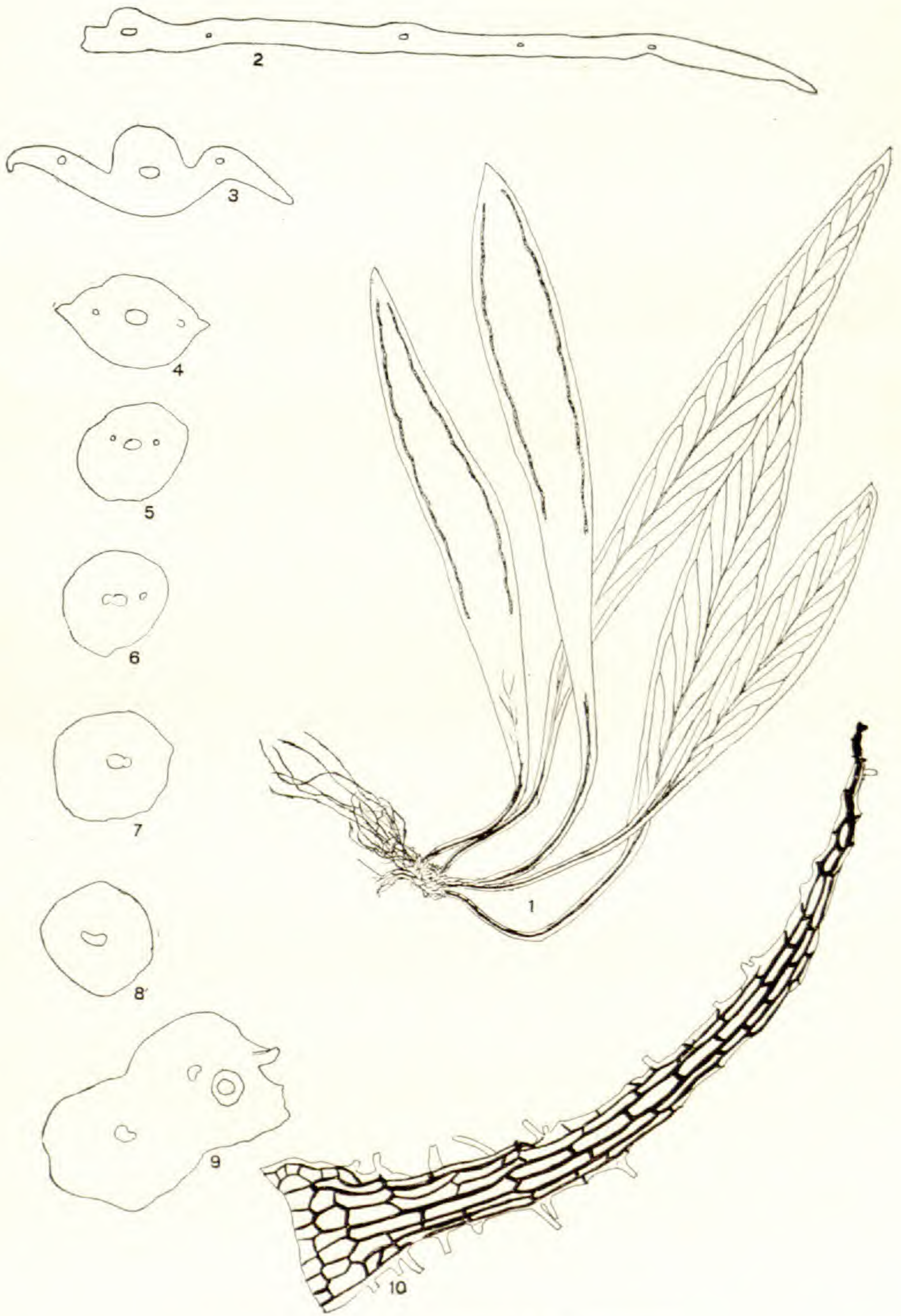
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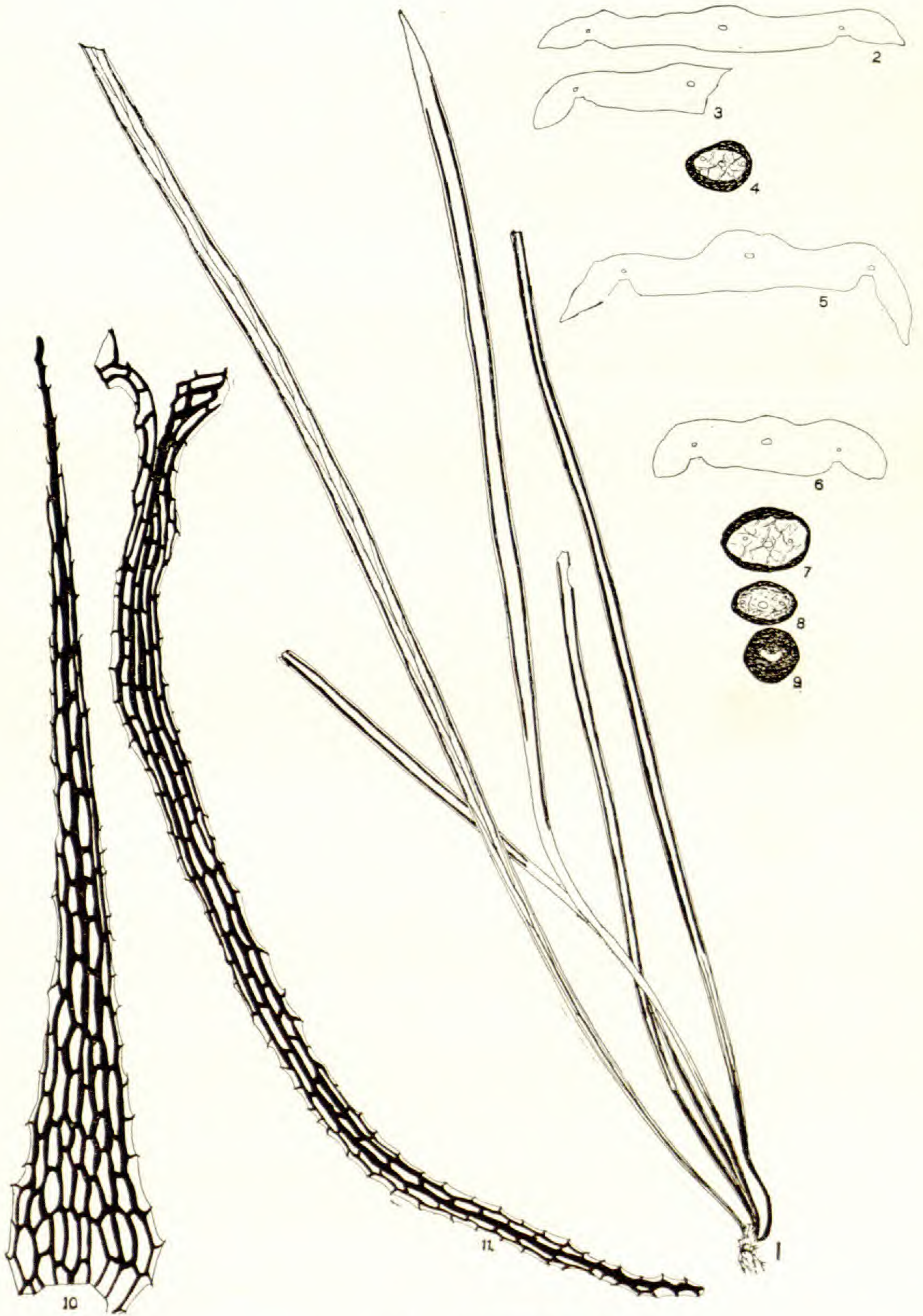
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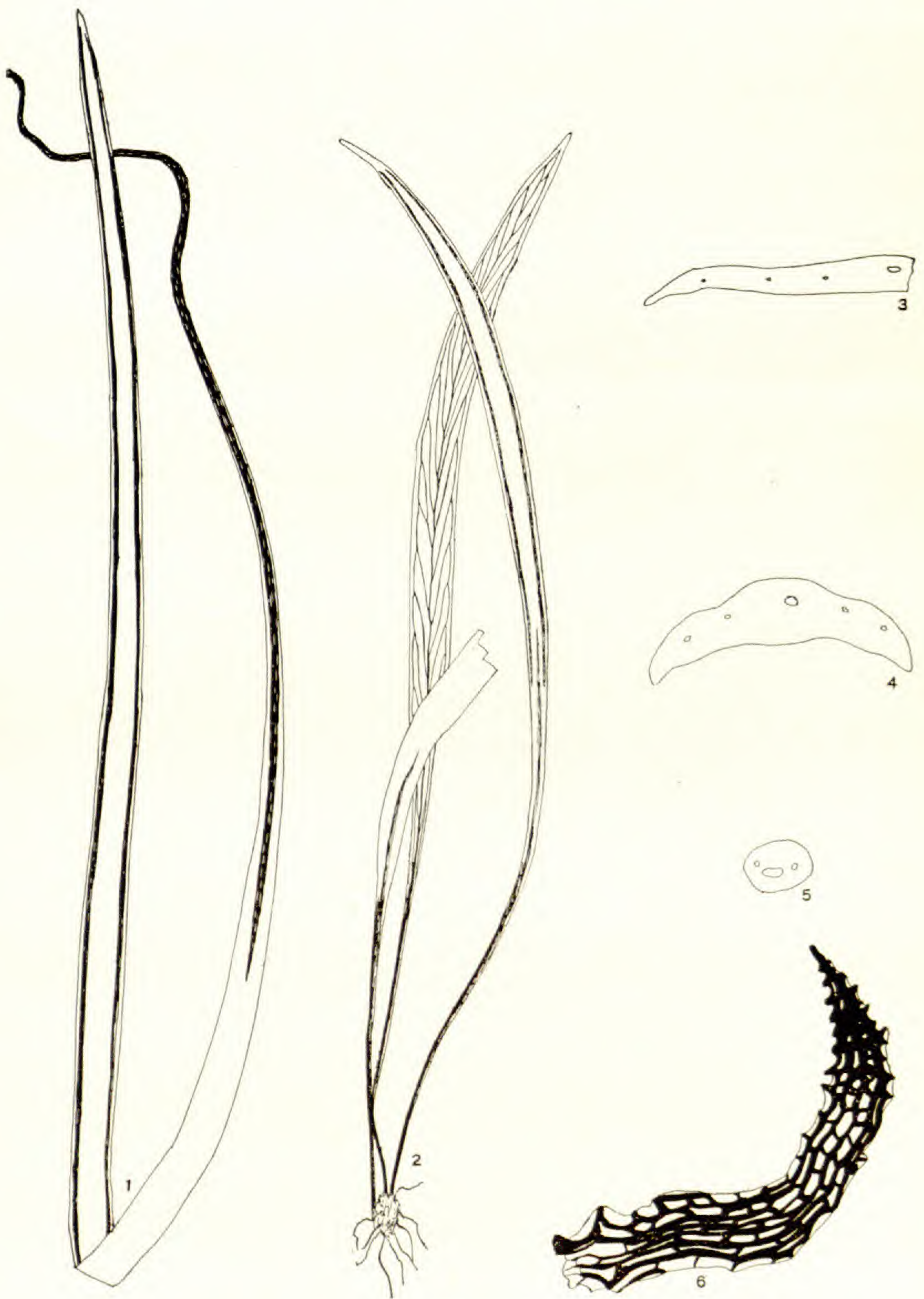
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### CONTENTS

A review of investigations of the mosaic disease of tobacco, together with a bibliography of the more important contributions . . . H. A. ALLARD 435

Phytogeographical notes on the Rocky Mountain region—III. Formations in the alpine zone . . . P. A. RYDBERG 459

INDEX TO AMERICAN BOTANICAL LITERATURE . . . 475

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BULLETIN  
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SEPTEMBER, 1914

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A review of investigations of the mosaic disease of tobacco, together with a bibliography of the more important contributions

H. A. ALLARD

Concerning the nature of the mosaic disease, many important facts have been published from time to time, both in America and in Europe. However, from the published accounts of earlier investigators, especially in Europe, it is now known that various pathological appearances entirely distinct from the true mosaic have been ascribed to this disease. In reviewing the literature of the subject one is at once impressed with the contradictory conclusions reached by different investigators and the conflicting results frequently obtained in their individual experiments, which oftentimes indicate that the controls were quite as subject to the disease as plants inoculated with the virus. Unquestionably, these discrepancies to a great extent can readily be accounted for in the light of facts recently brought out by the writer (59, 64)\* regarding insect agencies which may become active disseminators of infection and which have heretofore been overlooked in a study of the disease.

After several years of careful investigation, Iwanowski and Polowzoff (4) concluded that the term "Mosaikkkrankheit" had frequently been used to cover two very distinct diseases, i. e. true, infectious mosaic and "Pockenkrankheit." Mayer considered "Pockenkrankheit" simply a later phase of true mosaic and thus associated the two diseases under the term "Mosaik-

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\* The serial numbers in parentheses used in this paper refer to the "Index to the literature of mosaic," page 453.

[The BULLETIN for August (41: 391-434. pl. 15-20) was issued 25 Au 1914.]



krankheit." Likewise Koning, Heintzel, and Beijerinck failed to distinguish clearly between the two diseases. The published accounts of Prillieux and Delacroix, Marchal, Goutière, Perreau, and Bouygues indicate that in many instances these investigators had confined their attention entirely to "Pockenkrankheit" or some other leaf-spot disease. This failure to distinguish the true mosaic disease from various other pathological troubles finally led to considerable confusion as to the bacterial nature of the trouble supposed to be the true infectious mosaic disease described by Mayer.

Dr. Adolf Mayer (2), Director of the Experiment Station at Wageningen, Holland, appears to have given in 1886 the first scientific account of the mosaic disease of tobacco, terming it "Mosaikkkrankheit,"\* whence the common term "mosaic" for this disease. Although Mayer failed to distinguish between this disease and "Pockenkrankheit," his accurate description of various facts and symptoms of the disease with which he worked identifies the first phase without question as the true mosaic disease affecting American tobacco. The more important facts brought out by Mayer may be briefly stated as follows:

He first proved that the disease was communicable by artificial inoculation; that the sap of healthy plants was not infectious; that an incubation period of 10 or 12 days preceded the first observable symptoms; that the disease was persistent, appearing ultimately in all immature growing parts of affected plants; that diseased sap filtered once through filter paper still retained its virulence; that sap sufficiently heated lost its virulence; and that the seed of affected plants did not carry the disease to the next generation.

Mayer failed to produce the disease in other solanaceous plants. Further, he found that liming, crowding the plants, sudden atmos-

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\* According to Hunger, J. H. Swieten, as a result of investigations of a disease of tobacco in the Opper-Betuwe, possibly gave the first account of mosaic in 1857. Among the tobacco growers the disease was known as "rost," a term at the present time usually applied to the mosaic disease.

In the year 1866 Swieten spent several months in Cuba in connection with problems relating to tobacco culture, but did not mention the mosaic disease as occurring here. See *De tabaksteelt te Elst en omstreken in de Opper-Betuwe*. Tijdschrift ter bevordering van Nijverheid, 1857, tweede reeks, Deel 5, pp. 147-167, and *Beschrijving van te teelt en bereiding van de Cuba-tabak*. Tijdschrift voor Nijverheid en Landbouw in Ned-Indie, 1866. Deel XII, pp. 235-316.



pheric changes, unfavorable conditions of whatever sort affecting the roots, i. e., mechanical injury, nematodes, parasitic fungi, etc., were not in any way responsible for the origin of the disease, important conclusions which several workers in the United States seem not to have known. He recognized the sporadic occurrence of the disease in the field, and finally concluded that its spread must be through the soil, both in the field and in the seed bed. He recognized the fact, however, that a transfer of the disease by means of the soil had never been proved. It is plainly indicated that Mayer held the soil in some way responsible for the origin of the disease, since he advised renewal of soil in hotbeds, crop rotation, removal of the stubs of mosaic plants, the use of chemical rather than animal manures, etc. Although Mayer did not isolate any organisms responsible for the disease, he finally concluded that it was of bacterial origin.

In 1892 Iwanowski (7) brought out additional important facts relative to the mosaic disease and confirmed many of the conclusions of Mayer. He, like Mayer, found that the sap of mosaic plants produced the disease in healthy plants and also that it lost its virulence when heated nearly to the boiling point. His results with filtered sap did not agree with the conclusions of Mayer, who stated that twice filtering through common filter paper rendered the diseased juice innocuous. On the contrary, Iwanowski found that the sap retained its virulence even after it had been filtered. In agreement with Mayer, Iwanowski also held the view that the disease was bacterial or parasitic in its nature. He did not, however, isolate any organism specifically connected with the disease, although he claims to have seen such organisms in the tissues of affected plants.

In 1894 two French investigators, Prillieux and Delacroix (8) described a tobacco trouble occurring in France, which they believed to be the true mosaic disease. Its presence was indicated on the leaves by the occurrence of spots in which they found a motile bacillus united in chains. It appears, however, that the disease described by these investigators was entirely distinct from the true mosaic of Mayer.

In 1897 Marchal (9) published a paper, "La mosaïque du tabac." He stated that the leaves of affected plants became



covered with grayish spots in the tissue of which he found a motile bacillus which imparted a yellow color to culture media. He also reproduced this disease in healthy plants by experimental inoculation. Marchal found the disease prevalent in seed beds, especially those rich in organic matter. He recommended renewal of the seed beds and sterilization as practical methods of control. The malady described by Marchal appears not to have been the true mosaic disease at all. In all essential points the disease appears to be the same trouble that was previously mentioned by Prillieux and Delacroix (8).

In 1898 Beijerinck (10) published additional facts and observations regarding the true mosaic disease. He found that diseased sap so filtered as to be entirely free from bacteria still retained its power to infect healthy plants, in this respect confirming Iwanowski (7). He showed that a very minute quantity of this filtered juice produced the disease in immature, growing tissues. He held that dried mosaic material retained its infectious properties for some time, and, likewise, that it was not rendered innocuous by remaining in the soil throughout the winter. Like Mayer (2) and Iwanowski (7), he found that heating mosaic virus to the boiling point rendered it harmless. He proved that the virus traveled considerable distances in plants but produced obvious symptoms only in immature tissues. Beijerinck claimed that the soil around diseased roots may infect healthy roots and that plants in some instances apparently recovered from the disease temporarily. Previous to the work of Beijerinck all investigators of the disease were strongly inclined to establish a bacterial origin for it, although at that time no direct proof had been obtained. Beijerinck, on the other hand, obtaining only negative evidence with regard to bacteria, advanced his theories along somewhat different lines. He assumed that the virus must be an unorganized material, fluidlike in its nature, and capable of symbiotic growth in the presence of living cells. Just what Beijerinck wished to convey by these vague and indefinite terms it is rather difficult to conclude, although it would appear as if he were foreshadowing the enzymatic theory of mosaic diseases, a theory which later was developed more fully.

Shortly after Beijerinck (10) published his results, Sturgis (16)



in Connecticut presented a careful account of the mosaic or "calico" disease as it occurs around Hartford, Connecticut, together with a summary of work done by foreign investigators up to that time. He concluded that "mottled-top" was a less pronounced phase of "calico" developing in nearly mature plants. He likewise proved conclusively by growing seedlings from the seed of calicoed plants that the disease is not transmitted through the seed. From his extended observations in the Connecticut Valley, Sturgis found that calico was very sporadic in its occurrence and that it could not be attributed to parasitic fungi, nematodes, insects, mechanical injury of the roots, cultivation, etc. He was finally led to believe that the disease was purely physiological, as the following paragraphs of his summary indicate:

(2) "The disease occurs abundantly in some localities, notably on the close, clayey soils on the east side of the Connecticut River; sparingly in other localities, where the soil is open and porous.

(7) "It seems probable that the disease is purely a physiological one, caused primarily by sudden changes of atmospheric conditions which disturb the normal balance between evaporation of water from the leaves and its absorption by the roots, and secondarily by soil conditions which prevent the speedy restoration of that balance. This supposition is supported by numerous facts."

In 1899 Sturgis (17) published the results of various liming and shading experiments as a preventive of calico, and as additional proof of the supposed physiological origin of the disease. In this paper he concludes "that shading may reduce the amount of calico, there seems good reason to believe"; and, with respect to liming the soil, "that the use of lime may not, in all cases, exercise the deleterious effect on tobacco that some growers suppose it to, and that there is some reason for thinking that its use may tend to decrease the prevalence of calico."

As already shown, Beijerinck (10), in somewhat uncertain terms, seemed inclined to place the inciting cause of the disease somewhere between parasitic and non-parasitic agencies. Sturgis (17) completed the step and was the first to regard the disease as a purely physiological response to particular soil and climatic factors.



He did not, however, attempt to determine the exact nature of this response in affected plants.

In the *Verslag omtrent den staat van 'Slands Plantentuin te Buitenzorg over het jaar 1899* (19, pp. 73-78) the supposed bacterial nature of mosaic is discussed. Cultures of various organisms supposed to be responsible for mosaic were isolated from the tissues of such plants. These were inoculated into healthy plants, but with somewhat uncertain results. In many cases it was stated that only a slight indication of the disease followed, which, with the further development of the plants, often disappeared entirely. This was explained on the grounds that obscure conditions of one sort or another had weakened the virulence of the cultures.

It was shown that the so-called "wit kop" was simply a manifestation of mosaic. It was stated that sprinkling the virus upon healthy plants produced disease, as did placing finely cut mosaic material beneath the roots at transplanting. Sprinkling mosaic sap upon the soil ten days before transplanting, and working it into the soil did not produce mosaic.

Mosaic material was dried in the sun ten days and worked lightly into the soil. Other plots were similarly treated with mosaic material dried in the shade. It was stated that some mosaic followed each operation. In such tests, however, it may be said that there is no very certain means of determining to what extent this treatment of the soil was actually responsible for the disease until controls are taken into consideration. It is a well-known fact that mosaic may be prevalent in a field quite independently of any test.

Raciborski (19) in 1898-99 reported the results of his work with mosaic. He examined microtome sections of the leaves and stems of mosaic plants for bacteria, but found no evidence of organisms either in the cells or intercellular spaces. He determined the effects of different temperatures, exposure to the sun, etc., upon the virulence of the sap of mosaic plants. Some of his conclusions were as follows:

Mosaic sap did not lose its virulence when heated 5 minutes at 62° C. When heated one minute at 100° C. the sap still produced mosaic after 10-14 days. The virulence was lost entirely, however, when the sap was heated 15 minutes at 100° C.



When the virus was exposed to the sun in broad, shallow glass vessels for one day it was not rendered inert. An exposure for 4 or 5 days, however, destroyed its infectious nature. He concludes from this that exposure of the uppermost layers of the soil in the seed bed to the sun, will afford a practical and efficient means by which the planter can rid his soil of mosaic infection.

Mosaic sap lost its virulence when treated with potassium permanganate. Mosaic sap was treated with basic lead acetate and filtered, and the filtrate freed of lead with  $H_2S$ . Air was forced into the solution to remove the  $H_2S$ . The solution was then neutralized and sprinkled upon healthy plants. It appeared that the virulence was lost.

Water was then added to the precipitate obtained by adding basic lead acetate to the original virus. The lead was removed with  $H_2S$ , and this likewise was then driven off as before. The filtrate obtained, after filtering, was neutralized, and sprinkled upon healthy plants. The virulence was also lost.

A water extract was obtained from mosaic leaves dried in the shade. This solution was virulent when sprinkled upon plants.

Shade-dried mosaic material was then extracted with cold alcohol of 98 per cent. This extract was evaporated at  $70^\circ C$ . Water was added to the solid material and sprinkled upon healthy plants. The virulence was lost.

It appears that Raciborski tested the virulence of the mosaic sap following the different treatments by sprinkling it upon the leaves of healthy plants. As this method of inoculation is somewhat uncertain, however, conclusions based upon such inoculations are open to question.

In 1899 van Bijlert (20) mentions the occurrence of mosaic in the vicinity of the experimental station at Tandajong, Morawa. In one instance a narrow path one meter wide was a sharply dividing line between a field of tobacco which became badly mosaic and the experimental field which remained free from the disease.

From the fact that coolies did not work in the experimental field, van Bijlert is of the opinion that this largely accounts for the freedom of this field from mosaic, although surrounded on all sides by mosaic plants. Likewise, he considered that the path one meter wide served as an important means of checking the spread of the disease.



Since in the process of topping, suckering, etc., all mosaic portions removed from the plants are thrown upon the ground, Van Bijlert was convinced that the path checked the further spread of the disease through the soil by preventing rains from washing the virus of this material to the roots of neighboring healthy plants.

He considers that coolies are very largely responsible for the wholesale spread of mosaic in a field by carrying infection on their hands from plant to plant during the usual field operations of topping, suckering, etc.

Van Bijlert strongly recommended the laying out of paths one meter wide around experimental plats, not only to afford an easy means of access to different portions of the experimental field, but also to serve as an important means of preventing the spread of mosaic.

Koning (15), in 1899, largely confirmed the conclusions of previous investigators in Europe. In extensive field experiments he proved conclusively that in ordinary topping operations the disease is readily transferred from diseased to healthy plants. In fact, he claimed that in this manner as high as 88 per cent. of the healthy plants became affected with the disease. He likewise claimed that in some instances kainit and Thomas slag tended to diminish the extent of the disease.

Woods (18), in 1899, made a study of various morphological and physiological differences between healthy and discolored tissues in leaves affected with the mosaic disease and later (29) brought out certain facts relative to the disease, namely, that it is infectious, that excision of affected parts does not check its development in other parts, that the virus is generally distributed throughout the plant, and that interlacing root systems do not necessarily communicate the disease from a mosaic plant to a healthy plant. Like Sturgis (17) he concluded that the disease was a physiological response to certain unfavorable conditions. Woods went considerably farther than Sturgis, since he sought to define the actual pathological changes induced in plants as a result of this malnutrition, which he thought must involve the normal enzym activity of the plants. With regard to this point Woods (29) makes himself clear as follows:

“The disease is not due to parasites of any kind, but is the



result of defective nutrition of the young dividing and rapidly growing cells, due to a lack of elaborated nitrogenous reserve food accompanied by an abnormal increase in activity of oxidizing enzymes in the diseased cells. The unusual activity of the enzyme prevents the proper elaboration of reserve food, so that a plant once diseased seldom recovers. On the decay of the roots, leaves, and stems of both healthy and diseased plants, the enzyme in question is liberated and remains active in the soil. The enzyme is very soluble in water and appears to pass readily through plant membranes. If young plants take it up in sufficient quantity to reach the terminal bud, they become diseased in the characteristic way."

In 1900 Heintzel (22), independently of Woods, came to the conclusion that oxidizing enzymes are responsible for the origin of the disease in tobacco plants.

Loew (24) in 1900 published briefly on the mosaic disease of tobacco. The observations of a number of practical growers in Connecticut were mentioned, but opinions were shown to be widely different as to the origin of the disease. Loew showed that an entire field may become diseased in one year, followed by a healthy crop the next season. He noted the sporadic occurrence of the disease. The oxidase and peroxidase content of healthy and mosaic plants was also compared. Many popular notions were cited which are too much at variance, however, to be regarded as established facts.

In 1900 Koning (23) gave a rather full discussion of his work with mosaic. Although careful examinations were made for microorganisms in the diseased tissues, all results were inconclusive.

Koning inoculated many healthy plants with soil solutions from fields where mosaic was prevalent. He was never able to produce mosaic in this way, and concluded that the virus could not exist long in the soil in an active condition. He stated that filtering the sap once through a Chamberland filter did not render it inert, but that when twice filtered its infectious nature was lost. He finally concluded that the virus of mosaic contained microorganisms too small to be retained by the pores of the filter, and that these possessed vegetative and spore-forms. Other conclu-



sions were that absolute alcohol killed the virus of mosaic, that filtered mosaic sap allowed to stand 3 months without preservatives retained its virulence. Koning states that he was unable to obtain mosaic in *Datura Stramonium*, *Hyoscyamus niger*, *Solanum tuberosum* or *Petunia nyctaginifolia* with the sap of mosaic tobacco.

Hunger (27) in 1902 and also in 1904 (40) reported the results of his observations and experiments with the mosaic disease in Sumatra. He established many important facts. Although many of his experiments gave somewhat contradictory results under different conditions, he found that transplanting several times did not necessarily cause the disease to develop, although he was inclined to believe that seedlings pulled from dry soil possibly contracted the disease more readily than those pulled from wet soil. Although Hunger states that topping tobacco plants at six weeks of age produced more disease than topping them at three weeks of age, he also found that topping 1,200 plants grown elsewhere did not produce the disease in a single plant, although these plants were topped at various ages.

Hunger also grew plants from large, medium, and small seed, and concluded that medium-sized seed produced the highest percentage of mosaic plants. The large and small seed produced about the same percentage of mosaic plants. It is difficult to understand why size of seed, however, should bear any relation to the occurrence of this disease.

Hunger found that cuttings from diseased plants, whether rooted in soil or grafted upon healthy stocks, remained diseased. Many of his healthy cuttings also became diseased. He states that the trouble appeared to have no relation to fertilizer treatment. He was inclined to believe that the occurrence of the disease might be associated with extremely hot days and heavy rains.

It is interesting to note that Hunger regarded the mosaic disease as a physiological malady. He refused (33) to accept Wood's theory (18), however, that the disease was associated with the inhibitory action of oxidase and peroxidase upon diastatic action, since he maintained that these oxidizing enzymes did not inhibit the conversion of starch into sugar. He also maintained that these enzymes could not diffuse, so that plants would not be able to take them from the soil through their roots.



Hunger (36) also, in 1903, reported the results of various observations and experiments made in Deli, Sumatra, to determine how the mosaic disease was spread in a tobacco field. He showed that coolies in the operation of searching for caterpillars readily communicated the disease from diseased to healthy plants throughout the field. He stated that by touching a diseased plant first and then healthy plants "all touched plants without exception became diseased." He concludes that careless, inexperienced, and short-sighted coolies are largely responsible for the spread of the disease in a field. In this respect he confirmed the topping experiments reported previously by Koning (15).

Hunger again published, in 1903 (35), an interesting paper showing that the spread of mosaic in the Deli, Sumatra, fields is very largely due to coolies employed to search for tobacco worms. Very careful experiments were made with plats and rows, in such a way that a mosaic plant was the first plant touched. Beginning with this, only alternate plants, 3, 5, 7, 9, etc., were searched for worms. The plants represented by the even numbers were intended for controls and remained untouched. In all instances, practically every plant in the series beginning with the mosaic plant sooner or later became mosaic. At the same time, the controls, with few exceptions, remained healthy.

Hunger states that the less experienced coolies often become notorious as mosaic carriers. Coolies with this reputation are frequently troubled with defective vision as well. In the operation of worming, such coolies find it necessary to pause before each plant to determine if worms are present, and in the search the young, central leaves are handled more or less. On the other hand, the skilled, keen-eyed coolies pass rapidly from plant to plant without finding it necessary to touch the leaves in order to learn if a worm is present. Should a worm be seen it is skillfully removed. Mosaic infection under such conditions is reduced to the minimum through the operation of worming.

An instance is given of two coolies, who, from year to year, spread mosaic in all the fields they wormed. A medical examination indicated that both were very near-sighted.

Hunger (41), in 1904, also published the results of his experiments with the retransplanting of tobacco plants, before finally



transferring them to the field. This method, it seems, has been put into operation more or less generally at Deli. Experiments were made to determine what influence this practice had upon the subsequent occurrence of mosaic. The procedure was as follows: A mother seed bed *A* was prepared and sowed Feb. 17. This seed germinated Feb. 25. On the 14th of March, just 25 days from the sowing of the seed, 750 plants were transferred from *A* to bed *B* and set  $3 \times 2\frac{1}{4}$  inches apart. March 22, 500 plants were removed from bed *B* to bed *C* and set  $4\frac{1}{2} \times 2\frac{1}{4}$  inches apart. On March 29, 250 plants were removed from bed *C* to bed *D* and set  $9 \times 2\frac{1}{4}$  inches apart. All were fertilized alike.

On April 2, 250 plants from beds *A* and *B* were transferred to the field. On April 8, 250 plants from bed *C*, and on April 11, 250 plants from bed *D* were set in the field.

Topping was omitted and in every way the plants were similarly treated.

The results were as follows: Plants from the mother bed *A* were healthy and reached a height of about  $2\frac{1}{4}$  meters. Plants from bed *B* were not as tall and were more or less mosaic. Plants from bed *C* were very inferior in every way and badly mosaic in most instances. Plants from bed *D* were not over  $\frac{1}{2}$  meter in height and not a plant escaped mosaic. It is interesting to note that mosaic had appeared in beds *B*, *C* and *D* at the time of final transplanting to the field.

From these results Hunger concludes that these additional transplantings have nothing to recommend them, since they seriously interfere with the normal growth of the plants and likewise lead to the development of mosaic.

In 1904 Bouygues and Perreau (38) stated that they obtained, by selection, strains of tobacco resistant to the disease called by them "la nielle." The authors refer to a previous account of the disease and its symptoms by Bouygues. His careful description of the diseased plants makes it apparent that la nielle does not refer to true mosaic at all, but to some form of leaf-spot or rust.

In the same year F. Pirazzoli (43) published an interesting review of the literature of mosaic. She added somewhat to the confusion already existing between true mosaic and various leaf-spot diseases, since she, like Comes, called true mosaic, "Mal della bolla" and Pockenkrankheit, "mal del mosaico."



In 1904 Selby (44) reported briefly his results with the mosaic disease of tobacco in Ohio. He reviewed some of the more important practical experiments conducted by previous investigations and confirmed these results in some of his own experiments. He repeated a number of simple inoculation experiments with the virus of mosaic plants, and obtained symptoms of the disease in healthy plants after an incubation period of 9 to 12 days. He could see no difference in plants inoculated near the base and those inoculated in the tender portion. As a rule, the new growth alone showed the disease. He proved that a purely physiological chlorosis known as "yellow French" was not communicable to healthy plants by inoculation and that seed of mosaic plants produced healthy plants. The disease could not be transferred to healthy plants through the blossoms by inoculating these with the nectar of diseased plants. Contact experiments conducted with diseased and healthy plants showed an increase of 68.6 per cent. of disease in the healthy plants. In surrounding control plats the natural increase of the disease during this period was less than 3 per cent. These experiments were a further confirmation of similar experiments previously conducted abroad by Hunger and Koning.

Field observations in the Germantown district in 1903 and 1904 gave interesting results with respect to the occurrence of the mosaic disease. Considering 12 farms in the vicinity of Germantown, the percentage of diseased plants ranged from less than 1 per cent. to 43.5 per cent. On the station farm great variation was found in the prevalence of the disease in individual rows, some rows being entirely free, others showing 56 per cent. of the plants affected. Fertilized and unfertilized plats showed no difference. Preventive measures are recommended which in the main consist of the prompt removal of all diseased plants, both in the seed bed and in the field. Selby states that such diseased plants if allowed to remain become a menace to all healthy plants through the practical operations of worming, topping, suckering, etc.

In 1905 Hunger (46) further discussed the mosaic disease of tobacco. He carefully reviews the various theories of the disease, and gives a full discussion covering "Pockenkrankheit," which for



a long time was confused with "Mosaikkrankheit." Although he believed that the mosaic disease was a physiological disturbance arising from unfavorable conditions, Hunger held that an unorganized ferment of the toxophore group of Oppenheimer, rather than oxidizing enzymes, was responsible for the appearance of the disease.

In 1905 Jensen (47) published a paper in which he mentioned the different means by which the occurrence of mosaic could be lessened according to the views of various investigators, i. e., Mayer, Raciborski, Woods, Sturgis, Koning, Hunger, and others. He stated that since these workers regarded the soil in some way responsible for the origin of the disease, their attention was directed mainly to the treatment of the soil of the seed bed and the field. For the seed bed, sterilization, soil-removal, and the use of certain kinds of manures were generally recommended. For the prevention of the disease in the field, certain fertilizers were advised. Sturgis, in Connecticut, was inclined to believe that the use of shade lessened the occurrence of mosaic, Woods also considered that injury of any sort predisposed the young plants to the disease. For this reason he considered that root injury must be guarded against during transplanting, in order to reduce the amount of the disease in the field.

Jensen first reviews somewhat critically the methods employed by Sturgis, Iwanowski, and Hunger to show that the seed of mosaic mother plants produce healthy progeny. He describes in detail the results of special selection experiments which he carried on in Java with mosaic and healthy plants. He made careful comparison of the progeny of one self-fertilized healthy plant as a control and four mosaic plants grown side by side under identically the same conditions from the seed bed to the field. The percentage of mosaic plants occurring in each progeny was separately determined. Without exception mosaic plants appeared in every progeny in varying amounts.

From these experiments Jensen is inclined to believe that the progenies of the mosaic plants show greater susceptibility to mosaic than the progeny of the healthy plants, and that the careful selection of resistant races will prove to be a practical method of controlling the disease. However, from the amount of



mosaic shown by the single control progeny it seems fair to ask if Jensen's experiments have been extended sufficiently to warrant final generalizations as to the greater resistance of progenies of healthy over mosaic parents.

Delacroix (49), in 1906, reviewed rather fully previous investigations of the mosaic disease of tobacco.

As a means of preventing the disease, he advises making seed beds in new soil which has not previously grown tobacco. He also recommends crop rotation in the field, and cautions against the use of insufficiently rotted organic manure, and the choice of soils naturally too wet.

At the same time, Delacroix discusses a leaf-spot disease which he calls "la maladie des taches blanches" to distinguish it from a spot disease which he has previously described as "rouille blanche." He is convinced that the disease termed "mal del mosaico" by Comes and F. Pirazzoli is identical with his "maladie des taches blanches." Delacroix is not quite certain as to the relationship of "rouille blanche" and the "maladie des taches blanches."

Baur (50), in 1906, mentions the mosaic disease of tobacco in connection with a discussion of infectious chlorosis of the Malvaceae. He is inclined to believe that they are not essentially different in some respects. It is mentioned that the former is, however, transferred by other means than by grafting, and that the virus of mosaic is more stable, since the principle of infectious chlorosis can exist only within the living cells of the Malvaceae.

In 1907 Hunger (51) expressed his views concerning the effects of shade as a preventive of mosaic in tobacco. In a test of two plots with Deli tobacco, one shaded, and another unshaded as a control, he states that only 8 per cent of the plants became mosaic under shade, while 44 per cent became mosaic in the sun. He considers this a striking confirmation of Sturgis's results in Connecticut.

In explanation of these results, Hunger considers that shade so regulates the various physiological activities of the plant that the phytotoxin of mosaic is not generated. He contends that mosaic arises only when unfavorable external conditions stimulate the secretion of this specific toxin, which once formed has the



peculiar property of engendering a similar diffusible toxin within the cells. In some respects Hunger's toxin theory is not far removed from Beijerinck's "contagium vivum fluidum" theory.

Hunger remarks that the Deli-Sumatra tobacco, through intensive breeding, has become especially subject to mosaic. He mentions that soils most favorable to the production of the best type of Sumatra tobacco are also especially favorable localities for mosaic, while on "paja-soil" which produces the most inferior Deli wrappers, mosaic is almost unknown.

In 1908 Clinton (53), working in Connecticut, established an important fact concerning the mosaic disease. By artificial inoculation he showed conclusively that the mosaic disease of tobacco was communicable to healthy tomato plants and vice versa. This seems to be the first actual proof that this disease of tobacco is infectious to plants of other solanaceous genera.

Lodewijks (56), in 1910, reported his investigations concerning the effects of different kinds of light upon the development of the mosaic disease. By keeping the upper diseased portions of mosaic plants covered while at the same time the lower, healthy-appearing leaves were exposed, Lodewijks claims to have obtained remarkable results. Under these conditions he claims to have found that diffused light checked the disease, red light decreased it, and blue light completely cured plants of the malady. It was his opinion that an antiviral or antitoxin was thus formed in the lower, healthy leaves which destroyed or rendered inert the virus of the disease. These results are so radical that further investigation seems necessary in order to understand their meaning more fully.

In 1910 Westerdijk (57) published an account of the mosaic disease of tomato. She concludes that this disease is infectious to tomatoes, but that it is not communicable to tobacco. She likewise believes that the development of the disease is greatly dependent upon the intensity of light, strong sunlight increasing the intensity of the symptoms. In striking contrast to the mosaic disease of tobacco, she claims that the mosaic disease of tomato is carried to the next generation through seed produced by mosaic plants. Westerdijk stated that she was unable to communicate the mosaic disease of tobacco to healthy tomato plants by artificial



inoculation. Her results on this point, however, are somewhat open to question, since from the description of the plants one can not be sure that she worked with the true mosaic disease of tobacco.

Jensen (63) (1903-1911) reports his investigation of the mosaic disease of tobacco in the Dutch East Indies. A number of mosaic-free plants were selected in the field, and the progenies of these kept separate each year. By continuous selection of mosaic-free plants within these lines from 1903 to 1907, Jensen states that there was a very noticeable increase each year in the percentage of mosaic-free plants. He was led to believe that careful selection afforded an efficient means of decreasing mosaic by developing strains naturally resistant to mosaic infection.

Jensen describes and gives an illustration of a most remarkable tobacco plant found in 1899. With the exception of a single basal leaf which had developed to normal size, the growth of the leaves was limited to the development of the midribs alone. The plant was selfed but the entire progeny grown in 1910 was normal. It is very probable that this abnormal plant was an exceptionally severe form of mosaic.

Experiments were carried on to determine if excessive quantities of plant food had any influence on the susceptibility of plants to mosaic. It was found, however, that mosaic occurred quite as generally in the fertilized as in the non-fertilized plants.

Jensen (1911) states that attempts to develop mosaic-resistant lines from plants escaping mosaic infection in the field resulted in failure. At Kebon-Aroem, where mosaic is very prevalent, 93 healthy plants selected from a badly mosaic field were inoculated with the filtered sap of mosaic plants. Not a single plant escaped infection. The conclusion was finally reached that mosaic-free plants selected in a field, must be inoculated with the virus of mosaic before their resistance to mosaic can be determined.

In 1912 the writer (59) published briefly in *Science* additional facts concerning the mosaic disease of tobacco. It was shown that the disease is communicable to practically all genera of the solanaceous family, that the disease is dependent upon specific infection, and that simply cutting back plants does not produce the malady. It was also shown that particular kinds of aphides may be active disseminators of the disease.



In 1912 Egiz (60) in Russia published a paper concerning the growing of tobacco in southern and middle Russia. He mentions briefly the more important diseases affecting the tobacco plant in this region, i. e., rust (Pockenkrankheit), mosaic, and other diseases. He added nothing beyond what is already known concerning the mosaic disease of tobacco. Egiz considered that soil and climatic factors of one sort or another were responsible for the disease, i. e., soils too moist, soft rather than hard soils, hot sunshine together with great humidity, etc. As a means of preventing the occurrence and spread of the disease he recommended burning all diseased plants, keeping soils in the best tilth, the application of good quantities of lime, and the saving of seed from healthy plants. Egiz also mentioned another disease somewhat similar to mosaic in appearance which is not infectious and results from injuries to the roots from one cause or another. The leaves become marbled or variegated.

Chapman (61), in 1913, published the results of observations and experiments with the mosaic disease of tobacco and tomatoes. He pronounced the disease a purely physiological one, and contended that it was not of fungous or bacterial origin. He did not consider that a specialized virus was responsible for the occurrence of the disease. He regarded the theory of antagonistic enzyme action previously advanced by Woods as sufficient to explain the primary origin of the disease. Although Chapman believed that improper sterilization of infected seed beds actually increased the occurrence of mosaic in the seedlings, it is difficult to offer a satisfactory explanation for such results.

Since the time of Mayer the failure to distinguish between the true mosaic disease and various other diseased appearances has led to a literature filled with confusion and contradiction. Throughout Europe many investigators at first regarded a spot disease, "Pockenkrankheit," as a later or final phase in the development of the true mosaic disease or "Mosaikkrankheit." Others have contended that these appearances represent two distinct diseases. Throughout France especially, various leaf-spot diseases were described as the true mosaic of Mayer. Beijerinck (12) applies the term "la nielle" to the true mosaic disease. Perreau (38) speaks of "la nielle "ou" Mosaikkrankheit" and has in mind a



rust or spot disease. Delacroix (45) later designates true mosaic as "la nielle vrai."\*

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INDEX TO THE LITERATURE OF MOSAIC

The following is a list, arranged in time sequence, of the more important contributions referring to the mosaic disease of tobacco or mentioned in connection therewith.

1. 1885. **Mayer, Adolf.** Over de in Nederland dikwijk voorkomende Mozaiekziekte der Tabak. Landb. Tijdschr.
2. 1886. ———. Über die Mosaikkrankheit des Tabaks. Landwirtschaft. Versuchs-Stat. 32: 450-467. *pl.* 3. Abstract by Erwin F. Smith in Jour. Myc. 7: 382-385. 1894.
3. 1888. ———. Heilung der Mosaikkrankheit des Tabaks. Landwirtschaft. Versuchs-Stat. 35: 339-340.
4. 1890. **Iwanowski, D., & Polowzoff, W.** Rjabucha, bolesn Tabaka, eja pritschini i srelstwa borbi s neju. (Die Pockenkrankheit der Tabaksflanze.) 23 p. Mém. Acad. Imp. Sci. St. Pétersbourg, VII. 37.
5. 1890. **Linhart, György, & Mezey, Gyula.** A dohány mozaikbetegsége. Mezőgazdasági Szemle, p. 1-10.
6. 1892. **Iwanowski, D.** Über die Mosaikkrankheit der Tabakspflanze. Bull. Acad. Imp. Sci. St. Pétersbourg II. 3: 67-70.
7. 1892. ———. Über zwei Krankheiten der Tabakspflanze. Land- und Forstwirtschaft (Russisch). Abstract in Beih. Bot. Centralb. 3: 266-268. 1893.
8. 1894. **Prillieux, E. E., & Delacroix, Georges.** Maladies bacillaires de divers végétaux. Compt. Rend. Acad. Sci. Paris 118: 668-671.

These writers described a bacterial disease which they thought was true mosaic, but which later was shown to be "rouille blanche" (white rust).

\* Terms used to designate true mosaic:

*America:* Mosaic; calico; gray-top; mottled-top; mottling; foxy tobacco; brindle; mongrel; chlorosis; walloon; frenching.

*France:* La mosaïque vrai; la nielle vrai (Delacroix); la nielle (Delacroix) (Beijerinck).

*Italy:* Male della bolla.

*Netherlands:* Mozaiek-ziekte; vlek-ziekte; wit-kop.

*Germany:* Mosaikkrankheit; Flecken-krankheit.

*Brazil (Portuguese):* A molestia de "mosaico."



9. 1897. **Marchal, Émile.** La mosaïque du tabac. *Rev. Myc.* **19**: 13, 14.  
 Marchal appears to have studied "la rouille blanche" rather than true mosaic.
10. 1898. **Beijerinck, M. W.** Ueber ein Contagium vivum fluidum als Ursache der Fleckenkrankheit der Tabaksblätter. *Verhandel. Kon. Akad. Wetensch. Amsterdam II.* **6<sup>5</sup>**: 1-22. *pl.* 1, 2. Abstract in *Centralb. Bakt. Zweite Abt.* **5**: 27-33. 1899.
11. 1899. ————. Bemerkung zu dem Aufsatz des Herrn Iwanowsky über die Mosaikkkrankheit der Tabakspflanze. *Centralb. Bakt. Zweite Abt.* **5**: 310, 311.
12. 1899. ————. De l'existence d'un principe contagieux vivant fluide, agent de la nielle des feuilles de tabac. *Arch. Néerland. Sci. II.* **3**: 164-186. *pl.* 5, 6.
13. 1899. **Breda de Haan, J. van.** Voorloopige mededeelingen over het Peh-Sem of de mozaïek-ziekte in de tabak te Deli. *Teysmannia*, **9**: 567-584.
14. 1899. **Iwanowski, D.** Über die Mosaikkkrankheit des Tabakspflanze. *Centralb. Bakt. Zweite Abt.* **5**: 250-254. [Illust.]
15. 1899. **Koning, C. J.** Die Flecken- oder Mosaikkkrankheit des holländischen Tabaks. *Zeits. Pflanzenkrank.* **9**: 65-80. *f.* 1, 2; *pl.* 2.
16. 1899. **Sturgis, W. C.** Preliminary notes on two diseases of tobacco. *Ann. Rep. Connecticut Agr. Exp. Sta.* **22**: 242-260.
17. 1899. ————. On the effects, on tobacco, of shading and the application of lime. *Ann. Rep. Connecticut Agr. Exp. Sta.* **23**: 252-261.
18. 1899. **Woods, A. F.** The destruction of chlorophyll by oxidizing enzymes. *Centralb. Bakt. Zweite Abt.* **5**: 745-754.
19. 1899. **Raciborski, M.** Verslag omtrent den staat van 'Slands Plantentuin te Buitenzorg over het jaar 1899. 73-78; 108-110.
20. 1899. **Bijlert, A. van.** Opmerking, omtrent de verbreiding van een vlekziekte. *Mededeel. 'Slands Plantentuin* **43**: 49-52.
21. 1900. **Goutière, J. F.** Sur quelques maladies du tabac. *Jour. d'Agr. Prat.* **64<sup>1</sup>**: 569-571.
22. 1900. **Heintzel, Kurt.** Contagiöse Pflanzenkrankheiten ohne Microben, mit besonderer Berücksichtigung der Mo-



saikkrankheit der Tabaksblätter. Erlangen, 46 p.,  
1 pl. (Inaugural-Dissertation.)

23. 1900. **Koning, C. J.** Der Tabak: Die Flecken- oder Mosaik-  
krankheit des holländischen Tabaks. Studien über  
seine Kultur und Biologie. Amsterdam. pp. 71-86,  
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24. 1900. **Loew, Oscar.** Remarks on the mosaic disease of the  
tobacco plant. U. S. Dept. Agr. Rep. 65: 24-27.
25. 1900. **Woods, A. F.** Inhibiting action of oxidase upon diastase.  
Science, II. 11: 17-19.
26. 1901. **Iwanowski, D.** Über die Mosaikkrankheit der Tabaks-  
pflanze. Centralb. Bakt. Zweite Abt. 7: 148.
27. 1902. **Hunger, F. W. T.** De mozaiek-ziekte bij Deli-tabak.  
Deel I. Verslag van de op Deli met betrekking tot de  
mozaiek-ziekte genomen proeven in de jaren 1901-1902.  
Mededeel. 'Slands Plantentuin 63: 1-104.
28. 1902. **Iwanowski, D.** Die Mosaik- und Pockenkrankheit der  
Tabakspflanzen. Zeits. Pflanzenkrank. 12: 202, 203.
29. 1902. **Woods, A. F.** Observations on the mosaic disease of  
tobacco. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 18:  
1-24. *pl.* 1-6.
30. 1903. **Bouygues, H.** Sur la nielle des feuilles du tabac. Compt.  
Rend. Acad. Sci. Paris 137: 1303-1305.

A leaf-spot or rust disease is described, rather than the mosaic disease.

31. 1903. **Hunger, F. W. T.** Physiologische onderzoekingen over  
Deli-tabak. Mededeel. 'Slands Plantentuin 66, Hoof-  
dstuk 5.
32. 1903. **Roux, E.** Sur les microbes dits invisible. Bull. Inst.  
Pasteur, Revues et Analyses, 1, No. 1.

Roux considers it probable that organisms too small to be revealed by the  
microscope are responsible for mosaic.

33. 1903. **Hunger, F. W. T.** Bemerkung zur Wood'schen Theorie  
über die Mosaikkrankheit des Tabaks. Bull. Inst.  
Bot. Buitenzorg 17: 1-9.
34. 1903. ————. Een voorloopige verklaring omtrent het  
veelvuldig optreden der mozaiek-ziekte bij Sumatra-  
tabak. Tijdschrift voor Nijverheid en Landbouw in  
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35. 1903. ————. Het Rupsen-zoeken bij tabak in verband  
met het later optreden der mozaiek-ziekte. Teys-  
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37. 1903. **Iwanowski, D.** Über die Mosaikkrankheit der Tabakspflanze. *Zeits. Pflanzenkrank.* 13: 1-41. *pl.* 1-3.
38. 1904. **Bouygues H., & Perreau, —.** Contribution à l'étude de la nielle des feuilles de tabac. *Compt. Rend. Acad. Sci. Paris* 139: 309-310.

These investigators claim to have obtained by selection strains of tobacco resistant to the disease called by them "la nielle." This disease appears to be a rust of some sort, although it is mentioned in an abstract in the Experiment Station Record, U. S. Department of Agriculture, 16: 677, 1905, as the mosaic disease of tobacco.

39. 1904. **Hunger, F. W. T.** Over den aard der besmettelijkheid der mozaiek-ziekte bij de tabaksplant. *Handelingen, Achtste Vlaamsch Natuuren Geneeskundig Congres gehouden te Antwerpen op 24<sup>en</sup> en 25<sup>en</sup> September, afl. 3, p. 45-50.*
40. 1904. ————. Die Verbreitung der Mozaikkrankheit infolge der Behandlung des Tabaks. *Centralb. Bakt. Zweite Abt.* 11: 405-408.
41. 1904. ————. Invloed van het verspenen van tabaksbibit. *Korte berichten uit 's Lands Plantentuin. Teysmannia* 15: 58-64.
42. 1904. **d'Utra, Gustavo.** A molestia de "Mosaico" do fumo. *Boletim da Agricultura, São Paulo V. 2: 51-71.*

d'Utra merely reviews the work of a number of investigators connected with the mosaic disease of tobacco. His statement that the disease rarely ever occurs in successive years is of considerable interest.

43. 1904. **Pirazzoli, Francesca.** Male della bolla e del mosaico. *Bolletino Technico della Coltivazione dei Tabacchi* 3<sup>4</sup>: 1-41. *pl.* 1.
44. 1904. **Selby, A. D.** Tobacco diseases and tobacco breeding. *Ohio Agr. Exp. Sta. Bull.* 156: 87-114. *pl.* 1-8 + *f.* 1-3.
45. 1905. **Delacroix, Georges.** La rouille blanche du tabac et la nielle ou maladie de la mosaïque. *Compt. Rend. Acad. Sci. Paris* 140: 678-680.

Distinction is made here between "la rouille blanche" (white rust), a bacterial disease which Delacroix at first described as true mosaic, and "la nielle vrai" (true mosaic). He names the bacillus considered by him responsible for "la rouille blanche."



46. 1905. **Hunger, F. W. T.** Untersuchungen und Betrachtungen über die Mosaikkrankheit der Tabakspflanze. Zeits. Pflanzenkrank. **15**: 257-311.
47. 1905. **Jensen, Hjalmar.** Über die Bekämpfung der Mosaikkrankheit der Tabakpflanze. Centralb. Bakt. Zweite Abt. **15**: 440-445.
48. 1905. **Hunger, F. W. T.** Neue Theorie zur Ätiologie der Mosaikkrankheit des Tabaks. Ber. Deuts. Bot. Ges. **23**: 415-418.
49. 1906. **Delacroix, Georges.** La nielle du tabac et la "maladie des taches blanches." Ann. Inst. Nat. Agron. II. **5**: 158-205.
50. 1906. **Baur, E.** Über die infektiöse Chlorose der Malvaceen. Sitzungsber. Königl. Preuss. Akad. Wiss. 1906: 11-29.
51. 1907. **Hunger, F. W. T.** Beschaduwing als prophylaxis tegen de mozaiek-ziekte der tabak. Mededeel. Depart. Landbouw. **3**: 62-68.
52. 1909. **Sorauer, Paul.** Die Mosaikkrankheit des Tabaks. Handbuch der Pflanzenkrankheiten **1**: 678-683.

Mosaic is classed as a non-parasitic, enzymatic disease. The work of Bouygues and Perreau is cited as an example of what selection for resistance to mosaic can accomplish. The fact seems to have been overlooked that Bouygues and Perreau worked with a rust disease and not true mosaic.

53. 1909. **Clinton, G. P.** Notes on fungous diseases, etc., for 1908. Connecticut Agr. Exp. Sta. Bien. Rep. **1907-1908**: 857-858. *pl. 66, f. b.*
54. 1909. **Perreau, —.** Note sur la nielle des tabacs. Bull. Soc. Bot. France **56**: LIII-LV.

Perreau refers to the rust or leaf-spot disease previously mentioned by him and Bouygues in 1904. Perreau stated that the disease appeared on land which had not been grown to tobacco for 30 years. An abstract of these results is given under the heading "Notes on the mosaic disease of tobacco," in the Experiment Station Record, U. S. Department of Agriculture, **23**: 649. 1910.

55. 1910. **Hinson, W. M., & Jenkins, E. H.** The management of tobacco seed beds. Connecticut Agr. Exp. Sta. Bull. **166**: 1-11. *f. 1.*

These authors state that there is no evidence to show that infection arises from the stems plowed into the field.

56. 1910. **Lodewijks, J. A., Jr.** Zur Mosaikkrankheit des Tabaks. Rec. Trav. Néerland. **7**: 107-129. Abstract in Bot. Centralb. **114**: 518.



57. 1910. **Westerdijk, Johanna.** Die Mosaikkrankheit der Tomaten. Amsterdam, 19 p., 3 pl. (Mededeel. Phytopath. Lab. "Wille Commelin Scholten" Amsterdam, 1.)
58. 1911. **Russell, H. L.** Tomato breeding experiments. Wisconsin Agr. Exp. Sta. Bull. 218: 20.

Here it is claimed that the peach and cherry types are naturally resistant to the mosaic disease, and that crossing these with Earliana have given strains resistant to the disease.

59. 1912. **Allard, H. A.** The mosaic disease of tobacco. *Science* II. 36: 875, 876.
60. 1912. **Egiz, S. A.** Tabakovodstvo. Glavnoe Upravlenie Zemledeliia i Zemleustroistva, Department Zemledeliia, Obshchedostynnyiia Soobshcheniia sel'skokhoziaistvennykh Uchrezhdenii i Spetsialistov po Sel'skokhoziaistvennoi Chasti, (Russia), no. 9.
61. 1913. **Chapman, G. H.** Mosaic and allied diseases, with special reference to tobacco and tomatoes. Ann. Rep. Massachusetts Agr. Exp. Sta. 25: 94-104.
62. 1913. **Melchers, Leo E.** The mosaic disease of the tomato and related plants. *Ohio Naturalist* 13: 149-173. *pl.* 7, 8 + *f. 1.* 1913.
63. 1903-1911. **Jensen, Hjalmar.** Mozaiek-ziekte. Medeel. Profsta. Vorsten-Landsche Tabak. No. 5, 1913.
64. 1914. **Allard, H. A.** The mosaic disease of tobacco. U. S. Dept. Agr. Bull. 40: 1-33. *pl.* 1-5. Ja 1914.



Phytogeographical notes on the Rocky Mountain region  
III. Formations in the alpine zone

P. A. RYDBERG

As the writer is no ecologist and has dealt very little with plant societies, he knows that this paper will scarcely stand muster before experts in that line. The notes are mostly taken down from memory and casual observations made while collecting with taxonomy wholly in view. They must therefore be in many respects imperfect and in some cases faulty. As I have occasionally criticized ecologists and phytogeographers, even severely, for their work, I should expect criticism when I myself enter their field, but right here I wish to say that I not only expect, but rather wish, somebody to point out my errors or shortcomings, so that the truth may be had. My only excuse for writing on "Formations" is that very little has been published in this line on the Rocky Mountain region, and in every case it has been only small local regions that have been treated. I know that Professor Clements has been working for years on the ecology of the Pikes Peak region and when his book is out, I expect to see an expert treatise on the subject; but until then let us amateurs scribble down and publish our notes, and probably they may be of some value to the professional ecologists, and, in the meantime, of general interest to the plant-lovers.

Clements in his little article "Formation and Succession Herbaria"\* has given the best list of plants, arranged according to regions, formations, and successions, ever published from the Rocky Mountain region. The value of this list is increased by the fact that he has distributed a collection of exsiccatae illustrating it. Of course, his paper treats only of the region of Pikes Peak, Colorado. He assigns the following formations to the alpine region:

Alpine meadow formation  
Alpine bog formation

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\* University [Nebraska] Studies 4: 329-355. 1904.



Alpine lake formation  
Alpine mat formation  
Alpine rock-field formation

While my observations at other places in the Rockies agree essentially in most respects with Professor Clements' arrangement, it cannot be applied without modification to all localities in the Rockies, not even to all in Colorado. When the whole of the southern Rockies is considered, some modifications must be made, and if the alpine region of the northern Rockies is included, still more adjustment is needed. Here there are found formations of ericaceous plants, consisting of undershrubs, if not, as in the Alps, of shrubs. Perhaps I lay too much stress upon the moisture in the ground and soil, and therefore would be inclined to subdivide Professor Clements' alpine meadow formation.

The Rocky Mountains have received their name from the numerous loose rocks that cover their tops and sides. In naming plants from the Rocky Mountains, the specific name usually used has been *scopulorum*. This is really a misnomer, for it is not from *scopulum* (a projecting cliff) but from *saxum* (the loose rock), that the Rockies were named. When the mountain disintegrates it breaks up into large blocks. These in the Rockies cover large fields, or, as they are mostly on the slopes, they are often more or less in motion and are usually known as "rock-slides." The first form of vegetation which appears on a newly formed rock-slide is, of course, lichens. Whenever there has been deposited a little humus between the rocks a few flowering plants appear, mostly perennials, with strong root systems or with strong rhizomes. Thus arises the first formation, the

#### ROCK-SLIDE FORMATION

If the rocks disintegrate still more, they become broken up into smaller pieces and more humus is added and there arises a gravel-field. If the disintegrated portion is rather thin, as it usually is on the top of the peaks and along the ridges, the formation is a xerophytic one, as little of the water from the melting snow is retained. So we have our second formation, which corresponds to Dr. Clements' alpine mat formation. This may be called the



## MOUNTAIN CREST FORMATION

If the gravel field or rock field is situated on the sloping mountain side, either under a snowdrift or along the course of the drainage, in other words where the moisture is greater and where more humus has a chance to gather, we have our third formation, which I shall call in lack of a better word the

## MOUNTAIN SEEP FORMATION

This was included by Clements in the mountain meadow. While the mountain seeps have many plants in common with the meadows, there are found others wholly characteristic of these seeps, as for instance certain species of the saxifrage family and several willows. Where the ground is less sloping and the humus has had chance to gather still more, there is found the

## ALPINE MEADOW FORMATION

If the drainage is imperfect and the water becomes stagnant, the next formation occurs, the

## ALPINE BOG FORMATION

or if deeper, the

## ALPINE LAKE OR POND FORMATION

To this can also be added special formations. There are certain plants that grow only in the crevices of exposed cliffs. Hence, the

## CLIFF FORMATION

Another is found only below and around the melting snowdrifts, the

## SNOW-DRIFT FORMATION

Of these the rock-slides and mountain crest formations are decidedly xerophytic; the cliff formation mostly mesophytic but often xerophytic, the meadow and mountain seep formations mesophytic or the latter usually hydrophytic; of course, the bog and lake formations are hydrophytic.

## I. ALPINE MOUNTAIN CRESTS

I shall begin with this formation, as it is perhaps the most characteristic of the alpine formations. The plants are nearly all



very low, only a few inches high, but what they lack in size they make up in the coloration of their flowers. It is strange that the alpine plants should have such bright colors, when insects are comparatively rather scarce and the plants have all the facilities of wind-pollination. Most of the plants of this formation grow in clumps or mats, even the grasses and sedges growing there are more or less tufted.

One of the most common and, at the same time, conspicuous plants of this formation is *Alsinoopsis obtusiloba*. It is not conspicuous on account of its size or the beauty of its flowers, but on account of its mode of growth. It is found nearly everywhere in the most exposed places, in the crevices of the rocks or between the boulders, wherever the roots can find a foothold, even where there is scarcely a trace of soil. It grows in tussocks or mats from 1 to 12 inches in diameter, the stem lying flat on the rocks and only the peduncles rising 1-2 inches above them. *Draba oligosperma*, *D. andina*, and *D. densiflora* have a similar habit but grow in smaller mats and are more frequent between smaller stones and gravel on the ridges. In similar situations are found larger mats of *Dryas octopetala* and (in the northern Rockies) *D. Drummondii*, and smaller colonies of *Potentilla quinquefolia* and *Phlox caespitosa*. The latter is rather rare in the southern Rockies where its place is taken by a closely related species, *Phlox condensata*. *Silene acaulis*, the moss campion, resembles *Alsinoopsis obtusiloba* in habit, but prefers places with more humus. The vegetation of the bare rocks consists mostly of the above mentioned *Alsinoopsis* and less frequently *Sedum stenopetalum* and scattered patches of *Draba* and *Phlox*.

Two of the most widely distributed plants growing in gravelly places on the tops of the mountains are *Erigeron simplex* and *E. multifidus*. The following three species, closely related to the latter, are found in similar situations, but *E. trifidus* is more limited to the northern portion, extending even into the Arctics. *E. pinnatisectus* is confined to the southern Rockies and the original *E. compositus* to the northwest. In similar situations we find also *Smelowskia americana* and *Trifolium dasyphyllum*; in the southern Rockies also *Androsace carinata*, *Thlaspi coloradense*, *T. purpurascens*, and *Eritrichium argenteum*; and in the northern Rockies,



*Douglasia montana* and *Eritrichium elongatum*. *Acomastylis* (*Sieversia*) *turbinata* is found in a depauperate form on the crests and in better development in the meadows. The beautiful paint-brushes, *Castilleja occidentalis* and *C. Haydeni* (southern Rockies), are found mostly on the slopes, connecting the crests with the meadows.

Of the grasses, *Poa rupicola*, *P. Pattersonii*, *P. Lettermanni*, *Festuca brachyphylla*, *F. saximontana*, *F. supina*, and *Agropyron Scribneri* are mostly limited to the crest themselves, while *Trisetum subspicatum*, *Deschampsia curtifolia*, *Agropyron andinum*, and *A. latiglume* frequent the slopes or even run down into the meadows.

The following plants are the most common and most generally distributed alpine xerophytes belonging to this formation:

* <i>Calamagrostis purpurascens</i>	* <i>Heuchera parvifolia</i>
<i>Trisetum subspicatum</i>	<i>Potentilla quinquefolia</i>
<i>Deschampsia curtifolia</i>	<i>Acomastylis turbinata</i>
<i>Poa rupicola</i>	* <i>Dasiphora fruticosa</i>
* <i>Poa crocata</i>	<i>Dryas octopetala</i>
<i>Festuca brachyphylla</i>	* <i>Dasystephana affinis</i>
<i>Festuca saximontana</i>	<i>Trifolium dasyphyllum</i>
<i>Agropyron Scribneri</i>	* <i>Phlox caespitosa</i>
<i>Oreobroma pygmaea</i>	<i>Castilleja occidentalis</i>
<i>Alsinopsis obtusiloba</i>	<i>Antennaria media</i>
<i>Silene acaulis</i>	* <i>Antennaria aprica</i>
<i>Draba oligosperma</i>	* <i>Senecio Purshianus</i>
<i>Draba andina</i>	<i>Erigeron simplex</i>
<i>Draba densiflora</i>	<i>Erigeron compositus</i>
* <i>Draba aurea</i>	<i>Erigeron multifidus</i>
<i>Smelowskia americana</i>	<i>Erigeron trifidus</i>
* <i>Sedum stenosepalum</i>	

The following are common and important plants of this formation in the southern Rockies, but lacking or rare in the northern. Those with the asterisks are mostly found near or below the timber-line, those with the dagger are found in the northern Rockies but are rare:

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\* Those with asterisks are mostly found near the timber-line and also below.



† <i>Poa Pattersoni</i>	* <i>Draba streptocarpa</i>
<i>Poa Lettermanni</i>	<i>Draba saximontana</i>
<i>Avena Mortoniana</i>	<i>Androsace carinata</i>
* <i>Eriogonum xanthum</i>	* <i>Dasystephana Parryi</i>
<i>Paronychia pulvinata</i>	<i>Phlox condensata</i>
* <i>Arenaria Fendleri</i>	<i>Castilleja Haydeni</i>
<i>Thlaspi coloradense</i>	<i>Pentstemon Hallii</i>
<i>Thlaspi purpurascens</i>	† <i>Eritrichium argenteum</i>
<i>Cheirinia radiata</i>	<i>Erigeron pinnatisectus</i>
<i>Cheirinia nivalis</i>	* <i>Besseya plantaginea</i>
<i>Draba aureiformis</i>	* <i>Senecio Nelsonii</i>
<i>Draba chrysantha</i>	<i>Senecio Harbourii</i>
<i>Draba crassifolia</i>	

The following are important plants of this formation in the northern Rockies but lacking in the southern:

<i>Festuca supina</i>	<i>Douglasia montana</i>
<i>Agropyron andinum</i>	<i>Phacelia sericea</i>
<i>Agropyron latiglume</i>	<i>Phacelia alpina</i>
<i>Potentilla Macounii</i>	<i>Eritrichium elongatum</i>
<i>Dryas Drummondii</i>	<i>Dasystephana monticola</i>
<i>Aquilegia Jonesii</i>	

The following plants belong to this formation but are rather local:

#### Southern

<i>Poa epilis</i>	<i>Potentilla minutifolia</i>
<i>Festuca minutiflora</i>	<i>Potentilla tenerrima</i>
<i>Arenaria Tweedyi</i>	<i>Potentilla nivea</i>
<i>Cheirinia amoena</i>	<i>Potentilla nipharga</i>
<i>Draba crassa</i>	<i>Potentilla paucijuga</i>
<i>Parrya platycarpa</i>	<i>Gormaniana debilis</i>
<i>Oreoxis humilis</i>	<i>Aragallus podocarpus</i>
<i>Oreoxis Bakeri</i>	<i>Aragallus Hallii</i>
<i>Oreoxis alpina</i>	<i>Chaenactis pedicularia</i>
<i>Pseudocymopterus Tidestromii</i>	<i>Chaenactis alpina</i>
<i>Xylorrhiza coloradensis</i>	<i>Senecio petrocallis</i>
<i>Xylorrhiza Brandegei</i>	<i>Chrysopsis alpicola</i>
<i>Macronema pygmeum</i>	



## Northern

*Douglasia nivalis*  
*Phacelia Lyallii*

*Antennaria sedoides*  
*Macronema Lyallii*

## 2. ALPINE ROCK-SLIDES

Many parts of the Rocky Mountains are covered by loose rocks, often in more or less unstable conditions, sometimes forming sliding fields or moving together with the snow avalanches. These are not wholly without vegetation and there are certain plants that are characteristic of such rock-slides, scarcely growing anywhere else.

The most characteristic plant of the rock-slides is, perhaps, *Claytonia megarrhiza* with its large red root lodged far down among the rocks. Another is *Alsine americana* of the northern Rockies, which has a slender rootstock, sending up long shoots among the rocks, the proper leaves and flowers crowded at the ends of the branches. *Senecio carthamoides* and *C. Fremontii*, *Telesonix Jamesii* and *T. heucheriforme*, *Ribes montigenum* and *R. parvulum* are also confined to the rock-slides, the former of each pair found in the southern, the latter in the northern Rockies. *Hulsea carnosus* also I found only in the rock-slides of Montana and Yellowstone Park. *Primula Parryi* and *Oxyria digyna* frequent the rock-slides, but are not confined to them, the former being even found in the woods. The other rock-slide plants are rather local.

The following constitute for the most part the rock-slide vegetation:

## Southern Rockies

*Polemonium speciosum*  
*Polemonium confertum*  
*Primula Parryi*  
*Claytonia megarrhiza*  
*Telesonix Jamesii*  
*Heuchera Hallii*  
*Ribes montigenum*  
*Pentstemon Hallii*  
*Pentstemon Harbourii*

*Aquilegia saximontana*  
*Syntheris plantaginea*  
*Senecio carthamoides*  
*Oxyria digyna*  
*Selaginella densa*  
*Machaeranthera Pattersoni*  
*Pseudopteryx anisata*  
*Senecio invenustus*



## Northern Rockies

<i>Claytonia megarrhiza</i>	<i>Hulsea carnosia</i>
<i>Telesonix heucheriforme</i>	<i>Senecio Fremontii</i>
<i>Oxyria digyna</i>	<i>Alsine americana</i>
<i>Selaginella densa</i>	<i>Ribes parvulum</i>
<i>Pseudopteryxia Hendersonii</i>	<i>Polemonium viscosum</i>

## 3. ALPINE CLIFFS

While the following plants are found elsewhere, they are characteristic of the crevices of exposed cliffs:

* <i>Chondrosea Aizoon</i>	<i>Oxyria digyna</i>
* <i>Leptasea austromontana</i>	<i>Aquilegia saximontana</i>
<i>Antiphylla oppositifolia</i>	<i>Polemonium pulcherrimum</i>
<i>Anticlea coloradensis</i>	<i>Polemonium delicatum</i>
<i>Senecio petrocallis</i>	

## 4. ALPINE MOUNTAIN SEEPS

This formation usually is found between the mountain crests and the meadows, but is more moist than either. Often the mountain crest or mountain slope formation gradually changes into the meadow. This is usually the case where no melting snow-drift supplies the slope with more moisture throughout the summer; but where water is dripping or seeping down from the snow, along brooks, and above subterranean water courses, there is developed a formation, which as far as moisture is concerned could be classified with the wet meadow, but the ground is more rocky, the soil consists more exclusively of humus and most of the plants are different from those of the true meadow. The grasses and sedges are fewer both in number and in species, but otherwise the same as those of the meadow, although the three Poas mentioned below are characteristic of these seeps, rather than of the meadows. Characteristic plants of these seeps are the alpine willows, alpine clovers, *Sibbaldia procumbens*, *Rhodiola*, species of *Ranunculus*, *Senecio*, *Polemonium* and *Juncus*, *Taraxacum scopulorum*, *Mertensia alpina* and its relatives, *Myosotis alpestris*, and, above all, many species of *Saxifraga* and its allies.

In the northern Rockies there is found a plant association that may be counted here. On northern cold mountain slopes of



Montana, with a good deal of moisture, sometimes whole acres are covered with *Cassiope Mertensiana*. Except the ericaceous bog formation, made up of *Phyllodoce*, *Kalmia*, and *Ledum*, this is the only poor representation of the shrubby ericaceous formation, so characteristic of the Alps. This association of *Cassiope* suggests in many respects the arctic tundra. I have not visited the extreme northern part of the Rockies in British America, but I suspect that *Cassiope tetragona* and *Harrimanella hypnoides* there form similar associations. The only other plants in the alpine regions of the Rockies that I know of as forming similar mats are the dwarf alpine willows, *Salix saximontana*, *S. nivalis*, *S. petrophila*, *S. cascadiensis*, and *S. Dodgeana*. The last, the smallest willow of the world, I found forming similar mats near the top of Electric Peak, southern Montana, at an altitude of 11,000 feet. When it was first discovered I did not know that I had been walking on top of a willow forest before I dropped down on my knees, began to poke among the leaves, and found some minute catkins.

The following plants are common in the seep throughout the Rockies:

<i>Poa alpina</i>	<i>Sagina saginoides</i>
<i>Poa cenisia</i>	<i>Ranunculus pygmaeus</i>
<i>Poa arctica</i>	<i>Ranunculus hyperboreus</i>
<i>Juncoides spicatum</i>	* <i>Aquilegia coerulea</i>
<i>Salix petrophila</i>	<i>Draba fladnizensis</i>
<i>Salix saximontana</i>	<i>Rhodiola integrifolia</i>
<i>Oxyria digyna</i>	<i>Saxifraga cernua</i>
<i>Alsinopsis propinqua</i>	<i>Cerastium behringianum</i>
<i>Alsine baicalensis</i>	<i>Mertensia alpina</i>
<i>Alsine laeta</i>	<i>Myosotis alpestris</i>
<i>Muscaria adscendens</i>	<i>Taraxacum scopulorum</i>
<i>Micranthes rhomboidea</i>	<i>Artemisia scopulorum</i>
<i>Leptasea flagellaris</i>	<i>Senecio cymbalarioides</i>
<i>Sibbaldia procumbens</i>	<i>Juncus Drummondii</i>
<i>Trifolium Brandegei</i>	<i>Juncus Parryi</i>
<i>Trifolium Parryi</i>	<i>Juncus triglumis</i>
* <i>Vaccinium caespitosum</i>	<i>Juncus castaneus</i>
<i>Primula angustifolia</i>	<i>Chondrophylla americana</i>
<i>Polemonium pulcherrimum</i>	



The following are important plants belonging to this formation, but limited to the southern Rockies:

<i>Ranunculus Macauleyi</i>	<i>Oreochrysum Parryi</i>
<i>Rhodiola polygama</i>	<i>Artemisia saxatilis</i>
<i>Cerastium Earlei</i>	<i>Artemisia Pattersonii</i>
<i>Trifolium Brandegei</i>	<i>Saxifraga debilis</i>
Relatives of <i>Trifolium dasy-</i>	<i>Mertensia brevistyla</i>
<i>phyllum</i> ( <i>T. stenolobum</i> , <i>T.</i>	<i>Mertensia viridula</i>
<i>attenuatum</i> , <i>T. bracteolatum</i>	<i>Mertensia lateriflora</i>
and <i>T. lividum</i> )	<i>Mertensia Bakeri</i>
<i>Anthropogon barbellatum</i>	<i>Pentstemon stenosepalum</i>
<i>Polemonium confertum</i> and	<i>Salix pseudolapporum</i>
its relatives	<i>Senecio Holmei</i>
<i>Micranthes arnoglossa</i>	<i>Senecio taraxacoides</i>
<i>Leptasea chrysantha</i>	<i>Senecio Soldanella</i>
<i>Muscaria delicatula</i>	<i>Senecio crocatus</i>
<i>Tonestus pygmaeus</i>	

The following are common in the northern Rockies, but not found in the southern:

<i>Salix cascadiensis</i>	<i>Micranthes stellaris</i>
<i>Salix nivalis</i>	<i>Micranthes Rydbergii</i>
<i>Draba lonchocarpa</i>	<i>Micranthes hieracifolia</i>
<i>Draba nivalis</i>	<i>Dasystephana glauca</i>
<i>Saxifraga rivularis</i>	<i>Polemonium viscosum</i>
<i>Muscaria caespitosa</i>	<i>Ranunculus saxicola</i>

The following belong to this formation but are merely local or rare:

#### Southern

<i>Delphinium alpestre</i>	<i>Micranthes Vreelandii</i>
<i>Alsinopsis quadrivalvis</i>	<i>Leptasea Hirculus</i>
<i>Alsinopsis Rossii</i>	<i>Polemonium Brandegei</i>
<i>Sagina nivalis</i>	<i>Draba Parryi</i>
<i>Alsine polygonoides</i>	<i>Cerastium pulchellum</i>
<i>Chrysosplenium tetrandrum</i>	<i>Mertensia Parryi</i>
<i>Muscaria micropetala</i>	<i>Artemisia spithamaea</i>
<i>Micranthes brachypus</i>	<i>Artemisia Parryi</i>



## Northern

<i>Salix Dodgeana</i>	<i>Micranthes Vreelandii</i>
<i>Alsinopsis quadrivalvis</i>	<i>Leptasea Hirculus</i>
<i>Alsinopsis Rossii</i>	<i>Leptasea Van Bruntiae</i>
<i>Alsine polygonoides</i>	<i>Polemonium parviflorum</i>
<i>Chrysosplenium tetrandrum</i>	<i>Chondrophylla Fremontii</i>
<i>Muscaria monticola</i>	<i>Artemisia spithamea</i>
<i>Micranthes crenatifolia</i>	

## 5. ALPINE MEADOWS

The more or less mesophytic part of the alpine region may be called the alpine meadow. It is found in the less sloping parts of the mountains, where more humus and alluvial soil has had a chance to collect. Of course, the more characteristic plants in such localities are grasses and sedges.

The most important and most common of the grasses are the different species of *Poa*, *Phleum alpinum*, *Trisetum subspicatum*, *Agropyrum biflorum*, *Festuca saximontana*, and in the wetter places, especially on brook banks, *Deschampsia caespitosa* and *D. alpicola*. On the slopes *Festuca ingrata* and *F. Thurberi* are also important, but not to such an extent as they are in the subalpine and mountain region. The sedges and rushes occupy mostly the wetter parts, which stand on the borderland of bogs. There are, however, localities which must be classified as meadows, where the predominating plants are other than grasses and sedges. In many places many acres are covered with mostly *Acomastylis turbinata* or *Rydbergia grandiflora* in the southern, and *Acomastylis sericea* in the northern Rockies.

The common species of the meadow formations throughout the whole region are the following:

<i>Phleum alpinum</i>	* <i>Poa epilis</i>
<i>Deschampsia caespitosa</i>	<i>Poa leptocoma</i>
<i>Trisetum subspicatum</i>	* <i>Festuca ingrata</i>
<i>Trisetum majus</i>	<i>Festuca saximontana</i>
* <i>Danthonia intermedia</i>	<i>Festuca rubra</i>
* <i>Poa longiligula</i>	* <i>Agropyron caninum</i>
* <i>Poa Buckleyana</i>	<i>Agropyron biflorum</i>



<i>Juncoides spicatum</i>	* <i>Amarella strictiflora</i>
<i>Juncoides parviflorum</i>	* <i>Castilleja rhexifolia</i>
<i>Bistorta bistortoides</i>	* <i>Castilleja lauta</i>
<i>Bistorta linearifolia</i>	* <i>Castilleja lancifolia</i>
<i>Alsine laeta</i>	<i>Besseya alpina</i>
<i>Cerastium behringianum</i>	* <i>Campanula Parryi</i>
<i>Thalictrum alpinum</i>	<i>Campanula petiolata</i>
* <i>Aquilegia flavescens</i>	<i>Trifolium nanum</i>
<i>Clementsia rhodantha</i>	<i>Trifolium Parryi</i>
* <i>Potentilla diversifolia</i>	<i>Lloydea serotina</i>
<i>Potentilla glaucophylla</i>	* <i>Tium alpinum</i>
<i>Potentilla rubripes</i>	* <i>Atelophragma elegans</i>
<i>Acomastylis turbinata</i>	<i>Aragallus deflexus</i>
<i>Sieversia ciliata</i>	<i>Phacelia sericea</i>
* <i>Agrostis hyemalis</i>	<i>Phacelia ciliosa</i>
* <i>Alopecurus aristulatus</i>	* <i>Pedicularis racemosa</i>
<i>Juncus Drummondii</i>	<i>Pedicularis Parryi</i>
<i>Juncus Parryi</i>	<i>Aster apricus</i>
<i>Juncus triglumis</i>	<i>Rydbergia grandiflora</i>
<i>Juncus castaneus</i>	* <i>Senecio pseud aureus</i>
* <i>Primula Parryi</i>	<i>Solidago oreophila</i>
* <i>Vaccinium scoparium</i>	<i>Solidago decumbens</i>
* <i>Vaccinium oreophilum</i>	<i>Solidago ciliosa</i>
* <i>Androsace subumbellata</i>	* <i>Erigeron glabellus</i>
<i>Amarella plebeja</i>	

The following are common plants of the alpine meadow, but are restricted to either the southern or the northern Rockies:

#### Southern

<i>Blepharoneuron tricholepis</i>	<i>Draba streptocarpa</i>
<i>Deschampsia alpicola</i>	<i>Angelica Grayi</i>
<i>Poa alpicola</i>	<i>Primula angustifolia</i>
<i>Poa Grayana</i>	<i>Polemonium speciosum</i>
* <i>Poa Sheldoni</i>	<i>Polemonium confertum</i>
<i>Poa pudica</i>	<i>Polemonium mellitum</i>
* <i>Festuca Thurberi</i>	<i>Valeriana acutiloba</i>
<i>Anemone zephyrea</i>	<i>Castilleja brunescens</i>
* <i>Sidalcea candida</i>	<i>Campanula uniflora</i>



<i>Achillea subalpina</i>	<i>Pseudocymopterus purpureus</i>
<i>Arnica Parryi</i>	* <i>Mertensia alpina</i>
* <i>Senecio amplexans</i>	<i>Mertensia brevistyla</i>
<i>Oreochrysum Parryi</i>	<i>Aster alpinus</i>

## Northern

<i>Tofieldia palustris</i>	<i>Acomastylis sericea</i>
<i>Juncoides arcticum</i>	* <i>Trifolium Haydeni</i>
<i>Juncoides arcuatum</i>	<i>Phacelia alpina</i>
<i>Juncoides hyperboreum</i>	<i>Angelica Roseana</i>
<i>Juncus biglumis</i>	<i>Polemonium viscosum</i>
<i>Drymocallis pseudorupestris</i>	<i>Valeriana septentrionalis</i>

## 6. ALPINE BOGS

The principal hydrophytic formation of the alpine regions are the alpine bogs or wet meadows, situated on the mountain sides where the drainage is imperfect or where the water supply is greatly increased by melting snowdrifts above. These are of two kinds, either sedge bogs, where grasses and sedges are predominant, or willow bogs where the principal species are shrubs. The latter are rare above timber-line in the southern Rockies.

## SEdge BOGS

Little needs to be said of the sedge bogs, as they resemble similar bogs in any part of the colder regions, only that the individual species vary. With the sedges are usually mixed in a considerable amount of grasses as *Alopecurus aristulatus*, *Calamagrostis Langsdorfii*, *Poa leptocoma* and *Poa reflexa*, the cotton grass, *Eriophorum gracile*, and other more conspicuous plants as the little red elephant, *Elephantella groenlandica*.

The principal plants of this formation are:

<i>Carex</i> (many species)	<i>Calamagrostis Langsdorfii</i>
* <i>Eriophorum gracile</i>	<i>Poa leptocoma</i>
* <i>Eriophorum polystachyum</i>	* <i>Poa reflexa</i>
* <i>Alopecurus aristulatus</i>	* <i>Phleum alpinum</i>

\* These are found only near the timber-line, otherwise belonging to the subalpine region.



<i>Scirpus pauciflorus</i>	<i>Swertia palustris</i>
<i>Scirpus caespitosus</i>	* <i>Pyrola uliginosa</i>
<i>Bistorta bistortoides</i>	<i>Veronica Wormskjoldi</i>
<i>Bistorta vivipara</i>	* <i>Elephantella groenlandica</i>
<i>Ranunculus affinis</i>	<i>Amarella scopulina</i>
<i>Thalictrum alpinum</i>	<i>Amarella strictiflora</i>
<i>Vaccinium oreophilum</i>	<i>Antennaria nardina</i>
<i>Primula Parryi</i>	

To this formation belong also the following species restricted to a part of the region:

Southern	Northern
<i>Caltha rotundifolia</i>	<i>Caltha leptosepala</i>
<i>Ranunculus stenolobus</i>	<i>Caltha Cheledonii</i>
* <i>Senecio atratus</i>	
<i>Ligusticum Porteri</i>	

#### WILLOW BOGS

These willow bogs are not exclusively alpine, as most of the species there are found also in the subalpine region. They are not so common in the southern Rockies as they are in the northern. In Colorado, the shrubby species consist mostly of *Salix glaucops* and *Betula glandulosa*, although other species of willows, as for instance *S. chlorophylla*, are not rare. *Kalmia microphylla* is very local there. In the northern Rockies the number of species is increased. More species of *Salix* are found and *S. chlorophylla* becomes more predominant. *Alnus sinuata* is added to *Betula glandulosa*. Sometimes, especially in pockets on the northern slopes, the predominant plants are ericaceous, viz., *Kalmia microphylla*, *Ledum glandulosum*, *Phyllodoce empetriformis*, and *P. glanduliflora*. In the Canadian Rockies evidently are added to these, *Arctuos* and *Oxycoccus*. The herbaceous plants are mostly the same as in the sedge bogs, *Elephantella* and *Pyrola uliginosa* being conspicuous, especially in the subalpine regions.

The shrubby plants characteristic of the willow bogs are the following:

<i>Salix chlorophylla</i>	<i>Salix saximontana</i>
<i>Salix glaucops</i>	<i>Salix monticola</i>



* <i>Betula glandulosa</i>	<i>Phyllodoce glanduliflora</i>
* <i>Alnus sinuata</i>	<i>Kalmia microphylla</i>
<i>Phyllodoce empetriformis</i>	* <i>Ledum glandulosum</i>

In the Canadian Rockies are added to these:

<i>Salix alexensis</i>	<i>Salix Barattiana</i>
<i>Salix arbusculoides</i>	<i>Salix Drummondiana</i>

#### 7. SNOW DRIFT FORMATION

This special formation is made up of hydrophytic plants, nearly all of the family Ranunculaceae. The other plants are such as are only occasionally found in these peculiar situations. This formation could be included in the alpine seeps on account of their moisture, but the ground is neither rocky nor does it contain much humus. As a rule the soil is considerably clayey. In reality it is a part of the alpine meadow, modified by the slowly melting snowdrifts. The formation is found only in hollows or on gentle slopes, where large snowdrifts have lodged during the winter and the ground does not become bare before late in the summer. The grasses and most other meadow or bog plants could not withstand such severe conditions. Where the snowdrifts have been the ground is perfectly bare or nearly so, except for these peculiar plants, which appear as soon as the snow has melted and the ground has had time to thaw a few inches deep. Sometimes they even come up through the snow. Hence, the stories of the snow plants often heard of are not altogether "fakes."

This formation is principally made up of the following plants:

Southern	Northern
<i>Ranunculus adoneus</i>	<i>Ranunculus eximius</i>
<i>Ranunculus alismaefolius</i>	<i>Ranunculus alismaefolius</i>
<i>Ranunculus stenolobus</i>	<i>Caltha leptosepala</i>
<i>Caltha rotundifolia</i>	<i>Caltha Cheledonii</i>

#### 8. ALPINE LAKES

The aquatic flora of the alpine region is rather meagre. All the phanerogams and fernworts found there are found also in the subarctic region, in fact, are boreal plants of wide distribution.

The flora of the alpine lakes is limited to the following phanerogams and fernworts:



## Southern Rockies

*Sparganium angustifolium*  
\**Potamogeton alpinus*  
\**Utricularia vulgaris*  
*Callitriche palustris*  
*Isoetes paupercula*

## Northern Rockies

*Sparganium angustifolium*  
*Sparganium minimum*  
*Potamogeton alpinus*  
*Callitriche palustris*  
*Isoetes Bolanderi*

In the alpine brooks are found *Catabrosa aquatica* and *Phippsia algida*, the latter having been collected at one locality in Colorado.

NEW YORK BOTANICAL GARDEN



# INDEX TO AMERICAN BOTANICAL LITERATURE

1914

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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## CONTENTS

Notes on Rosaceae—VIII. . . . . PER AXEL RYDBERG 483

New or notable species of *Amaranthus* . . . . . PAUL C. STANDLEY 505

The introduced vegetation in the vicinity of Douglas Lake, Michigan,  
HENRY ALLEN GLEASON and FRANK THEODORE McFARLAND 511

INDEX TO AMERICAN BOTANICAL LITERATURE. . . . . 523

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BULLETIN  
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OCTOBER, 1914

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Notes on Rosaceae—VIII

PER AXEL RYDBERG

DRYAS

Little has been added to the knowledge of this genus in the last eighty years. Only one species has been added, *Dryas tomentosa* Farr.

*Dryas integrifolia* Wahl. Many authors regard this as merely a variety of *D. octopetala*, as intermediate forms are met with, but these have only been found where the two species grow together and are probably all of hybrid origin. Nathorst\* was inclined to regard these forms as hybrids, but he did not call them by a hybrid name, denoting them as *D. octopetala* f. *intermedia*. Hartz† held the same opinion, but apparently by a slip of the pen called them *D. integrifolia intermedia* Nathorst. This hybrid has also been collected in Alaska at Orca, Prince William's Sound, 1899, Coville & Kearney 1191.

*Dryas octopetala* L. Hartz, *loc. cit.*, admitted several varieties of *Dryas octopetala*, viz. var. *minor* Hook., var. *hirsuta* Hartz, and var. *argentea* Blytt. The last one of these seems to be furthest from the type, but by no means deserving specific rank. Simmons described a similar form of *D. integrifolia*, viz. *D. integrifolia canescens*.

*Dryas tomentosa* Farr. This species is closely related to *D. Drummondii* and perhaps not distinct. It may be only a variety

\* Öfvers. Kong. Sv. Vet. Akad. Hand. 41<sup>1</sup>: 24. 1884.

† Medd. Groenl. 18: 321. 1895.

]The BULLETIN for September (41: 435-482) was issued 8 O 1914.]



standing in the same relationship to *D. Drummondii* as *D. octopetala argentea* Blytt stands to *D. octopetala*. This species has also been collected in the Canadian Rockies, *Macoun 65125*.

### GEUM

*Geum vernum* (Raf.) T. & G. was originally described as *Stylopus vernus* Raf., and the writer is somewhat in doubt if this species should not be regarded as the type of a distinct genus. The habit is that of a typical *Geum*, but the receptacle in fruit becomes stalked above the hypanthium, and the bractlets are usually lacking. Occasionally, however, there are found minute bractlets in this species, and the receptacle is more or less stalked in *Geum rivale*. The generic characters of *Stylopus* do therefore break down, and it is perhaps better to regard it a *Geum*, especially as the general habit is not essentially different.

*Geum virginianum* L. This species has in general been very well understood. Murray, however, applied that name to *G. canadense* and redescribed the true *G. virginianum* as *G. laciniatum* Murr. Many have referred the latter synonym to *G. canadense* and Scheutz suggests that it may be the same as *G. agrimonioides* C. A. Mey., i. e. *G. Meyerianum* Rydb., but in my opinion it belongs to *G. virginianum* L.

*Geum camporum* Rydb. Some twenty years ago, the writer, when working over the Rosaceae of Nebraska, had trouble in determining some specimens of *Geum*, and did not know whether to refer them to *G. canadense* or to *G. virginianum*. These specimens had the thick leaves, the stout stem and branches, and the large fruiting head of the latter, but the receptacle was not glabrous and the achenes had the pubescence of *G. canadense*. When working up the material for the North American Flora, he found that the plant was more common in the prairie region of the Mississippi valley than was expected and that its range extended from Minnesota and South Dakota to Arkansas and Texas. As both *G. virginianum* and *G. canadense* are found in the region, *G. camporum* might be regarded as a hybrid of the two. These two have about the same distribution (except that *G. virginianum* is not found in Mexico), but *G. camporum* is not found except in the western part of their common range. It is, therefore, not probable that it is a



hybrid, and it is more likely a distinct species. The following specimens belong to it:

KANSAS: Manhattan, 1892, *Norton*; Riley County, 1895, *Norton 137*; Olathe, 1892, *Hitchcock*; Fort Riley, 1892, *Gayle 522*; Emporia, 1891, *E. Smith*; Cowley County, 1899, *Mark White 54*; Lawrence, *W. C. Stevens*.

NEBRASKA: Lincoln, 1887, *Webber*; Nehawka, *Swezey*; Sargent Bluffs, 1853 or 1854, *Hayden*; Franklin, 1893, *Laybourne*; Middle Loupe, 1893, *Rydberg 1608*; Glenwood, 1888, *T. A. Williams*.

SOUTH DAKOTA: Black Hills, Fort Meade, 1887, *Forwood 15*.

OKLAHOMA: *Waugh 175*.

TEXAS: San Marcos, 1898, *Stanfield*; Crab Apple, *Jermey 471*; Industry, 1893, *Wurzlow*.

MINNESOTA: Fort Snelling, 1890, *Mearns 346, 347*.

ARKANSAS: Whippe Expedition, *Bigelow*.

*Geum canadense* Jacq. This has usually been known under the name *Geum album* J. F. Gmel. The latter was arbitrarily substituted by Gmelin, probably because he thought that it was more appropriate. I say arbitrarily and without good cause, for he simply based his species on Jacquin's plate and original description of *G. canadense*.

*Geum album* (i. e. *G. canadense*) has been reported from the valley of Mexico. As that station was so far remote from the otherwise known range of *Geum canadense*, the nearest station being in Texas, the writer thought that the specimens from Mexico belonged to some other species and that it was merely a case of misidentification. He found, however, in the National Herbarium three sheets collected by Schiede, no. 580, at San Angel, not far from Mexico City, and these specimens can not be distinguished from specimens from the United States. It was also collected at Chinantla, 1841, *Liebmann 1743*.

*Geum Meyerianum* Rydb. C. A. Meyer\* gave a very good description of this species, but mistook it for *G. agrimonioides* Pursh, which is not a *Geum* at all, but *Drymocallis agrimonioides* (Pursh) Rydb., until lately usually known as *Potentilla arguta*. It was, therefore, necessary to give another name to *Geum agrimoni-*

\* Ind. Sem. Petrop. 11: Supl. 29, 1846.



*oides* of Meyer and the writer with pleasure dedicated it to the botanist who first distinguished it. It is strange that this species (or variety) of the *Geum canadense* group has not been recognized by any American authors. It was admitted and described also by Scheutz in his monograph.\* It is related to *G. canadense*, but the basal leaves and lower stem-leaves are pinnatifid and the stem is more hirsute. These characters are sometimes found in *G. hirsutum* Muhl. [*G. florum* (Porter) Bicknell], but the petals in *G. Meyerianum* are white and longer than the sepals, while in *G. hirsutum* they are pale yellow and much shorter.

The following specimens belong to *G. Meyerianum*:

NEW YORK: Fleishmann, Delaware County, 1892, *Hermann von Schrenk*; Tuxedo, 1896, *W. H. Lewis*; Oneida, 1903, *H. D. House*.

ONTARIO: Battersea, 1898, *Fowler*.

QUEBEC: Danville, 1894, *A. K. Berg*.

PENNSYLVANIA: New Danville, Pike Crossing, 1901, *Heller*; Bangor, 1899, *Porter*; Easton, 1899, *Porter*.

DISTRICT OF COLUMBIA: banks of canal, 1895, *Pollard*.

*Geum hirsutum* Muhl. This species has been well characterized by Porter and Bicknell under the names *G. album flavum* and *G. flavum*. It was also described by Fischer and Trautvetter, who mistook it for *G. canadense*, which they held distinct from *G. album*. The oldest name, however, is *G. hirsutum* Muhl. Muhlenberg listed it in his catalogue in 1813. In this publication it is to be regarded as a *nomen semi-nudum*, but nine years later Link gave it a short description, pointing out the essential characters.

*Geum decurrens* Rydb. Some specimens from New Mexico, Arizona and Colorado and named *G. strictum* seemed so different from all other specimens of that widespread and rather variable species, that the writer thought it advisable to propose in the North American Flora a new species based on these specimens. The essential characters are pointed out in that work. It is, however, advisable to cite some more specimens.

ARIZONA: Bakers Butte, Mogollon Mountains, 1887, *Mearns* 59.

NEW MEXICO: Mogollon Mountains, 1903, *Metcalf* 536.

COLORADO: Rico, 1898, *Crandall* 4109.

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\* Nov. Act. Soc. Sci. Upsala III. 7: 32. 1870.



*Geum oregonense* (Scheutz) Rydb. This was originally described as a variety of *G. urbanum* to which it is not closely related. Its relationship is with *G. macrophyllum*. Usually it is well distinguished from that species by its open inflorescence, smaller stem-leaves and smaller and usually paler petals, but intermediate forms are not lacking. Some of these at least may be regarded as hybrids. *Geum oregonense* is common throughout the Rocky Mountains, as well as the Sierra Nevada and the Cascades. In the southern Rockies, *G. macrophyllum* is not found, but it extends east to northern New England, where *G. oregonense* is not found at all. In California the characters separating the two species seem to be less marked, and considerable questionable material has been seen.

*Geum perincisus* Rydb. Many subarctic specimens which might have been referred to *G. oregonense* have the upper leaves deeply incised and the petals broader and in form approaching those of *G. strictum*. It is hard to say whether these should be regarded as a variety of *G. oregonense* or as a distinct species. I adopted the latter view, because all these specimens were far northern ones and some of them found much further east than any of the typical *G. oregonense*. The following specimens belong here:

ALASKA: Eagle, Yukon Valley, 1902, *Arthur Collier* 34, 35; Copper River region, 1902, *William L. Poto* 147.

YUKON: Fort Selkirk, 1899, *Tarleton* 120.

MACKENZIE: Fort Simpson, 1861-62, *Onion, Kennicott & Hardisty*; Fort Resolution, 1901, *Preble & Preble* 154.

ALBERTA: Cave Avenue, Banff, *McCalla* 2074.

MICHIGAN: Turin, 1901, *Barlow*.

*Geum strictum* Ait. is a very variable species. Usually the terminal leaflet is more or less rhombic, as it is commonly described, but not seldom it is rounded or subreniform as it is in *G. macrophyllum* or *G. oregonense*. It usually can be easily distinguished by its large rounded petals and always by its fruit. The lower portion of the style is never glandular and the upper portion has hairs about twice as long as those of the other two species. *Geum scopulorum* is the common form of *G. strictum* in the Rockies, a little less robust than in the East.



*Geum aleppicum* Jacq.\* has been regarded as a synonym of *G. strictum*. Being an older name it should have been substituted. But I think that it is well distinct from the North American plant. So are all specimens from Europe referred to *G. strictum*. Whether they should all be included or not in *G. aleppicum*, I could not tell, but it is evident that *G. strictum* should be excluded from the flora of Europe and Asia Minor.

*Geum mexicanum* Rydb. Specimens in habit much resembling *G. macrophyllum* have been collected in southern Mexico. They were also determined as that species. As *G. macrophyllum* has not been collected at any station nearer than Sierra Nevada in California, it is very improbable that that species should grow in southern Mexico. A closer examination of these specimens revealed that the petals and the fruit were essentially those of *G. strictum*. As the habit is quite different, a new species *G. mexicanum* was proposed and based upon these specimens. To this belong the following:

VERA CRUZ: Mount Orizaba, 1891, *Henry E. Seaton* 251.

HIDALGO: Sierra de Pachuca, 1901, *Rose & Hay* 5563; 1906, *Rose & Rose* 11489.

*Geum urbanum* L., a native of Europe and temperate Asia, has been introduced in this country and is well established at several places, especially at Cambridge, Massachusetts.

*Geum geniculatum* Michx. The type locality of this species was given as Canada. This must have been a mistake, for the plant is known only from the mountain slopes of North Carolina and eastern Tennessee.

*Geum rivale* L. This is a native of North America as well as Europe and Asia. Rafinesque thought that the American plant was different and redescribed it as *G. nutans* Raf. As there was an older *G. nutans*, Steudel proposed the name *G. Rafinesquianum* for the American plant, but this was unnecessary as that and the European one are identical.

#### HYBRIDS

Hybrids in *Geum* are not unknown in Europe; why should they be in America? *Geum intermedium* Ehrh., a hybrid of *G.*

\* Coll. 1: 80.



*rivale* L. and *G. urbanum* L., has been known for a long time. *Geum rivale* L. hybridizes also here in America and the following hybrids have been known. As the flowers of *G. rivale* are quite different from those of most species of the genus, its hybrids are easily distinguished.

*Geum rivale* × *strictum*, *G. auranthacum* Fries, was the first one to be recognized. It was described from garden material, but the following native specimens are to be referred here:

ALBERTA: *Macoun 20016*.

NEW YORK: Catskills, near Hunter, 1898, *Britton*; shores of Lake Champlain, 1900, *N. L. & E. G. Britton*.

*Geum macrophyllum* × *rivale*, *G. pulchrum* Fern., is represented by the following specimens:

VERMONT: Mendon, *Eggleston*.

QUEBEC: Bic, 1905, *Williams, Collins & Fernald*.

The hybrids between the species of the *G. strictum* group are not so easily distinguished, partly because the species themselves are closely related and seemingly grade into one another. As the intergrading forms are found in the region where the ranges of two species overlap, they may represent hybrids. As examples of such hybrids may be given the following specimens:

*Geum oregonense* × *strictum*.

UTAH: Logan, 1910, *George Zundel 206* (in part).

MONTANA: Helena, 1908, *Butler 798*.

COLORADO: Honnold, 1901, *Tweedy 4172*.

*Geum macrophyllum* × *oregonense*.

BRITISH COLUMBIA: Scagit Valley, 1905, *J. M. Macoun 69914*.

WYOMING: Crevasse Mountain, Yellowstone Park, 1902, *Mearns 2191*.

MONTANA: Tobacco Mountains, 1909, *Butler 4231*.

OREGON: Oregon City, 1905, *Lyon 60*.

*Geum macrophyllum* × *strictum*.

MONTANA: Lake McDonald, 1901, *MacDougal 959*.

## SIEVERSIA

This genus was based on *Sieversia anemonoides* and hence monotypic. In 1823 Robert Brown extended the genus to include all the *Geums* without articulate styles. This limitation was



retained up to 1906, when Dr. Greene segregated from it *Acomastylis* and *Erythrocoma*. In my opinion the former was rightly taken out, as it differs from *Sieversia* by the same character of the fruit that separates *Anemone* from *Pulsatilla*. *Erythrocoma* on the other hand I can not regard as distinct generically from *Sieversia*. Its species differ from the type of *Sieversia* only in the erect instead of spreading petals and a better developed hypanthium. If *Erythrocoma* should be kept distinct, *Geum rivale* should be taken out of *Geum*, as it differs by just the same characters, and still that species frequently hybridizes with the other species. Dr. Greene made the following statements which are not exactly true: "*Sieversia* was founded on a Siberian undershrub, low and slender, with almost rotate calyx and corolla, the former nearly chorisepalous, and its mature styles are long, filiform, plumose to the very apex." There are apparently three species which have gone under the name *Sieversia anemonoides*, of which one can be called an undershrub, the other two having the habit of *Dryas octopetala*, being strongly cespitose with the branches more or less covered by soil and moss. I think the type of *Sieversia* was one of these. The difference between this cespitose stem and the branching rootstock of *Erythrocoma* is indeed very small. The styles of *Sieversia anemonoides* Willd., or *S. pentapetala* (L.) Greene, are not plumose to the apex, for the upper part is naked, soft, withering, as it is in *Erythrocoma*, the only difference being that it is very short, scarcely 2 mm. long. This naked portion of the style is found not only in the type of *Sieversia* and in *S. ciliata* and its relatives, but also in the *S. montana* group, to which *S. radicata*, *S. Peckii* and *S. calthifolia* belong. The naked portion in most is rather persistent, although usually withering in age, but in some species or even individuals it breaks off. It is however never articulated to the lower portion of the style as in *Geum*, where the upper portion, which is usually hairy, falls off very early. C. P. Smith\* describes the style of *Erythrocoma ciliata* as follows: "Style hooked, or articulated [*italics mine*], the terminal portion often deciduous." I have seen it somewhat bent or even occasionally hooked, but never with a proper articulation. The soft upper naked portion, after it has withered, often falls off at

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\* *Muhlenbergia* 8: 7. 1912.



the junctions with the hard persistent lower portion, but there is no marked articulation at this point as there is in *Geum*.

As to the limitation of the species, it is impossible for me to follow Dr. Greene in his segregation. The original two species of Pursh's *Geum triflorum* and *Geum ciliatum* are apparently well distinct; the intermediate forms may be hybrids. *Erythrocoma campanulata* Greene seems also to be a good species. In the North American Flora I also admitted *Sieversia grisea* (Greene) Rydb., *S. canescens* (Greene) Rydb., *S. flavula* (Greene) Rydb. and *S. brevifolia* (Greene) Rydb. If the first two really are specifically distinct from *S. triflora* (Pursh) R. Br. and the last two from *S. ciliata* (Pursh) G. Don is questionable. The other species of *Erythrocoma* of Greene are nothing but forms of those mentioned, due to local conditions.

*Sieversia pentapetala* (L.) Greene (*S. anemonoides* Willd.) is an Asiatic species reported for America only from the Aleutian Islands. The only specimens I have seen from this region were collected by Dall.

*Sieversia glacialis* (R. Br.) Spreng. This species has the floral characters of the genus *Erythrocoma* Greene, but the habit suggests the species of *Acomastylis*. Some of the specimens are as follows:

ALASKA: York Plateau, near Ip-muk, Port Clarence, 1901, *Walpole 1906*; Port Clarence, 1901, *Collier*.

SIBERIA: Whalen, 1894, *J. T. White*.

*Sieversia campanulata* (Greene) Rydb. is the best species of *Erythrocoma* described by Dr. Greene. The broad reddish petals much exceeding the obtusish sepals and bractlets. It seems to be confined to the Olympic Mountains. The following specimens belong here:

WASHINGTON: Olympic Mountains, *Elmer 2529*; *Wilkes Expedition 352, 813* in part.

*Sieversia triflora* (Pursh) R. Br. This is distinguished from *S. ciliata* (Pursh) G. Don in the broader, less deeply cleft leaflets and the more persistent style-tips, as pointed out by C. P. Smith, but there is another character which seems to have been overlooked. In all the other species referred to *Erythrocoma*, the hypanthium is rounded or even sunken at the base, even at flowering time, and the bractlets are not much, if any, exceeding the



sepals in length; in *S. triflora* the hypanthium at least in anthesis is acute at the base and the bractlets much exceeding the sepals in length. If so characterized, *Sieverisa triflora* takes in all the forms growing on the prairies or plain region east of the Rockies and extending into Montana and Wyoming.

*Erythrocoma cinerascens* Greene and *E. affinis* Greene I can not distinguish from it. The former is a depauperate form, I take to be due to a higher altitude, represented by most specimens from the Black Hills and Wyoming. The latter is the high northern form with narrower leaflets and brighter coloration. If held distinct it had two older names than that of Dr. Greene, viz. *Sieversia rosea* Graham and *Geum Grahami* Steudel.

*Sieversia grisea* (Greene) Rydb. The following proposed species of *Erythrocoma*, viz. *E. grisea*, *E. arizonica*, *E. tridentata* and *E. aliena*, all by Greene, have many characters common with *S. triflora*, viz. the habit, leaf-form and tothing, pubescence, and styles, but the hypanthium is not acute at the base, the petals are broader and the bractlets shorter, slightly if at all longer than the sepals.

They were all described from Arizona and Chihuahua, but the same forms are common in Colorado and rarely as far north as Montana and Washington. They constitute the mountain representatives of *S. triflora*. Of these *Erythrocoma grisea* is the first one in the list. The type does not represent the common form, but is a depauperate form with short leaves, standing in the same relationship to the common form as *E. cinerascens* Greene stands to *Sieversia triflora*. The common better-developed form represents *E. arizonica* and is common in Colorado. *E. tridentata* is a form with looser pubescence and narrower leaflets, otherwise not distinguishable from *E. arizonica*. *E. aliena* is exactly the same as *E. grisea*.

*Erythrocoma australis* I regard as a hybrid between *Sieversia grisea* and *S. ciliata*. See my notes in the North American Flora.

*Sieversia canescens* (Greene) Rydb. The forms of *Erythrocoma* of the mountains of California, Oregon and Washington differ very little from *S. grisea*, as here understood, except in a denser pubescence and shorter bracts. It is doubtful if they should be regarded as a distinct species. I retained, although



with hesitation, the specific rank of these forms, on which *Erythrocoma canescens* Greene was based.

*Sieversia ciliata* (Pursh) G. Don. This species is confined to the Rocky Mountains and running down into the Cascades of Washington. It is found neither on the plains nor in the Sierra Nevadas. In most of its range it is associated with *S. grisea* and intermediate forms are not lacking; they are perhaps to be explained as of hybrid origin. The center of its distribution is in the northern Rockies, while that of *S. grisea* is more common in the southern. Its range barely touches that of *S. triflora* and only slightly overlaps that of *S. canescens*.

*Sieversia flavula* (Greene) Rydb. It was only with reluctance I admitted this as a species in the North American Flora. It is rather local in the mountains of Wyoming and Montana. The following specimens have been seen.

WYOMING: *A. Nelson* 829, 7501.

MONTANA: *Chestnut & Jones* 105; *Rydberg & Bessey* 4414.

*Sieversia brevifolia* (Greene) Rydb. This is a derivative of *S. ciliata*. It is confined to the mountains of central Utah. *S. Watson* 318, doubtfully referred here by Dr. Greene, I think should be referred to *S. ciliata*. The following specimens belong here:

UTAH: Panguitch Lake, *Jones* 6002g; Fish Lake, *Jones* 5779g, 54410; *L. F. Ward* 378.

*Sieversia Peckii* (Pursh) R. Br. This and the three following form a distinct natural group, which is represented in Europe by *Sieversia montana* and other species. *S. Peckii* has been confused with *S. radiatum* or has been made a variety of the same. It is, however, perfectly distinct. It is confined to the mountains of New Hampshire and Maine.

*Sieversia radiata* (Michx.) R. Br. This is closely related to the northwestern *S. calthifolia* (Menzies) D. Don. It is confined to the region of which Roan Mountain is the center, and the majority of the specimens in our herbaria are from that very mountain.

*Sieversia calthifolia* (Menzies) D. Don. This species is rather variable. In the high arctic regions it becomes stunted and more hairy (var. *congesta*), and then has a quite different appearance. Another cause for the many synonyms cited under the species



has been the supposition that there are two species in the northwest represented by *Geum calthifolium* Menzies and *Geum rotundifolium* Langsd. It is evident that *G. calthifolium* Menzies described in Rees' Cyclopaedia was based on the plant known as *Geum rotundifolium*. Scheutz seemed to be of a different opinion. He kept *Geum rotundifolium* and *G. calthifolium* distinct. His description of the latter (which by the way does not agree with that in Rees' Cyclopaedia) seems, however, to be drawn from specimens of *S. macrantha* Kearney or some related species and not from *S. calthifolia*.

*Sieversia macrantha* Kearney. This species was distinguished by Kearney and his description was found in the manuscript of the Flora of Alaska, which has been in preparation for many years by the botanists of the United States Department of Agriculture. As there was no telling when this work would be published, I adopted Kearney's name and description, with such slight modifications in form as to make it congruous with the general style used in the North American Flora. I have seen no specimens except those of the type collection. It may be possible that Scheutz drew his characterization of *G. calthifolium* from specimens of this species.

#### ACOMASTYLIS

As stated before, the writer agrees with Dr. Greene that the specimens referred to it should be removed from *Sieversia* as well as from *Geum*. They are closely related and the distinguishing characters are rather trivial, but as these trivial characters are supported by different ranges, the writer thinks they are of specific value.

*Acomastylis humilis* (R. Br.) Rydb. and *A. Rossii* (R. Br.) Greene. The former seems sometimes to grade into the latter, but as its range is much more limited than that of *A. Rossii*, it is at least a geographical species. It is confined in America to the Aleutian and Pribiloff Islands, but is also found in eastern Siberia, while *A. Rossii* extends well into Arctic America as far east as Melville Island.

*Acomastylis gracilipes* (Piper) Greene and *A. depressa* Greene are only known from the type collections. They are closely related to *A. sericea*, but the hypanthium is more flat, not turbinate as i



is in *A. sericea* and *A. turbinata*. *A. gracilipes* was first described as a *Potentilla*. In this respect it has had the same fate as *A. turbinata*.

*Acomastylis sericea* Greene has a more western and northern distribution than *A. turbinata* (Rydb.) Greene. The following specimens have been seen.

NEVADA: Ruby Mountains, *Heller 9139, 9359*; East Humbolt Mountains, *Watson 320*; same locality, *M. E. Jones 1897*.

IDAHO: Salmon River Mountains, *Henderson 4035*.

MONTANA: Indian Creek and Pony, *Rydberg & Bessey 4416, 4417*; Spanish Peaks, *Flodman 608*; Belt Mountains, *Scribner 40*; Rone Mountain, *Chestnut 9*.

WYOMING: Wind River Mountains, *V. Bailey*; northwestern Wyoming, *Rose 290*.

*Acomastylis turbinata* (Rydb.) Greene. The range of this species covers that of the preceding, but includes also Colorado, Utah, Arizona and New Mexico.

### COWANIA

*Cowania mexicana* D. Don is not found within the United States, and not even near the boundary. It is confined to central Mexico. The plant of southwestern United States and northern Mexico should be known as *C. Stansburiana* Torr., which differs in the form of the hypanthium and the lobing of the leaves. *C. mexicana* is represented by the following specimens:

MEXICO: Durango, 1896, *Palmer 12, 71*; *Nelson 4696*; Sierra Madre, *Seeman*; *Hartweg*.

*Cowania Davidsonii* Rydb. is closely related to *C. Stansburiana*, but differs in the elongated pedicels, the form of the hypanthium, etc. The following specimens belong to it:

ARIZONA: Blue River, September 8, 1902, *A. Davidson 754*; Castle Creek, Bradstran Mountains, 1892, *Toumey 129d*.

*Cowania alba* Goodding is unknown to me, except as to a poor fragment collected by Purpus and as to the descriptions. Purpus' specimens may well represent a hybrid of *C. Stansburiana* and *Kuntzia tridentata*.

*Cowania ericaefolia* Torr. and *C. Howardi* S. Wats. are the same. The writer has seen the types of the two, which are



identical, but no other specimens. The species must be very local.

### FALLUGIA

Three species have been proposed in this genus, viz. *F. paradoxa* (D. Don) Endl., *F. acuminata* Cockerell and *F. micrantha* Cockerell. Besides, the first has had two additional specific names, viz. *Geum cercocarpoides* DC. and *Fallugia mexicana* Walp. It has been impossible for the writer to distinguish more than one species, for the lobing or not lobing of the sepals is very inconstant, the same individual having both lobed and unlobed sepals, and the size of the petals is so variable, that no line can be drawn between *F. acuminata* and *F. micrantha*. In the essentially staminate plant the petals are usually larger.

### KUNTZIA vs. PURSHIA

Dr. Greene,\* when adopting the name *Kuntzia* instead of *Purshia*, made the following remarks: "A well-known rosaceous type of Rocky Mountain and Californian shrub, at first referred to the South American genus *Tigarea*, was taken up by the elder De Candolle in 1818, as a new genus, under the name *Purshia*. Sprengel, who about a year earlier, had himself published a genus *Purshia*, soon after proposed *Kuntzia* for the name of the Candollean *Purshia*; and this will apparently be the proper name for the western genus now called *Purshia*, which latter name is more than once revertible; for Rafinesque had a *Purshia* in print as early as 1813. I find no record of any earlier *Kuntzia* than this of Sprengel, which most writers who have mentioned it, say was substituted for the Candollean *Purshia* in Sprengel's *Systema*, 1825; but I find it four years earlier than that, in the first edition of Steudel's *Nomenclator* (1821)."

There is more than one correction to be made in the above statement. *Purshia* DC. was not published in 1818. The publication is usually cited as *Purshia* DC., *Trans. Linn. Soc. Bot.* 12: 157. 1818. The title page of that volume bears the year 1818, but the first part of it, in which *Purshia* appears, was published in 1817. The first publication of *Purshia* Sprengel was neither in his *Systema* (1825), nor in Steudel's *Nomenclator*, but in

\* *Pittonia* 2: 298. 1892.



Sprengel's *Anleitungen*,\* 1817. Then comes the question which was the earlier, *Purshia* DC. or *Purshia* Spreng. Fortunately, Sprengel himself when proposing *Kuntzia* gave under *Purshia* DC., which he replaces, a reference to the Supplement to Lamarck's *Encyclopedie Methodique*,† where Poiret publishes *Purshia* for De Candolle, the year before its technical publication by De Candolle in the Transactions of the Linnean Society. There is, therefore, no question concerning *Purshia* DC. antedating *Purshia* Spreng. But how about *Purshia* Raf.? I have been unable to find it mentioned in any of Rafinesque's writings of 1813. The Kew Index gives the publication of *Purshia* Raf. as "Am. Month. Mag. (1819) 191." At the place referred to we find only the following remarks under *Onosmodium*: "Sprengel has since given it the name *Purshia*, which had already been applied to another genus." Nobody can tell if this refers to an earlier *Purshia* Raf. It may just as well refer to the earlier *Purshia* DC. Apparently the first appearance of *Purshia* Raf. was in *Journal de Physique*‡ in 1819. It is evident that *Purshia* DC. can not be thrown out on any other ground than by regarding *Burshia* Raf. (1808) an error in orthography. It was not a misprint, for Rafinesque states that it was named after Mr. Bursh and on the unpublished plate of Rafinesque's, the original spelling is *Burshia*.

#### CHAMAEBATIA

*Chamaebatia australis* (Brand.) Abrams has been collected in Lower California by Orcutt and Miss Irish and in southern California by Pringle in 1882 and by Chandler, no. 5214.

#### CERCOCARPUS

*Cercocarpus macrophyllus* C. K. Schneider is the most common of the Mexican species of *Cercocarpus*. Most of the material labeled as *C. fothergilloides* belongs to this species. Some of the specimens are cited below.

VERA CRUZ: Orizaba, 1892, *J. G. Smith* 199; Cuerta de San Juan del Estada, *Liebman* 1719.

HIDALGO: Pachuca, 1905, *Purpus* 1139.

\* Ed. 2, 2: 450. 1817.

† v. 4: 623. 1816.

‡ 89: 257. 1819.



JALISCO: *Leon Dequet*.

OAXACA: 1894, *Pringle 5871*.

GUERRERO: Chipancingo, 1903, *Nelson 7068*; between Chilapa and Texla, 1894, *Nelson 2168*.

*Cercocarpus fothergilloides* HBK. To this species the following are to be referred.

PUEBLA: Cerro de Paxtle, *Purpus 4200*.

VERA CRUZ: Orizaba, *F. Mueller*.

*Cercocarpus Traskiae* Eastw. has not been collected outside of Santa Catalina Island, California.

*Cercocarpus mojadensis* C. K. Schneider. To this belongs the following specimens:

COAHUILA: Sierra Mojada, 1892, *M. E. Jones 134*; Sierra de Plata, 1905, *Purpus 1059*; San Lorenzo Canyon, 1905, *Palmer 537*.

*Cercocarpus Pringlei* (C. K. Schneider) Rydb. This was originally described as a variety of *C. mojadensis*, but I think it is specifically distinct.

*Cercocarpus macrurus* Rydb. This is the *C. parvifolius* of the Klamath and Siskiyou region of California and Oregon. It is nearest related to *C. montanus* Raf., differing in the longer leaves with more numerous lateral veins and the large fruit. Although the characters separating it from *C. montanus* on one hand and *C. Douglasii* on the other are not so striking, it is geographically separated from both, the former being limited to the Rockies and the latter to central and southern California. The following specimens belong to it:

CALIFORNIA: Siskiyou Mountains, 1880, *Engelmann* (fruit); same locality, 1866, *Henderson* (flowers); Ashland, 1866, *Henderson 259* (flowers and young fruit); Klamath River at Keno, *Cusick 2835*; Klamathon, 1903, *Copeland 3504*; no locality, *Wilkes Expedition 1167*.

OREGON: Weiner, 1898, *Walpole 81*; Barclay Springs, Modoc Point, *Coville 1523* in part.

*Cercocarpus montanus* Raf. There have been two species confused under the name of *C. parvifolius* Nutt. even from its first description in the Botany of Beechey's Voyage by Hooker & Arnott. These authors adopted Nuttall's manuscript name, but included in their description not only Nuttall's type from the Rockies but



also specimens collected by Douglas in California. The latter were the base of the description and figure in Hooker's *Icones*, plate 323. It is a question whether Hooker & Arnott did not have Douglas's specimens in mind when they drew the description of *C. parvifolius*. It would, therefore, be some doubt as to which the name *C. parvifolius* should be applied, the low shrub of the Rocky Mountains or the more tree-like one from southern and central California. Sargent referred both to *C. parvifolius*, while C. K. Schneider, who without question has done the best and most critical work on the genus, referred the latter to *C. betulaeifolius*, yes, even made it the "var. *typicus*" of that species. Schneider laid more stress on the form and size of the teeth of the leaves and in this respect Douglas's plant is more like *C. betuloides*. If the pubescence and leaf-form are considered, it resembles more the plant of the Rockies. As said before, it is doubtful which of the two should be regarded as *C. parvifolius*. As Nuttall's plant is included in the original description it must be regarded as the type, but unfortunately, or rather fortunately, it (i. e. the Rocky Mountain shrub) had already a name, *C. montanus* Raf., based on *C. fothergilloides* Torrey, not that of Humboldt, Bonpland and Kunth; and *C. parvifolius* becomes a synonym. Hence the more tree-like species of California, represented by Douglas's specimens, was left without a name, and the writer proposed the name *C. Douglasii* in the North American Flora.

*Cercocarpus Douglasii* Rydb. See the discussion above. Of this species I have seen many specimens. They are all from California, except the following:

ARIZONA: Jucumba Hot Springs, 1894, *Schoenfeldt* 335.

LOWER CALIFORNIA: Nachaguere Valley, 1894, *Schoenfeldt* 3432 and *Mearns* 3390.

*Cercocarpus rotundifolius* Rydb. This is related to the preceding species, but differs in the small broad rounded-oval leaves; in *C. Douglasii* the leaves are obovate or oblanceolate, distinctly cuneate at the base. To *C. rotundifolius* belongs the following specimens:

CALIFORNIA: Los Angeles County, 1901, *Grant* 3488; 1850, *C. C. Parry*; 1890, *H. E. Hasse*.

LOWER CALIFORNIA: mountains, 1882, *Pringle*.



*Cercocarpus alnifolius* Rydb. This is the same as *C. betulaeifolius Blancheae* of C. K. Schneider, mainly; although that author had included some specimens of *C. Douglasii* mixed in with the type. As a species had already been named after Mrs. Blanche Trask, viz. *C. Traskiae*, it would be bad taste to propose another one. Besides personally I dislike the use of the given name of a person as forming the specific name. I, therefore, adopted the more appropriate *C. alnifolius* instead of the varietal name *Blancheae*. This species is also endemic to Santa Catalina Island, California.

*Cercocarpus betuloides* Nutt. Hooker in his *Icones* changed the name to *C. betulaeifolius*, which form has been more commonly adopted than the original. It has also been regarded as a variety of *C. parvifolius* Nutt., i. e. of *C. montanus* Raf., but is evidently distinct.

*Cercocarpus minutiflorus* Abrams. Nothing further has been added to the knowledge of this species since its publication.

*Cercocarpus flabellifolius* Rydb. In Utah and northwestern New Mexico is found a mountain mahogany, having the pubescence of the Californian *C. betuloides* and the coarse toothing of the leaves of *C. montanus*. It has obovate leaves as the latter, but much broader and with more flaring teeth. This character is best seen in the type collected by L. F. Ward. The following specimens are to be referred here:

UTAH: Glenwood, 1875, *Ward 122*; western slope of La Sal Mountains, 1911, *Rydberg & Garrett 8566*; south side of Abajo Mountains, 9275; Juab, 1902, *Goodding 1073*; Silver Reef, 1894, *Jones 5163, 5163b*; Lacolite, *Jones 5663, 5204e*; Marysvale, *Jones 5405d*; Cedar City, *Jones 5208, 5404d*; Salina Canyon, *Jones 5441m*; Fish Creek Canyon, 1909, *Garrett 2523*.

NEW MEXICO: Aztec, 1899, *Baker 384*.

*Cercocarpus argenteus* Rydb. This is related to *C. montanus*, but the pubescence is appressed-silky, the leaves narrower, toothed above the middle with smaller teeth. The following specimens belong here:

TEXAS: Randall County, *Eggers*; Llano Estacado, *Bigelow* (Whipple Exp.); Guadalupe Mountains, 1901, *Bailey 436*.

NEW MEXICO: El Capitan Mountains, 1900, *Earle 209*; same



locality, *Plummer*; Winsor's Ranch, 1908, *Standley 4104*; Ratan Mountains, 1903, *Griffiths 5497*; White Mountains, 1907, *Wooton & Standley 3606*; Sacramento Mountains, 1899, *Wooton*; Las Vegas, 1891, *Dewey*; Folsom, 1903, *A. Howell 171*.

COLORADO: North Cheyenne Canyon, 1894, *E. A. Bessey*.

*Cercocarpus paucidentatus* (S. Wats.) Britton. This species was based on *Cercocarpus parvifolius paucidentatus* S. Wats. In order to determine the type of the species, we must find the type of the variety. The latter was based on *Shaffner 114*, *Parry & Palmer 224\** from San Louis Potosi, and *Wright 1056* from Texas or eastern New Mexico. The first, *Shaffner 114*, must be regarded as the type, but *Parry & Palmer 225* is the same. Upon this very number C. K. Schneider based his *C. Treleasii*, which therefore becomes a synonym. *Wright 1056* belongs to another species, the same as Wilcox's specimen from which Britton mainly drew his description of *C. paucidentatus*. This was without a specific name, and I adopted Schneider's varietal name for it. The following specimens belong to *C. paucidentatus* (S. Wats.) Britton or *C. Treleasii* C. K. Schneider.

SAN LOUIS POTOSI: *Shaffner 114*, 476, 635; *Parry & Palmer 225*.

HIDALGO: Ixmiquelpan, 1905, *Purpus 1383*.

*Cercocarpus eximius* (C. K. Schneider) Rydb. This is *C. paucidentatus* Britton, mainly as to the description, but not the type. Sargent regarded it as the same as *C. brevifolius* A. Gray. Schneider first admitted it as a variety *eximius*, but afterwards adopted Sargent's views. He, however, did not have a clear conception of the same, for *Rusby 125* and other specimens with better developed and more toothed leaves, he referred doubtfully to *C. betulaefolius*. Leaves toothed above the middle are not uncommon and sometimes found together with perfectly entire-margined leaves on the same bush. It is to be admitted that it is closely related to *C. breviflorus*, but differs in the spreading pubescence and the longer hypanthium. It is also much more common than *C. brevifolius* and its range extends through New Mexico, Arizona, Chihuahua and Sonora.

\* This is evidently a misprint for 225, because *Parry & Palmer 224* is a species of *Rubus* and also cited by Watson under *Rubus trivialis*. It is now known as *R. oligospermus* Thornber.



*Cercocarpus breviflorus* A. Gray. This has nearly the same range as the preceding, but is more eastern, being found also in western Texas and Coahuila. It is, however, lacking in Sonora and western Arizona.

*Cercocarpus ledifolius* Nutt. is the most widely distributed species of the genus. Its characters are rather constant. It varies, however, in the width of the leaves and in the margin being more or less revolute. *Cercocarpus ledifolius intercedens subglabra* C. K. Schneider is either an extremely narrow-leaved form or else a hybrid with *C. intricatus*.

*Cercocarpus hypoleucus* Rydb. This has been mistaken for both *C. ledifolius* and *C. intricatus*, but the villous pubescence of the lower surface of the leaves should exclude it from either, though it may cause some confusion with *C. arizonicus*. It has smaller, narrower leaves with sharper petioles than *C. ledifolius*, but larger leaves, less enrolled, and larger fruit than *C. intricatus* and *C. arizonicus*. The following specimens are referred here:

MONTANA: Melrose, 1895, *Rydberg 2695; Shear 3216; Red Rock, Shear 3349; Helena, 1908, Butler 713, 774; Tobacco Mountain, Butler 4236; Montana, Kelsey; Lombard, 1900, Blankinship.*

WYOMING: Wolf Creek Canyon, *A. Nelson 2292; between Sheridan and Buffalo, 1900, Tweedy 3236; Big Horn, 1899, Tweedy 2540; Powder River, 1901, Goodding 252; 1893, Evermann; Big Horn Basin, 1893, V. Bailey; Tongue River, 1898, Tweedy 39.*

IDAHO: Salmon River, *Henderson 3143 and 3790; V. Bailey 49.*

UTAH: Raft River, *S. Watson 313 in part.*

OREGON: Snake River, 1897, *Sheldon 8201.*

*Cercocarpus intricatus* S. Wats. M. E. Jones reduced this to a variety of *C. ledifolius*, claiming that they grade into each other; and still he proposed a new species *C. arizonicus*, which is much closer to *C. intricatus* than *C. ledifolius* is. I have seen the specimens from Willow Spring, Arizona, on which *C. arizonicus* was based and these are identical with Jones's own specimens from Deep Creek, determined by Jones as *C. ledifolius intricatus*. It is evident that Jones did not distinguish these species very well. Some of Jones's specimens are evidently hybrids. See below. The range of *C. intricatus* includes parts of Utah, Arizona and Nevada. A specimen from California, but with much shorter



leaves, scarcely 5 mm. long, is referred doubtfully to this species. It is *Vernon Bailey 2019* of the Death Valley expedition.

*Cercocarpus arizonicus* Jones. This species is much more local than *C. intricatus*. It is closely related to it, perhaps not distinct. If *C. hypoleucus* were found in the region this might be a hybrid between that species and *C. intricatus*.

UTAH: Deep Creek, 1891, *M. E. Jones*; Tropic, 1894, *Jones*.

NEVADA: Rock Mountains, 1898, *Purpus 6336?*

#### HYBRIDS

Mr. Coville has collected specimens which are without doubt a hybrid between *C. ledifolius* and *C. macrurus*. A specimen of the hybrid and one of each of the two parents is mounted on the same sheet, his *no. 1523* in the National Herbarium. When these two species hybridize, it would be expected that some of the more closely related species might do so. This may explain some of the intermediate forms between *C. betuloides* and *C. Douglasii*, between *C. montanus* and *C. flabellifolius*, and between *C. ledifolius* and *C. intricatus*.

Also a specimen collected by *M. E. Jones* at Silver Reef in 1894 seems to be a hybrid of *C. ledifolius* and *C. arizonicus*. A specimen of the latter is included under the same number, *5149k*, and *C. ledifolius* is found in the region.

NEW YORK BOTANICAL GARDEN







## New or notable species of *Amaranthus*\*

PAUL C. STANDLEY

The two new species of *Amaranthus* described below were detected by the author while revising this genus for the North American Flora. It was scarcely to have been expected that many undescribed species would be discovered in this group, most of whose members are widely distributed weeds of waste or cultivated ground. Some of the West American species, however, are restricted locally to rocky canyons, gravelly mesas, and sandy beaches; it is to this group that the two new species belong. There are included here notes upon some of the earlier species which have not been well understood. The distribution of *Amaranthus retroflexus* is also discussed.

### *Amaranthus Watsoni* Standley sp. nov.

*Amaranthus Torreyi suffruticosus* Uline & Bray, Bot. Gaz. 19: 272.  
1894.

Stems stout or slender, 1.5 to 10 dm. high, erect or ascending, branched, obtusely angled, glandular-puberulent or short-villous, densely glandular above; petioles slender or stout, 0.5-6.5 cm. long; leaf blades rhombic-oval to rounded-ovate or oblong, 1-8 cm. long, obtuse to truncate at the apex and usually emarginate or even deeply retuse, acutish or rounded at the base, sometimes slightly decurrent, rather thick, deep green or yellowish green, glandular-puberulent, at least beneath, often densely so on both surfaces; flowers dioecious, in axillary clusters, especially in the pistillate plants, and in terminal, often paniculate, erect or drooping spikes, these 4-16 cm. long and 6-14 mm. in diameter; bracts lanceolate, longer than the flowers, attenuate to the subulate tips, glandular-puberulent; sepals of the staminate flowers 3-4 mm. long, oblong, obtuse or acutish, 1-nerved, the nerve excurrent; sepals of the pistillate flowers slightly united at the base, broadly spatulate, 2.5 mm. long, broadly rounded at the apex, usually emarginate, 1-nerved, the nerve sometimes excurrent in the outer sepals; stamens 5; style branches 2; capsule subglobose, circumscissile; seeds dark reddish brown, 0.6 mm. in diameter, rotund.

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Type in the U. S. National Herbarium, 692084, collected in the vicinity of Guaymas, Sonora, Mexico, in 1887, by Dr. Edward Palmer (312).

This sheet consists of pistillate specimens. As typical of the staminate plant may be taken sheet no. 692083, collected at the same locality in the same year by Dr. Palmer, under his number 675. Additional specimens examined. SONORA: Guaymas, 1887, *Palmer 676*. LOWER CALIFORNIA: La Paz, near sea level, February 17, 1906, *Nelson & Goldman 7532*; between Santo Domingo and Matancita, alt. 15 to 30 meters, November 14-15, 1905, *Nelson & Goldman 7282*; Cape St. Lucas, *Xantus 100*.

The proposed species is related to *Amaranthus Palmeri* S. Wats., and the type collection was determined by Dr. Watson as that species. It is readily distinguished by its glandular pubescence, relatively broader, very obtuse, emarginate leaves, and shorter bracts. The staminate spikes, too, are less dense and usually considerably thicker. Both species were collected by Dr. Palmer at Guaymas, and it is possible that in some cases they were distributed under the same number.

*Amaranthus Torreyi suffruticosus* is doubtless to be placed here, although the specimens are so old and fragmentary that they do not represent the species well. It would be unfortunate to retain the name *suffruticosus*, since the plant is as truly herbaceous as all the other North American members of the genus.

#### ***Amaranthus myrianthus* Standley sp. nov.**

Stems prostrate or ascending, 3-10 dm. long, much branched, stout, succulent, glabrous or sparsely villous; petioles stout, 4-15 mm. long; leaf blades rounded-oval to oval or nearly orbicular, 6-20 mm. long, 5-15 mm. wide, rounded or emarginate at the apex, rounded to cuneate at the base, thick and firm, very conspicuously veined, villous beneath, at least when young; inflorescence dioecious, of numerous paniculate many-flowered spikes, these dense or sometimes interrupted below, 6-40 cm. long and 1-2 cm. thick in the pistillate plants, the spikes of the staminate plants shorter, somewhat interrupted, few-flowered, 7 mm. or less in diameter; bracts 2 or 3 at the base of each flower, ovate or broadly ovate, acute, sometimes pungent-tipped, usually half as long as the sepals but sometimes nearly equaling them; sepals of the staminate flowers oblong to oval, 2.5 mm. long, obtuse,



apiculate, thin and scarious except along the single green nerve; sepals of the pistillate flowers 2 mm. long, spatulate, or narrowly oblong and narrowed toward the base, broadly obtuse to acutish, glabrous, rather thick and firm, much thickened and united at the base, the midnerve usually excurrent; stamens 5; style branches 3, slender, elongate, divaricate; utricle obovoid, about equaling the sepals, thin-walled, nearly smooth, circumscissile; seed rotund, black and shining, about 1 mm. in diameter.

Type in the U. S. National Herbarium, 463205, collected in the vicinity of La Barra, 8 kilometers east of Tampico, Tamaulipas, Mexico, at sea level, February 1-8, 1910, by Dr. Edward Palmer (266). Additional material of the same collection is mounted on sheet 463206.

In general appearance this is similar to *Amaranthus Greggii* S. Wats., a species with indehiscent fruit. The form of the fruit and bracts would suggest a relationship with *A. Torreyi*, but that has erect stems, narrower leaves, larger flowers, and narrow bracts, while the form of the inflorescence is very unlike in the two species.

AMARANTHUS GREGGII S. Wats. Proc. Amer. Acad. 12: 274. 1877

Watson based this species upon specimens collected by Gregg in Mexico, at the mouth of the Rio Grande, in 1848 or 1849. Uline and Bray\* in their monograph of the North American species of *Amaranthus* say: "The fact that but one locality has ever been reported, and that only the pistillate flowers and the upper part of the plant are in existence, places this species on a rather perilous footing." Mr. G. L. Fisher, however, has re-collected the plant recently at Galveston, Texas. On September 8, 1912, he gathered pistillate specimens along the beach at Galveston (102), and on September 1, 1913 he revisited the locality, securing both staminate and pistillate plants (605, 612). His specimens agree very well with the type in the Gray Herbarium, which the writer has examined through the courtesy of Dr. B. L. Robinson. Mr. Fisher states that the plant is abundant on sand along the Gulf shore about 400 feet from water. The new locality represents a considerable extension of range for this species which no doubt will be found at intervening points along the Texan coast.

\* Bot. Gaz. 19: 271. 1894.



The species is very distinct, differing from most of its relatives in its tough-walled, indehiscent fruit. The branches are nearly a meter long or shorter, succulent, sparingly branched, and procumbent or ascending. Watson described the pistillate sepals as acute, but in both the type and the Texan specimens the inner ones are rounded or obtuse, while the outer ones are acute, or frequently obtuse.

AMARANTHUS BRACTEOSUS Uline & Bray, Bot. Gaz. 19: 314. 1894  
*Amaranthus viscidulus* Greene, Pittonia 3: 344. 1898.

The type of *A. bracteosus* (in the Gray Herbarium) was collected by Fendler (735), probably near Santa Fe, New Mexico. *Amaranthus viscidulus* was based upon Wooton's 300 from the White Mountains, New Mexico, the specimens having been collected at Gilmore's Ranch on Eagle Creek. Upon a superficial examination the two appear distinct, but more careful comparison has convinced the writer that they are the same species. The type of *A. bracteosus* appears to be a plant grown in wet soil, for it is very stout and has large leaves, while very little pubescence is present. The type of *A. viscidulus* is a smaller plant with a more slender stem, smaller leaves, and abundant viscid-villous pubescence. Both are very unlike any other American species. They agree perfectly in the peculiar form of the bracts and fruit, and in having the petioles longer than the leaf blades. These differences are probably correlated with habitat. A greater amount of moisture would be expected to produce a larger, less pubescent plant like *A. bracteosus*. No specimens corresponding to Fendler's plant have been collected recently in New Mexico, although several botanists have worked in the region from which it came. On the other hand, *Amaranthus viscidulus* has been collected several times, not only in the White Mountains but at Pecos (*Standley 5149*), a locality not far distant from Santa Fe. Fendler visited Pecos at least twice and it may be that he collected the type of *A. bracteosus* there.

In a recent treatment of the genus *Amaranthus*, Dr. Thellung\* has confused this with *A. pubescens* (Uline & Bray) Rydb., adopting the name *viscidulus* and citing *pubescens* as a synonym. His description applies wholly to the latter species. *Amaranthus*

\* In Asch. & Graebn. Syn. Fl. Mitt. Eur. 5: 289. 1914.



*viscidulus* is readily separated by its larger, rounded leaves, longer bracts, spicate rather than axillary inflorescence, and 5 instead of 3 sepals in the pistillate flowers.

In their original description of *A. viscidulus*, Uline and Bray cite also a cultivated specimen in the National Herbarium. This appears to be nothing more than a somewhat abnormal form of *A. hybridus*.

AMARANTHUS ACUTILOBUS Uline & Bray, Bot. Gaz. 19: 320. 1894  
*Euxolus emarginatus* A. Br. & Bouché, Ind. Sem. Hort. Berol. 1851; Linnaea 25: 297. 1853. Not *Amaranthus emarginatus* Salzm.; Uline & Bray, 1894.

This was originally described as having come from Mexico. The authors do not cite the name of the collector, and it is probable that the description was based upon cultivated plants grown from seeds believed to have come from Mexico. In the herbarium of the Missouri Botanical Garden is a specimen collected by A. Braun in 1857, in the Royal Botanical Garden at Berlin, where it is said to have escaped ("verwildert") from cultivation. No other collection than the original one has ever been reported from Mexico. Thellung\* reports the species as adventive in Germany at Berlin, Dresden, and Mannheim, and in Austria at Vienna and Prague.

Recently, while examining the *Amaranthus* material in the herbarium of the Missouri Botanical Garden, the writer found four sheets of a species which at first was not recognized. Upon examining the flowers it was soon apparent that the plants were *Amaranthus acutilobus*, although in general appearance they were unlike cultivated specimens of that species, having longer, less fleshy, more slender stems and smaller leaves. All four sheets are from southern Italy, one having been collected at Naples in 1871 or 1872, and three at Gioja, Calabria, in 1871 and 1872. Upon one of the sheets from Gioja is a specimen of *Amaranthus crassipes* Schlecht., a species known only from the West Indies and peninsular Florida. This indicates that the material was carelessly prepared, for it is not probable that this species has been introduced in Italy. The occurrence of *A. acutilobus* in Italy is of great interest, for it suggests a possibility that the

\* In Asch. & Graebn. Syn. Fl. Mitt. Eur. 5: 282. 1914.



species may be a native of that region rather than of Mexico. Until the plant is re-collected in the latter country, its occurrence there must remain very doubtful.

The name *acutilobus* adopted by Uline and Bray in renaming this species is an inappropriate one, for the lobes of the leaves are not acute but rounded or obtuse.

#### AMARANTHUS RETROFLEXUS L.

In practically every manual of North American botany the statement is made that this species has been introduced into the United States from tropical America. The writer has seen a large series of specimens of the plant from North America and from the Old World, but he has seen none from Mexico or Central America. Probably it does reach northern Chihuahua and Sonora, since it is found in New Mexico and Arizona not far from the Mexican border. The species is not known to occur in South America.

Linnaeus based his description upon plants said to come from Pennsylvania. It is probable that the species is a native of the southeastern part of the United States. It is apparently most abundant in the east, although it is found throughout the United States and in southern Canada. In the west it grows usually in localities where it might easily have been naturalized, but the same may be said of its occurrence in the east. *Amaranthus retroflexus* is now thoroughly established in many parts of Europe, Asia, and Africa.

WASHINGTON, D. C.



## The introduced vegetation in the vicinity of Douglas Lake, Michigan\*

HENRY ALLAN GLEASON AND FRANK THEODORE MCFARLAND

Throughout the eastern states the number of introduced species is one of the most remarkable features of the flora. These plants, originating in widely separated regions, are unusually well fitted by their habits of growth, by their physiological demands, by the amount of seed which they produce, or by the nature of their dissemination to exist in the immediate proximity of civilization. An increasing density of population, up to certain limits, merely creates new habitats for them, extends their old ones, or facilitates their seed dispersal. Most of them are unable to compete with native species, except when favored by human operations, and are not found far beyond cultivated ground. In this they differ radically from native plants, which rapidly decrease in number of species under the influence of civilization, so that there are in the eastern states very few species of native weeds.

The extensive areas of unsettled land in the vicinity of the biological station of the University of Michigan afford a good opportunity for the study of the distribution and behavior of the foreign species, and some of the results of this study are here presented.

Douglas Lake, just south of the Straits of Mackinac, lies in a gently rolling country of glacial origin. Most of the land to the south, west, and east of the lake is sand, and formerly supported a magnificent growth of white and Norway pines. This was lumbered about thirty years ago and no virgin area of pine forest now exists in the region. The pine land has been burned over repeatedly, and is now occupied by a sparse growth of aspens, *Populus grandidentata* predominating, mixed with various other species in smaller proportion. Practically none of this land is actually under cultivation.

North of the lake some morainic ridges rise high above the

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\* Publication no. 27 from the Biological Station of the University of Michigan.



surrounding country, and the soil is of clay or of sand well mixed with humus. Both soil types were occupied with a dense forest of hardwoods, chiefly *Fagus grandifolia* and *Acer saccharum*, with a good mixture of *Tsuga canadensis*. Most of this has been lumbered within the past five years, and only small untouched areas are now remaining. Besides these two predominating types of vegetation, there are some rather extensive swamps with a dense growth of *Thuja occidentalis*, smaller tamarack and sphagnum bogs, and the usual small areas of marsh and dune vegetation along the shore of the lake. A full account of these has been published by Gates.\*

On the north shore of the lake are some small and scattered farms, separated by woods or slashings, and several summer cottages. On the south side of the lake is one small summer resort, with about half a dozen cottages and the biological station and engineering camp of the University of Michigan. Otherwise the shore and immediate vicinity of the lake are uninhabited.

The known flora of the Douglas Lake region includes over 650 species of flowering plants and ferns. These species have been collected not merely over the unsettled area adjacent to the lake, but also from the settlements, extending in some directions as far as six miles away from the lake. Of these 650 species, 94 are considered as introduced into the Manual range by Robinson and Fernald in the seventh edition of Gray's Manual. Seventeen other species, considered to be native by these authors, are undoubtedly introduced into the Douglas Lake region. These are *Panicum capillare*, *Agrostis alba*, *Poa pratensis*, *Hordeum jubatum*, *Polygonum aviculare*, *Polygonum erectum*, *Amaranthus blitoides*, *Amaranthus graecizans*, *Euphorbia maculata*, *Euphorbia hirsuta*, *Verbena bracteosa*, *Plantago major*, *Silphium laciniatum*, *Silphium terebinthinaceum*, *Iva xanthifolia*, *Ambrosia psilostachya*, and *Helianthus annuus*. Nine other species are probably introduced, although the evidence is by no means certain. These are *Humulus Lupulus*, *Chenopodium hybridum*, *Lepidium virginicum*, *Lepidium apetalum*, *Lappula deflexa*, *Ambrosia artemisiifolia*, *Rudbeckia hirta*, *Achillea Millefolium*, and *Artemisia ludoviciana*.

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\* Frank C. Gates, The vegetation of the region in the vicinity of Douglas Lake, Cheboygan County, Michigan, 1911. 14th Rep. Mich. Acad. Sci. 46-106. pl. v-xxib. 1913.



The total number of introduced species is then apparently 120, or 18 per cent. of the total flora. This corresponds very closely to the proportion for the whole Manual range, which is 19 per cent., according to the tabulation in the seventh edition of the Manual. The systematic distribution of the 120 species is quite interesting, and differs markedly from that of the introduced flora of the whole Manual range. Among them are 24 composites, 16 grasses, 10 mints, 10 legumes, 9 mustards, 9 pinks, and 8 polygonads. These seven families include therefore nearly three quarters of the whole. The first two families contribute also about 76 native species to the flora of the region, but the last five are represented here chiefly by their 46 introduced species, and have but 31 native members in the known flora. For each of these seven families, the proportion of introduced species is considerably in excess of the general proportion for the Manual range. Of the pinks, 87 per cent. are introduced, compared with 47 per cent. in the Manual range, while for the other families the proportions are for the legumes 78 per cent., crucifers 53 per cent., polygonads 53 per cent., mints 47 per cent., composites 36 per cent., and grasses 34 per cent., compared with 20 per cent., 45 per cent., 24 per cent., 35 per cent., 17 per cent., and 17 per cent., respectively, for the Manual region as a whole. No definite reason can be assigned for the unusually large proportion of introduced species in these particular families, but it may be possible that the Douglas Lake region lies too far north for most of the native species.

Of these 120 species, a considerable number have been found only in the immediate vicinity of civilization and at a considerable distance from Douglas Lake. The railroad tracks and vacant lots at Pellston have furnished a number, and several more species have escaped from cultivation in the thickly settled neighborhoods east of the lake. These plants have shown no tendency to establish themselves in the uncultivated region, or to follow the progress of civilization into it, and will accordingly receive no further attention in this paper.

For convenience, the introduced flora will be considered under three heads, that of summer resorts, of roads and clearings in the hardwoods, and of roads and clearings in the aspen land.



## THE INTRODUCED FLORA NEAR SUMMER RESORTS

At Ingliside, at the northwest corner of the lake, are two permanent residences and several summer cottages. A wagon road leads to Levering, about five miles away, and is well travelled. Very few farming operations are under way in the vicinity, and the introduced species are practically confined to dooryards and kitchen gardens. The whole settlement occupies not to exceed six acres, and the following introduced species occur:

<i>Poa compressa</i>	<i>Brassica arvensis</i>
<i>Poa pratensis</i>	<i>Sedum acre</i>
<i>Agrostis alba</i>	<i>Trifolium repens</i>
<i>Phleum pratense</i>	<i>Trifolium pratense</i>
<i>Setaria viridis</i>	<i>Trifolium hybridum</i>
<i>Agropyron repens</i>	<i>Euphorbia Cyparissias</i>
<i>Bromus secalinus</i>	<i>Malva rotundifolia</i>
<i>Rumex elongatus</i>	<i>Cynoglossum officinale</i>
<i>Polygonum aviculare</i>	<i>Lappula deflexa</i>
<i>Polygonum Persicaria</i>	<i>Solanum nigrum</i>
<i>Polygonum Convolvulus</i>	<i>Verbascum Thapsus</i>
<i>Chenopodium album</i>	<i>Nepeta Cataria</i>
<i>Amaranthus retroflexus</i>	<i>Plantago major</i>
<i>Arenaria serpyllifolia</i>	<i>Plantago lanceolata</i>
<i>Cerastium vulgatum</i>	<i>Ambrosia artemisiifolia</i>
<i>Silene noctiflora</i>	<i>Iva xanthifolia</i>
<i>Lychnis alba</i>	<i>Anthemis Cotula</i>
<i>Lepidium virginicum</i>	<i>Achillea Millefolium</i>
<i>Capsella Bursa-pastoris</i>	<i>Chrysanthemum Balsamitae</i>
<i>Sisymbrium altissimum</i>	var. <i>tanacetoides</i>
<i>Sisymbrium officinale</i>	<i>Arctium minus</i>
var. <i>leiocarpum</i>	<i>Taraxacum officinale</i>

Of these 42 species, three are obviously escaped from cultivation, *Euphorbia Cyparissias*, *Sedum acre*, and *Chrysanthemum Balsamitae* var. *tanacetoides*.

About half a mile east of Ingliside along the lake shore is another summer colony of four cottages, located in a gravelly pastured field. The occupants reach their cottages chiefly by boat from Ingliside, thus reducing the opportunity for the chance introduction of plants. Here the introduced flora is composed of the following 26 species:



<i>Poa pratensis</i>	<i>Trifolium repens</i>
<i>Poa compressa</i>	<i>Trifolium pratense</i>
<i>Phleum pratense</i>	<i>Trifolium hybridum</i>
<i>Agrostis alba</i>	<i>Lappula deflexa</i>
<i>Setaria viridis</i>	<i>Cynoglossum officinale</i>
<i>Rumex Acetosella</i>	<i>Verbascum Thapsus</i>
<i>Rumex elongatus</i>	<i>Nepeta Cataria</i>
<i>Polygonum Convolvulus</i>	<i>Plantago major</i>
<i>Arenaria serpyllifolia</i>	<i>Plantago lanceolata</i>
<i>Silene noctiflora</i>	<i>Chrysanthemum Leucanthemum</i>
<i>Sisymbrium altissimum</i>	var. <i>pinnatifidum</i>
<i>Sisymbrium officinale</i>	<i>Cirsium lanceolatum</i>
var. <i>leiocarpum</i>	<i>Taraxacum officinale</i>
<i>Capsella Bursa-pastoris</i>	<i>Lepidium virginicum</i>

About half a mile beyond this settlement, or a mile from Ingliside, is the most remote of the summer settlements, consisting here of but two cottages. They are located in a hardwood forest and have practically no cleared land around them. Here there is no introduced flora whatever, although some daisies planted around a veranda show a slight tendency to spread. Just behind these cottages along an abandoned logging road nineteen species of introduced plants occur.

These data, showing the reduction in the introduced flora from 42 species to none in a distance of a mile, indicate clearly the inability of the species to migrate without some effective human aid. The same feature is illustrated by the flora around or near Bryant's hotel, on the south side of the lake. Here is a wagon road from Pellston, and during the summer months the travel is quite heavy. All vehicles stop at or near the hotel, and persons desiring to reach the farther cottages walk down the beach. In the immediate vicinity of the hotel nineteen species occur. These are:

<i>Poa compressa</i>	<i>Polygonum Persicaria</i>
<i>Poa pratensis</i>	<i>Polygonum Convolvulus</i>
<i>Poa annua</i>	<i>Rumex elongatus</i>
<i>Agrostis alba</i>	<i>Rumex Acetosella</i>
<i>Phleum pratense</i>	<i>Chenopodium album</i>
<i>Polygonum aviculare</i>	<i>Chenopodium hybridum</i>



<i>Amaranthus retroflexus</i>	<i>Plantago major</i>
<i>Lepidium virginicum</i>	<i>Anthemis Cotula</i>
<i>Malva rotundifolia</i>	<i>Taraxacum officinale</i>
<i>Nepeta Cataria</i>	

In the dooryards of the cottages just beyond the hotel the number is reduced to thirteen:

<i>Poa compressa</i>	<i>Cerastium vulgatum</i>
<i>Poa pratensis</i>	<i>Trifolium repens</i>
<i>Agrostis alba</i>	<i>Trifolium hybridum</i>
<i>Phleum pratense</i>	<i>Verbascum Thapsus</i>
<i>Rumex elongatus</i>	<i>Achillea Millefolium</i>
<i>Rumex Acetosella</i>	<i>Taraxacum officinale</i>
<i>Chenopodium album</i>	

In the dooryards of the three cottages farthest from the hotel the number of species is reduced to seven only:

<i>Poa pratensis</i>	<i>Verbascum Thapsus</i>
<i>Poa compressa</i>	<i>Achillea Millefolium</i>
<i>Agrostis alba</i>	<i>Taraxacum officinale</i>
<i>Rumex elongatus</i>	

A quarter of a mile farther, in the small clearing around an abandoned Indian hut, *Dianthus barbatus* is escaped from cultivation, and fourteen introduced species occur. All of these are found also in the vicinity of the hotel, except *Capsella Bursa-pastoris* and *Trifolium pratense*.

Around the premises of the biological station a few species of introduced plants occur, but so far as known only one of them has been introduced since the opening of the station in 1909. The station occupies the site of a logging camp abandoned many years before, and the introduced flora is probably a relic of that time. Besides the species listed below, a solitary plant of *Satureja Acinos* was found in 1912, and young plants from its seeds were found again in 1914. It was probably introduced in packing material.

<i>Poa compressa</i>	<i>Secale cereale</i>
<i>Poa pratensis</i>	<i>Agropyron repens</i>
<i>Agrostis alba</i>	<i>Setaria viridis</i>
<i>Phleum pratense</i>	<i>Rumex Acetosella</i>
<i>Avena sativa</i>	<i>Rumex elongatus</i>



<i>Polygonum Convolvulus</i>	<i>Brassica arvensis</i>
<i>Chenopodium album</i>	<i>Trifolium pratense</i>
<i>Silene noctiflora</i>	<i>Verbascum Thapsus</i>
<i>Cerastium vulgatum</i>	<i>Achillea Millefolium</i>
<i>Lepidium virginicum</i>	<i>Taraxacum officinale</i>
<i>Capsella Bursa-pastoris</i>	

One interesting colony of introduced plants is found in a small clearing occupying a somewhat elevated spot in the midst of a cedar swamp. An old man has lived there alone for several years, but the clearing contained no introduced species until two years ago. At that time a small summer cottage was built there, and the new additions to the flora were probably brought in in packing material. At least most of them are found immediately in front of the door, where any goods would probably be unpacked. An area not more than a hundred feet in diameter contains 24 species. Most of them are found around other clearings also, but among them are a few not known to occur elsewhere in the uncultivated region. These are:

<i>Salsola Kali</i>	<i>Portulaca oleracea</i>
var. <i>tenuifolia</i>	<i>Solanum nigrum</i>
<i>Amaranthus blitoides</i>	<i>Sonchus asper</i>

These data summarized indicate that not to exceed 56 species out of 120 have succeeded in establishing themselves in the vicinity of the remote dwellings in this uncultivated region, and that the largest settlement, with two houses permanently occupied, supports 42 of these.

#### THE INTRODUCED FLORA OF HARDWOOD CLEARINGS

Near the northeastern end of Douglas Lake a large tract of beech-maple-hemlock hardwoods was lumbered in the winter of 1910-11 and has been left undisturbed since. During the last three years the usual clearing vegetation has developed, consisting at first of *Epilobium angustifolium*, *Erigeron canadensis*, and *Erechtites hieracifolia*, followed by a tangle of *Sambucus racemosa*, *Rubus idaeus* var. *aculeatissimus*, and young beech and maple saplings. Within this dense vegetation no introduced species is found. At intervals small cleared spots, seldom more than twenty feet across, mark places where horses were fed or lunches eaten



during the logging operations. Each of these shelters from four to twelve introduced species, as follows:

<i>Poa pratensis</i>	<i>Trifolium repens</i>
<i>Phleum pratense</i>	<i>Trifolium hybridum</i>
<i>Agrostis alba</i>	<i>Lappula deflexa</i>
<i>Rumex Acetosella</i>	<i>Cynoglossum officinale</i>
<i>Polygonum Convolvulus</i>	<i>Verbascum Thapsus</i>
<i>Chenopodium album</i>	<i>Cirsium lanceolatum</i>
<i>Lepidium virginicum</i>	<i>Cirsium arvense</i>
<i>Capsella Bursa-pastoris</i>	<i>Taraxacum officinale</i>

The chief logging road leading from this tract is nearly overgrown with thickets, but is still marked by numerous introduced species. These include every one of the preceding list and the following in addition:

<i>Poa compressa</i>	<i>Trifolium pratense</i>
<i>Rumex elongatus</i>	<i>Chrysanthemum Leucanthemum</i>
<i>Lychnis alba</i>	var. <i>pinnatifidum</i>

Mention has already been made of the fact that nineteen introduced species occur along a road in another part of the hardwood region. Among these are four not mentioned above, *Cerastium vulgatum*, *Silene noctiflora*, *Nepeta Cataria*, and *Plantago major*.

West of Bryant's hotel there formerly stood a grove of hardwood, lumbered in the winter of 1912-13. Observations of the flora made in 1911 showed one introduced species, *Cirsium lanceolatum*, while in 1912 no introduced species was seen. At the present time 29 such species occur along the principal road through it, leading from Pellston to Bryant's hotel. These are:

<i>Poa compressa</i>	<i>Polygonum Convolvulus</i>
<i>Poa pratensis</i>	<i>Chenopodium album</i>
<i>Phleum pratense</i>	<i>Cerastium vulgatum</i>
<i>Agropyron repens</i>	<i>Silene noctiflora</i>
<i>Secale cereale</i>	<i>Lepidium virginicum</i>
<i>Agrostis alba</i>	<i>Sisymbrium altissimum</i>
<i>Rumex elongatus</i>	<i>Trifolium repens</i>
<i>Rumex Acetosella</i>	<i>Trifolium pratense</i>
<i>Polygonum aviculare</i>	<i>Trifolium hybridum</i>
<i>Polygonum Persicaria</i>	<i>Lappula deflexa</i>



<i>Solanum nigrum</i>	<i>Chrysanthemum Leucanthemum</i>
<i>Verbascum Thapsus</i>	var. <i>pinnatifidum</i>
<i>Nepeta Cataria</i>	<i>Cirsium lanceolatum</i>
<i>Plantago major</i>	<i>Cirsium arvense</i>
<i>Achillea Millefolium</i>	<i>Taraxacum officinale</i>

Back of this road in soil exactly the same, and like the road covered until two years ago with a dense forest, there is now a tangle of brush heaps, with a dense growth of *Epilobium angustifolium* and young maple seedlings. In it the eleven introduced species are strictly confined to small open places and feeding grounds, and are exceedingly few in number of individuals. The following occur:

<i>Poa pratensis</i>	<i>Trifolium hybridum</i>
<i>Phleum pratense</i>	<i>Solanum nigrum</i>
<i>Rumex Acetosella</i>	<i>Verbascum Thapsus</i>
<i>Polygonum Convolvulus</i>	<i>Cirsium lanceolatum</i>
<i>Chenopodium album</i>	<i>Taraxacum officinale</i>
<i>Trifolium repens</i>	

In all, only 26 species have been observed in areas formerly occupied by hardwoods, and these are in every case confined to the logging roads and feeding grounds. This does not include seven other species growing along the public road near Bryant's hotel.

#### THE INTRODUCED VEGETATION IN THE ASPEN REGION

As in other types of vegetation, the introduced species among the aspens are again almost confined to the immediate vicinity of the roads. In this case, quantitative studies of their distribution were made by the quadrat method. In one hundred places chosen at random, a strip of 2-meter quadrats was observed. These were so placed that the first quadrat was adjacent to the wagon track of the main road through the aspens, and the others extended in a strip perpendicular to the roadway. Observations were continued on each strip until two successive quadrats showed no introduced species whatever. In most cases no introduced plants were found beyond the fifth quadrat, and in no case was one found beyond the tenth. This indicates that in the thirty years since the pines were lumbered, introduced species have been



able to penetrate, in general, less than twenty meters into the aspen thickets. Even yet they are most numerous in the quadrats nearest the roadway, as shown by the following table, in which the data for the one hundred series have been collected. The first figure after each species indicates the number of *first* quadrats in which it occurs, the second figure the number of *second* quadrats, and so on.

	1	2	3	4	5	6	7	8	9	10
<i>Poa compressa</i> .....	65	40	29	29	17	11	4	2	1	
<i>Poa pratensis</i> .....	63	28	27	20	15	7	4	2		
<i>Agrostis alba</i> .....	59	10	8	8	10	3			1	
<i>Phleum pratense</i> .....	40	4	9	4	6	3	2			
<i>Trifolium repens</i> .....	21	15	5	7	6	5	4	2	2	
<i>Trifolium pratense</i> .....	16	7	7	3	2	5	3		1	
<i>Rumex Acetosella</i> .....	13	9	18	25	25	24	10	4	5	1
<i>Agropyron repens</i> .....	13	6	8	2	3	2	2			
<i>Trifolium hybridum</i> .....	9	1	1	1						
<i>Lepidium virginicum</i> .....	5	3	2	2		1	1	1		
<i>Dactylis glomerata</i> .....	3	1								
<i>Taraxacum officinale</i> .....	1			1						
<i>Chrysanthemum Leucanthemum</i> var. <i>pinnatifidum</i> .....	1									
<i>Verbascum Thapsus</i> .....				2	3			1		
Total.....	309	124	114	104	87	61	30	12	10	1

These figures clearly indicate the close dependence of the introduced species upon human operations. Besides these fourteen species, *Avena sativa*, *Polygonum aviculare*, *Cerastium vulgatum*, and *Achillea Millefolium* also occur in the same association.

A deep ravine traverses a part of the aspen region, and some springs at its bottom make it a favorite camp ground and watering place for horses. In the small flat clearing at the bottom of this ravine fourteen introduced species occur, including besides those listed above *Secale cereale*, *Arenaria serpyllifolia*, and *Cirsium lanceolatum*. In all, 21 introduced species are known to occur in the aspen region.

Only three species of the introduced group are apparently establishing themselves in the aspen association, in spite of the open vegetation and the abundant space available for plants. Of these the most successful is *Rumex Acetosella*, now found widely scattered throughout the association, with a frequency index of from 10 to 15. *Lepidium virginicum* is common along most roadsides, and in some places these colonies occur away from the



roads, giving the species in some parts of the aspen association a frequency index of 2 or 3. *Verbascum Thapsus* occurs in scattered patches, usually grouped around a single plant of the previous year. The year 1914 has apparently been unusually favorable for this species, since many more such patches occur than ever before.

The close dependence of all the introduced species upon cultivation is well shown at the edge of the uncultivated area, and may be illustrated here by data from the margin of the aspen association east of Douglas Lake. A field planted to rye in 1913 stood idle in 1914, and was well overgrown with various species of weeds. It is separated by a wire fence from the uncultivated land to the west. A strip of fifteen 2-meter quadrats, extending from the fence into the field, was counted, and showed a total of 21 species. Of these fourteen were introduced, with an average frequency index of 44, and seven were native, with an average frequency of 31. The field on the other side of the fence is well grown up with thickets of oak and aspen, but has been pastured and supports a good bluegrass sod. A similar list of quadrats showed in it sixteen species, of which only three were introduced, *Poa pratensis*, *Verbascum Thapsus*, and *Taraxacum officinale*.

#### CONCLUSIONS

1. Of 120 introduced species in the region, only 56 have been observed within the uncultivated region. All of these occur in the vicinity of dwellings; 26 along recent logging roads or camp grounds in the hardwood region; 21 along roads or camp grounds among the aspens; and only three show a tendency to establish themselves among the native species.

2. The great reduction in the number of introduced species around the more remote settlements shows that they are in many cases dependent upon human aid for their dispersal.

3. Among these 56 species are many with efficient means of dispersal. Their limitation to the immediate vicinity of roads, camp grounds, or dwellings is accordingly due, not to lack of mobility, but to inability to compete successfully with the native species.







# INDEX TO AMERICAN BOTANICAL LITERATURE

1908-1914

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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### CONTENTS

Further observations on the relationship between the number of ovules formed and the number of seeds developing in <i>Cercis</i> . . .	J. ARTHUR HARRIS	533
A superficial study of the pine-barren vegetation of Mississippi	ROLAND M. HARPER	551
INDEX TO AMERICAN BOTANICAL LITERATURE. . . . .		569

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# THE TORREY BOTANICAL CLUB

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BULLETIN  
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TORREY BOTANICAL CLUB

---

NOVEMBER, 1914

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Further observations on the relationship between the number of ovules formed and the number of seeds developing in *Cercis*

J. ARTHUR HARRIS

(WITH FOUR TEXT FIGURES)

I. INTRODUCTORY REMARKS

In an earlier paper,\* I discussed upon large masses of data drawn from series of trees in different habitats the relationship between the number of seeds maturing and the number of ovules formed in the legume, *Cercis canadensis*. The analysis of the more homogeneous collections from individual trees was then reserved. This is now undertaken.

II. ANALYSIS OF DATA

A. *The Meramec Highlands Collections*

For convenience of treatment merely, I recognize two series, the first comprising 10 trees from which a relatively large number of pods were taken and the second embracing 100 trees from which 50-100 pods each were gathered.†

Table I gives the data and Table II the essential constants for the 13 large samples.

That the samples differ from tree to tree is especially conspicuous in the averages. Means such as 3.56, 3.75, 3.88, 4.26,

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\* Harris, J. Arthur. On the relationship between the number of ovules formed and the number of seeds developing in *Cercis*. Bull. Torrey Club 41: 243-256. 1914.

† From three trees of this latter collection a much larger number of pods was taken; they are, therefore, included here. The first hundred pods are also treated below, where the small samples from individual trees are discussed.

[The BULLETIN for October (41: 483-532) was issued 28 O 1914.]



TABLE I  
OVULES AND SEEDS DEVELOPING PER POD

Number of Individual	1/2	2/2	1/3	2/3	3/3	1/4	2/4	3/4	4/4	1/5	2/5	3/5	4/5	5/5	1/6	2/6
1	18	32	24	72	90	18	49	137	144	2	13	25	35	28	1	—
2	1	2	1	9	5	2	18	31	35	4	14	36	37	45	—	2
3	2	3	3	14	12	3	18	45	49	1	3	12	29	38	—	—
4	6	14	9	45	66	3	28	45	81	—	—	3	5	13	—	—
5	4	15	4	63	117	7	61	156	212	—	7	11	28	12	—	—
6	—	—	—	—	—	—	—	1	1	—	—	6	5	7	—	3
7	—	2	2	12	19	3	31	72	95	1	10	29	63	53	—	2
8	2	11	17	45	95	13	44	140	204	3	3	13	36	40	—	1
9	3	11	6	20	12	10	31	77	48	6	48	137	210	213	8	31
10	—	1	—	4	1	—	6	10	8	3	1	10	30	30	—	1
115	—	1	2	6	12	1	15	41	69	1	12	23	58	85	—	—
116	—	—	—	2	3	—	11	50	40	—	16	81	159	126	—	3
118	—	—	—	2	5	—	3	11	36	—	—	13	50	95	—	—

3/6	4/6	5/6	6/6	2/7	3/7	4/7	5/7	6/7	7/7	2/8	4/8	5/8	6/8	7/8	8/8	Totals
—	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—	695
4	12	10	5	—	—	—	—	—	1	—	—	—	—	—	—	274
—	—	5	3	—	—	—	—	1	—	—	—	—	—	—	—	242
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	318
—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	698
10	6	18	10	—	1	5	8	11	4	1	—	4	—	—	—	111
4	9	5	6	—	—	—	—	—	—	—	—	—	—	—	—	418
1	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	672
97	219	328	209	6	16	27	59	61	40	—	1	3	1	3	1	1,942
2	5	13	18	1	—	—	3	2	3	—	—	—	—	—	—	152
6	17	20	30	—	—	—	—	1	—	—	—	—	—	—	—	400
45	78	136	82	1	3	4	10	20	9	—	—	—	—	1	—	880
1	23	70	104	—	1	1	6	16	14	—	—	—	—	—	—	451

TABLE II  
PHYSICAL CONSTANTS FOR THIRTEEN INDIVIDUALS

Plant	Pods	Ovules			Seeds		
		Average	Standard Deviation	V	Average	Standard Deviation	V
1	695	3.760 ± .021	.832 ± .015	22.12	2.935 ± .026	1.023 ± .018	34.87
2	274	4.671 ± .033	.811 ± .023	17.37	3.555 ± .046	1.142 ± .033	32.14
3	242	4.268 ± .035	.812 ± .025	19.02	3.496 ± .048	1.114 ± .034	31.88
4	318	3.563 ± .027	.710 ± .019	19.92	2.965 ± .036	.966 ± .026	32.57
5	698	3.768 ± .016	.638 ± .011	16.94	3.129 ± .021	.835 ± .015	26.68
6	111	6.153 ± .052	.808 ± .036	13.12	4.585 ± .075	1.174 ± .053	25.60
7	418	4.409 ± .024	.743 ± .017	16.86	3.555 ± .032	.985 ± .023	27.70
8	672	3.887 ± .018	.689 ± .013	17.74	3.231 ± .025	.969 ± .018	30.00
9	1,942	5.542 ± .016	.931 ± .011	16.79	4.281 ± .022	1.276 ± .016	29.80
10	152	5.131 ± .050	.908 ± .035	17.70	4.230 ± .070	1.285 ± .050	30.37
115	400	4.765 ± .028	.821 ± .019	17.24	4.012 ± .037	1.099 ± .026	27.38
116	880	5.375 ± .018	.782 ± .012	14.55	4.293 ± .024	1.070 ± .017	24.93
118	451	5.466 ± .027	.856 ± .019	15.65	4.913 ± .032	1.001 ± .022	20.37



TABLE III

DIFFERENCES AND PROBABLE ERRORS OF DIFFERENCES IN THE STANDARD DEVIATION OF OVULES AND SEEDS AND IN THE CORRELATION OF OVULES AND SEEDS FOR SELECTED INDIVIDUALS OF CERCIS

Individuals Compared	Ovules		Seeds		Ovules and Seeds	
	Differences in Standard Deviation	Ratio	Differences in Standard Deviation	Ratio	Differences in Correlation	Ratio
1 and 5	.193 ± .019	10.28	.189 ± .024	7.93	.071 ± .025	2.77
7 and 9	.187 ± .021	9.04	.291 ± .028	10.47	.053 ± .028	1.93
8 and 10	.219 ± .037	5.87	.316 ± .053	6.00	.089 ± .036	2.44
4 and 118	.146 ± .027	5.42	.035 ± .034	1.02	.073 ± .027	2.72
5 and 9	.292 ± .016	18.04	.441 ± .022	20.32	.048 ± .025	1.91
6 and 10	.100 ± .051	1.98	.111 ± .073	1.52	.302 ± .065	4.66

TABLE IV

RELATIONSHIP BETWEEN NUMBER OF OVULES PER POD AND NUMBER OF SEEDS PER POD

Tree	Number of Pods	C. F.	$r_{08}$	$r_{02}$	$r_{02}/E_{r_{02}}$
1	695	.7807	.573 ± .017	-.074 ± .025	2.93
2	274	.6709	.488 ± .031	-.060 ± .058	1.03
3	242	.8189	.679 ± .023	+.112 ± .063	1.77
4	318	.8323	.648 ± .022	+.047 ± .056	.82
5	698	.8304	.502 ± .019	-.152 ± .025	6.08
6	111	.7452	.342 ± .056	-.178 ± .092	1.94
7	418	.8062	.497 ± .025	-.128 ± .032	3.94
8	672	.8311	.556 ± .018	-.043 ± .026	1.64
9	1,942	.7724	.550 ± .012	-.016 ± .015	1.03
10	152	.8243	.645 ± .032	+.081 ± .080	1.01
115	400	.8420	.607 ± .021	-.028 ± .034	.82
116	880	.7987	.531 ± .016	-.062 ± .023	2.73
118	451	.8989	.720 ± .015	-.070 ± .032	2.19

4.76, 5.13, 5.54 and 6.15 with probable errors always in the second place of decimals and ranging from .016 to .057 for ovules are so clearly significantly different that it is needless to calculate probable errors. The differences for mean number of seeds are also clearly significant.

The standard deviations for both ovules and seeds present a problem more difficult of solution by mere inspection. Values like .63, .68, .71, .74, .78, .85 and .93 with probable errors not exceeding .04 in any case appear to be significant. Differences exceeding their probable error as widely as those for the few random pairs given in Table III certainly indicate that the trees must be regarded as individual in variability as well as type.

For both ovules and seeds the coefficients of variation differ



conspicuously, ranging from 13.12 to 22.12 for ovules and from 20.37 to 34.87 for seeds. Unless the values of means and standard deviations are perfectly correlated—an assumption which we have no reason to make—one would expect the coefficients of variation to show considerable fluctuation in magnitude from the influence of the means alone.

Since the constants showing the mean values and the variabilities of ovules and seeds per pod and perhaps those for the correlation of these two characters as well (see Table III) differ significantly from individual to individual it is clear that there may be serious disadvantages in lumping together the materials from different trees to form a large sample to be used in the investigation of delicate correlations.

Turn now to the correlation coefficients. Table IV gives the results. Here as in the two random samples and their combination there is a considerable correlation between the number of ovules per pod and the actual number of seeds developing.

Trees 1, 5, 7, 8, and 9 have been selected for the test of linearity of regression because of the large number of pods available. The equations to the regression straight lines are given in the

Tree	Equation to Regression Straight Line	Deviation*
1	$s = .284 + .705 o$	.065
5	$s = .653 + .657 o$	.042
7	$s = .652 + .658 o$	.050
8	$s = .194 + .781 o$	.030
9	$s = .100 + .754 o$	.048

accompanying table. The average weighted deviation of observation from theory of each tree is also given. Graphs have been made showing the empirical means and the fitted straight line for each tree. Only that for tree 9 need be given, as figure 1. Perhaps the fit is slightly better than for some of the others, but the observations are numerous. All of the graphs show unusually good agreements of theoretical and empirical means. The theoretical and the empirical means differ on an average by only about five-hundredths of a seed.

\* Weighted mean deviation, disregarding signs, of observed from theoretical mean number of seeds per pod.



The coefficients for the correlation between the number of ovules per pod and the capacity of the pods for developing their ovules into matured seeds as determined from the formula

$$r_{oz} = \frac{r_{os} - v_o/v_s}{\sqrt{1 - r_{os}^2 + (r_{os} - v_o/v_s)^2}}$$

are all very low and are either positive or negative in sign, for these individual trees — presumably more homogeneous than the

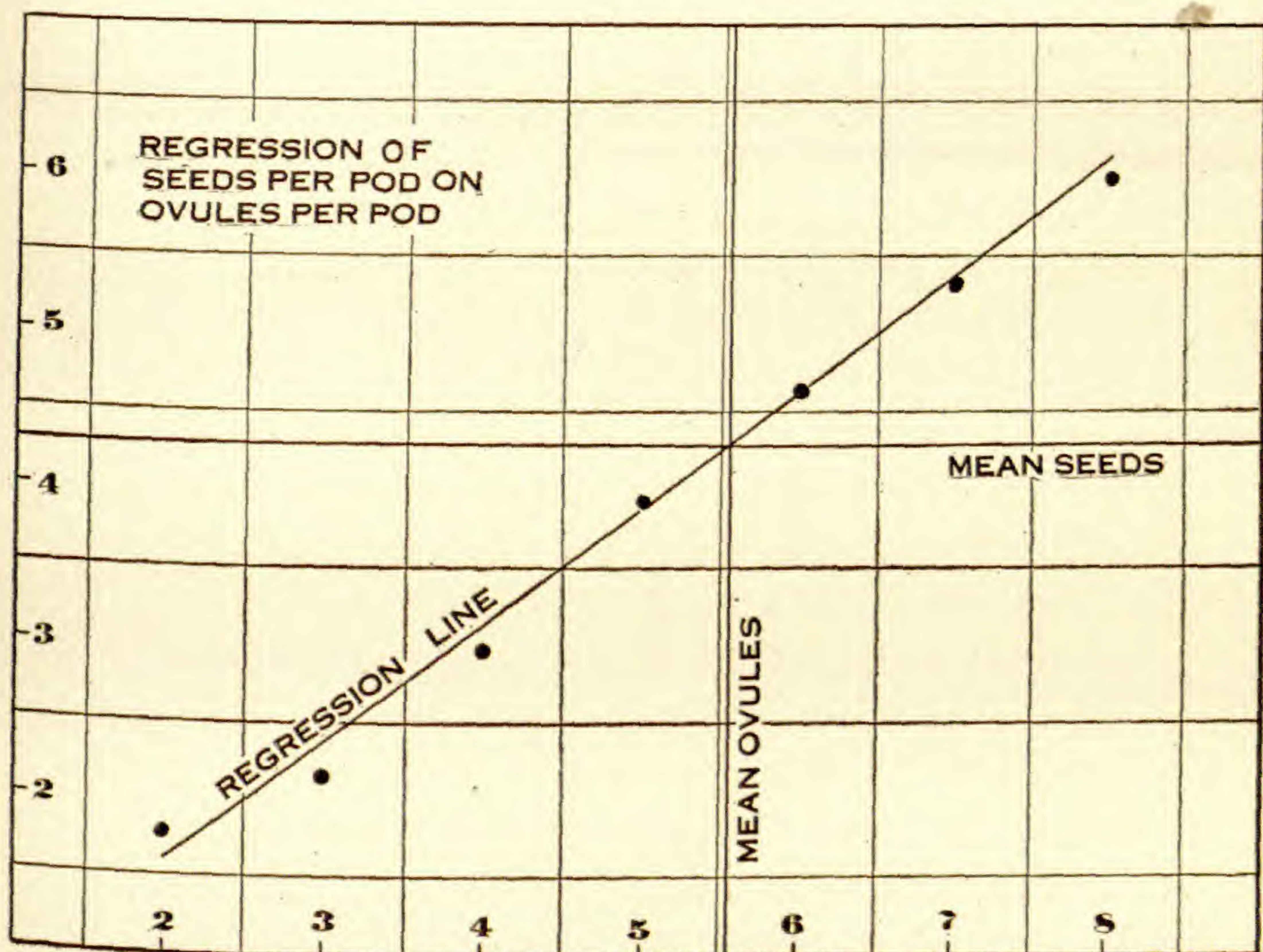


FIG. 1. Regression line and empirical means for tree 9.

general samples. Regarding probable errors, only four of the thirteen can be considered to differ significantly from 0. Ten of the thirteen are negative. All those which are significant with regard to their probable error are negative in sign.

Smaller collections from 100 trees were gathered shortly after those described above for the purpose of having more numerous individual samples for testing the results already stated. Separate correlation tables showing the relationship between the number of ovules formed and the number of seeds developing were drawn up for each tree. Of course it is impossible to publish all these.

The constants which interest us here are (a) the coefficient of



correlation for the number of ovules formed and the number of seeds developing per pod, and (b) the coefficient of correlation between the number of ovules per pod and the deviation of the number of seeds per pod from the probable number on the assumption that the number of seeds per pod is proportional to the number of ovules. These constants are presented in Table V in a form which will be clear without further comment.

The values for all the trees (large and small collections) are seriated in Table VI.

At the outset of the work I had thought that perhaps by the collection of a sufficiently wide series of individuals I might find some in which the coefficient of correlation between the number of ovules formed and the number of seeds developing would be very low. The results for the 110 trees show, however, that not only are all the values positive but that in every case they are of a substantial order. The lowest value entered in Table VI is .325 and the highest .850.

The constants of these correlation coefficients calculated with Sheppard's correction, are:

Mean,	.5994 $\pm$ .0075
Standard Deviation,	.1165 $\pm$ .0053
Coefficient of Variation,	19.431

It seems of considerable interest for our present problem to try to ascertain whether this observed variation in the magnitudes of the correlations between the number of ovules and seeds represents a real biological difference in the individual trees examined, or whether it is merely a statistical result, attributable to the fact that constants for each tree are based upon a small, not immensely large, sample of its pods. I believe we may make some progress as follows.

The standard deviation of random sampling of  $r$  is  $(1 - r^2)/\sqrt{n}$ , where  $n$  is the number of individuals included in the sample on which  $r$  is calculated. Let us assume now that the true value of  $r$  is the same for each individual tree and that it has the value found as our mean, say  $r = .600$ . This seems reasonable.

If  $n$  for each individual were 100, a condition holding for 60 of the trees but only with rough approximation for the remaining 50, one would expect



TABLE V

CORRELATIONS FOR SERIES OF PODS FROM INDIVIDUAL TREES

Tree	N	$r_{08}$	$r_{02}$	Tree	N	$r_{02}$	Tree	N	$r_{08}$	$r$	
11	100	.336	-.245	45	100	.562	.077	79	100	.663	-.073
12	100	.342	-.291	46	100	.630	.064	80	100	.655	-.070
13	100	.444	-.275	47	87	.716	.283	81	100	.506	-.253
14	100	.455	-.098	48	97	.442	-.248	82	73	.707	.019
15	100	.609	.151	49	93	.463	-.156	83	83	.597	-.201
16	100	.578	-.014	50	100	.576	-.077	84	76	.598	-.095
17	100	.704	.121	51	86	.728	.197	85	100	.683	-.010
18	100	.665	.157	52	100	.510	-.120	86	100	.720	.122
19	100	.477	-.164	53	100	.720	.152	87	69	.569	.004
20	100	.527	-.090	54	68	.522	-.022	88	100	.702	.154
21	88	.618	.065	55	100	.596	-.009	89	100	.647	.072
22	85	.460	-.051	57	100	.522	-.278	90	91	.709	.116
23	100	.681	.172	58	100	.688	-.062	91	100	.633	-.032
24	100	.684	.111	59	86	.752	.282	92	100	.486	-.036
25	100	.510	-.186	60	100	.641	-.116	94	80	.591	-.011
26	100	.691	.127	61	100	.732	-.029	95	97	.717	.081
27	100	.662	.048	62	98	.747	.112	96	100	.680	-.025
28	100	.618	-.106	63	74	.661	.011	98	74	.551	.045
29	100	.593	-.048	64	79	.630	.030	100	65	.490	-.185
30	91	.604	-.031	65	100	.808	-.070	101	100	.545	-.107
31	80	.436	-.034	66	80	.644	-.080	102	99	.560	-.171
32	85	.659	.053	67	70	.698	-.088	107	100	.440	-.192
33	95	.429	-.220	68	100	.716	.050	108	100	.600	-.010
34	100	.357	-.189	69	73	.789	-.106	109	69	.500	-.026
35	83	.437	-.053	70	100	.461	-.132	111	67	.428	-.198
36	100	.560	-.058	71	100	.678	.086	112	80	.579	.004
37	90	.563	.055	72	100	.803	.012	113	72	.742	.119
38	100	.645	.083	73	100	.750	.016	114	100	.475	-.004
39	100	.745	.167	74	100	.662	-.047	115	100	.807	.150
40	88	.667	.041	75	80	.659	-.063	116	100	.506	.090
41	76	.723	.226	76	100	.747	-.085	117	100	.393	-.166
42	100	.343	.011	77	100	.596	-.078	118	100	.688	-.106
43	62	.454	.012	78	94	.707	-.189	119	50	.854	.085
44	100	.618	.097								

TABLE VI

DISTRIBUTION OF COEFFICIENTS OF CORRELATION,  $r_{08}$

Center of Correlation Grade	$f$	Center of Correlation Grade	$f$
.325	1	.600	9
.350	4	.625	6
.375	—	.650	12
.400	1	.675	9
.425	4	.700	9
.450	7	.725	8
.475	4	.750	6
.500	9	.775	—
.525	3	.800	4
.550	6.5	.825	—
.575	6.5	.850	1



$$\sigma_r = \frac{1 - .60^2}{\sqrt{100}} = .0640.$$

This would have its probable error

$$.67449 \times .0640 / \sqrt{220} = .0029.*$$

By comparison we get:

$$\text{Empirical, S. D.} = .1165 \pm .0053,$$

$$\text{Theoretical, S. D.} = .0640 \pm .0029,$$

$$\text{Difference} = .0515 \pm .0060.$$

The difference is over 8 times its probable error and I think indicates that there are real biological differences in the individuals.

The constants for the correlation between the number of ovules per pod and the deviation of the number of seeds from their probable value,  $r_{oz}$ , for the 60 trees with 100 pods per tree and for the 40 other trees with less than 100 pods are summarized from Table V in Table VII. For a grand total of 110 trees I add

TABLE VII  
FREQUENCIES OF VALUES OF  $r_{oz}$  FOR SERIES OF INDIVIDUALS

Ovules and Capacity, $r_{oz}$	60 Trees, 100 per Tree	40 Trees, Less Than 100	Total 110 Trees
-.325 - -.275	2	—	2
-.275 - -.225	3	1	4
-.225 - -.175	3	5	9
-.175 - -.125	3	2	7
-.125 - -.075	10	4	14
-.075 - -.025	11	6	20
-.025 - +.025	8	7	16
+.025 - +.075	4	6	11
+.075 - +.125	8	5	15
+.125 - +.175	8	—	8
+.175 - +.225	—	1	1
+.225 - +.275	—	1	1
+.275 - +.325	—	2	2

the constants obtained for the 10 individuals from which all the pods were taken.

These results are also shown graphically in Fig. 2. Here the length of the lines indicates the magnitude of the correlation, i. e., the amount by which it deviates from 0, and the nature and

\* The 10 trees yielding more than 100 pods each have been included.



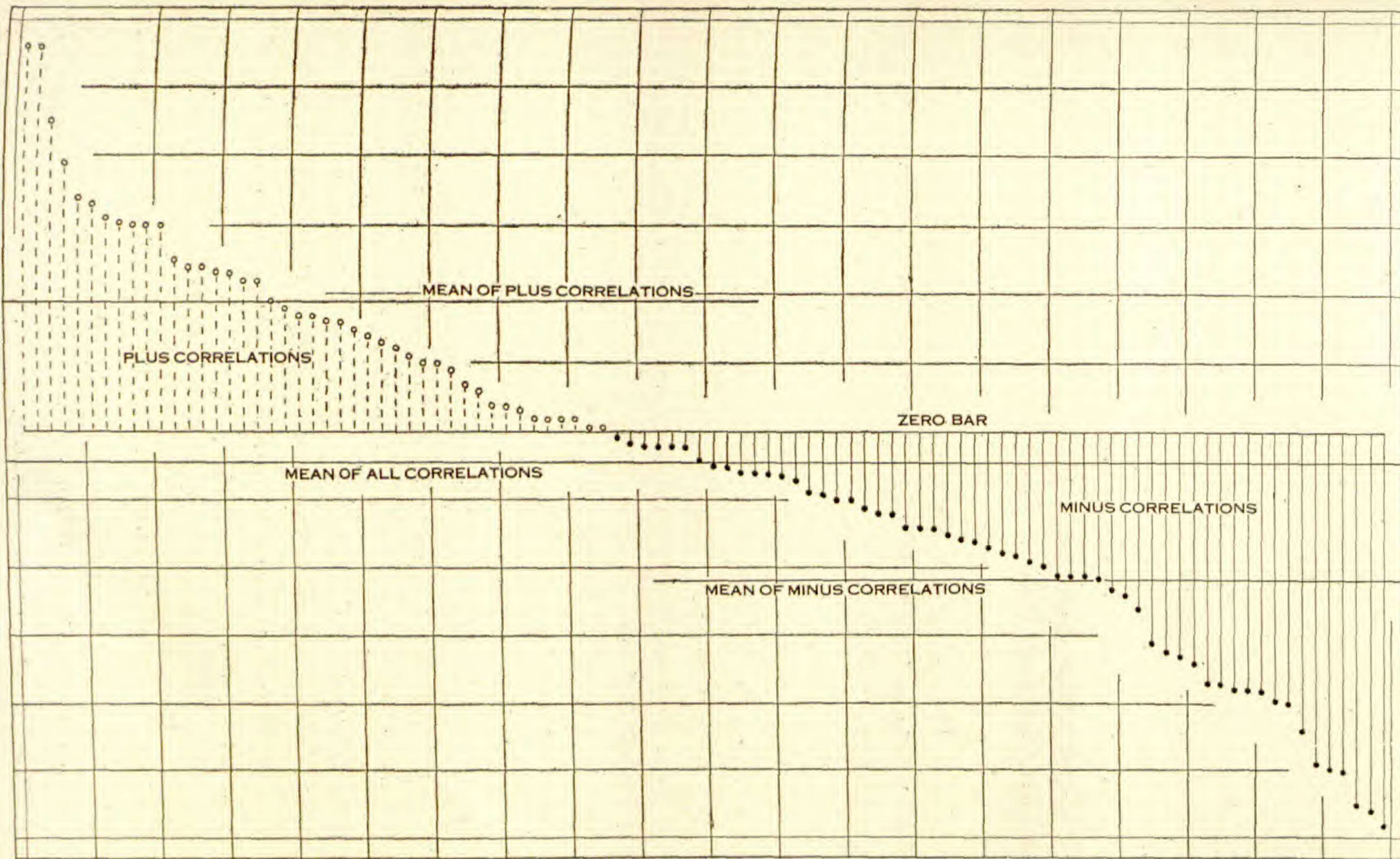


FIG. 2. Values of  $r_{02}$  for 100 individual trees from Meramec Highlands. Each coefficient is represented by a line. For  $r$ , 1 space is equal to .050.



the direction of this line, the sign. The firm lines and solid dots below the zero bar stand for negative coefficients, while the broken lines and circles above the zero bar indicate the magnitude of positive coefficients. The ten large trees are omitted.

Taking these results as they stand it would appear that the relationship between the number of ovules per pod and the capacity of the pod for maturing its seeds may vary, being sometimes positive and sometimes negative. The light and dark line areas in the diagram are *nearly* equal, and their means lie *about* equally distant from the zero bar.

But one cannot accept any statistical constant—average standard deviation or coefficient of correlation—as absolutely correct as a description of the material from which the sample investigated was drawn; all are too large or too small by an amount known to mathematicians as the probable error of random sampling. Is it not possible that the considerable range of variation in the constants tabled here is due to purely statistical causes and has no biological significance whatever? I think we may proceed as follows.

Assuming that there is no relationship between the number of ovules per pod and the capacity of the pod for maturing its seeds—i. e., that  $r_{oz} = 0$ —the deviation of the empirical means and the empirical standard deviation due to the probable errors of random sampling from the theoretical 0 may be determined. I illustrate with the 60 trees furnishing each 100 pods.

The standard deviation of the coefficient of correlation is as pointed out above  $(1 - r^2)/\sqrt{n}$ . Clearly where  $n = 100$  and  $r_{oz}$  is actually 0 one would expect a standard deviation of 0.10 due merely to the errors of random sampling. But this standard deviation itself would have a probable error which for the 60 trees from which I have 100 pods would be  $.67449(0.1/\sqrt{120})$ , or .0062.

One must expect, therefore, if  $r_{oz}$  be actually 0, to find a standard deviation of  $0.1000 \pm .0062$  in the coefficients for the 60 trees with 100 pods each *due to no organic cause whatever but solely to the errors of random sampling*.

The probable error of the mean is  $.67449\sigma_r/\sqrt{n}$ . Substituting values with  $\sigma = 0.1$  as just indicated I find



$$E_a = .67449 \times 0.1/\sqrt{60} = .0087.$$

This line of argument has been followed out in the preparation of Table VIII where for convenience I assumed that  $n = 100$  for each tree.\* In this table, the constants actually found are compared with the values one should expect them to have if the corre-

TABLE VIII  
MEAN VALUES OF  $r_{oz}$  FOR THE INDIVIDUAL TREES

	60 Trees	40 Trees	110 Trees
Theoretical mean. . . . .	.0000 $\pm$ .0087	.0000 $\pm$ .0107	.0000 $\pm$ .0064
Calculated mean. . . . .	-.0292 $\pm$ .0106	-.0175 $\pm$ .0154	-.0232 $\pm$ .0080
Difference. . . . .	-.0292 $\pm$ .0137	-.0175 $\pm$ .0187	-.0232 $\pm$ .0102
Theoretical standard deviation	.1000 $\pm$ .0062	.1000 $\pm$ .0075	.1000 $\pm$ .0045
Calculated standard deviation.	.1218 $\pm$ .0075	.1440 $\pm$ .0108	.1242 $\pm$ .0056
Difference. . . . .	.0218 $\pm$ .0097	.0440 $\pm$ .0131	.0242 $\pm$ .0072

lation between the number of ovules per pod and their capacity for maturing their seed were actually 0, and the constants as found from actual collections were due merely to the errors of random sampling.

For all three series the mean differs from 0 by less than 2.5 times its probable error. For the standard deviations the difference between the observed and the theoretical values is less than 2.5 in the case of the 60 trees and only about 3.3 times its probable error in the other two series.

Notwithstanding these low values of the means and the nearly equal areas of plus and minus values on the diagram, one must not lose sight of the facts, (a) that there are more negative than positive coefficients, the ratio being 57 : 43 for the smaller collections and 64 : 46 for the series from all the individual trees, and (b) that all the means are negative in sign.

This series like those discussed above seems to indicate that if there is any relationship between the number of ovules per ovary and the capacity of the ovary for maturing its ovules into seeds it is of such a nature that the ovaries with the larger numbers of ovules are slightly less capable than those with the smaller numbers.

\* This is not strictly true; I think that the approximation is quite close enough for present purposes. Sheppard's correction was used for the empirical distribution.



*B. The Individuals from the Vicinity of Lawrence, Kansas*

The relationship for the whole material has already been discussed. For the individual trees the results as shown in Table IX are most interesting. Of the 22 values of  $r_{oz}$ , only 1 has

TABLE IX

## CORRELATIONS FOR INDIVIDUALS

Tree	$r_{os}$ and $E_{r_{os}}$	$r_{oz}$ and $E_{r_{oz}}$
1	.671 ± .037	-.134 ± .066
2	.692 ± .035	+.099 ± .099
3	.595 ± .044	-.052 ± .067
4	.604 ± .043	-.204 ± .065
5	.580 ± .045	-.172 ± .065
6	.549 ± .047	-.131 ± .066
7	.400 ± .057	-.182 ± .065
8	.380 ± .058	-.189 ± .065
9	.365 ± .058	-.341 ± .060
10	.365 ± .058	-.319 ± .061
11	.554 ± .047	-.174 ± .065
12	.394 ± .057	-.189 ± .065
13	.609 ± .042	-.030 ± .067
14	.391 ± .057	-.263 ± .063
15	.381 ± .058	-.274 ± .062
16	.543 ± .048	-.117 ± .067
17	.537 ± .048	-.253 ± .063
18	.181 ± .065	-.322 ± .060
19	.572 ± .045	-.022 ± .067
20	.644 ± .039	-.212 ± .064
21	.514 ± .050	-.085 ± .067
22	.635 ± .040	-.288 ± .062

the positive sign. Taking the ratios of the constants to their probable errors to test their significance I find that the single positive constant deviates from 0 by an amount equal to its probable error; hence no significance can be attached to it. Of the 21 negative coefficients 14 differ from 0 by more than 2.5 times their probable error. The whole situation is summed up graphically in diagram 3 in which these ratios are plotted out with the signs of the correlations. If there were no real biological correlation between the number of ovules per pod and their capacity for maturing their seeds, the distribution of these ratios would be centered at 0, marked by the "theoretical mode and mean" line, with the deviations about equally distributed above



and below. What one does find is that the empirical mode falls on the class  $-3.50$  to  $-2.50$ . The area of the polygon which is composed of statistically significant constants is shaded in.

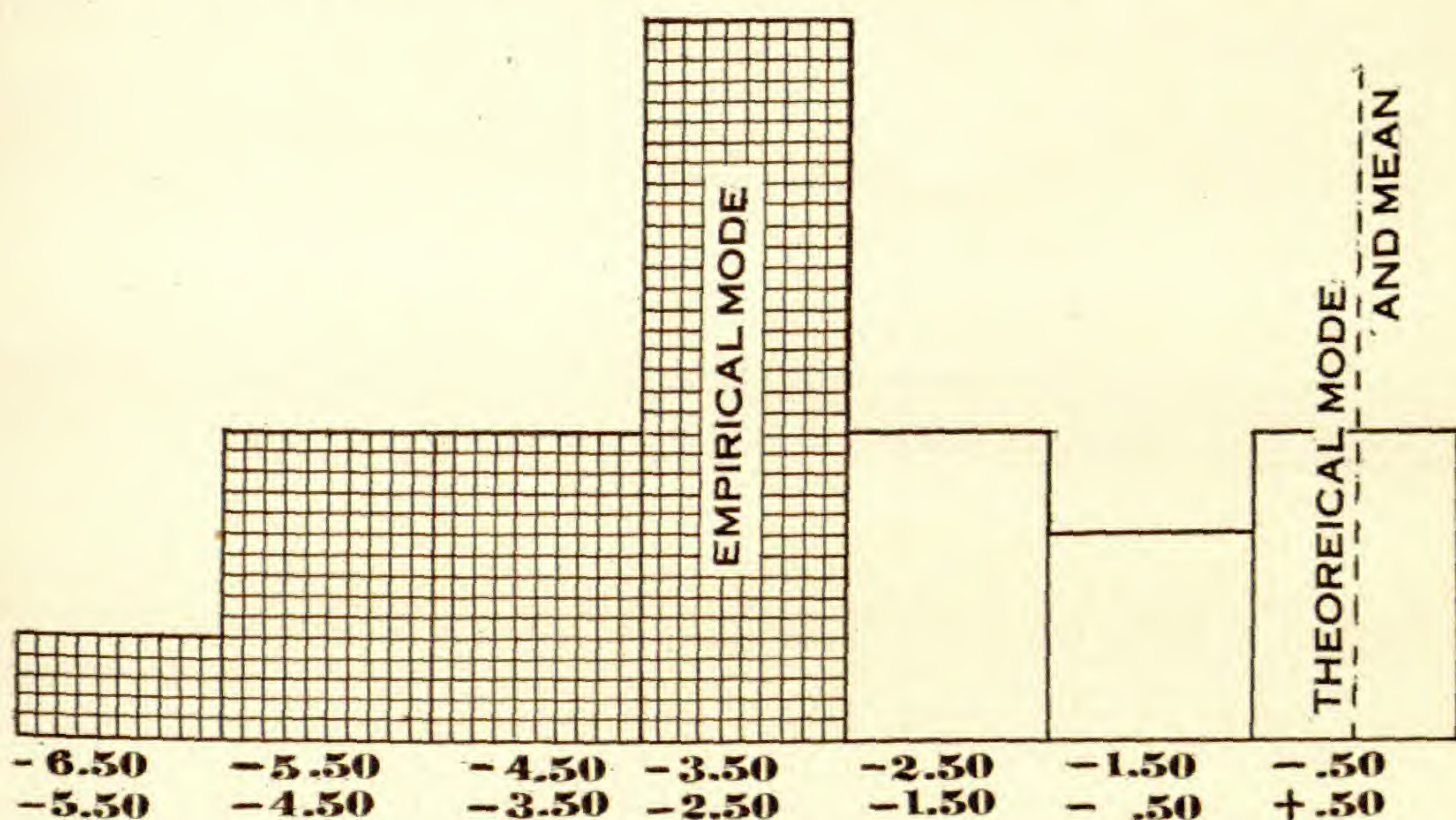


FIG. 3. Distribution of ratios of  $r_{02}$  coefficients to their probable errors, showing large number of significantly negative correlations for the eastern Kansas series.

### C. *The Individuals from the Vicinity of Sharpsburg, Ohio*

In this collection, the lumped data gave values of  $r_{0s} = .455 \pm .009$ ,  $r_{02} = -.034 \pm .011$ . Thus the correlation between number of ovules and the capacity of the ovary for maturing its ovules into seeds while negative in sign is not only low but is only 3.15 times its probable error.

The calculated correlations for the individuals are set forth in Table X.

These results differ essentially from those secured for the Kansas series in two regards; (a) only 6 out of the 26 may be considered statistically significant with regard to their probable error as compared with 14 out of 21 in the Kansas series; (b) the constants are about evenly distributed between positive and negative, there being 14 positive and 12 negative signs. The general average is, however, negative.

Again, the ratios of the constants to their probable errors are plotted out in a polygon (FIG. 4) showing the scatter of the constants on either side of zero.



TABLE X  
CORRELATIONS FOR INDIVIDUALS

Tree	$r_{os}$ and $E_{r_{os}}$	$r_{oz}$ and $E_{r_o}$
1	.511 ± .041	-.079 ± .055
2	.790 ± .021	+.078 ± .055
3	.566 ± .037	+.022 ± .055
4	.614 ± .034	+.205 ± .055
5	.310 ± .050	-.066 ± .055
6	.581 ± .036	+.184 ± .055
7	.396 ± .046	+.083 ± .055
8	.426 ± .045	-.057 ± .055
9	.254 ± .051	+.020 ± .055
10	.425 ± .045	-.058 ± .055
11	.324 ± .049	-.060 ± .055
12	.485 ± .042	+.056 ± .055
13	.614 ± .034	-.074 ± .055
14	.119 ± .054	-.164 ± .054
15	.524 ± .040	+.047 ± .055
16	.567 ± .037	+.108 ± .054
17	.400 ± .046	-.280 ± .051
18	.454 ± .044	+.071 ± .055
19	.440 ± .044	+.041 ± .055
20	.342 ± .049	+.137 ± .054
21	.338 ± .049	-.183 ± .053
22	.470 ± .043	-.062 ± .055
23	.614 ± .034	-.075 ± .055
24	.416 ± .045	-.064 ± .055
25	.386 ± .047	-.089 ± .055
26	.262 ± .051	-.086 ± .055

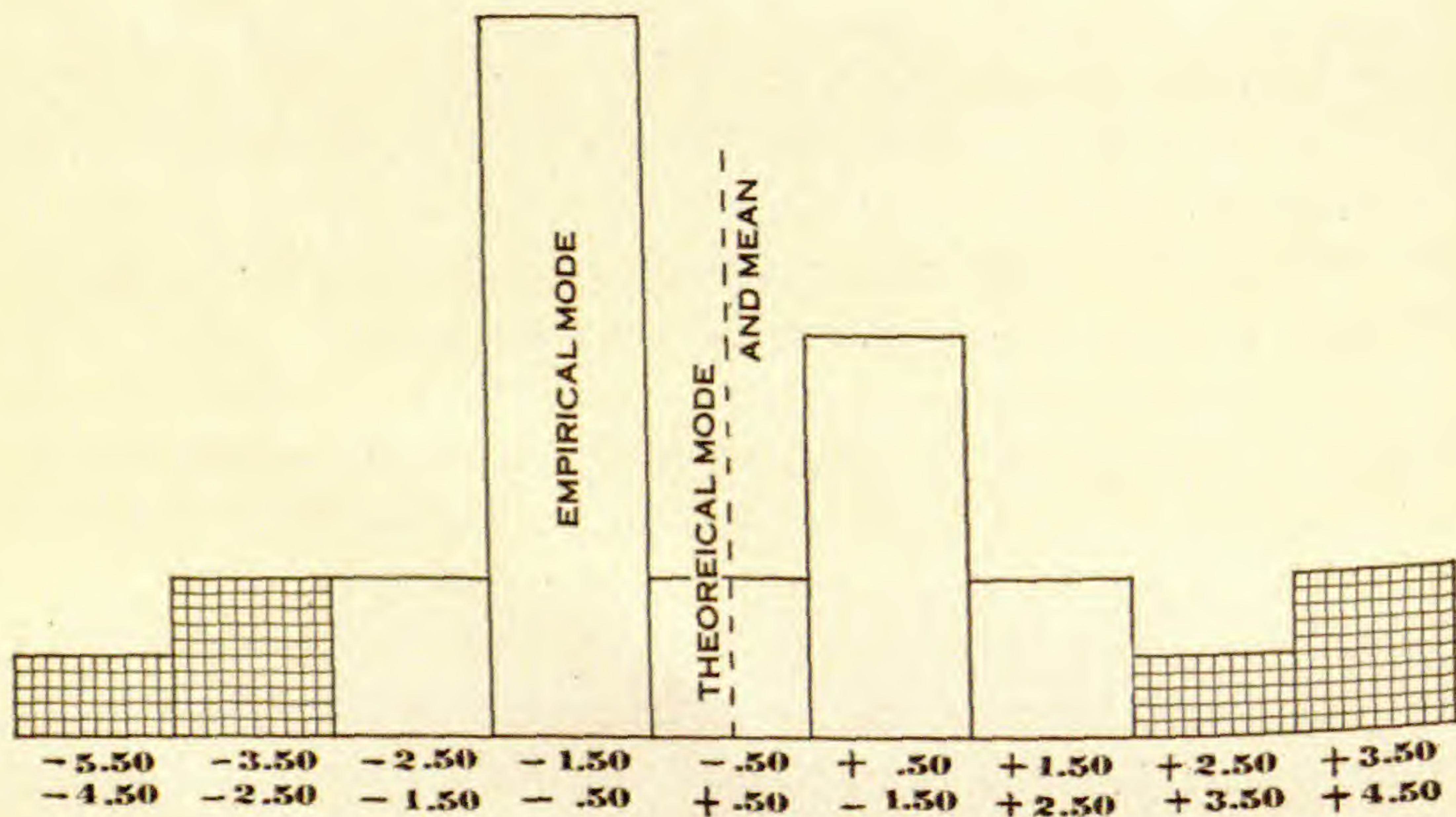


FIG. 4. Distribution of ratios of  $r_{oz}$  to  $E_{r_{oz}}$ , Ohio series.



## III. SUMMARY AND DISCUSSION

The investigations described in this and the preceding paper establish several points concerning fertility and fecundity. The following may now be cited.

(a) The physical constants — type, variability, and correlation—of the number of ovules per pod and the number of seeds developing per pod in *Cercis canadensis* differ sensibly from individual to individual and from habitat to habitat. The data do not, however, justify the conclusion that the trees from the different habitats are to be distinguished taxonomically.

(b) The correlations for number of ovules formed and number of seeds developing per pod,  $r_{os}$ , have always been found positive and of a moderate, considerable or even high intensity.

This is true for the pods of an individual tree as well as for a mixed sample from a considerable series of trees. The correlation coefficient is slightly raised by the combination of collections from different individuals.

(c) Regression is sensibly linear, both within the series of pods from the same individual and in a population of pods from many individuals. Possibly, however, there is a departure from linearity in the pods with eight ovules, but in my largest series there are only 36 of these pods out of a total of 28,554; this number is too small to be given great importance.

The significance of the linearity of regression is two-fold. Statistically, it justifies describing the interdependence between the number of ovules formed and the number of seeds maturing by the coefficient of correlation. Biologically, it shows that the rate of increase in number of seeds developing per pod remains the same as we pass from pods with the lowest to pods with the highest numbers of ovules.

(d) Wherever large series of pods have been examined, the correlation between the number of ovules per pod and the capacity of the pods for maturing their seeds,  $r_{oz}$ , has a negative sign and a low, usually a very low, magnitude. When the number of pods is relatively small — say about 100 as in the case of the correlations from individual trees — the coefficient is sometimes positive. These results may well be due to the probable errors of random sampling which, with samples of this small size, may be quite large enough to screen such a slight relationship.



In such cases the number of negative values is generally larger than the number of positive coefficients, and their mean numerical magnitude is always higher. For every large series examined the value of  $r_{oz}$  has been over 2.5 times its probable error and sometimes many times its probable error. These evidences can leave little doubt of the existence of a slight negative relationship between the number of ovules formed and the capacity of the pod for maturing its ovules into seeds, the pods with the larger number of ovules producing relatively fewer seeds.

This conclusion has also been reached in an earlier paper for the dwarf varieties of *Phaseolus vulgaris* as a whole.

(e) The foregoing conclusions and other statements made in these pages apply exclusively to the one species considered and should not be extended to others except on the basis of actual data. There is no reason to assume that species may not differ in this regard. The data available for another of the Leguminosæ, *Robinia*,\* indicate that quite different conditions from those found in *Cercis* may prevail. If the correlations found for *Sanguinaria*† are based on sufficiently large and representative samples they lead to the same conclusion. There are strong evidences that some strains of *Phaseolus* differ from others in the sign of this relationship. Indeed the Kansas series of *Cercis* differs rather conspicuously from others in the intensity of the negative correlation.

The conclusions concerning capacity for seed development here drawn are based upon mature pods only. One of the most important things to be done is to determine the relation of this phenomenon to the intra-individual selective elimination of ovaries, if it occurs in *Cercis*. All of the data here discussed were collected before this differential failure of ovaries in *Staphylea* was demonstrated. As yet I have been unable to obtain adequate materials for solving the problem for *Cercis*.

(f) This paper is exclusively a statement of observed facts. I have no explanation to offer of the relationships which have been regularly found when adequately large series of data have been analyzed. Theories as to the causes underlying the conditions

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\* Harris, J. Arthur. *Biometrika* 6: 441-442. 1909.

† Harris, J. Arthur. *Biometrika* 7: 321-324. 1910.



observed seem to me, in view of the numerous difficulties of the problem, premature. Upon the painstaking collections of facts in regard to natural phenomena, whether or not they can be lined up with current theories, seems to me to rest the real advance of biology. When more comprehensive data are available—many of which are already collected and in an advanced stage of reduction—it will be much safer to consider causal phases of the phenomena.

COLD SPRING HARBOR







# A superficial study of the pine-barren vegetation of Mississippi

ROLAND M. HARPER

(WITH THREE TEXT-FIGURES)

In Mississippi *Pinus palustris* is confined to the southern half of the state, and the region in which it is the dominant tree, constituting the pine-barrens, covers about 13,000 square miles, or less than one third of the state. The pine-barrens proper (in Mississippi but not in any of the states farther east) are confined to the area underlaid by a non-calcareous formation supposed to be of late Tertiary age, which has been called Grand Gulf in Mississippi and Alabama and Altamaha Grit in Georgia. The boundary between this and the limestone region which borders it on the north seems much less distinct in Mississippi than in Georgia,\* but is approximately 100 miles from the coast. In western Mississippi this formation is overlaid by a brownish silty loam of supposed aeolian origin, known as the loess, which is many feet thick along the Mississippi River but thins out gradually eastward and disappears entirely in the neighborhood of the Pearl River. Where the loess forms the surface the long-leaf pine is absent and other pines scarce, and the forests are mainly of the ordinary southern hardwood type, much as in the northern parts of the state.

*Previous literature.*—The following list is believed to contain all the more important papers bearing on the phytogeography of the Mississippi pine-barrens, except a few for the whole state which were cited in my paper on northern Mississippi last year,† and a few primarily geological ones. The arrangement is chronological.

(Mrs.) **Martha B. Flint.** Notes from the Mississippi pine barrens. Bot. Gaz. 7: 43. Apr. 1882.

— The exogenous flora of Lincoln Co., Mississippi, from October to May. Bot. Gaz. 7: 74-76, 79-81. June and July 1882.

\* See Bull. Torrey Club 32: 144. 1905.

† Bull. Torrey Club 40: 377-399. pl. 21, 22. Au 1913.



**B. D. Halsted.** Southern Mississippi floral notes. Gard. and For. 4: 250-251. 27 May 1891.

Relates to the vicinity of Ocean Springs, in May.

— The giant sundew heliotropic. Bull. Torrey Club 18: 212-213. July 1891.

Relates to the plant now known as *Drosera filiformis Tracyi* (Macfarlane) Diels,\* and a few other species observed around Ocean Springs.

**Charles Mohr.** The timber pines of the southern United States. U. S. Forestry Bull. 13. 1896 and 1897.

Notes on long-leaf pine in Mississippi on pages 42-43.

**C. L. Pollard.** Studies in the flora of the central Gulf region. Bull. Torrey Club 24: 148-158. Mar. 1897.

**Andrew Allison.** Notes on the winter birds of Hancock County, Mississippi. The Auk 23: 44-47. Jan. 1906.

Contains about a page of interesting notes on the vegetation.

**R. M. Harper.** Midwinter observations in southeastern Mississippi and eastern Louisiana. Torrey Club 6: 197-205. f. 1. Oct. 1906.

**J. S. Holmes & J. H. Foster.** Condition of cut-over long-leaf pine lands in Mississippi. U. S. Forest Service Circular 149. 8 pp. May 1908.

— A study of forest conditions of southwestern Mississippi. Miss. Geol. Surv. Bull. 5. 56 pp. and folded colored map. Dated January, 1908, on title-page and March 17, 1909, in letter of transmittal, but not distributed until 1910 or 1911.

**E. N. Lowe.** A preliminary study of the soils of Mississippi. Miss. Geol. Surv. Bull. 8. 220 pp., outline map, and 23 half-tones, mostly in text. 1911.

Contains copious notes on vegetation.

**W. N. Logan.** The soils of Mississippi. Miss. Exp. Sta., Technical Bull. 4. 49 pp. and folded colored map. 1913.

**R. M. Harper.** The forest regions of Mississippi in relation to the lumber industry: a geographical and statistical study. Southern Lumberman 70<sup>935</sup>: 27-28. 23 Aug. 1913.

Includes a small geographical map. Also reprinted in octavo size, with 8 pages.

**E. N. Lowe.** Note on the flora of Mississippi. Miss. Geol. Surv. Bull. 11: 137-166, including full-page geographical map. Dec. 1913.

This paper divides the state into nine divisions, and sketches the vegetation of each. It has also been issued separately as a 32-page pamphlet with the title "A brief note on the floral regions of Mississippi." The remainder of Bulletin 11 consists of Bulletins 5 and 7 reprinted, with the addition of three half-tone plates copied from other publications, and a 3-page statistical supplement on the lumber industry of Mississippi.

\* Described in Engler's Pflanzenreich 4<sup>112</sup>: 92. 1906.



The government soil surveys of Lincoln, Wayne and Forrest Counties and the McNeill, Biloxi and Scranton areas, published in recent years, are valuable in this connection, but not as much so as if their authors had been more familiar with previous literature and the local geography, geology and flora, and if chemical analyses of soils had been included.

*Itinerary.*—In December, 1905, I spent a day in the pine-barren region of Mississippi near Hattiesburg, and the next day observed the vegetation from the train between Lumberton and the Pearl River *en route* to New Orleans. A few days later, in January, 1906, I traveled the whole length of the Mississippi coast by rail, with a brief stop at Gulfport. On October 18, 1908, traveling northward on the Mobile & Ohio R. R., I entered the state at State Line, in the northeastern corner of Greene County, and left the pine-barrens near Waynesboro, about 20 miles farther on. On July 20, 1911, I walked into Mississippi a few miles northeast of Buckatunna,\* in Wayne County, and traveled on the Mobile & Ohio R.R. from Buckatunna to State Line and beyond. In July, 1913, I entered the region under consideration from the west somewhere near Brookhaven, on the Mississippi Central R.R., and traveled through it for about 300 miles, via Wanilla, Foxworth, Columbia, Maxie, Gulfport, Pascagoula (formerly Scranton), Evanston, Beaumont, and Laurel.† On this trip notes were taken from the train nearly every mile, and also on the ground for a few minutes or hours in the vicinity of Columbia, Biloxi,‡ Fontainebleau, Pascagoula, and Moss Point.

#### PHYSICAL FEATURES

*Soils.*—The soil of the pine-barren region is in the main a sandy loam, the proportion of clay increasing with the depth. On the uplands the soil is usually grayish and the subsoil brick-red, and in some places the red clay comes nearly or quite to the surface. There is at present some difference of opinion among geologists as to whether the surface sand and clay of this and

\* Misspelled "Bucatumna" by the U. S. Post Office Department.

† All the places mentioned in this sentence are railroad junctions, but some of them are so new that they can be located only on the most modern maps.

‡ At (or rather near) Biloxi I enjoyed the hospitality of Professor S. M. Tracy, as many other botanists had done in previous years.



other pine-barren regions represent distinct formations of late Tertiary or Quaternary age (Columbia and Lafayette), or are merely products of weathering from the underlying marine Tertiary formations.\*

Deep beds of sand, such as are common on the left sides of creeks and rivers in the corresponding parts of Georgia, are rare in Mississippi, and the Mississippi pine-barren soils seem to average a little richer than those farther east. But in comparison with soils farther inland these are poor in available mineral plant food, especially near the coast, where the diminished seasonal fluctuation of the ground-water seems to limit the supply of available potash, etc., in a manner not yet fully understood, but perhaps simply by preventing aeration. The richest soils in this region are along streams which pass through calcareous regions farther inland, and west of the Pearl River where the influence of the loess is felt.

The following partial analyses extracted from Dr. Hilgard's report on Mississippi in the 5th volume of the Tenth Census will serve as a basis for comparing these soils with those of northern Mississippi and other nearby or similar regions. They are from three localities, a pine ridge in Simpson County, the hammock or second bottom of the Pearl River in Marion County, and the "pine meadows" of Jackson County. In the first two cases both soil and subsoil were analyzed. The percentages of only lime (CaO), potash (K<sub>2</sub>O), "phosphoric acid" (P<sub>2</sub>O<sub>5</sub>), and magnesia (MgO) are given here.

All of these, especially the last, are considerably below the

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\* Advocates of the latter hypothesis claim that the process of weathering tends to wash out the clay and concentrate the sand on the surface. If this were universally true then the oldest soils would be the sandiest; but in the interior hardwood region (e. g., in Middle Tennessee, Kentucky, etc.), where the soils are residual from Paleozoic rocks, and have been exposed to weathering processes many times longer than the region under consideration, clay predominates on the surface, and sand is chiefly confined to the beds of streams. Even on the Cumberland Plateau, where the rocks are mostly sandstone, the soils are decidedly loamy. To explain this difference between the soils of Tennessee and southern Mississippi it will probably be necessary to take into consideration the seasonal distribution of rainfall. In Middle Tennessee and a great deal of neighboring territory the summers are pretty dry, while in the region under consideration, as in most other parts of the coastal plain, summer is the rainy season; which must make a considerable difference in the processes of weathering.



	Lime	Potash	Phos. Acid	Magnesia
Simpson County ridge . . . . .	.061	.074	.069	.112
Subsoil of same . . . . .	.038	.169	.041	.229
Pearl River hammock . . . . .	.113	.124	.169	.141
Subsoil of same . . . . .	.054	.169	.059	.212
Jackson County pine meadow . . . . .	.023	.061	.021	.069

average in fertility, which explains why this and other pine-barren regions still retain so much of their native vegetation. The density of population and amount of woodland remaining are pretty closely correlated with the soil characters. In 1910 the portions of the pine-barren region west of the Pearl River had about 40 inhabitants to the square mile (which is pretty close to the state average), the three coast counties about 25, and the whole region about 30. The amount of woodland varies from 69 per cent. west of the Pearl River to 90 per cent. east of there, while for the whole state it is 64 per cent.

But notwithstanding the poverty of pine-barren soils in mineral plant food, they are easily tilled at all seasons, and respond readily to applications of commercial fertilizers, and for the last few decades farmers have been taking possession of them very rapidly. From 1900 to 1910 the population of the region under consideration increased 45 per cent. (over 50 per cent. east of the Pearl River, where the poorer soils are located), and similar developments were going on in the corresponding parts of other southeastern states at the same time, necessitating among other things the building of many new railroads and the creation of several new counties, and thus keeping map-makers busy.

*Topography and hydrography.*—The topography is very similar to that which I have already described for the corresponding parts of Georgia,\* Florida,† and Alabama.‡ In the parts most remote from the coast it is moderately hilly, and some of the smallest valleys that contain permanent streams may be as much as 50 feet deep. Toward the coast, where erosional forces have been less active on account of the lesser elevation, the local relief is less, and ponds and swamps are more frequent. In some places, especially in Jackson County, the country is almost perfectly

\* Bull. Torrey Club 32: 146. 1905; Ann. N. Y. Acad. Sci. 17: 24. 1906.

† Ann. Rep. Fla. Geol. Surv. 3: 218-219. 1911.

‡ Geol. Surv. Ala., Monog. 8: 114-115. 1913.



flat for miles, forming the "pine meadows" described by Hilgard\* and others; but usually the country is a little undulating right down to the coast.

As in the pine-barrens of Georgia and Alabama, the streams that rise within the region carry little sediment and do not fluctuate much. The Pearl and Pascagoula Rivers drain parts of the Eocene red hills to the northward and are therefore somewhat muddy. In the lower and flatter parts of the region the groundwater is of course always near the surface (for it can hardly sink below sea-level), and the soil is therefore always damp. The most typical or characteristic pine-barren plants are found in such situations. The existence of a large paper mill at Moss Point, at the mouth of the Escatawpa River, one of the typical coffee-colored pine-barren streams, is probably correlated with the freedom of the water from mineral substances in suspension or solution.

*Climate.*—The following climatological data, extracted from the annual summary of the Mississippi section of the U. S. Weather Bureau for 1911, will give an idea of the salient features of the climate of this region. Eight stations have been selected, as follows: Waynesboro and Jackson, just north of the region, Brookhaven, about on its western edge, Natchez and Woodville, farther west, and Pearlinton, Bay St. Louis and Biloxi, on the coast. The data given here are mean temperature for January and July, average annual rainfall, and proportion of the total rainfall in the four warmest months, June to September, and the six warmest months, May to October. The first two columns of figures are degrees Fahrenheit, the third inches, and the last two percentages.

It may be observed at once that not only is the rainfall more copious toward the coast, but also a larger proportion of it comes in summer there, so that if absolute instead of relative figures for summer rainfall were given the contrast between the coast and the interior stations in this respect would be still greater. Less comprehensible, but perhaps more interesting, is the fact that

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\* Geol. and Agric. Miss. 368-371. 1860. See also McGee, 12th Ann. Rep. U. S. Geol. Surv. 1: 368, 475. 1892; Mohr, U. S. Forestry Bull. 13: 60, 81. 1896; Contr. U. S. Nat. Herb. 6: 123-124. 1901; Harper, *Torreya* 6: 204-205. 1906.



Stations	January Temperature	July Temperature	Annual Rainfall	Percentage in	
				4 Months	6 Months
Waynesboro.....	47.2	80.9	50.50	35.9	47.2
Jackson.....	47.3	81.3	50.57	30.7	42.4
Brookhaven.....	48.0	81.6	58.42	33.3	44.4
Natchez.....	49.8	81.8	54.59	31.9	43.2
Woodville.....	50.1	81.4	59.55	35.3	47.4
Pearlington.....	52.0	80.9	57.92	41.8	52.4
Bay St. Louis.....	50.8	81.4	59.82	41.5	51.9
Biloxi.....	51.5	81.9	60.75	42.9	53.8

the summers are relatively drier west of the Pearl River, where the soils are richer, than in the more typical pine-barrens to the eastward. It is easy to imagine how the seasonal distribution of rainfall might affect the soils somewhat, as suggested on a preceding page, but in this case the loess near the Mississippi River must owe its location and character to geological causes rather than to any local climatic factors; and it may be that the soil itself, perhaps through the vegetation, influences the rainfall reciprocally to some extent.\*

#### VEGETATION

From the notes taken in the five different years above mentioned a rough quantitative analysis of the vegetation has been derived.† The 1913 trip has furnished more data than all the others combined, partly because of its greater duration (over four days), and partly because it was made at a season when the number of flowers in the pine-barrens is near its maximum.

\* See Bull. Torrey Club 37: 415-416. 1910; Torreyia 12: 140-141. 1912; Geol. Surv. Ala. Monog. 8: 19, 24. 1913.

† One of the objects of this paper is to show how a botanical reconnaissance survey of an essentially homogeneous area of 13,000 square miles can be made in less than a week. At this rate a person sufficiently familiar with the flora could cover an area the size of New England, New York or Michigan in about a month, or the whole United States in five years, even if the country were made up of two or three hundred quite dissimilar areas of the size of the one here treated. Or five interested persons could cover the country in one year, or twenty persons (if so many phytogeographers could be found) in one summer. Even such hasty work brings out some fundamental and significant facts not previously known, and if more time can be devoted to it the results of course are still more satisfactory. (In view of these possibilities it looks like misdirected energy to spend months or years, as many botanists have done, in trying to make a complete collection of the plants of a single county or other restricted area, and publishing a list of them, which usually establishes no general principles and is therefore of very little scientific value.)



The list of plants given below is of course far from complete, for there must be nearly a thousand species of flowering plants in the area examined. But it probably contains most of the trees and shrubs that could be found, and most of the larger herbs. In a quantitative analysis of vegetation bulk is more important



FIG. 1. Looking east across Bayou St. Martin, near southwest corner of Jackson County. Pine-barrens on both sides (*Pinus Elliottii* at edge, *P. palustris* on higher ground), passing abruptly, with no intervening fringe of shrubs or hardwoods, into brackish marsh vegetation consisting mostly of *Juncus Roemerianus*. (The absence of a strip of hammock vegetation at the edge of the marsh probably indicates that the fires which keep the pine forest clear of underbrush sweep right across the bayou through the rushes.) July 16, 1913.

than number of species or individuals, and the herbs too small to recognize from a moving train, however interesting they may be to systematists, probably constitute less than 1 per cent. of the total volume of vegetation. The difficulty of recognizing some plants from a train has been partly counterbalanced, however, by the fact that I spent several hours on the ground near the coast, where typical pine-barren plants are most abundant.

To indicate as nearly as possible relative abundance, which is not necessarily the same as frequency, wherever a species was noted as abundant I have counted it three times in tabulating the returns, where common it is counted twice, and where rare it is not counted at all. (Even this does not do justice to the abundance of the



conifers, and if the figures for them were multiplied by two or three it would probably make the proportions more nearly correct.) Species seen less than four times are omitted entirely from the list. Trees, shrubs and herbs are separated, and evergreens are indicated by bold-face type, as usual. The names of plants are followed by a few words on habitat, which may be of interest to some readers.

## TREES

283	<b>Pinus palustris</b>	Mostly on uplands, abundant throughout
152	<i>Nyssa biflora</i>	Small swamps, etc.
140	<b>Pinus Elliottii</b>	Small swamps and shallow ponds
126	<b>Magnolia glauca</b>	Non-alluvial swamps
122	<b>Pinus Taeda</b>	Low grounds, in richer soils
72	<i>Quercus marylandica</i>	Dry loamy uplands
64	<i>Liquidambar Styraciflua</i>	Richer soils mostly
46	<i>Cornus florida</i>	Loamy uplands mostly
40	<i>Taxodium imbricarium</i>	Small swamps and ponds, coastward
37	<i>Liriodendron Tulipifera</i>	Low grounds
36	<i>Quercus falcata</i>	Dry loamy uplands
31	<b>Pinus glabra</b>	Hammocks, etc.
25	<b>Magnolia grandiflora</b>	Hammocks, etc.
23	<i>Quercus Catesbaei</i>	Dry sandy soils
23	<b>Pinus echinata</b>	Dry loamy uplands
22	<i>Fagus grandifolia</i>	Hammocks, etc.
22	<i>Quercus cinerea</i>	Sandy uplands
21	<i>Acer rubrum</i>	Non-alluvial swamps
20	<i>Salix nigra</i>	River-banks and low grounds
18	<i>Taxodium distichum</i>	Swamps of larger streams
11	<b>Quercus nigra</b>	Creek-bottoms mostly
10	<i>Hicoria alba?</i>	Loamy uplands
9	<i>Nyssa sylvatica</i>	Loamy uplands
9	<b>Ilex opaca</b>	Hammocks, etc.
8	<i>Nyssa uniflora</i>	Along larger streams
8	<i>Oxydendrum arboreum</i>	Hammocks, etc.
8	<b>Quercus geminata</b>	Sand near coast
7	<b>Quercus laurifolia</b>	Hammocks, etc.
6	<i>Quercus Phellos</i>	Bottom lands
6	<i>Carpinus caroliniana</i>	Bottoms, etc.
5	<i>Quercus stellata</i>	Loamy uplands
5	<i>Diospyros virginiana</i>	Various situations
5	<b>Quercus virginiana</b>	Near coast
5	<i>Magnolia macrophylla</i>	Richer soils
5	<b>Chamaecyparis thyoides</b>	Sour swamps
4	<i>Quercus Michauxii</i>	Bottoms

## SHRUBS AND WOODY VINES

68	<b>Ilex glabra</b>	Moist pine-barrens
42	<b>Serenca serrulata</b>	Low pine-barrens, coastward



32	<b>Cyrilla racemiflora</b>	Branch-swamps, etc.
29	<b>Smilax laurifolia</b>	Non-alluvial swamps
27	<b>Myrica pumila</b>	Low pine-barrens
24	<b>Hypericum fasciculatum</b>	Around ponds and branches
22	<b>Rhus copallina</b>	Uplands mostly
16	<b>Rubus nigrobaccus?</b>	A weed
13	<b>Aralia spinosa</b>	Hammocks
12	<b>Myrica cerifera</b>	Hammocks
11	<b>Alnus rugosa</b>	Branch-swamps, etc.
8	<b>Rhus glabra</b>	Near Pearl River
7	<b>Cliftonia monophylla</b>	Sourest non-alluvial swamps
7	<b>Viburnum nudum</b>	Non-alluvial swamps
6	<b>Ilex myrtifolia</b>	Shallow ponds near coast
6	<b>Callicarpa americana</b>	Hammocks, etc.
5	<b>Bignonia crucigera</b>	Bottoms mostly
4	<b>Vitis aestivalis</b>	Bottoms mostly
4	<b>Sassafras variifolium</b>	Mostly a weed
4	<b>Diospyros virginiana</b>	Various situations
4	<b>Phoradendron flavescens</b>	Mostly on <i>Nyssa biflora</i>

## HERBS

93	<b>Eriocaulon decangulare</b>	Wet pine-barrens
50	<b>Helenium tenuifolium</b>	A weed, on roadsides, etc.
45	<b>Rhexia Alifanus</b>	Pine meadows, etc.
39	<b>Eupatorium rotundifolium</b>	Low pine-barrens
36	<b>Sarracenia Sledgei</b>	Wet pine-barrens
34	<b>Sabbatia macrophylla</b>	Wet pine-barrens
29	<b>Lophiola aurea</b>	Wet pine-barrens
26	<b>Dichromena latifolia</b>	Wet pine-barrens
26	<b>Tillandsia usneoides</b>	Mostly in swamps
26	<b>Eupatorium capillifolium</b>	A weed
26	<b>Sabbatia campanulata</b>	Low pine-barrens
26	<b>Juncus Roemerianus</b>	Brackish marshes along coast
23	<b>Anastrophus compressus</b>	A weed
23	<b>Cracca virginiana</b>	Dry pine-barrens
23	<b>Polygala ramosa</b>	Low pine-barrens
22	<b>Campulosus aromaticus</b>	Low pine-barrens
22	<b>Eupatorium compositifolium</b>	A weed, in dry soils
21	<b>Tofieldia racemosa</b>	Wet pine-barrens
20	<b>Oxypolis filiformis</b>	Wet pine-barrens, etc.
18	<b>Cladium effusum</b>	Fresh or slightly brackish marshes
17	<b>Rynchospora Chapmani</b>	Wet pine-barrens, coastward
16	<b>Polygala cymosa</b>	Cypress ponds mostly
16	<b>Chondrophora nudata</b>	Low pine-barrens
14	<b>Stokesia laevis</b>	Low pine-barrens
13	<b>Anchistea virginica</b>	Shallow cypress ponds, etc.
12	<b>Eupatorium purpureum</b>	Branch-swamps
11	<b>Centella repanda</b>	Low pine-barrens
9	<b>Drosera filiformis Tracyi</b>	Wet pine-barrens



9	<i>Osmunda cinnamomea</i>	Non-alluvial swamps, etc.
8	<i>Hibiscus aculeatus</i>	Low pine-barrens
7	<i>Sabbatia angularis</i>	Low pine-barrens
7	<i>Scleria Baldwinii</i>	Cypress ponds, etc.
7	<i>Panicum dichotomum?</i>	Low pine-barrens
7	<i>Xyris</i> sp.	Low pine-barrens
6	<i>Rhexia lutea</i>	Low pine-barrens
6	<b><i>Aristida stricta</i></b>	Dry pine-barrens mostly
6	<b><i>Chrysopsis graminifolia</i></b>	Dry pine-barrens mostly
6	<i>Sagittaria lancifolia</i>	Estuarine marshes
6	<i>Polygala cruciata</i>	Low pine-barrens
5	<i>Azelia cassioides</i>	Low pine-barrens
5	<i>Cyperus pseudovegetus</i>	Ditches, etc.
5	<i>Ludwigia pilosa</i>	Ponds and ditches
5	<i>Rhynchospora corniculata</i>	Shallow ponds, etc.
5	<i>Baldwinia uniflora</i>	Low pine-barrens
5	<i>Habenaria nivea</i>	Low pine-barrens
5	<i>Linum floridanum</i>	Low pine-barrens
5	<i>Spartina polystachya</i>	Brackish marshes
4	<i>Leptilon canadense</i>	A weed
4	<b><i>Sarracenia psittacina</i></b>	Low pine-barrens
4	<i>Rhynchospora semiplumosa</i>	Low pine-barrens
4	<i>Helianthus angustifolius</i>	Low pine-barrens
4	<i>Trilisa odoratissima</i>	Low pine-barrens
4	<i>Rhynchospora axillaris</i>	Low pine-barrens
4	<i>Saururus cernuus</i>	Swamps
4	<i>Carphephorus Pseudo-Liatris</i>	Low pine-barrens
4	<b><i>Lycopodium alopecuroides</i></b>	Low pine-barrens
4	<i>Rynchospora Baldwinii</i>	Low pine-barrens
4	<i>Xyris flexuosa*</i>	Low pine-barrens

If we add together the figures for evergreens we find that 55.3 per cent. of the trees (six conifers and seven angiosperms) and 68.4 per cent. of the shrubs (counting *Cyrilla* as half evergreen) are evergreen. Of course a great deal of the most abundant tree, *Pinus palustris*, has been cut for lumber, much more proportionately than the cypress and hardwoods, which makes the percentage of evergreens lower than it would be for virgin forests. If a careful analysis of the forests of this region could have been made half a century ago the proportion of evergreens would probably have been found to be something like 75 per cent. This is in striking contrast with the northern half of the state, where the soils are more clayey and (therefore?) richer in potash, and where no natural region seems to have more than 20 per cent. of its trees evergreen.†

\* *X. torta* of most nineteenth-century authors. See Torrey 5: 129. 1905.

† See Bull. Torrey Club 40: 395-396. 1913.



The Ericaceae and allied families are usually pretty well represented in pine-barrens and other sandy regions, and therefore it is rather surprising that only one member of this family, *Oxydendrum*, was seen more than three times in all the travels above outlined. This may be correlated with the fact that the soils in southern Mississippi are a little richer than those of the average pine-barrens; but on the other hand, the Leguminosae, which seem to prefer soils pretty well supplied with potash, etc. but poor in humus, as in areas frequently burned over, seem equally scarce here, only one species, *Cracca Virginiana*, being listed



FIG. 2. Flat damp pine-barrens, with trees mostly *Pinus palustris*, stunted and rather scattered, about half a mile north of Fontainebleau, Jackson County. July 17, 1913.

above. More extensive explorations are needed to solve the problem.

*Comparisons with other pine-barren regions.*—It will be instructive to compare the foregoing list of plants with quantitative lists previously published for the corresponding parts of Georgia\* and Alabama.† In this way some conclusions can be drawn that would be utterly impossible with qualitative lists of the usual

\* Plant World 15: 244. Oct. 1912.

† Geol. Surv. Ala. Monog. 8: 116-117. June 1913. (This includes trees only.)



type. It is quite evident that the following species are more abundant in Georgia:—*Taxodium imbricarium*, *Quercus Catesbaei*, *Pinus serotina*,\* *Quercus cinerea*, *Cliftonia*, *Ilex myrtifolia*, *Nyssa Ogeche*,\* *Serenoa*, *Quercus pumila*, *Aristida stricta*, *Eupatorium compositifolium*, *Sarracenia flava*,\* *Chondrophora nudata*, *Eriogonum tomentosum*,\* *Baptisia perfoliata*,\* and *Kuhnistera*; and the following in Mississippi:—*Pinus Taeda*, *Liquidambar*, *Quercus marylandica*, *Cornus florida*, *Pinus glabra*, *Magnolia grandiflora*, *Fagus*,† *Pinus echinata*, *Taxodium distichum*, *Nyssa sylvatica*,† *N. uniflora*, *Oxydendrum*,† *Magnolia macrophylla*,† *Chamaecyparis*,† *Rhus copallina*, *R. glabra*,† *Sassafras*, *Sarracenia Sledgei*,† *Sabbatia macrophylla*, *Lophiola*, *Eupatorium capillifolium*, *Juncus Roemerianus*,† *Cladium*,† *Stokesia*, *Drosera filiformis Tracyi*, and *Carphephorus Pseudo-Liatris*. It is significant that practically all the species here enumerated for Georgia are typical pine-barren plants, while most of those noted as being more abundant in Mississippi are more characteristic of richer soils (and drier summers) farther inland. Several of the species common to Georgia and Mississippi, such as *Pinus Elliottii*, *Taxodium imbricarium*, *Pinus glabra*, *Quercus geminata*, *Chamaecyparis*, *Cliftonia*, *Lophiola*, *Drosera filiformis Tracyi*, and *Sarracenia psittacina*, are not known west of the Mississippi River, while several others grow in Louisiana but not in Texas. All this tends to confirm the suggestion made a few years ago‡ that the principal center for pine-barren plants is in Georgia, where they also extend farther inland than they do elsewhere.

Very few quantitative studies of forests for areas larger than single counties have been made as yet, but from a few that have been published by the writer for other pine-barren regions the following percentages of evergreens have been computed:

Pine-barrens of New Jersey (July) 74.3 per cent.§

Cape Fear pine-barrens, North Carolina (July) 60 per cent.||

\* Not known in Mississippi at all.

† Not known in the Altamaha Grit region of Georgia, but all except *Sarracenia Sledgei* have been found elsewhere in South Georgia. *Juncus Roemerianus* and *Cladium* are chiefly confined to the neighborhood of the coast.

‡ Torrey 7: 43. 1907.

§ Bull. Torrey Club 37: 426. 1910.

|| Bull. Torrey Club 37: 416. 1910.



Fall-line sand-hills of South Carolina (March) 59 per cent.; (July) 37.5 per cent.\*

Pine-barrens of southern South Carolina (March) 72.4 per cent.; (July) 53.8 per cent.†

Flat pine-barrens of southeastern Georgia and northeastern Florida (March) 66 per cent.‡

Altamaha Grit region of Georgia (December) 56.9 per cent.§

Lime-sink region of Alabama (original forests) 75 per cent.; (present condition) 65 per cent.||

Southwestern pine hills of Alabama (original forests) 84 per cent.; (present condition) 72 per cent.¶

All these figures, except those for Alabama, are based almost entirely on car-window notes, like those for Mississippi, and are doubtless too low, for such notes do not do justice to the abundance of the conifers. The winter figures for evergreens are higher than the corresponding summer ones, on account of the difficulty of recognizing some of the deciduous trees in winter.

#### NOTEWORTHY SPECIES

The following notes on distribution are based on the trip of 1913, unless otherwise indicated.

*Pinus Elliottii* Engelm. The northwesternmost stations I have observed for this species, in different years, are as follows: (1) On the Mobile & Ohio R.R. between Winchester and Waynesboro, Wayne County; (2) on the New Orleans, Mobile & Chicago R.R. in the upper edge of Perry County; (3) on the Mississippi Central R.R. a little west of Hattiesburg; (4) on the Columbia branch of the Gulf & Ship Island R.R. in the lower edge of Lamar County a little west of Lumberton. These points may be taken as marking approximately the limits of its range in that direction.\*\* Like most other typical pine-barren plants in Mississippi, it is not known west of the Pearl River, and is most abundant

\* Bull. Torrey Club 37: 413. 1910; 38: 224. 1911.

† Bull. Torrey Club 37: 410. 1910; 38: 226. 1911.

‡ Bull. Torrey Club 38: 231. 1911.

§ Plant World 15: 244. 1912.

|| Geol. Surv. Ala. Monog. 8: 109-111. 1913.

¶ Ibid. 116-118.

\*\* See *Torreya* 6: 200, 201, 203. 1906; Bull. Torrey Club 37: 603; 38: 236. 1911.



near the coast. *Pinus Taeda*, on the other hand, is common in the Pearl River bottoms, and rare coastward.

*Pinus glabra* Walt. is rather common near the Pearl and Leaf Rivers, and rare elsewhere in the pine-barren region. The same might be said of *Taxodium distichum*.



FIG. 3. Edge of cypress pond about a mile north of Fontainebleau, showing *Taxodium imbricarium* and *Pinus Elliottii*. July 17, 1913.

*Taxodium imbricarium* (Nutt.) Harper (*T. ascendens* Brong.). On the 1913 trip first seen about 15 miles north of Gulfport, and last near Merrill, George County,\* about 50 miles inland. (On the Mobile & Ohio R.R. it does not seem to reach the point where the railroad crosses the Alabama-Mississippi line.) In the Carolinas and Georgia it extends about as far inland as *T. distichum* does, but the inland limits of the two species are far apart in Alabama and still more so in Mississippi and Louisiana.

*Chamaecyparis thyoides* (L.) BSP. Rather common in estuarine swamps of the Escatawpa River (not the Pascagoula, which is muddy) near Moss Point, and seen also in a branch-swamp near the middle of Jackson County.

*Campulosus aromaticus* (Walt.) Trin. Seen first in Forrest County, last in Jones County. Usually in damp pine-barrens with *Rhexia Alifanus*, as in the Carolinas.

\* This county was created from parts of Greene and Jackson Counties in 1910.



*Dichromena latifolia* Baldw. First noticed in the lower edge of Forrest County and last in the upper part of Jackson County. Usually accompanied by *Lophiola aurea*.

*Serenoa serrulata* (Michx.) B. & H. In Mississippi this is rarely seen more than five miles from the coast.

*Eriocaulon decangulare* L. Seen first in the eastern part of Marion County and last in Jones County; extending farther inland than many of the more typical pine-barren plants.

*Lophiola aurea* Ker. First in the lower edge of Forrest County, last in the lower edge of George County.

*Myrica inodora* Bartr. Arborescent in a non-alluvial swamp near Moss Point, Jackson County.

*Quercus pumila* Walt. What I take to be this species was seen from the train three or four times in dry pine-barrens in Jackson County on July 18th. It does not seem to have been reported from Mississippi before, or even from Alabama; but Professor Tracy tells me that he has seen it somewhere west of Biloxi.

*Quercus Catesbaei* Walt. In Mississippi this seems to be commonest between 50 and 75 miles from the coast. I have seen it as far inland as Marion, Perry and Wayne Counties.

*Sarracenia Sledgei* Macfarlane. This species, which takes the place of *S. flava* in Mississippi, was seen in 1913 first in the lower part of Lamar County and last near Lucedale, George County; both localities being about 45 miles inland. Along the Mobile & Ohio R.R., however, it extends up into the southeastern corner of Wayne County, about 63 miles from Mobile.

*Sarracenia rubra* Walt. A few specimens were seen in low pine-barrens northeast of Buckatunna in 1911.

*Magnolia macrophylla* Michx. Occasional in rich soil near the Pearl and Leaf Rivers. More common in the loess region west of the pine-barrens, in Franklin County, as was noted by Hilgard in 1860.\*

*Crataegus aestivalis* (Walt.) T. & G. In shallow ponds, where the red clay is near the surface, near Agricola, George County, July 18, 1913; and perhaps also near Buckatunna, Wayne County, October 18, 1908.

*Polygala cymosa* Walt. Seen first near Ten Mile, Harrison

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\* Geol. & Agric. Miss. 323-324. (§ 703).



County (about 27 miles inland), and last in the upper edge of Jackson County. Commonest within a mile or two of the coast. *P. ramosa* is more widely distributed, extending inland to Marion and Jones Counties.

*Drosera filiformis Tracyi* (Macfarlane) Diels. First about two miles north of Ocean Springs, Jackson County (not far from Professor Tracy's home), and last in the lower edge of George County.

*Cliftonia monophylla* (Lam.) Sarg. Extends inland to near Nugent, Harrison County, and Lucedale, George County. *Cyrilla racemiflora*, which sometimes associates with it, prefers richer soils and is less restricted in range.

*Ilex myrtifolia* Walt. In shallow ponds, Jackson County.

*Ilex glabra* (L.) Gray. Extends inland to Marion and Jones Counties, like *Eriocaulon decangulare*.

*Rhexia Alifanus* Walt. (*R. glabella* Michx.). Extends inland to the eastern part of Marion County and the southern part of Perry, but still farther in Alabama, as does the preceding.

*Oxypolis filiformis* (Walt.) Britton. Noticed first near Mississippi City, Harrison County, and last between Moss Point and the Escatawpa River, five or six miles from the coast.

*Sabbatia macrophylla* Hook. First near Lumberton, last between Hintonville and Glazier, Perry County.

*Sabbatia decandra* (Walt.) Harper. In a shallow pond near the middle of Jackson County, July 18, 1913.

*Sabbatia gentianoides* Ell. Flat damp pine-barrens near Fontainebleau and Moss Point, Jackson County.

*Stokesia laevis* (Hill) Greene. Noticed first in Forrest County, and last between Bexley and Merrill, George County. Commonest in the upper part of Harrison County; and not observed within 14 miles of the coast. I have also seen it a few times in Mobile County, Alabama, and once in the corresponding part of Georgia.\*

*Carphephorus Pseudo-Liatris* Cass. In flat damp pine-barrens near the coast, Jackson County.

Many of the species above mentioned show a tendency to extend farther inland eastward than westward (and still more so in Alabama and Georgia), which appears to be correlated with the seasonal distribution of rainfall as much as anything else.

\* See Bull. Torrey Club 32: 167. 1905.







# INDEX TO AMERICAN BOTANICAL LITERATURE

1906-1914

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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Includes *Bremiella* gen. nov. and *Peronospora Lepidii*, *P. Chamaesycticis*, and *P. minima*, spp. nov.



# BULLETIN

OF THE

# TORREY BOTANICAL CLUB

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## CONTENTS

Report on the Hepaticae of Alaska. (Plate 21.) . . . ALEXANDER W. EVANS 577

Branched cells in the prothallium of *Onoclea sensibilis* L. (Plates 22 and 23.)  
 CAROLINE A. BLACK 617

The correct name for the hemlock spruce . . . . . OLIVER A. FARWELL 621

INDEX TO AMERICAN BOTANICAL LITERATURE. . . . . 631

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BULLETIN  
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DECEMBER, 1914

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Report on the Hepaticae of Alaska\*

ALEXANDER W. EVANS

(WITH PLATE 21 AND THREE TEXT FIGURES)

INTRODUCTION

Through the kindness of Professor T. C. Frye, of the University of Washington, the writer has recently received a large collection of Alaska Hepaticae for determination. It was made in 1913 under the auspices of the Kelp Investigation Expedition of the United States Bureau of Soils. The vast majority of the specimens were collected by Professor Frye himself, but his collection is supplemented by a few specimens collected by Mr. A. B. Foster, Dr. G. B. Rigg, and Dr. R. B. Wylie. The specimens were all gathered near the coast, the easternmost locality being Verdure Creek, near the upper end of Portland Canal, and the westernmost, Mitrofanina Bay on the Alaska Peninsula. In spite of the fact that the region visited represents a relatively small portion of Alaska, the collection is the most comprehensive which has yet been brought back from the territory. It includes seventy species in condition to be identified, twenty being new to Alaska (or not before reported), seven new to America, and three new to science. The next largest collection, that of the Harriman Alaska Expedition, contained sixty-three species, thirty-nine of which were reported from Alaska for the first time. Of these thirty-nine species six were new to America and one, *Scapania cordifolia* K. Müll., was new to science, although it was at first confused with another species.

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\* Contribution from the Osborn Botanical Laboratory.

[The BULLETIN for November (41: 533-576) was issued 28 N 1914.]



The present report is based on Professor Frye's collection, but it reviews also what is known from other sources about the Hepaticae of Alaska and compares the species found in the territory with those occurring in other parts of the world. In addition to the seventy species represented in the present material, forty other species have been reported from Alaska. Five of these reports, however, were based on incorrect determinations or insufficient evidence, so that only thirty-five of the species can actually be accredited. The total number of species now known from Alaska is, therefore, 105. This number will probably be more than doubled when the flora has been more thoroughly explored.

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In the writer's report on the Hepaticae of the Harriman Expedition the literature of the Alaskan species is reviewed up to the close of 1900. Since that time a small collection of species has been reported upon by the writer, and another small collection by Howe, while a few additional species have been recorded by K. Müller and Stephani. The more important papers dealing with Alaskan species or containing scattered references to them are the following, only those which give actual new records being included:

1. **Cooley, Grace E.** Plants collected in Alaska and Nanaimo, B. C., July and August, 1891. Bull. Torrey Club **19**: 239-249. 1892.  
A list of thirteen Hepaticae from Alaska is given on pages 246 and 247, six of the species being reported for the first time.
2. **Coville, F. V.** Botany of Yakutat Bay, Alaska. II.—Botanical report. Contr. U. S. Nat. Herb. **3**: 334-353. 1896.  
A list of eight Hepaticae is given on page 351, two being reported for the first time.
3. **Evans, A. W.** Papers from the Harriman Alaska Expedition. V. Notes on the Hepaticae collected in Alaska. Proc. Wash. Acad. Sci. **2**: 287-314. *pl. 16-18.* 1900.  
Sixty-three species are listed, including thirty-nine additions to the Alaska flora; two other additions are mentioned incidentally.
4. **Evans, A. W.** Hepaticae collected by William A. Setchell in northern Alaska. Zoe **5**: 129-132. 1901.  
Twenty-three species are listed, two for the first time.
5. **Gottsche, C. M., Lindenberg, J. B. G., and Nees von Esenbeck, C. G.** Synopsis Hepaticarum. Hamburg. 1844-47.  
Four species are reported from Alaska, all for the first time.



6. **Howe, M. A.** The North American species of *Porella*. Bull. Torrey Club 24: 512-527. 1897.

Two species are noted from Alaska, one for the first time.

7. **Howe, M. A.** The Hepaticae and Anthocerotae of California. Mem. Torrey Club 7: 1-208. *pl.* 88-122. 1899.

Several species are reported from Alaska, three for the first time.

8. **Howe, M. A.** Contributions to the botany of the Yukon territory. I. An enumeration of the Hepaticae collected by R. S. Williams, 1898-1899. Bull. N. Y. Bot. Gard. 2: 101-105. *pl.* 14. 1901.

Several of the species listed, including two additions, came from Alaska. One of the species, *Scapania imbricata*, is described as new and figured.

9. **Merriam, C. H.** Plants of the Pribilof Islands, Bering Sea. Proc. Biol. Soc. Wash. 7: 133-150. 1892.

A list of three Hepaticae is given on page 150, the records being new but containing no additions to the Alaska flora.

10. **Müller, K.** Neue und kritische Lebermoose. Bull. Herb. Boissier II. 3: 34-44. *pl.* 1. 1903.

A new species, *S. cordifolia*, is described from Alaska specimens.

11. **Müller, K.** Monographie der Lebermoosgattung *Scapania* Dum. Nova Acta Kaiserl. Leop.-Carol. Acad. 88: 1-312. *pl.* 1-52. 1905.

Several species are quoted from Alaska, a few of the records being new, although no additions to the Alaska flora are reported.

12. **Pearson, W. H.** List of Canadian Hepaticae. 1-31. *pl.* 1-12. Montreal. 1890.

Several species are quoted from Alaska, one record being new.

13. **Rothrock, J. T.** Sketch of the flora of Alaska. Rept. Smithsonian Institution for 1867: 433-463. 1867.

A list of six Hepaticae, all representing additions to the flora of Alaska, is given on page 462.

14. **Stephani, F.** Hepaticae von der Halbinsel Alaska, gesammelt 1881/1882 von den Doctoren Arthur und Aurel Krause. Bot. Jahrb. 8: 96-99. *pl.* 3, *f.* 9-11. 1887.

Twenty-two species are listed, sixteen for the first time. Of these sixteen species four are described as new, viz., *Scapania albescens*, *Radula arctica*, *R. Krausei*, and *Frullania chilcootiensis*. The *Scapania*, however, is synonymous with *S. Bolanderi*, while *R. arctica* is probably synonymous with *R. Bolanderi* and *R. Krausei* with *R. complanata*.

15. **Stephani, F.** Species Hepaticarum. Bull., Mém., and Compl. au Bull. Herb. Boissier. 5 vols., the fifth in course of publication. 1898-1914.

Several species are recorded from Alaska, three for the first time.



16. Underwood, L. M. A preliminary list of Pacific Coast Hepaticae. *Zoe* 1: 361-367.

Among the species quoted from Alaska two represent additions to the flora.

#### LOCALITIES VISITED BY THE KELP EXPEDITION

The portion of Alaska investigated by the Kelp Expedition falls almost entirely within the Pacific Coast Forest region, as defined by the United States Forest Bureau. One or two of the westernmost stations, where arctic conditions prevail, offer the only exceptions to this statement. All of the localities visited are on or near the coast and are characterized by a heavy rainfall and low temperatures, although extremes of cold are rarely encountered. These conditions are unusually favorable for the growth of Hepaticae, and it is not surprising that they form a significant element of the flora.

With five exceptions the localities where the Hepaticae were collected are situated in the southeastern part of Alaska, a district containing numerous islands separated from one another and from the mainland by narrow channels. Forests abound everywhere, the prevailing tree being the western hemlock, *Tsuga heterophylla* (Raf.) Sarg. Another conspicuous tree is the Sitka spruce, *Picea sitchensis* (Bong.) Carr., while the Alaska cypress, *Chamaecyparis nootkatensis* (Lamb.) Spach, and the mountain hemlock, *Tsuga Mertensiana* (Bong.) Carr., are of frequent occurrence. Among deciduous trees the red alder, *Alnus rubra* Bong., is perhaps the most abundant. The five stations which are not in the southeastern part of Alaska represent a portion of the territory where the western hemlock, the Sitka spruce, and the mountain hemlock reach the northern and western limits of their ranges and gradually disappear. The balm-of-Gilead, *Populus balsamifera* L., is a deciduous species occurring in the same region.

The accompanying map (TEXT FIG. 1), after a sketch by Professor Frye, will show how most of the localities where specimens were collected are situated, and the following data, likewise supplied by Professor Frye, will give further information about the localities. The numbers correspond with those on the map.

1. AATS BAY. North shore of Coronation Island. The collections were made about the south end of the west arm and on the



peak to the southward. About latitude  $55^{\circ} 53'$  and longitude  $134^{\circ} 15'$ .

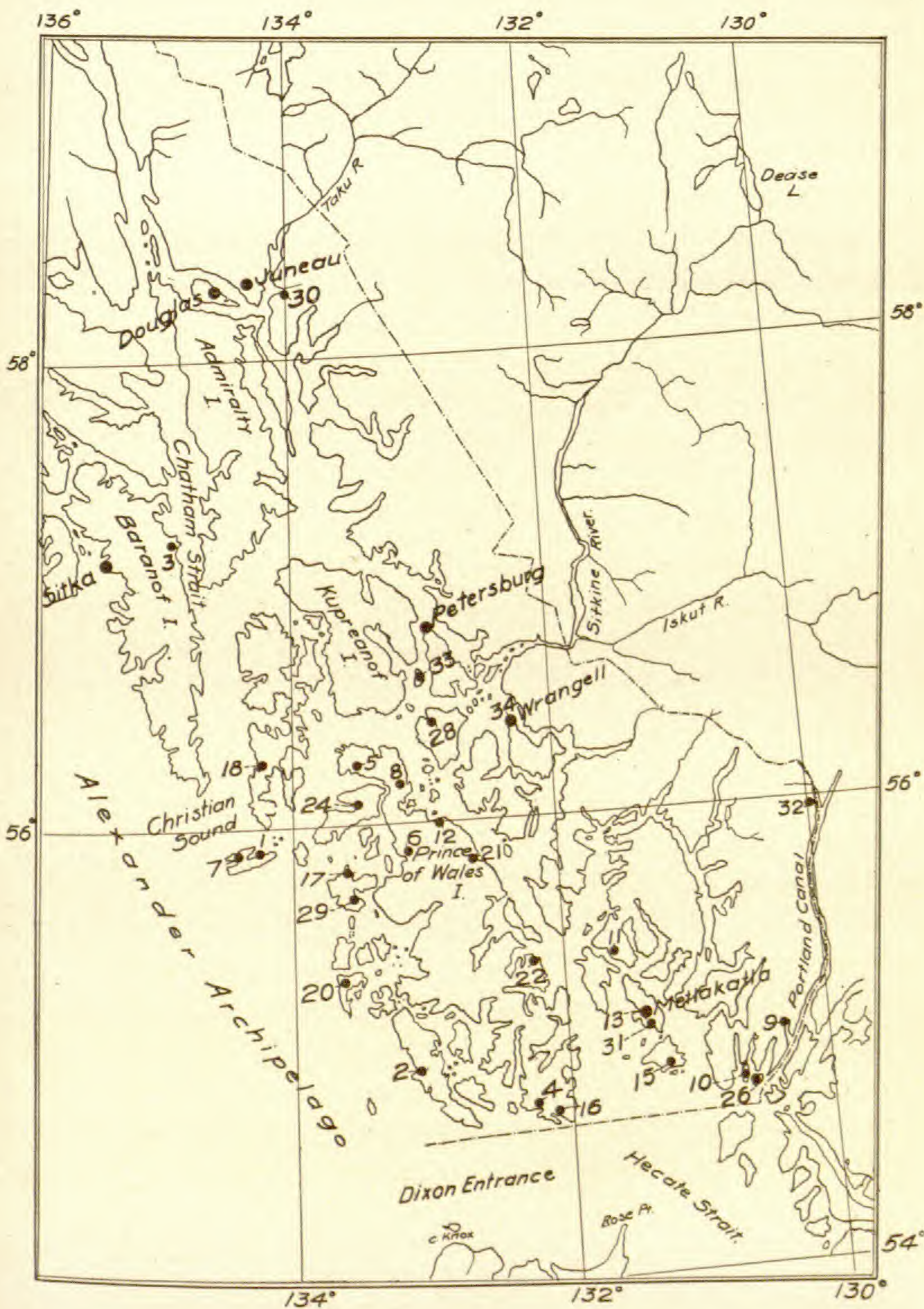


FIG. 1. Map of southeastern Alaska, showing most of the localities visited by the Kelp Expedition. Drawn by Mr. S. J. Berard, after a sketch by Professor T. C. Frye.



2. AUGUSTINE BAY. West shore of Dall Island, just north of Cape Augustine. The collections were made within a half mile of the head of the Bay. About latitude  $54^{\circ} 58'$  and longitude  $133^{\circ} 11'$ .

3. BARANOF. Post office and warm springs on Warm Spring Bay, east shore of Baranof Island. The collections were all made within 300 yards of the warm springs. About latitude  $57^{\circ} 5'$  and longitude  $134^{\circ} 50'$ .

4. BROWNSON BAY. South shore of Prince of Wales Island. The collections were made on a trip from the head of the Bay westward to the head of a large lake about a mile and a half distant, then down the east side of the lake to its outlet and diagonally back to the head of the Bay. About latitude  $54^{\circ} 46'$  and longitude  $132^{\circ} 15'$ .

5. CALDER. Post office and quarry on Shakau Bay, Prince of Wales Island. The collections were made within quarter of a mile of the quarry. About latitude  $56^{\circ} 10'$  and longitude  $133^{\circ} 27'$ .

6. DEWEYVILLE. Indian village on Prince of Wales Island at Sarkar Cove, an indentation opening on El Capitan Passage. The collections were made at the head of the Cove within quarter of a mile of the village. About latitude  $55^{\circ} 57'$  and longitude  $133^{\circ} 14'$ .

7. EGG HARBOR. North shore of Coronation Island. The collections were made near the south end of the Harbor and along a stream to the westward for about a mile. About latitude  $55^{\circ} 54'$  and longitude  $134^{\circ} 19'$ .

8. EXCHANGE COVE. Shore of Prince of Wales Island, southeast of Zarembo Island. The collections were made on the north shore of a stream flowing into the Cove. About latitude  $56^{\circ} 12'$  and longitude  $133^{\circ} 5'$ .

9. HIDDEN INLET. An arm of Pearse Inlet near the mouth of Portland Canal. The collections were made at the mouth of the Inlet, on the west shore. About latitude  $54^{\circ} 56'$  and longitude  $130^{\circ} 20'$ .

10. KANAGUNUT ISLAND. Very near the southeast corner of Alaska. The collections were made along the east shore and about a quarter of a mile from the north end. About latitude  $54^{\circ} 5'$  and longitude  $130^{\circ} 43'$ .

11. KETCHIKAN. Town on Tongass Narrows. The collec-



tions were made chiefly along a creek. About latitude  $55^{\circ} 21'$  and longitude  $131^{\circ} 38'$ .

12. LAKE BAY. Northeast shore of Prince of Wales Island, south of Zarembo Island. The collections were made near the shore and about quarter of a mile north of the cannery. About latitude  $56^{\circ} 1'$  and longitude  $132^{\circ} 55'$ .

13. METLAKATLA. Town on the west shore of Annette Island. The collections were made near the shore eastward and along a stream with a waterfall, the outlet of a lake about two miles from the town. About latitude  $55^{\circ} 7'$  and longitude  $131^{\circ} 33'$ .

14. MITROFANIA BAY. Southeast shore of Alaska Peninsula, northeast of the Shumagin Islands. About latitude  $56^{\circ} 0'$  and longitude  $158^{\circ} 45'$ . Not shown on the map.

15. MORSE COVE. South shore of Duke Island. The collections were made along the shore of the Cove and about two miles to the southwestward. About latitude  $54^{\circ} 55'$  and longitude  $131^{\circ} 16'$ .

16. NICHOLS BAY. South shore of Prince of Wales Island, near Cape Chacan. The collections were made on and near the west side of the Bay. About latitude  $54^{\circ} 43'$  and longitude  $132^{\circ} 8'$ .

17. PORT ALICE. North shore of Heceta Island. The collections were made along the west shore of an inlet and near the head. About latitude  $55^{\circ} 48'$  and longitude  $133^{\circ} 35'$ .

18. PORT MALMSBURY. West shore of Kuiu Island. The collections were made along the west shore and near the head of the second arm to the southward. About latitude  $56^{\circ} 12'$  and longitude  $134^{\circ} 9'$ .

19. PORT CHATHAM. Near the western end of Kenai Peninsula at the mouth of Cook Inlet. The collections were made along the north shore. About latitude  $59^{\circ} 14'$  and longitude  $151^{\circ} 45'$ . Not shown on the map.

20. PORT SAN ANTONIO. East shore of Baker Island. About latitude  $55^{\circ} 22'$  and longitude  $133^{\circ} 37'$ .

21. RATZ HARBOR. East shore of Prince of Wales Island, opposite Etolin Island. The collections were made near the south arm of the Harbor, close to the mouth of the salt water lagoon. About latitude  $55^{\circ} 53'$  and longitude  $132^{\circ} 35'$ .

22. SALTERY COVE. An indentation of Kasaan Bay, on the



east shore of Prince of Wales Island. The collections were made at the head of the Cove, within quarter of a mile of the cannery. About latitude  $55^{\circ} 24'$  and longitude  $132^{\circ} 19'$ .

23. SEWARD. South shore of Kenai Peninsula. About latitude  $60^{\circ} 8'$  and longitude  $147^{\circ} 45'$ . Not shown on the map.

24. SHIPLEY BAY. Northwest shore of Prince of Wales Island. The collections were made at the head of the Bay near the mouth of a creek. About latitude  $58^{\circ} 5'$  and longitude  $133^{\circ} 8'$ .

25. SHUYAK ISLAND. North of Afognack Island. The collections were made along the shore of an unnamed bay, at the southwest corner of the Island. About latitude  $58^{\circ} 30'$  and longitude  $152^{\circ} 27'$ . Not shown on the map.

26. SITKLAN ISLAND. Southeast corner of Alaska. The collections were made along the southwest shore. About latitude  $54^{\circ} 44.5'$  and longitude  $130^{\circ} 41'$ .

27. SNUG HARBOR. Southeast shore of Knight Island in Prince William Sound. About latitude  $60^{\circ} 16'$  and longitude  $147^{\circ} 45'$ . Not shown on the map.

28. ST. JOHN HARBOR. Northwest shore of Zarembo Island. The collections were made within two miles of the shore. About latitude  $56^{\circ} 26'$  and longitude  $132^{\circ} 56'$ .

29. SWIFTS CANNERY. Southeast shore of Heceta Island. The collections were made within quarter of a mile of the cannery. About latitude  $55^{\circ} 43'$  and longitude  $133^{\circ} 29'$ .

30. TAKU INLET. South of Juneau, receiving the Taku and Turner rivers. The collections were made along the east shore of the Inlet at the mouth of Turner River and about four miles south of Taku Glacier. About latitude  $58^{\circ} 25'$  and longitude  $134^{\circ} 0'$ .

31. TAM GAS HARBOR. South shore of Annette Island. The collections were made near the shore from Crab Point northwestward for a distance of about a mile and a half. About latitude  $55^{\circ} 4'$  and longitude  $131^{\circ} 33'$ .

32. VERDURE CREEK. A small stream emptying into Portland Canal near the upper end and about one mile north of Verdure Point. The collections were made near the mouth of the Creek. About latitude  $55^{\circ} 45'$  and longitude  $130^{\circ} 10'$ .

33. WOEWODSKI ISLAND. South entrance to Wrangell Strait.



The collections were made within a quarter of a mile of the abandoned Olympic Mine. About latitude  $56^{\circ} 31'$  and longitude  $133^{\circ} 2'$ .

34. WRANGELL. Near the mouth of the Stikene River. The collections were made within a few miles of the town. About latitude  $56^{\circ} 28'$  and longitude  $132^{\circ} 22'$ .

#### HEPATICAE COLLECTED BY THE KELP EXPEDITION

In the following enumeration the numbers in parentheses refer to the papers listed in the Bibliography, see page 578. Only those records are quoted which were new at the time they were published. Unless otherwise noted the specimens listed were collected by Professor Frye. The arrangement adopted is that of Schiffner in Engler & Prantl's *Die natürlichen Pflanzenfamilien*.

#### MARCHANTIACEAE

##### 1. CONOCEPHALUM CONICUM (L.) Dumort.

On wet soil. Aats Bay (904); Augustine Bay (584); Hidden Inlet (59); Ketchikan (18); St. John Harbor (240); Swifts Cannery (693). Previously reported by Rothrock (13, as *Fegatella conica*), Stephani (14, p. 99, as *F. conica*), Miss Cooley (1, p. 246), and the writer (3, p. 290; 4, p. 129).

##### 2. PREISSIA QUADRATA (Scop.) Nees

On soil among stones. Aats Bay (937). Previously reported by Stephani (14, p. 99), Miss Cooley (1, p. 247, as *P. hemisphaerica*), and the writer (3, p. 290; 4, p. 129).

##### 3. MARCHANTIA POLYMORPHA L.

On damp soil. Calder (829); Woewodski Island (964). Previously reported by Rothrock (13), Stephani (14, p. 99), Miss Cooley (1, p. 247), and the writer (3, p. 291; 4, p. 129).

#### METZGERIACEAE

##### 4. RICCARDIA LATIFRONS Lindb.

On bogs, sticks, and wet soil. Calder (827 in part); Exchange Cove (261); Ketchikan (505); Nichols Bay (391); Port San Antonio



(609, 618); Swifts Cannery (700). Previously reported by the writer (3, p. 291).

5. RICCARDIA MULTIFIDA (L.) S. F. Gray

On wet rocks and logs. Port Alice (728 in part); Port Malmsbury (994). New to Alaska.

6. METZGERIA CONJUGATA Lindb.

On rocks, trees, and logs. Aats Bay (900 in part, 907, 916, 927); Augustine Bay (574, 579 in part); Brownson Bay (476); Exchange Cove (267); Hidden Inlet (58); Nichols Bay (369, 392 in part, 399 in part, 401); Ratz Harbor (321); St. John Harbor (221, 250). New to Alaska.

7. METZGERIA PUBESCENS (Schrank) Raddi

On wet rocks. Hidden Inlet (80). Previously reported by Stephani (14, p. 98) and Miss Cooley (1, p. 247).

8. PALLAVICINIA FLOTOWIANA (Nees) Lindb.

On moist soil. Seward (*Rigg 1216*). Previously reported by the writer (3, p. 291, as *P. hibernica*).

9. PELLIA NEESIANA (Gottsche) Limpr.

On wet soil. Aats Bay (901); Baranof (1080); Ketchikan (10, 17); Ratz Harbor (301); St. John Harbor (241); Swifts Cannery (704). Previously reported by the writer (3, p. 293).

## JUNGERMANNIACEAE

10. GYMNOMITRIUM OBTUSUM (Lindb.) Pears.

On rocks. Brownson Bay (481); Nichols Bay (380). Previously reported by the writer (3, p. 293, *pl. 16, f. 1-3*).

11. MARSUPELLA EMARGINATA (Ehrh.) Dumort.

On wet rocks, soil, and decayed logs. Ketchikan (9); Nichols Bay (373); Port Malmsbury (993); St. John Harbor (223, 234, 251); Verdure Creek (35). Previously reported by the writer (3, p. 295; 4, p. 130) and Howe (8, p. 102).



12. *NARDIA SCALARIS* (Schrad.) S. F. Gray

On wet soil. Ketchikan (502); Port Malmsbury (992); Shuyak Island (*Rigg 1230*). Previously reported by the writer (3, p. 296).

13. *GYROTHYRA UNDERWOODIANA* M. A. Howe

On wet rocks. Augustine Bay (545). New to Alaska.

14. *JUNGERMANNIA ATROVIRENS* Schleich.

On wet rocks. Port Alice (730). Previously reported by the writer (3, p. 299; 4, p. 131).

15. *JUNGERMANNIA CORDIFOLIA* Hook.

On a log in a streamlet. Port San Antonio (601). Previously reported by Stephani (14, p. 97) and Howe (8, p. 102).

The specimens in the present collection are sterile and are aberrant in having better developed trigones than is usual in the species. In this respect they agree with the specimens cited by Howe.

16. *LOPHOZIA FLOERKEI* (Web. & Mohr) Schiffn.

In a swampy place. Baranof (1084 in part). Previously reported by the writer (3, p. 304; 4, p. 131) and Howe (8, p. 103).

17. *LOPHOZIA INCISA* (Schrad.) Dumort.

On decayed logs. Lake Bay (208); Nichols Bay (402); Ratz Harbor (307); Port San Antonio (623); Sitklan Island (44); Swifts Cannery (692, 702); Tam Gas Harbor (146). Previously reported by the writer (3, p. 303; 4, p. 131).

18. *LOPHOZIA INFLATA* (Huds.) M. A. Howe

In pools. Nichols Bay (388); St. John Harbor (227). Previously reported by the writer (3, p. 304; 4, p. 131).

19. *LOPHOZIA PORPHYROLEUCA* (Nees) Schiffn.

On logs and moist soil. Exchange Cove (275); Port Chatham (*Rigg 1225* in part); Swifts Cannery (759); Taku Inlet (1027). Not before reported from Alaska. The species was collected, however, by Miss Lois Clark at Douglas, in October, 1908.



## 20. LOPHOZIA QUINQUEDENTATA (Huds.) Cogn.

On earth. Mitrofanía Bay (*Rigg 1233*). Previously reported by the writer (3, p. 304).

## 21. SPHENOLOBUS EXSECTUS (Schmid.) Steph.

On earth. Mitrofanía Bay (*Rigg 1219* in part). New to Alaska.

## 22. SPHENOLOBUS MINUTUS (Crantz) Steph.

On rocks. Verdure Creek (31). Previously reported by Stephani (12, p. 97, as *Jungermannia minuta*), the writer (3, p. 305, as *Lophozia minuta*) and Howe (8, p. 103, as *L. minuta*).

## 23. ANASTREPTA ORCADENSIS (Hook.) Schiffn.

*Jungermannia orcadensis* Hook. Brit. Jung. *pl.* 17. 1814.

*Mesophylla orcadensis* Dumort. Hep. Europ. 130. 1874.

*Jungermannia (Anastrepta) orcadensis* Lindb.; Lindberg & Arnell, Kgl. Svenska Vet. Akad. Handl. 23<sup>5</sup>: 40. 1889.

*Anastrepta orcadensis* Schiffn.; Engler & Prantl, Nat. Pflanzenfam. 1<sup>3</sup>: 85. 1893.

In a swampy place. Baranof (1084 in part). New to America.

The geographical distribution of *Anastrepta orcadensis* presents several points of interest. In Europe it is more or less abundant in the higher mountain ranges, reaching lower altitudes in the British Isles, the Faroe Islands, and Scandinavia. Then it reappears in the Himalayas, in China, and in the Hawaiian Islands. Its discovery in Alaska marks a very noteworthy extension of its known range.

Although Lindberg knew the plant from sterile material only, he pointed out the fact that it differed markedly from the species of *Jungermannia*, subgenus *Eujungermannia*, section *Lophozia*—the genus *Lophozia* of most recent writers—and proposed the new section *Anastrepta* for its reception. This section was soon raised by Schiffner to generic rank, although he was still in ignorance of the reproductive branches. At the time of its publication as a genus *Anastrepta* was monotypic, but Stephani has recently transferred to it two additional species from the Straits of Magellan.

The habit of *Anastrepta* differs strongly from that of *Lophozia*, the stems being erect or ascending and forming loose tufts. The



leaves are succubous and bidentate at the apex, much as in *Lophozia*, subgenus *Dilophozia* K. Müll., but the line of attachment is strongly arched, the leaves being slightly decurrent at the postical base. In this respect the genus shows a relationship to *Plagiochila*. The leaves in *A. orcadensis* are imbricated and spread somewhat widely from the stem. The margin at the antical base is more or less revolute but this condition is much more pronounced at the postical base, the narrow revolute portion being quite unlike anything found in *Lophozia*. The apical sinus and lobes are subject to considerable variation. The sinus is always shallow and is sometimes scarcely apparent, the apex of the leaves appearing truncate. The lobes are sometimes nothing more than rounded corners and are usually rounded or very obtuse even when more distinct. Occasionally, however, they are more sharply pointed. The leaf-cells are small, measuring about  $16\ \mu$  in diameter in the middle of the leaf and  $20 \times 16\ \mu$  at the base. Their walls are thin and their small trigones have concave or straight sides. The cuticle is smooth.

Soon after Schiffner published *Anastrepta* as a genus the androecia and perianths were described by Jörgensen from Norwegian material, and K. Müller has recently added an account of the sporophyte from specimens collected by J. Velenovský near Prague. According to Jörgensen\* the perianths are slightly laterally compressed, but K. Müller was unable to confirm his observations and describes the perianths as bluntly four-angled in the upper part and plicate at the contracted mouth. The perianths, therefore, are essentially like those of *Lophozia*, and the same thing may be said of the androecia and sporophytes. At the same time the peculiar features of the vegetative organs are sufficient to justify the maintenance of *Anastrepta* as a genus. The specimens from Baranof are not abundant and lack sexual organs. Some of the leaves, however, bear clusters of the characteristic two-celled gemmae, which are deeply pigmented with purple and often show an angular outline. K. Müller† and Macvicar‡ may be consulted for descriptions and figures of the

\* Bergens Mus. Aarb. 1894-95<sup>18</sup>: 3-5. pl. 1; 1901<sup>4</sup>: 3-5. pl. 1.

† Rabenhorst's Kryptogamen-Flora 6: 753. f. 336, 337. 1910.

‡ Student's Handb. British Hepat. 213. f. 1-4. 1912.



species, while Schiffner\* has given a full account of its more important forms.

24. *PLAGIOCHILA ASPLENIOIDES* (L.) Dumort.

On damp rocks, soil, and logs. Augustine Bay (544); Hidden Inlet (60); Lake Bay (205); Mitrofanina Bay (Rigg 1219 in part); Port Alice (724, 728 in part); Shipley Bay (767, 778); St. John Harbor (230, 246); Swifts Cannery (691); Tam Gas Harbor (130). Previously reported by Coville (2) and the writer (3, p. 305; 4, p. 131).

25. *Plagiochila alaskana* sp. nov.

On logs. Nichols Bay (392 mostly, 399 mostly). No. 399 may be designated the type. The accompanying species are *Metzgeria conjugata* (mixed with both numbers), *Diplophyllum albicans* (mixed with 392), and *Frullania nisquallensis* (mixed with 399).

Yellowish or brownish green, not glossy, growing in compact tufts: stems mostly 2–3 cm. long and about 0.15 mm. in diameter, rigid, ascending, simple or sparingly and irregularly branched, the branches all intercalary, obliquely spreading, similar to the stems: rhizoids sometimes present near the base: leaves alternate, more or less imbricated, spreading at an angle of 45 degrees or less, postically secund and often deflexed in the outer part, more or less convex, ovate, mostly 1–1.4 mm. long (from middle of base to apex) and 0.7 mm. wide, long-decurrent antically, less decurrent postically, the decurrent portions narrow and the line of attachment strongly arched; antical margin revolute to about the middle, straight or slightly outwardly curved (on explanate leaves), entire to about the middle, sharply dentate or ciliate-dentate in the outer part; postical margin more strongly outwardly curved, sometimes slightly dilated toward the base, sharply dentate or ciliate-dentate; apex broad and rounded with teeth like those on the postical margin; total number of teeth mostly twenty to twenty-five, unequal, three to six cells long, one to three cells wide at the base; leaf cells plane, averaging  $14\ \mu$  in the apical portion,  $21 \times 14\ \mu$  in the middle, and  $40 \times 14\ \mu$  at the base, walls more or less thickened with well-developed triangular trigones, sometimes with bulging sides, and rare intermediate thickenings, coalescence between thickenings frequent, especially in median and basal regions, cuticle smooth: underleaves very minute:

\* Ber. naturw.-med. Ver. Innsbruck 31 (Beilage): 22–31. 1908.



inflorescence dioicous: ♀ inflorescence borne on the stem or on a leading branch, often with one or two subfloral innovations; bracts similar to the leaves and intergrading into them; innermost bracts about 1.5 mm. long and 1 mm. wide, the marginal teeth about twenty-five, usually longer than those on the leaves, an occasional tooth sometimes attaining a length of seven or eight cells; perianth narrowly obovate, about 2.7 mm. long and 1 mm. wide, strongly compressed, the sharp keels destitute of wings, sharply and densely ciliate at the truncate mouth: ♂ inflorescence and sporophyte not seen. (PLATE 21, FIGS. 1-6.)

This and the following species are closely allied but have no near relatives among the other species known from North America. Some of the East Indian species resemble them to a certain extent, and the same thing is true of various Andean species. The writer finds it impossible, however, to refer them to any described species and therefore proposes them as new, in spite of the fact that the species of *Plagiochila* are already so numerous and so incompletely understood.

In *P. alaskana* the following characters are perhaps the most important from a diagnostic standpoint: the simple or sparingly branched stems; the intercalary branches; the postically secund and often deflexed leaves; the narrowly arched line of attachment, the antical base being remarkably long-decurrent; the dentate or ciliate-dentate leaf-margins; the group of elongated cells at the base of the leaves; the exalate perianths. These peculiarities would place the species in Schiffner's section *Denticulatae*,\* a well-marked group which Stephani unfortunately does not recognize.

Among the species of this group growing in tropical Asia mention may be made of two, *P. renitens* Nees,† of Java, Sumatra, and India, and *P. trapezoidea* Lindenb.,‡ of Java. In both of these species the characters just enumerated for *P. alaskana* are more or less clearly exhibited. Both species, however, are considerably larger, the stems sometimes attaining a length of 10 cm. and the leaves a length of 2.5 mm. or more. The leaves, moreover, are

\* Die Hepaticae der Flora von Buitenzorg. Fl. Buitenzorg 4: 106. 1900.

† Lindenberg, Monogr. Hepat. Gen. *Plagiochilae* 90. pl. 17, f. 1-6. 1844 (= *Jungermannia renitens* Nees, Enum. Plant. Crypt. Javae 1: 76. 1830).

‡ L. c. 112. pl. 22, f. 1-18. 1844.



relatively broader, the ratio of width to length being 0.9 instead of only 0.7–0.75 as in *P. alaskana*. The greater relative breadth is due largely to a strong dilation at the postical base. The marginal teeth in the two Asian species are much like those in *P. alaskana* but usually number from thirty to forty. In *P. renitens* the decurrent portion at the antical base is entire, but in *P. trapezoidea* it is distinctly dentate and the species is further remarkable on account of the short and narrow lamina or paraphyllum which runs parallel with the decurrent portion and is situated in its near vicinity. In *P. renitens* the deflexed and postically secund habit is particularly well marked. The cells in both Asian species are somewhat larger than in *P. alaskana*, those in the apical portion measuring about  $20\ \mu$  in diameter those in the middle about  $30 \times 20\ \mu$ , and the elongated basal cells about  $60 \times 20\ \mu$ ; the trigones, especially in *P. trapezoidea*, are more clearly defined than in *P. alaskana*, coalescence being less prevalent.

To a considerable extent the section *Denticulatae* of Schiffner corresponds with the section *Heteromallae* of Spruce.\* Of this group, to which Spruce refers thirteen South American species, the following may be profitably compared with *P. alaskana*: *P. pachyloma* Tayl.,† *P. oxyphylla* Spruce,‡ and *P. fragilis* Tayl.,§ all of Ecuador. These three species show most of the characters emphasized under *P. alaskana*, although the elongation of the basal cells is not apparent in either *P. pachyloma* or *P. oxyphylla*, nor is the deflexed and postically secund habit always marked.

In *P. pachyloma* the leaves are almost as broad as long and measure about 2.2 cm. in length in the specimens studied by the writer, although Spruce gives a length of 2.75 mm. and Stephani a length of 3 mm. The postical base is strongly dilated, the antical margin is entire except near the apex, while the postical margin and the apical region are sharply spinose-dentate. The total number of teeth being about thirty. The species is peculiar in the brownish pigmentation of the teeth, in the strongly thickened

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\* Hep. Amaz. et And. 458. 1885.

† Jour. Bot. 5: 267. 1846.

‡ Hep. Amaz. et And. 480. 1885.

§ Jour. Bot. 7: 284. 1848.



walls of their elongated cells, and in the elongated cells with thickened walls which form a border along the antical margin.

In *P. oxyphylla* the leaves are relatively narrower than in *P. pachyloma*, measuring about  $2 \times 1.6$  mm. The antical margin is entire, the apex is usually tipped with a single acuminate tooth, although a second smaller tooth is sometimes present at the antical base of the apical tooth, or the apex may even be subequally bispinose. The postical margin bears from fifteen to eighteen sharp teeth or cilia, which are crowded toward the base and more scattered toward the apex.

In *P. fragilis* the leaves are always deflexed and postically secund, and the basal leaf-cells are always distinctly elongated. When well developed the leaves measure about 1.7 mm. in length and 1.4 mm. in width, ratio of width to length thus being about 0.8. The antical leaf-margin is entire, the dilated postical margin bears from twelve to sixteen spinose teeth, and the apex is usually unequally bidentate, the larger tooth being longer than the postical teeth. In some cases there is only one apical tooth. The leaf-cells in *P. fragilis* measure about  $20 \mu$  in diameter at the apex,  $30 \times 20 \mu$  in the middle, and  $50 \times 20 \mu$  in the basal region. The trigones, separated from one another by narrow pits, are unusually well developed, making the cell-cavities distinctly stellate; coalescence between trigones is not infrequent.

#### 26. *Plagiochila Fryei* sp. nov.

On a dry tree base. Augustine Bay (579). A slight admixture of *Metzgeria conjugata* is present.

Yellowish or brownish green, not glossy, growing in compact tufts: stems mostly 2-3 cm. long and 0.15 mm. in diameter, rigid, ascending, mostly simple, rarely with an occasional branch, the branches all intercalary, obliquely spreading, similar to the stems: rhizoids sparingly produced: leaves alternate, more or less imbricated, spreading at an angle of 45 degrees or less, postically secund and often deflexed in the outer part, more or less convex, orbicular-ovate to orbicular (exclusive of the decurrent portions), about 1.4 mm. long (when well developed) and 1.2-1.4 mm. wide, long-decurrent antically, less decurrent postically, the decurrent portions narrow, line of attachment strongly arched; antical margin revolute to about the middle, outwardly curved (on explanate leaves), entire to the middle or beyond, sometimes bearing



one to three broad and short teeth in the outer part; postical margin strongly outwardly curved and dilated toward the base, sharply spinose-dentate; apex broad and rounded with teeth like those along the postical margin; total number of teeth mostly twelve to fifteen, unequal and variable, pointing in various directions, mostly acuminate but sometimes merely acute, mostly two to six cells long and one to five cells wide at the base; leaf-cells plane, averaging  $14\ \mu$  in the apical portion,  $22 \times 14\ \mu$  in the middle, and  $40 \times 14\ \mu$  at the base, walls more or less thickened with well-developed but poorly defined trigones, the sides being straight or concave; coalescence between the trigones frequent especially in the median and basal portions, cuticle smooth: underleaves minute: remaining parts not seen. (PLATE 21, FIGS. 7-9.)

It will be seen from the above description that *P. Fryei* and *P. alaskana* are very closely related species and that most of the vegetative characters emphasized under *P. alaskana* are exhibited equally well by *P. Fryei*. In spite of these facts it still seems justifiable to consider the two plants distinct. The differences between them are found in the form of the leaves and in the peculiarities of the marginal teeth. The leaves of *P. alaskana* are relatively narrower than in *P. Fryei*, the ratio of width to length being only 0.7-0.75 instead of 0.85-1. As in the two species of tropical Asia, discussed under *P. alaskana*, the greater relative breadth in *P. Fryei* is due to the marked dilation of the postical base, a feature which appears to be constant. The marginal teeth in *P. alaskana* are more numerous than in *P. Fryei* and tend to be narrower and more sharply pointed; they extend farther back toward the antical base and usually spread out widely from the margin, instead of being variously directed. The cell-structure is very much the same in the two species, the middle lamellae are usually discernible, and the cell-measurements are practically identical. In *P. alaskana* the trigones are somewhat more distinct and sometimes have bulging sides; in *P. Fryei* the trigones, although well-developed, more frequently coalesce, thus making the walls appear uniformly thickened, and their sides are concave or straight. These differences, however, can not be regarded as very important in such a genus as *Plagiochila*, where the thickenings in the walls are subject to considerable variation.

The Asian and South American species contrasted with *P. alaskana* may be considered in connection with *P. Fryei* also.



They approach this species rather more closely than they do *P. alaskana* in having broader leaves more constantly and more strongly dilated at the postical base, but most of the other differences which distinguish them from *P. alaskana* would distinguish them from *P. Fryei* as well.

27. MYLIA ANOMALA (Hook.) S. F. Gray

In a bog. Metlakatla (105). New to Alaska.

28. MYLIA TAYLORI (Hook.) S. F. Gray

On logs. Augustine Bay (*Foster* 575; 760); Ketchikan (542); Morse Cove (440); Nichols Bay (370); Port Alice (*Foster* 787 in part); Port Chatham (*Rigg* 1225 in part); Port Antonio (608); Saltery Cove (327); St. John Harbor (248). Previously reported by the writer (3, p. 305).

29. LOPHOCOLEA CUSPIDATA (Nees) Limpr.

On a tree. Swifts Cannery (686). Previously reported by the writer (3, p. 306).

30. CHILOSCYPHUS PALLESCENS (Ehrh.) Dumort.

On a wet log. Aats Bay (911). New to Alaska.

31. CHILOSCYPHUS RIVULARIS (Schrad.) Loeske

On wet rocks and soil. Egg Harbor (945); Saltery Cove (333). Previously reported by Miss Cooley (1, p. 246, as *Ch. polyanthus*, var. *rivularis*).

32. GEOCALYX GRAVEOLENS (Schrad.) Nees

On moist soil. Snug Harbor (*Rigg* 1222). New to Alaska.

33. CEPHALOZIA BICUSPIDATA (L.) Dumort.

On logs, rocks, and soil, often in very damp localities. Aats Bay (918); Augustine Bay (572, 585, 587, 588); Exchange Cove (263, 266, 272); Ketchikan (498); Morse Cove (454); Nichols Bay (381, 403); Port San Antonio (622); Ratz Harbor (308); Snug Harbor (*Rigg* 1217); St. John Harbor (228); Swifts Cannery (695, 703, 718); Tam Gas Harbor (137, 149). Previously reported by the writer (3, p. 306).



## 34. CEPHALOZIA LEUCANTHA Spruce

On earth. Port Chatham (*Rigg 1225* in part). Previously reported by the writer (3, p. 306, *pl.*: 42, *f.* 18-26).

## 35. CEPHALOZIA MEDIA Lindb.

On rocks and soil. Augustine Bay (589, 595); Port San Antonio (610); Ratz Harbor (300). Previously reported by Miss Cooley (1, p. 246, as *C. multiflora*), Coville (2, as *C. multiflora*), and the writer (3, p. 306).

## 36. CEPHALOZIELLA BYSSACEA (Roth) Warnst.

On humus. Woewodski Island (*Foster 966*). Previously reported, as *Cephalozia divaricata*, by Coville (2) and the writer (3, p. 308; 4, p. 131).

## 37. CALYPOGEIA NEESIANA (Massal. &amp; Carest.) K. Müll.

On logs. Augustine Bay (594); Egg Harbor (943). Not before reported from Alaska. A specimen, however, from Columbia Fiord, Prince William Sound, *Coville & Kearney 1399*, belongs here. Reported by the writer (3, p. 308, as *Kantia Trichomanis*).

## 38. CALYPOGEIA TRICHOMANIS (L.) Corda

On logs and wet soil. Morse Cove (444); Port San Antonio (624); Verdure Creek (34). Previously reported, as *Kantia Trichomanis*, by Miss Cooley (1, p. 246), Coville (2), and the writer (3, p. 308).

## 39. BAZZANIA PEARSONI Steph.

*Bazzania Pearsoni* Steph. *Hedwigia* 32: 212. 1893.

*Mastigobryum Pearsoni* Steph. *Bull. Herb. Boissier* II. 8: 852. 1908.

*Pleuroschisma Pearsoni* K. Müll. *Rabenhorst's Kryptogamen-Flora* 6<sup>2</sup>: 272. 1913.

Among mosses at the base of a tree. Metlakatla (109 in part, 113). New to America.

The discovery of this very rare European species in Alaska is of much interest from the standpoint of geographical distribution. It was based on material collected at Killarney, Ireland, by Stewart



and Holt in 1885. It was found a second time at Slievemore, Achill Island, off the western coast of Ireland, by Jones and Duncan in 1911. No other stations have been reported. Through the kindness of Miss Haynes the writer has been enabled to compare material from both Irish stations with the specimens from Alaska, and finds that they agree in all essential respects. In No. 109 the species grew mixed with *Herberta adunca*.

In size and general habit *B. Pearsoni* bears a strong resemblance to the typical forms of *B. tricrenata*. The leaves, especially when dry, are imbricated and strongly decurved in both species, while the apex is usually bi- or tridentate with variable teeth. The distinctive characters of *B. Pearsoni* are the following: the strongly dilated antical portion of the leaves, the lack of distinct teeth on the underleaves, the very large trigones in the cells of both leaves and underleaves. The antical portion is so strongly dilated that it makes the leaf arch considerably beyond the axis and forms a cordate expansion at the base. The trigones in typical cases are separated by narrow pits with straight sides, the cell-cavities being distinctly stellate; the sides of the trigones are strongly convex or truncate, and coalescence of trigones is not infrequent. The middle lamellae are very distinct. The underleaves are contiguous to imbricated and are rounded or subcordate at the base; in outline they vary from orbicular to broadly ovate, the lateral margins are somewhat outwardly curved and are often reflexed at the base, and the apex is truncate or slightly retuse. Full descriptions of *B. Pearsoni*, with figures, may be found in Pearson's *Hepaticae of the British Isles* (p. 133, *pl.* 50) and in Macvicar's *Student's Handbook of British Hepatics* (p. 319, *f.* 1-4).

Among exotic species which are allied to *B. Pearsoni*, the Hawaiian *B. Didericiana* (Gottsche) Steph.\* may be particularly noted. In this species, which is about as large as *B. Pearsoni*, the leaves are much less convex and are also less dilated in the antical portion, while the underleaves are almost constantly toothed at the truncate apex, the teeth being very variable. The leaves

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\* See C. M. Cooke, Jr. *Trans. Connecticut Acad.* 12: 15. *pl.* 4, *f.* 1-13. 1904. In his *Species Hepaticarum* (*Bull. Herb. Boissier* II, 8: 775. 1908) Stephani has changed the name of this species to *Mastigobryum Didrichsenii*.



differ further in the fact that they are less narrow toward the apex. The leaf-cells with their large and strongly developed trigones are much the same in the two species.

40. *BAZZANIA TRICRENATA* (Wahl.) Trevis.

On rocks and logs. Aats Bay (908); Augustine Bay (543, 571, 578, 590); Exchange Cove (278, 279); Hidden Inlet (63, 86); Lake Bay (210); Morse Cove (452); Nichols Bay (368); Port Alice (*Foster* 785, *Foster* 786, *Foster* 787 in part); Port Malmsbury (980, 982); Port San Antonio (606, 616, 617, 645); Ratz Harbor (298); Shipley Bay (762, 763, 774); Sitklan Island (47, 50); Snug Harbor (*Rigg* 1221); St. John Harbor (865); Swifts Cannery (687, 690); Tam Gas Harbor (119, 134, 136, 148); Verdure Creek (23). Previously reported by Stephani (14, p. 97, as *Mastigobryum deflexum*), Miss Cooley (1, p. 246, as *Bazzania deflexa*), and the writer (3, p. 308, as *B. deflexa*).

41. *BAZZANIA TRILOBATA* (L.) S. F. Gray

On rocks in woods. Baranof (1084 in part); Verdure Creek (21). New to Alaska and apparently to the Pacific Coast region.

42. *LEPIDOZIA FILAMENTOSA* (Lehm. & Lindenb.) Lindenb.

On rocks and soil. Augustine Bay (581); Port San Antonio (644, *Foster* 1120); Shipley Bay (1124); Verdure Creek (30). Previously reported by Howe (7, p. 138) and the writer (3, p. 308).

43. *LEPIDOZIA REPTANS* (L.) Dumort.

On rocks, soil, and logs. Augustine Bay (595 in part); Baranof (1088); Exchange Cove (271); Taku Inlet (1035). Previously reported by Miss Cooley (1, p. 246), Coville (2), and the writer (3, p. 308).

44. *LEPIDOZIA SANDVICENSIS* Lindenb.

*Lepidozia sandvicensis* Lindenb.; G. L. & N., Syn. Hep. 201. 1845.  
Lindenberg & Gottsche, Sp. Hep. 6: 12. pl. 1, f. 1-5. 1846.  
C. M. Cooke, Jr., Trans. Connecticut Acad. 12: 7. pl. 2, f. 1-12.  
1904.\*

\* A few synonyms are recorded here.



On soil in very damp woods. Augustine Bay (684, Foster 2475); Port San Antonio (652). New to America. Heretofore known only from the mountains of the Hawaiian Islands, where it was collected many years ago by Tolmie and more recently by Baldwin.

It may perhaps appear hazardous to refer an Alaskan plant to a species of the Hawaiian Islands, but a careful comparison of the specimens noted above with material collected by Baldwin on the island of Maui has failed to bring to light any essential differences. It should be admitted, however, that *L. sandvicensis* is known from the Hawaiian Islands in sterile condition only and that the Alaskan material is equally destitute of female inflorescences. It is possible, therefore, that the discovery of perichaetial bracts and perianths may bring to light differential characters necessitating the segregation of the American plant as a distinct species.

The description and figures of Lindenberg give a clear general idea of the species, while a number of additional details are supplied by Cooke. *L. sandvicensis* belongs to a fairly well-defined group of *Lepidoziae* which are mostly of tropical distribution. They are characterized by pinnate stems with subdivided branches, the stems being limited in growth and blunt, the branches being likewise limited in growth but tapering out into slender flagella. The branches are of about the same length and give the entire shoot system a loosely plumose appearance. The group is further characterized by very minute leaves and underleaves, which are mostly far apart. Most of the photosynthesis is therefore carried out by the green axes, and the plants, in some cases at least, look almost as if they belonged to the thallose genus *Riccardia*.

In *L. sandvicensis* the main stem is somewhat flattened dorso-ventrally, measuring about  $0.5 \times 0.3$  mm. in section, and is bounded by a layer of short cells arranged in from forty to sixty longitudinal rows. These cells have thickened walls and measure about  $20 \mu$  in width. The internal cells average about  $15 \mu$  in width and have somewhat thinner walls. Rhizoids are wanting except near the tips of some of the flagelliform branches. The leaves and underleaves are so well described by Cooke that only a few of their more important features need be noted here. The stem leaves are almost transversely attached and extend obliquely outward, scarcely, if at all, projecting beyond the stem. The antical edge



is a little longer than the postical, the leaf thus being slightly unsymmetrical. In well-developed leaves the antical edge is about 0.3 mm. long, the postical about 0.2 mm. and the breadth at the base of the leaf about 0.4 mm. The leaves are normally quadrifid to below the middle with subulate acute lobes, ending in a single cell or in a row of two or three cells, and usually separated by acute sinuses. The underleaves are similar but smaller, being only 0.25 mm. in width. The leaf-cells measure about  $30 \times 22 \mu$  in the middle of the leaf and have thickened walls with indistinct trigones. The cuticle is smooth throughout.

The specimens from Augustine Bay show male inflorescences and indicate that the species is probably dioicous. The androecia occupy very short postical branches growing in the axils of the underleaves on the main stem. They are not abundant, the highest number observed on an individual stem being five. The concave bracts are crowded and borne in from two to four pairs, each bract enclosing one or two antheridia in its axil. No case of proliferation was observed, a condition apparently associated with the delicacy of the entire inflorescence. The individual bracts are subject to considerable variation in size and complexity. One of the best developed was 0.45 mm. long and 0.6 mm. wide. It was four-lobed to about the middle, the divisions and sinuses being acute. The margins of the divisions, although mostly entire, showed an occasional small tooth formed by a projecting cell. Other bracts showed only three lobes and sometimes the marginal denticulation was more pronounced. A well-developed bracteole measured 0.15 mm. in length and 0.25 mm. in width, and was likewise quadrifid to about the middle with acute entire lobes and sinuses, each lobe being two or three cells long and two cells wide at the base. The cells of both bracts and bracteoles are characterized by thin walls with vague indications of trigones toward the apices of the lobes. In the bracts the cells measure about  $30 \times 24 \mu$ . The antheridia are about 0.15 mm. in diameter.

There is no danger whatever of confusing *L. sandvicensis* with any of the other species of *Lepidozia* now known from the Pacific Coast region of North America. In both *L. reptans* and *L. filamentosa*, which occur in the present collection, the leaves are much larger and are often imbricated, so that the shoots bear no re-



semblance to those of *Riccardia*. In *L. setacea*, reported from Alaska and probably occurring in British Columbia, the plants are much smaller, while the deeply quadrifid, crowded, concave leaves with slender divisions are relatively much larger. Among European species *L. Pearsoni* Spruce,\* of the British Isles and Norway, comes somewhat nearer to *L. sandvicensis* on account of its lax habit and distant leaves and underleaves. But in this species the leaves and underleaves are considerably larger than in *L. sandvicensis*, the leaves are occasionally five- or six-lobed, the androecia are usually terminal on long lateral branches and the antheridia occur singly. Since *L. Pearsoni* has been found in company with *Anastrepta orcadensis* there is a possibility that it may yet be discovered in Alaska. At the present time the perianths are unknown, although the female inflorescence has been described.

45. BLEPHAROSTOMA TRICHOPHYLLUM (L.) Dumort.

On soil, rocks, and logs. Aats Bay (932); Augustine Bay (573); Hidden Inlet (67); Sitklan Island (43); Verdure Creek (37). Previously reported by Rothrock (13, as *Jungermannia trichophylla*), Coville (2), and the writer (3, p. 308; 4, p. 132).

46. ANTHELIA JULACEA (L.) Dumort.

On rocks. Port Malmsbury (986). Previously reported by the writer (3, p. 309; 4, p. 132).

47. HERBERTA ADUNCA (Dicks.) S. F. Gray

On trees and rocks. Aats Bay (925); Augustine Bay (561, Foster 677); Brownson Bay (470, Foster 517); Metlakatla (Wylie 76, Wylie 97, 109 in part); Morse Cove (446); Nichols Bay (384); Port San Antonio (605, 649); Ratz Harbor (309); Saltery Cove (320). Previously reported by Underwood (16, p. 366), Merriam (9), and the writer (3, p. 309).

48. PTILIDIUM CALIFORNICUM (Aust.) Underw. & Cook

On trees, bushes, and logs. Hidden Inlet (92); Port Malmsbury (980); Shipley Bay (Foster 779); Verdure Creek (26). Previously reported by the writer (3, p. 309).

\* Jour. Bot. 19: 34. 1881. See also Pearson, Hep. British Isles 121. pl. 45, 1900; Macvicar, Student's Handb. British Hepat. 325. f. 1-5. 1912; and K. Müller, Rabenhorst's Kryptogamen-Flora 6<sup>2</sup>: 284. f. 86. 1914.



## 49. PTILIDIUM CILIARE (L.) Nees

On rocks. Taku Inlet (1026). Previously reported by Stephani (14, p. 97) and the writer (3, p. 309; 4, p. 132).

## 50. PTILIDIUM PULCHERRIMUM (Web.) Hampe

On logs and stumps. St. John Harbor (245); near Wrangell (Foster 1122). Previously reported by Stephani (15, vol. 4, p. 43).

## 51. DIPLOPHYLLUM ALBICANS (L.) Dumort.

On logs, trees, and soil. Calder (835); Brownson Bay (474); Exchange Cove (276); Lake Bay (197, 211); Morse Cove (439); Port San Antonio (647); Shuyak Island (Rigg 1227); Swifts Cannery (696); Tam Gas Harbor (128). Previously reported by Rothrock (13, as *Jungermannia albicans*) and the writer (3, p. 309, as *Diplophylleia albicans*).

## 52. DIPLOPHYLLUM OVATUM (Dicks.) Steph.

On logs and trees. Brownson Bay (473); Nichols Bay (386); Port Malmsbury (989 in part). Previously reported by the writer (3, p. 305, as *Lophozia ovata*).

## 53. DIPLOPHYLLUM PLICATUM Lindb.

On trees and rocks. Baranof (1084 in part); Exchange Cove (274); Ratz Harbor (293); Saltery Cove (331). Previously reported by the writer (3, p. 309, pl. 17, 18, f. 27-35, as *Diplophylleia plicata*).

## 54. DIPLOPHYLLUM TAXIFOLIUM (Wahl.) Dumort.

On rocks and logs. Deweyville (Foster 789); Seward (Rigg 1228); St. John Harbor (243); Verdure Creek (27). Previously reported by Gottsche, Lindenberg, and Nees von Esenbeck (5, p. 76, as *Jungermannia albicans*, var. *taxifolia*), Merriam (9), and the writer (3, p. 309, as *Diplophylleia taxifolia*; 4, p. 132, under the same name).

## 55. SCAPANIA BOLANDERI Aust.

On logs, trees, and rocks. Augustine Bay (582); Brownson Bay (469); Hidden Inlet (79, 89, 90); Lake Bay (207, 209, 213); Morse Cove (441, 442, 443); Port Alice (Foster 787); Port Chatham



(Rigg 1226, 1234) Port Malmsbury (984); Port San Antonio (600, 604, 613); Ratz Harbor (295, 304); Sitklan Island (48); Snug Harbor (Rigg 1218); St. John Harbor (232); Swifts Cannery (698, 712); Tam Gas Harbor (117, 118, 124, 125); Verdure Creek (22). Previously reported by Stephani (14, p. 96, *pl.* 3, *f.* 9, as *Scapania albescens*), Pearson (12, p. 14), the writer (3, p. 311), and K. Müller (11, p. 186).

56. SCAPANIA CORDIFOLIA K. Müll.

*Scapania cordifolia* K. Müll. Bull. Herb. Boissier II. 3: 38. 1903.  
Nova Acta Kaiserl. Leop.-Carol. Acad. 88: 91. *pl.* 7b, *f.* 1-7.  
1905.

*Scapania paludosa papillosa* K. Müll.; L. Clark, Bull. Torrey Club  
36: 306. *pl.* 20, *f.* 12-17. 1909.

On wet rocks and soil, often in running water. Augustine Bay (593); Morse Cove (424); Port Malmsbury (999, 1000); Saltery Cove (328); St. John Harbor (218). Previously reported by K. Müller (10, p. 38), as noted above. The following stations to the southward of Alaska may likewise be quoted: near Skidegate, Queen Charlotte Islands, British Columbia, *W. Spreadborough* 83171, July, 1910; near Hume's Glacier, Queets River valley, Olympic Mountains, Washington, *T. C. Frye* 88, August, 1907 (type of *S. paludosa papillosa*).

The present species was based on Alaska material collected at Columbia Fiord by Coville and Kearney, while members of the Harriman Expedition (No. 1383). In the writer's account of the Hepaticae of this expedition these specimens were referred to *S. undulata*, a species then understood in a much broader sense than at the present time (3, p. 365). In proposing *S. cordifolia* as a new species Müller spoke of the great diversity which he found between sterile plants and those bearing perianths, and he emphasized the fact that the fertile plants were scarcely distinct from *S. dentata*, a species not definitely known from America at that time but since then reported from numerous scattered localities. The writer now finds, upon examining Coville and Kearney's material again, that some of the perianth-bearing plants agree fully with the sterile plants of Müller's description, and that the discrepancies between sterile and fertile plants which he em-



phasizes do not actually exist. It would appear, in fact, that what he considered to be fertile material of *S. cordifolia* is really *S. dentata* and that *S. cordifolia*, as originally understood, was a composite species. This being the case two courses are possible. *S. cordifolia* might be regarded as a simple synonym of *S. dentata*, since the fertile plants of *S. cordifolia*, as understood by Müller, belong to *S. dentata*; or the name *S. cordifolia* might be retained for the sterile plants which Müller studied. It is evident that he laid most stress on these sterile plants and that he drew all of his figures from them except figure 7. The writer suggests, therefore, that the second course be followed and that the species *S. cordifolia* be retained with emended characters.

The plants of *S. cordifolia* are robust and more or less pigmented with purplish red. The leaves are imbricated and are especially remarkable on account of their very short and usually arched keels. The antical lobe spreads obliquely while the postical keel extends at almost a right angle from the stem. Both lobes are strongly dilated just beyond the keel, thus giving the leaf a cordate appearance. Both lobes are minutely and sharply denticulate, and most of the teeth are unicellular, although an occasional tooth may be two cells long. In some cases both lobes are abruptly and narrowly decurrent, but this condition is by no means constant, some of the leaves being only slightly or not at all decurrent. The leaf-cells are subject to considerable variation in size. In one case the cells at the apex of the postical lobe were found to measure about  $16\ \mu$  in diameter, those in the middle about  $30 \times 24\ \mu$ , and those at the base about  $40 \times 24\ \mu$ . In other cases the median and basal cells were only  $18\ \mu$  wide, and the measurements given by Müller show further slight differences. Along the margin of the lobes the cell walls appear to be uniformly thickened with poorly developed trigones, but toward the middle the deeply pigmented and clearly defined trigones usually form a conspicuous feature of the cells. Even here, however, the trigones are not always distinct and the walls may appear to be of about the same thickness throughout. The cuticle is distinctly verruculose.

The perianths are borne on the main stems or on leading branches, and the bracts are much like the leaves. The innermost bracts differ in having a slightly longer keel and more obliquely



spreading lobes, and in lacking the cordate dilations so marked on both lobes of typical leaves at the end of the keel. In one inflorescence studied particularly the antical lobe was ovate, and measured  $1.6 \times 1.2$  mm. The apex was very bluntly pointed and the margin, throughout the greater part of its length, bore scattered, short, sharp teeth, each consisting usually of a single cell. The postical lobe was oblong-ovate and measured  $2.8 \times 1.5$  mm. The apex was more rounded and the margin like that of the antical lobe. The perianth was obovate with a broad truncate mouth and measured  $3 \times 1.8$  mm. The mouth bore about fifty teeth, variously directed and irregularly scattered, each being one or two cells long. None of the inflorescences studied had been fertilized, so that the characteristics of the sporophyte are still unknown.

In his original description, Müller compares *S. cordifolia* with *S. dentata* and *S. uliginosa*. As emended above the plant is evidently much closer to *S. uliginosa* than to *S. dentata*, and shows further a marked resemblance to certain forms of *S. paludosa* K. Müll. The writer, in fact, would consider the var. *papillosa* of *S. paludosa* a synonym of *S. cordifolia*, as indicated above. In both *S. uliginosa* and *S. paludosa* the keels of the leaves are short and usually strongly arched, the lobes are more or less dilated just beyond the end of the keel, and both lobes are more or less decurrent at the base, the decurrence sometimes being very strongly pronounced. In *S. cordifolia* the first two of these features are exhibited in a marked degree, but the third feature is sometimes less conspicuous and may be lacking altogether as Müller's description indicates. *S. uliginosa* is distinguished at once by the fact that the margins of the leaves are entire throughout, although the mouth of the perianth occasionally bears a few scattered teeth. *S. paludosa* is distinguished by its paler color and more delicate texture, the walls of the leaf-cells being only slightly thickened, by its more distant leaves, by the entire margins of its antical lobes, and by the less marked denticulation of its postical lobes.

#### 57. SCAPANIA DENTATA Dumort.

On wet rocks, often in running water. Aats Bay (906); Augustine Bay (540); Mitrofanina Bay (Rigg 1231); Port San Antonio (603); Saltery Cove (323). See notes under *S. cordifolia*, where *S. dentata* is reported for the first time from Alaska.



## 58. SCAPANIA IRRIGUA (Nees) Dumort.

On moist earth. Mitrofanía Bay (*Rigg 1232*); the specimens are scanty and not altogether typical. Previously reported by the writer (3, p. 312) and K. Müller (11, p. 80).

## 59. SCAPANIA NEMOROSA (L.) Dumort.

On rocks and soil. Aats Bay (912, 938); Morse Cove (435); Port Alice (*Foster 784*). Previously reported by Rothrock (13, as *Jungermannia nemorosa*), Stephani (14, p. 97), and Miss Cooley (1, p. 247).

## 60. SCAPANIA ULIGINOSA (Sw.) Dumort.

In running water. Ketchikan (504). New to Alaska.

## 61. SCAPANIA UMBROSA (Schrad.) Dumort.

On logs and trees. Calder (827 in part); Ratz Harbor (305); Swifts Cannery (*Foster 761*). Previously reported by the writer (3, p. 312).

## 62. SCAPANIA UNDULATA (L.) Dumort.

On wet rocks and soil, often in running water. Ketchikan (3); Morse Cove (438); Port Malmsbury (978, 997); Port San Antonio (599); Snug Harbor (*Rigg 1220*); Swifts Cannery (688). Previously reported by the writer (3, p. 311; 4, p. 131) and Howe (8, p. 104).

## 63. RADULA BOLANDERI Gottsche

On rocks, trees, and logs. Augustine Bay (546, 580, 586, *Foster 758*); Deweyville (*Foster 1123*); Exchange Cove (260); Hidden Inlet (73); Ratz Harbor (297, 312); Shipley Bay (*Foster 788*). Previously reported by the writer (3, p. 312; 4, p. 132).

Whether the *Radula arctica* of Stephani (14, p. 98, *pl. 3, f. 11*) is to be considered a synonym of *R. Bolanderi* is still a matter of some doubt. *R. arctica* was based on sterile material collected by the Krause brothers at Chlowak and Chilcoot (No. 17). On the basis of Stephani's original description and figure Howe (7, p. 159, footnote) suggests that it probably represents a juvenile condition of *R. Bolanderi*. Stephani, however, does not accept this suggestion and still maintains that *R. arctica* is a valid species



(3, vol. 4, p. 220, 1910). He states that the material of *R. arctica* is not juvenile, that it shows well-developed and richly branched plants, that the stem- and branch-leaves are well preserved, that the leaves and the cell structure are very different from those of *R. Bolanderi*, and that it would be quite out of the question to consider the two species identical. A comparison of Stephani's figure of *R. arctica* with Pearson's figure of *R. Bolanderi* (12, pl. 4, as *R. spicata*) shows that Howe's suggestion is certainly well supported, and a study of Stephani's latest description of *R. arctica* does not bring out any differences which are at all convincing. At the same time the question cannot be regarded as definitely settled until the type specimen of *R. arctica* has been re-examined.

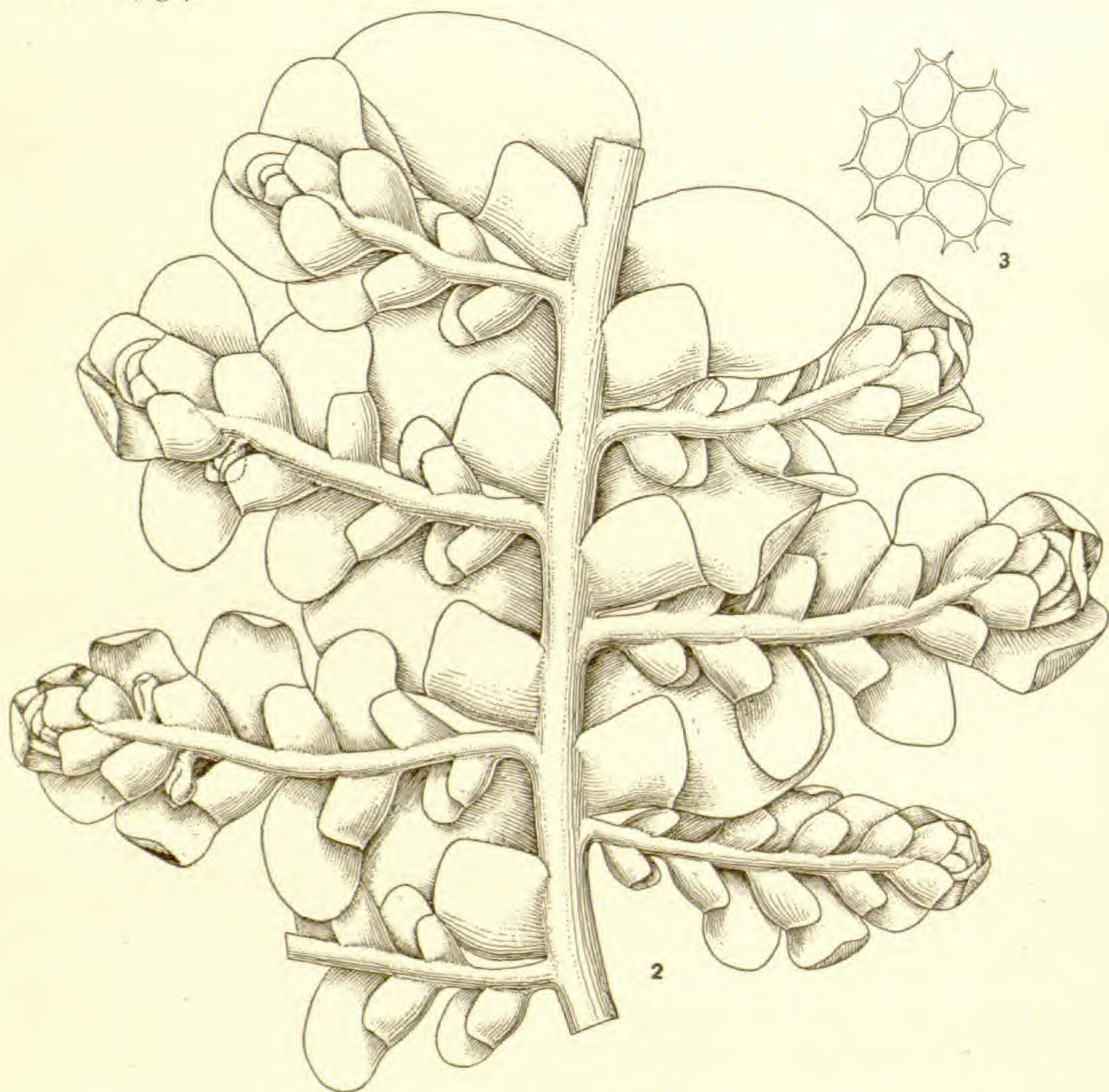
#### 64. *Radula polyclada* sp. nov.

On rocks. Aats Bay (900 mostly). The accompanying species are *Metzgeria conjugata* and *Frullania nisquallensis*.

Yellowish green, becoming brownish with age, not glossy, growing in loose tufts: stems mostly 2-3 cm. in length and 0.2 mm. in diameter, copiously and regularly pinnate, a branch usually arising behind each stem leaf, the branches widely spreading, 0.12 mm. in diameter, with smaller leaves than the stem, usually limited in growth after reaching a length of 0.5 cm. or less, often simple but sometimes bearing a few scattered and very short branches, 0.5 mm. long and 0.06 mm. in diameter, with still smaller leaves; rhizoids none: stem leaves contiguous to loosely imbricated, the lobe convex and sometimes revolute at the apex, spreading at an angle of about 80 degrees, slightly falcate, broadly ovate, about 1 mm. long and 0.85 mm. wide, attached by an almost longitudinal line, antical margin slightly or not at all dilated at the base, straight or somewhat rounded and arching partially across the axis, very rarely slightly beyond it, strongly outwardly curved to the broad and rounded apex, postical margin somewhat outwardly curved, forming a slight indentation at junction, with the slightly arched and scarcely decurrent keel; lobule subrhombiform in outline, about 0.55 mm. long and 0.4 mm. wide, more or less inflated along keel and in basal portion, otherwise appressed to the lobe, inner margin attached for almost its entire length by a nearly longitudinal line, not dilated, free margin parallel with keel and forming an angle of about 80 degrees with the inner margin, outer margin subparallel with the inner margin, apex rounded; leaf-cells plane, averaging 11  $\mu$  along the antical margin, 16  $\mu$  in the middle, and 22  $\mu$  at the base, the walls



thin but with small trigones having concave sides, cuticle smooth: leaves of primary branches more or less imbricated, the lobe convex, more obliquely spreading than in the stem-leaves, ovate, about  $0.45 \times 0.35$  mm.; the lobule trapezoidal in outline, the free margin being shorter than the keel, about  $0.3 \times 0.2$  mm.: leaves of secondary branches still more obliquely spreading, subequally bilobed, the lobes about  $0.18 \times 0.1$  mm.: inflorescence unknown. (TEXT FIGS. 2, 3.)



FIGS. 2, 3. *Radula polyclada* Evans. FIG. 2. Part of a stem showing seven branches, postical view,  $\times 25$ . FIG. 3. Cells from the middle of a lobe,  $\times 330$ . The figures were both drawn from the type specimen.

The numerous branches with their limited growth give the shoots of *R. polyclada* a distinctly plumose appearance, so that they bear a certain resemblance to the secondary shoots found in *Porella* and in the tropical genus *Bryopteris*. They look in fact as if they also might be secondary shoots arising from a prostrate



caudex, and the absence of rhizoids adds to the plausibility of this idea. Unfortunately no signs of such a caudex can be demonstrated in the present material. Neither can the position which the shoots occupy in nature be made out, although they are probably pendulous or ascending.

Among Alaskan species *R. Bolanderi* is apparently the closest ally of *R. polyclada*. It is, however, a somewhat smaller plant, the stems being only 1-2 cm. in length and 0.12 mm. in diameter, while the maximum size of the stem-leaves is about  $0.85 \times 0.65$  mm. It differs further in its less regular habit; in its more obliquely spreading stem-leaves, the angle formed with the stem being about 60 degrees; in the presence of rhizoids on its lobules; and in the apices of the lobules of its stem-leaves, which are obtuse or subacute instead of being rounded. The leaf-cells are much the same in the two species, both in size and in the characteristics of the cell-walls.

A still closer ally is the recently described *R. prolifera* Arnell,\* known only from the type specimen, which was collected in 1898 by H. Nilsson-Ehle at Bulkur, in the valley of the Lena, Siberia. Through the kindness of Dr. Arnell the writer has been enabled to compare a portion of this type specimen with the material of *R. polyclada* and finds that, in spite of their close relationship, the two species cannot be considered synonymous.

In *R. prolifera* the branching is usually just as copious as in *R. polyclada*, and there seems to be an equal lack of rhizoids; the branches, however, are of a somewhat different character. A very small number are essentially like the main stem, their leaves resembling the stem-leaves in all essential respects; but the vast majority are more nearly comparable with the small-leaved secondary branches of *R. polyclada*, except that they are shorter and more often subdivided. They represent the "flagella" of Arnell's description and possibly act as propagula in multiplying the species vegetatively. The stem-leaves of *R. prolifera* differ from those of *R. polyclada* in having a less arched or even straight keel, a scarcely evident indentation at the end of the keel, a more sharply pointed and differently shaped lobule (the outer margin being only about half as long as the inner margin), and sometimes

\* Ark. för Botanik 13<sup>2</sup>: 12. pl. 1, f. 1, 2. 1913



a greater dilation at the antical base of the lobe so that the margin arches beyond the stem. The leaves of the flagella are distant and subequally bilobed. So far as measurements go the two species are much the same, the lobes of the stem-leaves in *R. prolifera* measuring about  $1 \times 0.85$  mm., the lobules about  $0.5 \times 0.4$  mm., and the lobes of the flagella about  $0.2 \times 0.15$  mm. In the stem-leaves the cells of the lobes average about  $12 \mu$  in diameter along the antical margin, about  $18 \mu$  in the middle, and about  $20 \mu$  at the base, so that these, too, agree closely with the cell-measurements in *R. polyclada*; and an equally close agreement may be found between the characters derived from the cell-walls.

65. PLEUROZIA PURPUREA (Lightf.) Lindb.

*Jungermannia purpurea* Lightf. Fl. Scotica 778. 1777.

*Jungermannia cochleariformis* Hook. Brit. Jung. pl. 68. 1814.

*Radula cochleariformis* Dumort. Syll. Jung. 38. 1831.

*Pleurozia cochleariformis* Dumort. Recueil d'Obs. sur les Jung. 15. 1835.

*Physiotium cochleariforme* Nees, Naturg. Europ. Leberm. 3: 79. 1838.

*Pleurozia purpurea* Lindb. Musc. Scand. 3. 1879.

In very wet places, Brownson Bay (482); Metlakatla (III); Nichols Bay (376). New to America. The species was originally described from specimens collected in Scotland, where it is now known to be widely distributed. It is known also from Ireland, the Faroe Islands, and Norway, and reappears in the Himalyas and in the Hawaiian Islands. Its geographical distribution, therefore, coincides in most respects with that of *Anastrepta orcadensis*, except that its range in Europe is more circumscribed.

The genus *Pleurozia* is one of the most clearly defined genera of the Hepaticae and includes ten species, all of which were known to Jack when he monographed the genus in 1886.\* With the exception of *P. purpurea* the species are confined to tropical regions, four being cited by Jack from the Hawaiian Islands. The plants are all of large size, the stems in some of the species attaining a length of 12 cm., and all are characterized by a more or less marked

\* Monographie der Lebermoosgattung *Physiotium*. Hedwigia 25: 49-87. pl. 1-10. 1886.



purple pigmentation. One of the most remarkable features of the genus is found in the apical cell, which has only two cutting faces instead of three, as in all the other genera of the leafy hepatics. This interesting peculiarity was first pointed out by Goebel,\* who naturally associated with it the total lack of underleaves. Even more interesting features, however, are found in the leaves. These, except in a single species, are bilobed and complicate, the postical lobe forming a highly complex water-sac, the mouth of which is closed by a complicated valve. The details of this singular structure are fully described by Goebel, in the place just quoted, so that it is unnecessary to include an account of them here.

The only species with which *P. purpurea* need be especially compared are *P. gigantea* (Web.) Lindb.† and *P. conchaefolia* (Hook. & Wils.) Aust.‡ both of which occur in the Hawaiian Islands, although not confined to them. In all three species the entire postical lobe takes part in the formation of the water-sac. In *P. purpurea*, however, the antical lobe is shortly bilobed at the apex with triangular spinose-dentate lobes, while in *P. gigantea* the antical lobe is usually quite undivided and much less sharply toothed. In *P. conchaefolia* the postical lobe is relatively much larger than in *P. purpurea*, instead of being about half as long, while the antical lobe is truncate or only slightly emarginate and otherwise entire in the apical portion. A full description of *P. purpurea*, with figures, is given by Macvicar,§ and an account of a well-developed perianth with its bracts has recently been published by Schiffner.||

66. PORELLA NAVICULARIS (Lehm. & Lindenb.) Lindb.

On trees. Brownson Bay (479); Kanagunut Island (41); Port San Antonio (Foster 1121); Ratz Harbor (296); Shipley Bay (768); Tam Gas Harbor (135). Previously reported by Gottsche, Lindenberg, and Nees von Esenbeck (5, p. 297, as *Madotheca navicularis*), Stephani (14, p. 98, as *M. navicularis*), and the writer (3, p. 313).

\* Flora 77: 453. 1893.

† Hep. Scand. Exs. No. 5. 1874 (= *Jungermannia gigantea* Web.).

‡ Bull. Torrey Club 5: 17. 1874 (= *Jungermannia conchaefolia* Hook. & Wils.).

§ Student's Handb. British Hepat. 394. f. 1-3. 1912.

|| Oesterr. Bot. Zeitschr. 62: 11. f. 1-3. 1912.



## 67. PORELLA RIVULARIS (Nees) Trevis.

On rocks. Seward (*Rigg 1215, 1229*); Shipley Bay (765). Previously reported by Howe (6, p. 523; 7, p. 60) and the writer (3, p. 312).

## 68. PORELLA ROELLII Steph.

On trees and logs. Hidden Inlet (65, 76). New to Alaska.

## 69. FRULLANIA FRANCISCANA M. A. Howe

On branches of bushes. Port San Antonio (614). Previously reported by the writer (3, p. 313).

## 70. FRULLANIA NISQUALLENSIS Sulliv.

On trees, bushes, and rocks. Aats Bay (900 in part); Augustine Bay (583); Brownson Bay (471); Exchange Cove (277); Hidden Inlet (78, 84); Kanagunut Island (51); Metlakatla (102); Morse Cove (455); Nichols Bay (374); Port Alice (*Foster 731*); Port Malmsbury (989 in part); Ratz Harbor (294); Shipley Bay (772, 776, *Foster 780*); Tam Gas Harbor (115, 127, 132). Previously reported by Stephani (14, p. 98), Coville (2), and the writer (3, p. 312).

## ADDITIONAL HEPATICAE KNOWN FROM ALASKA

As in the preceding list the numbers in parentheses refer to the Bibliography on page 578, and the species are arranged according to Schiffner.

MARCHANTIACEAE. 1. *Sauteria alpina* (Nees & Bisch.) Nees (Howe, 7, p. 39). 2. *Grimaldia fragrans* (Balb.) Corda (Evans, 3, p. 290).

METZGERIACEAE. 3. *Riccardia major* Lindb. (Evans, 4, p. 129, as *Aneura major*). 4. *Metzgeria hamata* Lindb. (Miss Cooley, 1, p. 247). 5. *Pellia epiphylla* (L.) Corda (Miss Cooley, 1, p. 247). 6. *P. Fabroniana* Raddi (Evans, 3, p. 293, as *P. endiviaefolia*). 7. *Blasia pusilla* L. (Evans, 3, p. 293).

JUNGERMANNIACEAE. 8. *Gymnomitrium concinnatum* (Lightf.) Corda (Stephani, 14, p. 96). 9. *G. corallioides* Nees (Stephani, 14, p. 96; Merriam, 9; Howe, 7, p. 102). 10. *G. crenulatum* Gottsche (Stephani, 15, vol. 1, p. 143, as *Acolea crenulata*). 11. *Marsupella sphacelata* (Gieseke) Dumort. (Stephani, 14, p. 96, as



*Sarcoscyphus sphacelatus*). 12. *Nardia compressa* (Hook.) S. F. Gray (Evans, 3, p. 290). 13. *N. Geoscyphus* (DeNot.) Lindb. (Evans, as *N. haematosticta*, 3, p. 296; 4, p. 130). 14. *N. obovata* (Nees) Carringt. (Evans, 3, p. 297). 15. *Jungermannia caespiticia* Lindenb. (Evans, 4, p. 130). 16. *J. lanceolata* L. (Evans, 3, p. 299). 17. *J. sphaerocarpha* Hook. (Evans, 3, p. 298). 18. *Anastrophyllum Reichardtii* (Gottsche) Steph. (Evans, 3, p. 299; pl. 16, f. 4-17). 19. *Lophozia attenuata* (Lindenb.) Dumort. (Evans, 3, p. 304; 4, p. 131). 20. *L. guttulata* (Lindb. & Arnell) Evans (Evans, 3, p. 302). 21. *L. heterocolpa* (Thed.) M. A. Howe (Evans, 3, p. 304). 22. *L. lycopodioides* (Wallr.) Cogn. (Howe, 8, p. 103). 23. *L. obtusa* (Lindb.) Evans (Evans, 3, p. 303). 24. *L. quadriloba* (Lindb.) Evans (Evans, 3, p. 304). 25. *L. ventricosa* (Dicks.) Dumort. (Stephani, 14, p. 97, as *Jungermannia ventricosa*; Evans, 3, p. 301). 26. *Sphenolobus saxicola* (Schrad.) Steph. (Stephani, 14, p. 97, as *Jungermannia saxicola*). 27. *Temnoma setiforme* (Ehrh.) M. A. Howe (Stephani, 14, p. 97, as *Jungermannia setiformis*; Evans, 3, p. 308, as *Blepharostoma setiforme*). 28. *Anthelia Juratzkana* (Limpr.) Trevis. (Evans, 3, p. 309). 29. *Diplophyllum argenteum* (Tayl.) Spruce (Underwood, 16, p. 366). 30. *D. imbricatum* (M. A. Howe) Steph. (Howe, 8, p. 104, pl. 14, as *Scapania imbricata*). 31. *Scapania curta* (Mart.) Dumort. (Evans, 3, p. 312; 4, p. 132). 32. *Radula arctica* Steph. (Stephani, 14, p. 98, pl. 3, f. 11). 33. *R. complanata* (L.) Dumort. (Stephani, 14, p. 97, pl. 3, f. 10, as *R. Krausei*; Coville, 2, as *R. Krausei*; Evans, 3, p. 312; 4, p. 132). 34. *Porella platyphylla* (L.) Lindb. (Gottsche, Lindenberg, and Nees von Esenbeck, 5, p. 279, as *Madotheca platyphylla*; Stephani, 14, p. 98, as *M. platyphylla*; Miss Cooley, 1, p. 247). 35. *Frullania chilcootiensis* Steph. (Stephani, 14, p. 98).

The following species have likewise been reported from Alaska but on insufficient evidence:

1. *Asterella fragrans* (Schleich.) Trevis. (Howe, 7, p. 39). The record was based on a specimen collected at Telegraph Creek, British Columbia (close to the Alaska boundary), by G. M. Dawson. The species is surely to be expected in Alaska.

2. *A. tenella* (L.) Beauv. (Rothrock, 13, as *Fimbriaria tenella*). A species of eastern North America. Rothrock's specimens, as



already noted by the writer (3, p. 288), have disappeared, so that it is impossible to determine upon which species his record was based.

3. *Chiloscyphus polyanthus* (L.) Corda (Evans, 3, p. 306). The report was based on very fragmentary specimens which, in view of the recent critical work done on the genus *Chiloscyphus*, are hardly in a condition to be determined.

4. *Lepidozia setacea* (Web.) Mitt. (Evans, 3, p. 308). The specimens listed belong to the subgenus *Microlepidozia* but are unfortunately sterile; their reference to a definite species is therefore uncertain.

4. *Frullania Tamarisci* (L.) Dumort. (Gottsche, Lindenberg, and Nees von Esenbeck, 5, p. 439). This species has not been collected recently in the Pacific Coast region. The specimens recorded in the Synopsis Hepaticarum are referred to the variety *laxa*, and possibly belong to *F. nisquallensis*. Unfortunately they have not been accessible to the writer.

#### DISCUSSION OF THE HEPATIC FLORA OF ALASKA

The general features of the hepatic flora of Alaska have already been pointed out by the writer (3, p. 289). In the northern part of the territory the flora is essentially like that of other northern regions; in the southern and southeastern parts the northern species become mingled with species characteristic of the Pacific Coast region of North America. The predominance of northern elements is apparent from the fact that sixty-nine of the species known from Alaska occur also in northern Europe and Asia, eighteen occur in northern Europe but have not yet been reported from Asia, while one, *Diplophyllum plicatum*, occurs in northern Asia but is unknown in Europe. Of the remaining eighteen species seventeen are Pacific Coast species and one, *Lepidozia sandvicensis*, occurs also in the Hawaiian Islands.

The seventy-one species common to both Europe and Asia are circumpolar in their distribution with the exception of *Metzgeria hamata*, *Anastrepta orcadensis*, and *Pleurozia purpurea*. These three species, although found in northern Europe, are limited in Asia to tropical regions, so far as known at the present time. Although it is hardly advisable to give a complete list of the cir-



cumpolar species, a list of the species which are known from Europe but not from Asia follows. It is needless to state that this list will probably be diminished when the hepatic flora of Asia is more fully known.

<i>Riccardia major</i>	<i>Lophozia obtusa</i>
<i>Pallavicinia Flotowiana</i>	<i>Lophocolea cuspidata</i>
<i>Gymnomitrium crenulatum</i>	<i>Cephalozia leucantha</i>
<i>G. obtusum</i>	<i>Bazzania Pearsoni</i>
<i>Nardia compressa</i>	<i>Herberta adunca</i>
<i>N. Geoscyphus</i>	<i>Diplophyllum ovatum</i>
<i>N. obovata</i>	<i>Scapania nemorosa</i>
<i>Jungermannia caespiticia</i>	<i>S. uliginosa</i>
<i>Anastrophyllum Reichardtii</i>	<i>S. umbrosa</i>

Of the European species occurring in Alaska the following belong to the so-called Atlantic species, being restricted in Europe to the neighborhood of the Atlantic coast:

<i>Metzgeria hamata</i>	<i>Herberta adunca</i>
<i>Gymnomitrium crenulatum</i>	<i>Pleurozia purpurea</i>
<i>Bazzania Pearsoni</i>	

The characteristic Pacific coast species occurring in Alaska are listed below. All are endemic to North America and several are known only from Alaska.

<i>Gyrothyra Underwoodiana</i>	<i>Radula arctica</i>
<i>Plagiochila alaskana</i>	<i>R. Bolanderi</i>
<i>P. Fryei</i>	<i>R. polyclada</i>
<i>Lepidozia filamentosa</i>	<i>Porella navicularis</i>
<i>Ptilidium californicum</i>	<i>P. Roellii</i>
<i>Diplophyllum argenteum</i>	<i>Frullania chilcootiensis</i>
<i>D. imbricatum</i>	<i>F. franciscana</i>
<i>Scapania Bolanderi</i>	<i>F. nisquallensis</i>
<i>S. cordifolia</i>	

A most surprising feature of the hepatic flora of Alaska is the group of species which are found also in the Hawaiian Islands. Some of these have already been mentioned on the preceding pages, but a complete list, as follows, may be of interest:

<i>Marchantia polymorpha</i>	<i>Lepidozia sandvicensis</i>
<i>Riccardia multifida</i>	<i>Diplophyllum albicans</i>
<i>Anastrepta orcadensis</i>	<i>Pleurozia purpurea</i>



The occurrence of Atlantic species and of Hawaiian species in Alaska is of much interest, although it is impossible to point out at the present time what its significance may be. Such a species as *Pleurozia purpurea*, which is evidently a stable species of great age, may originally have been much more abundant and more evenly distributed than at the present time. Then, through the encroachment of other species at various portions of its range, it may have become restricted to the isolated regions where it is now found. This might explain the occurrence of the species in both western Europe and Alaska and its absence from the intervening regions. There is little evidence, however, that the volcanic Hawaiian Islands were ever connected with either North America or with the mainland of Asia, so that it is difficult to account for any close connection between the plants of the Islands and those of Alaska or the Himalyas.

The most remarkable species in the present collection came from southeastern Alaska, and it is probable that many other Hepaticae remain to be discovered in this interesting region. Such a species as *Scapania planifolia* (Hook.) Dumort., for example, which often grows in company with *Pleurozia purpurea* in western Europe ought surely to be expected, especially since it occurs also in the Himalyas and in the Hawaiian Islands. And, in view of the presence of the very rare *Bazzania Pearsoni* in Alaska, other Atlantic species of circumscribed range may come to light. In any case southeastern Alaska is recommended to collectors as an unusually favorable region for careful study.

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#### Explanation of plate 21

*Plagiochila alaskana* Evans. 1. Part of a stem with perianth, antical view,  $\times 23$ . 2. Part of a stem with perianth, lateral view,  $\times 23$ . 3. Leaf spread out,  $\times 23$ . 4. Bract spread out,  $\times 23$ . 5. Cells from the middle of a leaf,  $\times 300$ . 6. Marginal tooth of a leaf,  $\times 300$ . The figures were all drawn from the type specimen.

*Plagiochila Fryei* Evans. 7, 8. Leaves spread out,  $\times 23$ . 9. Cells from the middle of a leaf,  $\times 300$ . The figures were all drawn from the type specimen.



## Branched cells in the prothallium of *Onoclea sensibilis* L.

CAROLINE A. BLACK

(WITH PLATES 22 AND 23)

The fern gametophyte offers an interesting field for experimental culture work, not only in regard to the reproductive organs as various writers have shown, but in the germination of the spore and the development of the prothallium. Material is readily procured and the growing conditions may be easily controlled. The average fern spore will germinate on water or moist soil and the prothallium lives about three or four months or until a sporophyte has been established. Many have been known to live much longer.

The normal development of the gametophyte of different ferns has been described by various writers. In a recent research on the prothallium of *Camptosorus rhizophyllus* (L.) Link, Pickett (1) found that the prothallia showed a wide variation in size and form. The apical group is usually unsymmetrically placed and the typical wedge shaped apical cell is rarely seen. Old prothallia were found with several marginal growing regions and proliferations capable of independent growth were produced. In some very interesting experiments with this fern Pickett (2) had already shown that the drought resisting character of these prothallia was an efficient factor in the establishing of this fern to its habitat.

The dioecious prothallia of *Onoclea Struthiopteris* (L.) Hoffm. have been the subject of a physiological problem by Miss Wuist, (3) who has obtained monoecious forms in this fern by growing prothallia in culture solutions. Monoecious prothallia were also observed in soil cultures. Miss Wuist mentions the appearance of irregular and filamentous forms, some exceedingly long, in these cultures. Mottier (4) working with the same fern finds that about 12 per cent. of the prothallia are monoecious under optimum culture conditions. Branched filamentous prothallia have been described by Miss Pace (5) in fern gametophytes. Many examples



of the retention of the filamentous form of gametophyte due to feeble light and poor nutritive conditions and even of a reversion to the formation of cell threads, after an expanded prothallium had been established when nutritive conditions became unfavorable are given in Goebel's *Organography* (6, pp. 202-205).

Some very irregular filamentous prothallia, evidently the result of feeble light and poor nutritive conditions, were found by the writer in an old culture of *Onoclea sensibilis* L. A rather unusual character of these prothallia was the tendency of certain cells to branch. It was thought that a description of them might be of interest to others investigating fern prothallia.

Spores of *Onoclea sensibilis* were sown upon sterile distilled water for class use. Through oversight, the covered glass dish containing the culture was left undisturbed in somewhat dim light for approximately six weeks. When it was then observed the culture appeared green and healthy. Upon examining the culture, part of the prothallia were floating on the surface of the water and some smaller clumps were entirely submerged near the bottom of the dish. Slides were prepared from both sources. The prothallia taken from the surface presented the typical form with a well-defined apical region as shown in FIG. 1. Some of them consisted of thirty to fifty cells and bore a few antheridia.

The submerged prothallia were found to differ considerably from the normal gametophyte. In these prothallia the cells were greatly elongated and contained few chloroplasts scattered throughout. It was of interest to note that many cells had produced one or more outgrowths without cutting off the usual cross wall. FIG. 2 shows a five-celled prothallium, the last two cells of which are unusually long. The enlarged end of the apical cell is turned, indicating an abrupt change in the direction of growth. In FIG. 3 a small cell arises from the elongated apical cell. This cell is so turned that it is growing in the opposite direction from the main apical cell. This cell resembles a rhizoid except for its size and the presence of chlorophyll. In FIG. 4, the end of the filament forms an acute angle with the main cell-thread. This is due to a change in the direction of growth of the apical cell. A very small outgrowth is cut off laterally from the apical cell. The abrupt turning of the branches is not caused by contact with



the wall of the glass dish as none of the submerged prothallia examined were observed near the side of the dish. Fig. 5 seems a more normal prothallium having average sized cells. The end of the filament is turned so that there is a possibility of two growing regions here.

An extreme case of the tendency to form branched cells is seen in FIG. 6. Two cells of this filament have well defined protuberances, one of which is considerably elongated. The tip of the apical cell is also somewhat curved. A two-armed prothallium is seen in FIG. 7, due to the branching of one cell. This is an unusually long filamentous prothallium. The shorter branch consists of two cells. FIGS. 8 and 9 show great variety in the apical cell, each having a number of lobes. This suggests considerable diversity in the subsequent growth of the prothallium. In each case the apical cell is curved with two lobes at the extreme tip. FIG. 10 shows a young stage of a two-armed prothallium. In FIG. 11, three branches are found with their origin in one cell. Two of these branches are limited by cross walls. The increased activity of the cells where one or more branches are produced may be explained by considering that the active cell was once the apical cell and in a normal prothallium would remain the center of growth.

In sowing fern spores it is not unusual to find sporangia or a fragment of leaf in the culture. It was thought that an attached sporangium or bit of leaf caused the sinking of some of the spores, thus changing their environment by completely surrounding the developing prothallia with water. The dish was covered with a loosely fitting lid so that prothallia growing on the surface of the water would receive a sufficient supply of oxygen. The amount of oxygen would necessarily be limited in the prothallia growing below the surface of the water. It is suggestive that the oxygen requirement may have been a factor in producing these irregular gametophytes.

Besides the filament of elongated cells characteristic of impoverished prothallia, the accompanying drawings show that these prothallia differ from the normal gametophyte in one or more of the following characteristics:

1. A change in the direction of growth of the filament may occur by the apical cell forming an acute angle with the main cell thread (FIG. 4).



2. The production of an irregularly lobed apical cell (FIGS. 2, 8, 9).

3. An individual cell in the filament may develop an outgrowth or branch without forming a cross wall at the base (FIGS. 6, 7, 10).

4. A branched filamentous prothallium may have the proliferations originating in one cell (FIGS. 7, 10, 11).

5. An increase in the number of growing regions. (FIGS. 3-11).

An exact knowledge of the optimum physiological conditions under which fern prothallia will grow and the changes that occur when this condition is modified would be of interest since the fern gametophyte has shown itself to possess great potentiality.

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#### Explanation of plates 22 and 23

All the figures were drawn with the aid of a camera lucida.

FIG. 1. Normal prothallium from the surface of culture showing typical form with a well-defined apical region.

FIG. 2. A five-celled prothallium with an unusually long apical cell, swollen at the end, which is turned, indicating an abrupt change in the direction of growth.

FIG. 3. The end of the filament forms an acute angle with the main cell thread.

FIG. 4. A small cell cut off from the apical cell is growing in the opposite direction.

FIG. 5. A normal gametophyte with the possibility of two growing points.

FIG. 6. An extreme case of branched cells; two cells have well-defined protuberances.

FIG. 7. Two filaments originating in a two-armed cell.

FIGS. 8, 9. Irregularly lobed apical cells.

FIG. 10. A two-armed prothallium due to the branching of one cell.

FIG. 11. Three branches originating in one cell.



## The correct name for the hemlock spruce\*

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A casual perusal of the local floras covering eastern North America shows that the white spruce passes under the name of *Picea canadensis* (Mill.) BSP. and the hemlock spruce, of *Tsuga canadensis* (L.) Carr. Now, although Britton, Stearns, and Poggenberg quote Miller as the original author of the specific name *canadensis* of the white spruce, it becomes very evident through a perusal of Miller's description that his specific name is derived from the Linnaean *Pinus canadensis* and, therefore, that the proper citation (under article 41 of the Vienna rules) should include the name of Linnaeus, in parentheses, as the original author, instead of that of Miller. Here is, then, the anomalous position of two distinct species bearing the same specific name and both being derived from the same author, publication, and description, a condition contrary to all laws of botanical nomenclature, which provide that the specific name can be maintained for only one element of an aggregate when that aggregate is segregated. It remains, therefore, to determine which one of these two species shall retain the specific name *canadensis*. The first step is to determine if possible, what the Linnaean type of *Pinus canadensis* may be; if that can be determined, the rest will be easy, for the type element of an aggregate will retain the specific name upon segregation.

The description of *Pinus canadensis* in the 2d edition of the *Species Plantarum*, 1763, on page 1421, is as follows:—

10. PINUS foliis solitariis linearibus obtusiusculis *canadensis* submembranaceis.

*Abies* foliis solitariis confertis obtusis membranaceis. *Gron. virg.* 191.\*

*Abies* foliis piceae brevioribus, conis parvis biuncialibus laxis. *Mill. dict. t.* 1.

*Habitat in America septentrionali.* 2.

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\* Contributions to the Botany of Michigan, No. 10. Read at the St. Louis meeting of the Botanists of the Central States, October 17, 1914.



As there is no specific mention of a type we may arrive at one by considering (1) the herbarium specimens, (2) the description, (3) the synonyms, and (4) the specific name and habitat. *Pinus canadensis* is represented in the Linnaean Herbarium, but Mr. B. D. Jackson, in his Index to the Linnaean Herbarium, shows that the specimen was not received until later than 1767, several years after the publication of the species, and that it is not authenticated by Linnaeus; it may therefore be disregarded as not bearing upon the point in question.

The descriptive phrase of Linnaeus is not distinctive and can not limit his species to any one form; he took no consideration of the cones whatever; he described the leaves as solitary, linear, somewhat obtuse, and submembranaceous, characters that apply to the leaves of a number of species of the solitary-leaved Abietae and therefore can not be considered as specific in character. The first synonym cited is that of Gronovius. Gronovius' species was published as follows on page 191 of the 1st edition of the *Flora Virginica*, part 2, 1743:

*ABIES foliis solitariis confertis obtusus membranaceis.*

*Abies minor pectinatis foliis Virginiana conis parvis, subrotundis. Plukn. Alm. p. 2 t. 121 Fig. 1*

*Abies minor Taxifoliis, conis parvis subrotundis, deorsum spectantibus. Clayton N. 547*

*Folia linearis, plana, tenuissima, carinata, obtusa, confertim natam solitaria. Coni magnitudine fragae, ovati, acuminati, squamis numerosis planis subrotundis obtusissimis.*

In this connection it may properly be remarked that the plant of Plukenet, which is presumably the type of his figure 1, plate 121, is preserved in the Herb. Sloane, volume 95, folio 1, and is the hemlock spruce, generally known as *Tsuga canadensis* Carr.; also that the plant of Clayton, No. 547, upon which Gronovius based his species, is preserved at the British Museum and is the same thing.

Here we have not only a very accurate description of the leaves and cones but herbarium specimens and a published figure to supplement the descriptions, all of which, taken together, accurately limit the species defined to the hemlock spruce commonly known as *Tsuga canadensis* Carr. Apparently this should be



definite enough to fix the status of *Pinus canadensis* L. But let us go a little deeper into the question before taking up the next synonym. *If we take the first synonym enumerated under a species as the type of that species, in case no type is specifically named, then Pinus canadensis* L. becomes a pure synonym of *Pinus balsamea* L., for the first synonym cited under both species is the same Gronovian species, which is the hemlock spruce! Let us, therefore, investigate the *Pinus balsamea* of Linnaeus, published on page 1002 of the 1st edition of the *Species Plantarum* in 1753, as follows:

*Balsamea.* 9. PINUS foliis solitariis subemarginatis: subtus linea duplici punctata.

*Abies* foliis solitariis confertis obtusis membranaeis. *Gron. virg.* 191.\*

*Abies* minor, pectinatis foliis, virginiana, conis parvis subrotundis. *Pluk. alm.* 2. t. 121. f. 1.  
*Raj. dendr.* 8.

*Habitat* in Virginia, Canada. ♀

*Habitus* antecedentis [*Pinus Picea*], sed Folia latiora, obtusiora, utrinque per ramos pectinatim digesta, at duplici serie, superiore sc. breviora, subtus sunt picta linea duplici glauca: singula ex 8 ordinibus longitudinalibus punctorum alborum. Apex foliorum saepe bifidus.

A careful inspection of the above shows that it is an aggregate and composed of such divergent species as the balsam firs with *erect* cones and the hemlock spruce with *hanging* cones. To which element, then, under the rules of botanical nomenclature, does the name *Pinus balsamea* L. belong? There is unfortunately no rule covering this point in the Vienna rules nor, so far as the writer is aware, in any other code. There are no generic descriptions in the *Species Plantarum* and while there are specific diagnoses, these, from the modern point of view, are drawn so loosely in many cases that they are of little diagnostic value. Furthermore, the *Species Plantarum* is not considered to be a descriptive work but a mere application of the binomial system to the then known species—those that already had been published under the polynomial system by various older authors—and the species therein



enumerated are considered to be based upon citations rather than upon the descriptive phrases. Should then the most emphasis be placed upon the description or upon the citations? This is an important principle upon which no agreement has been reached; it ought to be definitely settled by a botanical congress, since very often, as in the present instance, widely different results may be obtained by different authors following out the different methods of treatment. Some authors prefer to adopt the descriptive matter as their guide, others the synonyms cited; so that we have such expressions as *Sonchus alpinus* L., as to character; or, as to the synonymy; or, as to the habitat, as the case may be. In the present instance, and it might be said in all instances of the kind, the best way is to let the internal evidence decide, adopting the name for that element which receives the preponderant weight of evidence. *If citations are considered to carry the greatest weight, for the Species Plantarum is par excellence the work in which the binomial system is applied to citations, then the name Pinus balsamea L. belongs to the hemlock spruce, for all the citations under that name are of this species.* The Linnaean herbarium contains no specimen which can be designated as the type, since it contained no specimen of the species at the time of its publication. Let us now look at the descriptive matter—the diagnostic phrase and the note under *Habitus*. There is absolutely nothing in the descriptive matter that will limit it to any one species; the cones are not at all considered; the characters ascribed to the leaves are applicable to other species than the balsam fir; in other words they are of a group or groups of a higher order than that of a species, i. e., an aggregate. The same may be said of the habitat given, which is Virginia and Canada; the specific name is *balsamea*, and this alone is indicative of what Linnaeus may have had in view as the type of his species. As a matter of fact, the *Pinus balsamea* of Linnaeus is so broadly drawn that it may be appropriately considered a huge pit into which *all* the *spruces* and *firs* of eastern North America may be conveniently dropped to form a conglomerate whole. Notwithstanding the fact that the *Species Plantarum* is primarily a publication founded upon the work of earlier botanists and that the binomials therein are mostly based upon and applied to the citations enumerated from those earlier



botanists, we may be justified, in the present instance, in following precedent and in disregarding the synonyms cited and the description also, allowing the name to represent the balsam fir; for this is undoubtedly the interpretation Linnaeus intended it to have as is indicated by the specific name.

Having excluded the hemlock synonyms from consideration under *Pinus balsamea* and having settled the status of that species we may resume consideration of *Pinus canadensis*. We have already shown that the first citation refers definitely to the hemlock spruce. We will now consider the Millerian synonym and endeavor to determine its status. This carries us back to the 7th edition of the "Gardeners Dictionary" published in 1759 and the "Figures" published in 1760. In the former work, Philip Miller has segregated the Linnaean aggregate and described four species from America under *Abies* as follows:

3. *ABIES minor, pectinatis foliis, Virginiana, conis parvis subrotundis. Pluk. Alm.* The Virginian Fir Tree, with small roundish Cones, commonly called Hemlock Fir.
4. *ABIES piceae foliis brevibus, conis minimus. Rand.* The Pitch-leaved Fir Tree, with small Cones, commonly called The Newfoundland Black Spruce Fir.
5. *ABIES piceae foliis brevioribus, conis parvis biuncialibus laxis. Rand.* The shortest Pitch-leaved Fir Tree with loose Cones, commonly called The Newfoundland White Spruce Fir.
6. *ABIES taxi foliis, odora, Balsami Gileadensis, Raii Hist. App.* The Balm of Gilead Fir.

Here we have, so far as the writer is aware, the first post-Linnaean description of the species as they are understood at the present time. Unfortunately, Miller had not at that time accepted the binomial nomenclature of Linnaeus and consequently his species received no specific appellations; his work, however, can not be ignored any more than can the *Species Plantarum* itself. The descriptions and the notes on the following page as to the native habitats, habits, etc., and the culture of the various plants in England leave no doubt whatever as to the identity of the species. No. 5 was illustrated in the following year, 1760, in the "Figures," and this is the species cited by Linnaeus under



his *Pinus canadensis*. I have not seen the plate published by Miller but, considering the fact that he had a very clear conception of the various species and access to living material of all, I doubt not but that it is characteristic of the white spruce.\* We have no choice but to consider the 7th edition of the Gardeners Dictionary to be the publication in which the delimitation or segregation of our spruces and firs began and to be guided accordingly. It has become very clear from the foregoing that the *Pinus canadensis* of Linnaeus is an aggregate consisting of the hemlock spruce and the white spruce. The habitat gives us no clue as to which may be considered the type but the specific name, as in the case of *Pinus balsamea*, may. The white spruce is most characteristically a Canadian species, while the hemlock spruce is characteristically American, using the latter term as equivalent to the United States; hence the specific name indicates the white spruce. Also what more than likely that Linnaeus in establishing his *Pinus canadensis* was guided more by the *recently published but specifically unnamed* plate of Miller, than by the old description of Gronovius? We must also consider the fact that the *Plukenetian species, also illustrated and the true hemlock spruce, was left under Pinus balsamea*. The very fact that the hemlock spruce was divided between the two species is paramount in itself to proof positive that the author did not consider it the type of either. A careful weighing and consideration of the above problems leads to the conclusion that the Millerian synonym, *not the Gronovian*, is the type of *Pinus canadensis* L.

To sum up: *Pinus balsamea* L. of the 1st edition of the Species Plantarum is an aggregate which may be considered to include *all* of the firs, spruces, and hemlocks.

Miller, in 1759, segregated the Linnaean aggregate, recognizing four species, but did not name them under the binomial system.

Linnaeus, in 1763, recognized, in part, the work of Miller and established *Pinus canadensis*, on, we shall claim, the Millerian species (No. 5) but probably intended it to contain all species with *drooping* cones. Unfortunately he neglected to remove the

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\* Since writing the above I have received a communication from Mr. A. Gepp, of the British Museum, in which he informs me that the plate of Miller referred to is considered by Mr. A. Bruce Jackson, an authority on the Coniferae, to be the *Picea canadensis* BSP., thus confirming the deductions above drawn.



Plukenetian synonym from *Pinus balsamea* which, very likely, was intended to include all species with *erect* cones. Five years afterward, 1768, Miller published the 8th edition of the Gardeners Dictionary and in this work he not only recognized the four species of the 7th edition, but the binomial system also and consequently gave specific appellations to the species.

The balm of Gilead fir or balsam fir (species No. 6 of the 7th edition) becomes *Abies balsamea*, species No. 3.

The white spruce fir (species No. 5 of the 7th edition) becomes *Abies canadensis*, species No. 4.

The black spruce fir (species No. 4 of the 7th edition) becomes *Abies mariana*, species No. 5.

The hemlock fir (species No. 3 of the 7th edition) becomes *Abies americana*, species No. 6.

Nos. 4 and 6 are described as follows:

4. ABIES (*Canadensis*) foliis linearibus obtusiusculis submembranaceis. *The Newfoundland White Spruce Fir.*

*Abies* foliis piceae brevioribus, conis parvis biuncialibus laxis.  
Rand.

6. ABIES (*Americana*) foliis linearibus obtusiusculis bifariam versis conis subrotundis. *The Hemlock Spruce Fir.*

A careful comparison of the descriptions of *Abies canadensis* Mill. and *Pinus canadensis* L. shows them to be identical in everything except the Gronovian synonym which Miller has removed from the Linnaean species and described and named as *Abies americana*. Under the Vienna Code, Articles 46 and 47 govern; the latter provides that in segregating a species, the specific name is retained for the element first published; and the former provides that where two or more groups are of the same date the author chooses and his choice cannot subsequently be modified. The conclusions we have arrived at from the above study are:

(1) Linnaeus published *Pinus balsamea* in 1753 and made it broad enough to include all east North American Abietae with single leaves.

(2) Miller, in 1759, segregated the Linnaean aggregate, recognizing four species.

(3) Linnaeus, in 1763, retained *Pinus balsamea* and described *Pinus canadensis* (dividing the hemlock spruce and placing a part



under each so that it can not be considered typical of either), thus recognizing only two of Miller's four species from America.

(4) Miller, in 1768, reestablished his four species, and gave them specific appellations under the binomial system as follows: the balsam fir or balm of Gilead fir became *Abies balsamea*; the white spruce, *Abies canadensis*; the black spruce, *Abies mariana*; and the hemlock spruce, *Abies americana*.

Under Articles 46, 47, 48, 50, and 51 of the Vienna Rules this choice of specific names by Miller for these plants can not be modified and the proper names and leading synonyms of the species are as follows:

ABIES BALSAMEA (L.) Mill. Gard. Dict. Ed. 8, No. 3. 1768.

*Abies taxifoliis*, odora, Balsami Gileadensis, Raii Hist. App.

Mill. Gard. Dict. Ed. 7, No. 6. 1759.

*Pinus balsamea* L. Sp. Pl. Ed. 1, 1002. 1753; Ed. 2, 1421.  
1763 (as to name only).

*Picea balsamea* Loudon, Arb. Brit. 4: 2339. f. 2240-2242.  
1844.

PICEA CANADENSIS (L.) BSP. Prel. Cat. N.Y. 71. 1888.

*Abies piceae* foliis brevioribus, conis parvis biuncialibus laxis.

Rand. Mill. Gard. Dict. Ed. 7, No. 5. 1759; Figures,  
pl. 1. 1760.

*Pinus canadensis* L. Sp. Pl. Ed. 2, 1421. 1763 (as to syno-  
nym of Miller).

*Abies canadensis* Mill. Gard. Dict. Ed. 8, No. 4. 1768.

*Pinus alba* Ait. Hort. Kew. 3: 371. 1789.

*Abies alba* Michx. Flor. Bor. Amer. 2: 207. 1803 (not of Miller,  
1768).

*Picea alba* Link, Linnaea 15: 519. 1841.

PICEA MARIANA (Mill.) BSP. Prel. Cat. N.Y. 71. 1888.

*Abies piceae* foliis brevibus, conis minimis. Rand. Mill.

Gard. Dict. Ed. 7, No. 4. 1759.

*Abies mariana* Mill. Gard. Dict. Ed. 8, No. 5. 1768.

*Pinus mariana* Du Roi, Obs. Bot. 38. 1771.

*Pinus nigra* Ait. Hort. Kew. 3: 370. 1789.

*Abies nigra* Du Roi, Handb. Baumg. 2: 182. 1800.

*Picea nigra* Link, Linnaea 15: 520. 1841.



***Tsuga americana*** (Mill.) nov. comb.

*Pinus balsamea* L. Sp. Pl. Ed. 1, 1002. 1753; Ed. 2, 1421.  
1763 (as to synonyms).

*Abies minor*, pectinatis foliis, Virginiana, conis parvis subrotundis, Pluk. Alm. Mill. Gard. Dict. Ed. 7, No. 3. 1759.

*Pinus canadensis* L. Sp. Pl. Ed. 2, 1421. 1763 (as to synonym of Gronovius).

*Abies americana* Mill. Gard. Dict. Ed. 8, No. 6. 1768.

*Pinus americana* Du Roi, Obs. Bot. 39. 1771.

*Abies canadensis* Michx. Fl. Bor. Am. 2: 206. 1803 (not of Miller, 1768).

*Picea canadensis* Link, Linnaea 15: 524. 1841.

*Tsuga canadensis* Carr. Trait. Conif. 189. 1855.

I wish here to thank Mr. A. Gepp, of the British Museum (Natural History), and Miss Mary A. Day, of the Gray Herbarium, most heartily for many valuable notes and kind assistance.

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# INDEX TO AMERICAN BOTANICAL LITERATURE

1910-1914

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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## INDEX TO VOLUME 41

New names and the final members of new combinations are in **bold face type**.

- Abies, 625; alba, 628; americana, 627, 628, 629; balsamea, 627, 628; canadensis, 627, 628, 629; mariana, 627, 628; nigra, 628
- Abrus precatorius, 107
- Abutilon Lemmoni, 303
- Acacia Berteriana, 8; lentiscifolia, 8; suffrutescens, 303
- Acaena, 323, 324; agrimonioides, 323, 324; californica, 324, 325; elongata, 323, 324; elongata gracilis, 324; elongata robusta, 324; laevigata, 323, 324; lappacea, 323, 324; pinnatifida, 324; torilicarpa, 324; tridactyla, 324; trifida, 324
- Acalypha alopecuroidea, 12
- Acanthospermum hispidum, 13
- Acer floridanum, 214, 219; rubrum, 559; saccharum, 512
- Acetabula, 158
- Achillea borealis, 102; lanulosa, 100; Millefolium, 355, 358, 512, 514, 516, 517, 519, 520; multiflora, 102; subalpina, 100, 471
- Achroanthus unifolia, 29, 32, 35
- Acolea crenulata, 612
- Acomastylis, 490, 491, 494; depressa, 494; gracilipes, 494, 495; humilis, 494; Rossii, 100, 494; sericea, 100, 469, 471, 494, 495; turbinata, 100, 463, 469, 470, 495
- Adenostoma, 330, 331; brevifolium, 330; fasciculatum, 330; fasciculatum densifolium, 330; fasciculatum hirsutum, 330; fasciculatum obtusifolium, 330; sparsifolium, 331
- Adiantum Capillus-veneris, 44, 308; **rimicola**, 308
- Aesculus octandra, 29, 34, 38; Pavia, 214
- Aethusa Cynapium, 84
- Azalia cassioides, 561; macrophylla, 29, 35, 45; pectinata, 212
- Agaricus, 179; campestris, 111
- Agrimonia, 325; Bicknellii, 328; Brittoniana, 329; Eupatoria, 325, 326, 328; Eupatoria glabra, 326; Eupatoria hirsuta, 326; Eupatoria mollis, 327; Eupatoria parviflora, 329; gryposepala, 326; incisa, 329, 330; macrocarpa, 326; microcarpa, 327, 329; mollis, 327; parviflora, 326, 329, 330; platycarpa, 327, 329; polyphylla, 329; Pringlei, 327, 329; pubescens, 327, 328; pumila, 327; rostellata, 326, 328, 329; serrifolia, 329; striata, 325, 327, 328, 329; suaveolens, 329
- Agropyron andinum, 99, 463, 464; biflorum, 96, 99, 469; caninum, 96, 469; latiglume, 99, 463, 464; repens, 514, 516, 518; Scribneri, 101, 463
- Agrostis, 359, 362; alba, 359, 360, 512, 514, 515, 516, 518; hyemalis, 470; perennans, 308
- Akebia quinata, 367
- Alaska, Observations on the edge of the forest in the Kodiak region of, 381; Report on the Hepaticae of, 577
- Alchemilla, 319, 320; achilleaefolia, 322; alpina, 319; domingensis, 321; filicaulis, 320; glomerulans, 320; hirsuta campestris, 321; nivalis, 321; orbiculata, 320; pectinata, 320; pinnata, 321, 322; pratensis, 320; sibbaldiaefolia, 321; speciosa, 222; vulgaris, 320; Wichurae, 320
- Algites americana, 297
- ALLARD, H. A., A review of investigations of the mosaic disease of tobacco, together with a bibliography of the more important contributions, 435
- Allium, 358; canadense, 358; cernuum, 356, 358
- Allocarya hispidula, 341
- Alnus rubra, 580; rugosa, 560; sinuata, 472, 473; tenuifolia, 338, 340
- Aloe ferox, 126
- Alopecurus aristulatus, 470, 471
- Alsine americana, 99, 465, 466; baicalensis, 467; dichotoma, 99; laeta, 97, 99, 467, 470; longipes, 97; polygonoides, 99, 468, 469
- Alsinopsis obtusiloba, 462, 463; propinqua, 95, 467; quadrivalvis, 96, 468, 469; Rossii, 96, 468, 469; verna, 95, 96
- Althea officinalis, 127
- Amaranthus, New or notable species of, 505
- Amaranthus, 505, 507, 508, 509; acutifolius, 509; blitoides, 512, 517; bracteosus, 508; crassipes, 509; emarginatus, 509; graecizans, 512; Greggii, 507; hybridus, 509; **myrianthus**, 506;



- Palmeri, 506; pubescens, 508; retroflexus, 505, 510, 514, 516; Torreyi, 507; Torreyi suffruticosus, 505, 506; viscidulus, 508, 509; **Watsoni**, 505
- Amarella Amarella, 96; arctophila, 102; monantha, 96; plebeja, 96, 470; propinqua, 102; scopulina, 472; strictiflora, 470, 472; tenella, 96
- Ambrosia artemisiifolia, 357, 360, 512, 514; psilostachya, 512
- Amelanchier Cusickii, 341; florida, 340; sp. 214
- Amomum Melegueta, 107, 127
- Amorpha canescens, 355, 356
- Ananas sativa, 153
- Anastrepta, 588, 589; orcadensis, 588, 589, 601, 610, 614, 615
- Anastrophyllum Reichardtii, 613, 615
- Anastrophus compressus, 560
- Anchistea virginica, 560
- Ancistrum, 323
- Andromeda Cooki, 298; grandifolia, 298; novae-caesareae, 298; Parlatorii, 298
- Andropogon furcatus, 354, 355, 357, 363; scoparius, 354, 357; virginicus, 28, 33, 35
- Androsace albertina, 96; carinata, 96, 462, 464; Chamaejasme, 96; septentrionalis, 102; subumbellata, 470
- Anemiopsis, 232
- Anemone, 490; canadensis, 29, 35; globosa, 101; narcissiflora, 96; parviflora, 94; tetonensis, 101; zephyra, 96, 470
- Anethum graveolens, 84
- Aneura major, 612
- Angelica atropurpurea, 107; Grayi, 101, 470; Roseana, 471
- Anisacanthus Thurberi, 303
- Anneslia colletioides, 18; **enervis**, 18
- Antennaria alpina, 97, 102; aprica, 463; media, 97, 463; monocephala, 102; nardina, 472; plantaginifolia, 356, 357; rosea, 339; sedoides, 465; umbrinella, 97
- Anthelia julacea, 601; Juratzkana, 613
- Anthemis Cotula, 514, 516; nobilis, 126
- Anthonomus grandis Thurberiae, 301
- Anthropogon barbellatum, 99, 468; ciliatum, 99
- Anticlea coloradensis, 466
- Antiphylla oppositifolia, 466
- Antrophyum minimum, 398; Werckleanum, 398
- Aphanes, 319, 320, 321; arvensis, 320; australis, 320; cuneifolia, 320; macrosepala, 320; occidentalis, 320
- Aphyllon, 231
- Apium graveolens, 107, 127; Petroselinum, 107, 127
- Apocynum androsaemifolium, 109, 340; cannabinum, 109, 359
- Appearance of polar bodies in the spermatogenous tissue of Ricciocarpus natans (L.) Corda, The, 333
- Aquilegia brevistyla, 100; coerulea, 467; flavescens, 470; Jonesii, 464; saximontana, 100, 465, 466
- Aragallus deflexus, 100, 470; foliolosus, 100; Hallii, 464; podocarpus, 97, 464
- Aralia groenlandica, 298; nudicaulis, 83; racemosa, 222; Ravniana, 298; spinosa, 28, 32, 35, 41, 42, 44, 46, 214, 560; Washingtoniana, 296
- Araliaceae, 83
- Araliopsis, 296, 297; breviloba, 296; cretacea, 296; cretacea dentata, 296; cretacea salisburiaefolia, 297
- Araucaria bladenensis, 297; marylandica, 297
- Archangelica officinalis, 126
- Arctium Lappa, 121; minus, 514
- Arctostaphylos Uva-ursi, 415
- Arctuos, 472
- Arenaria Fendleri, 464; serpyllifolia, 514, 515, 520; Tweedyi, 464
- Aristida dichotoma, 29, 36; stricta, 561, 563
- Aristolochia reticulata, 107; Serpentaria, 107, 127
- Arnica cordifolia, 339; montana, 107, 126; Parryi, 471
- Aronia nigra, 29, 35, 421
- Artemisia, 110; arctica, 102; borealis, 96; ludoviciana, 338, 340, 512; norvegica, 96; Parryi, 101, 468; Pattersonii, 101, 468; pauciflora, 107; Richardsoniana, 102; saxatilis, 468; saxicola, 96; scopulorum, 101, 467; spithamaea, 96, 468, 469
- Aruncus Aruncus, 28, 33, 35
- Asarum arifolium, 214, 216
- Asclepias, 109; incarnata, 358; linearis, 303; mexicana, 340; Sullivantii, 29, 32, 36, 38, 356, 358; syriaca, 358; tuberosa, 109, 355, 356; variegata, 29, 32, 34, 38; verticillata, 355, 360
- Ascobolus, 161, 172, 179, 183, 195, 196; carbonarius, 159, 160, 162, 163, 164, 166, 172, 187, 192, 193, 194, 197; furfuraceus, 159, 160, 161, 179, 180, 181, 183, 184, 186, 187, 188, 189, 193, 194, 195; glaber, 160, 193; immersus, 186, 190, 194; Leveillei, 189, 190, 194; magnificus, 181, 183, 185, 186, 192, 193, 196, 197; mirabilis, 162, 166; pusillus, 193; Winteri, 186, 189, 194
- Ascodesmis, 161, 181, 190, 192, 193; nigricans, 159, 184
- Ascophanus carneus, 159, 160, 172, 193; pilosus, 159
- Ascyron hypericoides, 28; multicaule, 33, 35



- Asimina parviflora*, 212  
*Aspergillus*, 169, 171, 182, 193; *flavus*, 289; *herbariorum*, 159, 161; *niger*, 290; *repens*, 159  
*Asperula*, 225  
*Aspidiophyllum*, 296, 297; *trilobatum*, 297  
*Asplenium cecilensis*, 297; *Dicksonianum*, 296; *montanum*, 29, 32, 36; *pinnatifidum*, 28, 33, 36  
*Aster*, 13; *adnatus*, 13, 14; *alpinus*, 94, 471; *apricus*, 470; ***bahamensis***, 13, 14; *Bracei*, 13, 15; ***Burgessii***, 13, 14; *carneus*, 15; *divaricatus*, 28, 33, 35; *Douglasii*, 338; *dumosus*, 13, 15; *expansus*, 15; *exilis*, 13, 15; *foliaceus frondosus*, 338; ***Grisebachii***, 13, 14; *inconspicuus*, 13, 15; *laevis Geyeri*, 338, 340; *lucayanus*, 13, 14; *macrophyllum*, 29, 35; *marginatus*, 14; *multiflorus*, 354, 360; *Novae-Angliae*, 357; *oreganus*, 339, 340; *paniculatus*, 359; *sericeus*, 354; *squamatus*, 13, 15; *Trifolium*, 15; *tripolium*, 15  
*Asterella fragrans*, 613; *tenella*, 613  
*Astragalus alpinus*, 93; *Purshii*, 340; *villosus*, 212  
*Atelophragma elegans*, 470  
Atlantic coastal plain, Contributions to the Mesozoic flora of the, X—Maryland, 295  
*At:iplex angustifolia*, 303  
*Atropa Belladonna*, 107, 125  
ATWELL, R. S. The appearance of polar bodies in the spermatogenous tissue of *Ricciocarpus natans* (L.) Corda, 333  
*Avena*, 225; *americana*, 100; *Mortoniana*, 100, 464; *sativa*, 516, 520  
*Avicennia*, 231  
*Azalea glauca*, 413; *hispida*, 413; *lutea*, 29, 30, 32, 35; *nitida*, 413; *viscosa*, 413  
  
*Bacillus mycoides*, 290; *prodigiosus*, 290; *pyocyaneus*, 290; *subtilis*, 290; *Tetani*, 267  
*Baeomyces roseus*, 159  
BAILEY, V. Wild cotton plant (*Thurberia thespesioides*) in Arizona, The, 301  
*Baldwinia uniflora*, 561  
*Balsamia*, 182  
*Balsamorhiza sagittata*, 342  
*Baptisia bracteata*, 355; *perfoliata*, 563  
*Barosma betulina*, 107, 110  
*Batodendron arboreum*, 212, 214  
*Batrachospermum*, 161, 167, 171, 172, 173  
*Bauhinia marylandica*, 297  
*Bazzania deflexa*, 598; *Didericiana*, 597; *Pearsoni*, 596, 597, 615, 616; *tricrenata*, 597, 598; *trilobata*, 598  
*Belairia parvifoliola*, 19  
  
BENEDICT, R. C. Revision of the genus *Vittaria*, J. E. Smith, A, 391  
*Berberis Aquifolium*, 127; *repens*, 341  
*Bernhardia dichotoma*, 56; *ramulosa*, 57  
BERRY, E. W. Contributions to the Mesozoic flora of the Atlantic coastal plain, X.—Maryland, 295  
*Besseya alpina*, 100, 470; *plantaginea*, 464; *plantaginifolia*, 100  
*Betula glandulosa*, 472, 473; *lutea*, 28, 32, 35, 44; *nigra*, 28, 33, 35; *papyrifera alaskana*, 381  
BICKNELL, E. P. The ferns and flowering plants of Nantucket,—XII, 71; XIII, 411  
*Bidens aristosa*, 30, 35  
*Bignonia crucigera*, 214, 560  
*Bistorta bistortoides*, 100, 470, 472; *linearifolia*, 100, 470; *vivipara*, 93, 472  
BLACK, C. A. Branched cells in the prothallium of *Onoclea sensibilis* L., 617  
Black-soil prairie station in northeastern Illinois, A., 351  
*Blasia pusilla*, 612  
*Blephariglottis lacera*, 29, 34, 38; *peramoena*, 29, 31, 35  
*Blepharoneuron tricholepis*, 470  
*Blepharostoma setiforme*, 613; *trichophyllum*, 601  
*Boletus*, 179  
*Bonnemaisonia*, 167  
*Bonnetia*, 20; *anceps*, 20  
*Botrytis cinerea*, 290; *vulgaris*, 290  
*Bourreria*, 10; *grandiflora*, 11; ***moaensis***, 10; ***mucronata***, 10; ***Nashii***, 11; *pauciflora*, 11; *setoso-hispida*, 10  
BOWMAN, H. H. M. Mechanical tissue development in certain North American vines, 365  
*Brachyphyllum macrocarpum*, 297; *macrocarpum formosum*, 297  
*Brachysiphon*, 223  
Branched cells in the prothallium of *Onoclea sensibilis* L., 617  
*Brassica arvensis*, 514, 517  
*Brauneria pallida*, 355; *purpurea*, 30  
*Brickellia californica*, 303  
BRITTON, N. L. Studies of West Indian plants—V, 1  
*Bromus Kalmii*, 356; *secalinus*, 514  
*Bryonia alba*, 126; *dioica*, 126  
*Bryopteris*, 608  
*Bumelia lanuginosa*, 214; *praenuntia*, 298  
*Bupleurum americanum*, 100; *purpureum*, 100; *ranunculoides*, 100  
*Burmannia*, 229; *candida*, 230; *Championii*, 222, 230; *coelestis*, 230  
*Burshia*, 497  
  
Cactaceae, 71  
*Cactus missouriensis*, 47; *Opuntia*, 71



- Calamagrostis arundinacea*, 95; *canadensis*, 97, 358, 359; *Langsdorfii*, 97, 471; *purpurascens*, 95, 463  
*Calliandra collettioides*, 18; *erophylla*, 303; *prehensilis*, 8; *revoluta*, 5; *Saman*, 8  
*Callicarpa americana*, 214, 560; *Hitchcockii*, 12  
*Callistemon*, 153  
*Callithamnion*, 174, 177  
*Callitriche palustris*, 474  
*Calluna vulgaris*, 415, 416, 417; *vulgaris pubescens*, 417  
*Calosiphonia*, 176  
*Caltha biflora*, 99; *cheledoni*, 99, 472, 473; *leptosepala*, 99, 472, 473; *rotundifolia*, 99, 472, 473  
*Calypogeia Neesiana*, 596; *Trichomanis*, 596  
*Campanula americana*, 363; *lasiocarpa*, 102; *Parryi*, 470; *petiolata*, 470; *rotundi rotundifolia*, 339; *uniflora*, 93, 94, 470  
*Camptosorus rhizophyllus*, 617  
*Campulosus aromaticus*, 560, 565  
*Cannabis sativa*, 107, 121  
*Capnoides sempervirens*, 29, 35  
*Capsella Bursa-pastoris*, 514, 515, 516, 517, 518  
*Capsicum fastigiatum*, 107  
*Cardamine bellidifolia*, 102; *rotundifolia*, 30  
*Carduus undulatus*, 341; *virginicus*, 30  
*Carex*, 471; *Clarkii*, 298; *costellata*, 28, 35; *floridana*, 214; *sp.*, 357  
*Carphephorus Pseudo-Liatris*, 561, 563, 567  
*Carpinus caroliniana*, 559  
*Carpites liriophylli*, 297  
*Carpolithus septloculus*, 298  
*Carthamus tinctorius*, 126  
*Carum Carvi*, 107, 127  
*Cassandra*, 421  
*Cassia acutifolia*, 107; *angustifolia*, 107; *Chamaecrista*, 354, 360; *nictitans*, 28, 35  
*Cassiope Mertensiana*, 98, 467; *tetragona*, 98, 102, 467  
*Castanea dentata*, 28, 33, 35  
*Castilleja brunescens*, 470; *coccinea*, 356; *Haydeni*, 99, 463, 464; *lancifolia*, 470; *lauta*, 470; *miniata*, 339; *occidentalis*, 100, 463; *pallida*, 99, 100, 102; *rhexifolia*, 470  
*Catabrosa aquatica*, 474  
*Ceanothus americanus*, 212; *sanguineus*, 339  
*Celastrophyllum crenatum*, 298; *undulatum*, 298  
*Celastrus arctica*, 298  
*Centella repanda*, 560  
*Cephalozia bicuspidata*, 595; *divaricata*, 596; *leucantha*, 596, 615; *media*, 596; *multiflora*, 596  
*Cephaloziella byssacea*, 596  
*Cerastrium alpinum*, 94, 96; *Behringianum*, 96, 99, 467, 470; *Earlei*, 99, 468; *pulchellum*, 99, 468; *vulgatum*, 514, 516, 517, 518, 520  
*Ceratostoma*, 161, 183, 184  
*Cercis canadensis*, 214, 219, 243, 244, 251, 256, 533, 547, 548; *Siliquastrum*, 224  
*Cercis*, On the relationship between the number of ovules formed and the number of seeds developing in, 243; Further observations, 533  
*Cercocarpus*, 331, 497; *alnifolius*, 500; *argenteus*, 500; *arizonicus*, 502, 503; *betulaefolius*, 499, 500, 501; *betulaefolius Blancheae*, 500; *betulaefolius typicus*, 499; *betuloides*, 499, 500, 503; *breviflorus*, 501, 502; *brevifolius*, 501; *brevifolius eximius*, 501; *Douglasii*, 498, 499, 500, 503; *flabellifolius*, 500, 503; *fothergilloides*, 497, 498, 499; *hypoleucus*, 502, 503; *intricatus*, 502, 503; *ledifolius*, 502, 503; *ledifolius intercedens subglabra*, 502; *ledifolius intricatus*, 502; *macrophyllus*, 497; *macrurus*, 498, 503; *minutiflorus*, 500; *mojadensis*, 498; *montanus*, 498, 499, 500, 503; *parvifolius*, 498, 499, 500; *parvifolius paucidentatus*, 501; *paucidentatus*, 501; *Pringlei*, 498; *rotundifolius*, 499; *Traskiae*, 498, 500; *Treleasii*, 501  
*Cereus grandiflorus*, 124  
*Chaenactis alpina*, 464; *Douglasii*, 341; *pedicularia*, 464  
*Chaetomium*, 183; *fimeti*, 182, 183  
*Chamaebatia*, 331, 497; *australis*, 497  
*Chamaecyparis nootkatensis*, 580; *thyoides*, 559, 563, 565  
*Chamaedaphne calyculata*, 414  
*Chamaenerion angustifolium*, 74, 75  
*Chamaepericlymenum canadense*, 86  
*Cheirinia amoena*, 100, 464; *asperrima*, 100; *nivalis*, 100, 464; *Pallasii*, 102; *radiata*, 100, 464; *Wheeleri*, 100  
*Chenopodium album*, 514, 515, 516, 517, 518, 519; *ambrosioides*, 107, 127; *hybridum*, 512, 515  
*Chiloscyphus*, 614; *pallescens*, 595; *polyanthus*, 614; *polyanthus rivularis*, 595; *rivularis*, 595  
*Chimaphila maculata*, 28, 33, 411; *umbellata*, 308, 411, 415  
*Chiogenes hispidula*, 426  
*Chionanthus virginica*, 212, 214  
*Chloranthus*, 232  
*Choiromyces*, 182  
*Chondrophora nudata*, 560, 563  
*Chondrophylla americana*, 467; *Fremontii*, 469  
*Chondrosea Aizoon*, 94, 466  
*Chrysanthemum Balsamitae tanacetoides*,



- 514; *Leucanthemum pinnatifidum*, 515, 518, 519  
*Chrysoma laricifolia*, 303  
*Chrysopsis alpicola*, 464; *aspera*, 212; *graminifolia*, 561; *mariana*, 29, 35  
*Chrysosplenium alternifolium*, 97; *americanum*, 28, 35; *tetrandrum*, 97, 468, 469  
*Cicuta bulbifera*, 84; *maculata*, 84, 359  
*Cilia aggregata*, 341  
*Cinchona Calisaya*, 126; *officinalis*, 126; *succirubra*, 126  
*Cinnamomum Newberryi*, 296, 297  
*Circaea alpina*, 28, 32, 35; *lutetiana*, 82  
*Cirsium arvense*, 518, 519; *discolor*, 355; *Hillii*, 356; *lanceolatum*, 515, 518, 519, 520  
*Cissites formosus magothiensis*, 298; *Newberryi*, 298  
*Citrullus Colocynthis*, 107, 126, 127  
*Cladium effusum*, 560, 563  
*Cladonia* sp., 212  
*Cladophlebis socialis*, 296  
*Clavaria* sp., 214, 215  
*Claytonia linearis*, 339; *megarrhiza*, 101, 465, 466; *perfoliata*, 339; *sibirica*, 339  
*Clematis hirsutissima*, 340  
*Clementsia rhodantha*, 470  
*Clerodendron calcicola*, 12  
*Clethra alnifolia*, 411, 414  
*Clethraceae*, 411  
*Cliftonia monophylla*, 560, 563, 567  
*Coccolobites cretaceus*, 298  
*Coelopleurum actaeifolium*, 85  
*Coffea*, 149; *arabica*, 149  
*Colchicum autumnale*, 107, 126  
*Coleochaete*, 192  
*Coleogyne*, 331  
*Coleosanthus grandiflorus*, 340  
*Collema*, 164, 169, 179, 196; *microphyllum*, 165, 192; *pulposum*, 157, 159, 162, 163, 164, 166, 192, 197  
*Collinsia tenella*, 339  
*Collinsonia canadensis*, 109  
*Collomia grandiflora*, 341  
*Colutea obovata*, 297; *primordialis*, 297  
*Commandra umbellata*, 354  
*Comocladia*, 9; *acuminata*, 9; *cuneata*, 9; *Dodonaea*, 9; *glabra*, 9; *pinnatifolia*, 9; *platyphylla*, 9  
*Compsomyces verticillatus*, 161  
*Condrophylla americana*, 96; *Fremontii*, 99; *humilis*, 99; *prostrata*, 96  
*Conium maculatum*, 83, 107; sp., 127  
*Conocephalum conicum*, 585  
*Conopholis americana*, 214, 215  
Contributions to the Mesozoic flora of the Atlantic coastal plain, X—Maryland, 295  
*Convallaria*, 225  
*Convolvulus Scammonia*, 126; *sepium*, 355, 358, 360  
*Conyza squamata*, 15  
*Copernicia*, 20; *Cowellii*, 17; *hospita*, 20; *macroGLOSSA*, 20; *rigida*, 17  
*Corallina*, 178  
*Cordia apiculata*, 298  
*Coreopsis major Oemleri*, 212  
*Coriandrum sativum*, 85, 107, 127  
*Cornaceae*, 86  
*Cornus*, 363; *Amomum*, 87, 362; *canadensis*, 86; *cecilensis*, 298; *florida*, 86, 214, 216, 219, 559, 563; *Forchhammeri*, 298; *stolonifera*, 28, 36, 338  
*Corylus americana*, 362  
*Cowania*, 495; *alba*, 495; *Davidsonii*, 495; *ericaefolia*, 495; *Howardi*, 495; *mexicana*, 495; *Stansburiana*, 495  
*Cracca virginiana*, 212, 560, 562  
*Crataegus aestivalis*, 566; *brevispina*, 341; *Michauxii*, 211, 214; sp. 214, 362  
*Crepis barbiger*, 339; *gracilis*, 339  
*Crossosma Bigelovii*, 303  
*Croton*, 230; *nummulariaefolius*, 12  
*Crotonophyllum cretaceum*, 297  
*Crucianella*, 223, 225  
*Cruoriopsis*, 196; *cruciata*, 175  
*Cudonia*, 180  
*Cunilla originoides*, 28, 33, 35  
*Cupressinoxylon Bibbinsi*, 298  
*Cuscata californica*, 341  
*Cynoglossum officinale*, 514, 515, 518  
*Cynomorium*, 222  
*Cynoxylon florida*, 86  
*Cyperus comosus*, 1; *pseudovegetus*, 561; sp. 358  
*Cypripedium*, 229; *acaule*, 28, 32, 35, 36, 415; *Reginae*, 30  
*Cyrilla racemiflora*, 560, 561, 567  
*Cytisus scoparius*, 107, 124  
*Czekanowskia capillaris*, 296  
  
*Dalbergia severnensis*, 297  
*Dammara borealis*, 299; *cliffwoodensis*, 299  
*Danthonia intermedia*, 469  
*Dasiophora fruticosa*, 30, 463  
*Dasyilirion Wheeleri*, 302, 303  
*Dasystephana affinis*, 463; *frigida*, 96; *Froelichii*, 96; *glauca*, 95, 468; *monticola*, 464; *Parryi*, 464; *Romanzovii*, 96  
*Dasystoma laevigata*, 28, 33, 35; *quercifolia*, 214  
*Datura*, 121; *ferox*, 127; *Stramonium*, 107, 121, 444; *Tatula*, 121  
*Daucus Carota*, 86, 360  
*Decodon verticillatus*, 73  
*Delphinium alpestre*, 101, 468; *Consolida*, 107, 121; *Menziesii*, 340; *Stephisagria*, 107, 127  
*Dendropanax*, 9; *cuneifolium*, 10; *filipes*, 9  
*Dentaria heterophylla*, 28, 35  
*Denticulatae*, 591, 592  
*Dermonema*, 194; *dichotomum*, 172



- Deschampsia alpicola*, 98, 469, 470;  
*caespitosa*, 93, 96, 98, 469; *curtifolia*,  
 96, 463  
*Desmodium illinoense*, 355  
*Dianthus barbatus*, 516  
*Dichromena latifolia*, 560, 566  
*Digitalis*, 115; *alba*, 116, 122, 123; *am-*  
*bigua*, 116, 122, 123; *Buxbaumi*, 122,  
 123; *canariensis*, 116, 122, 123, 124;  
*gloxiniaeflora*, 116, 122, 123; *gloxiniaeflora*  
*alba*, 117; *gloxiniaeflora rosea*, 116;  
*grandiflora*, 122, 123; *lanata*, 116, 122,  
 123; *lutea*, 122, 123; *macrantha*, 122,  
 123; *maculata Iveryana*, 116; *mon-*  
*strosa*, 122, 123; *purpurea*, 116, 122;  
*purpurea alba*, 122, 123; *purpurea*  
*maculata superba*, 122; *purpurea rosea*,  
 122, 123; *sibirica*, 116, 122, 123  
*Dilophozia*, 589  
*Dioscorea* sp., 214  
*Diospyros primaeva*, 297, 298; *rotundi-*  
*folia*, 298; *vera*, 297; *virginiana*, 28, 34,  
 559, 560  
*Diplophylleia albicans*, 602; *plicata* 602;  
*taxifolia*, 602  
*Diplophyllum albicans*, 590, 602, 615;  
*argenteum*, 613, 615; *imbricatum*, 613,  
 615; *ovatum*, 602, 615; *plicatum*, 602,  
 614; *taxifolium*, 602  
*Disporum majus*, 339  
*Dodecatheon Meadia*, 29, 32, 35, 356,  
 357; *puberulum*, 339  
 DODGE, B. O. The morphological rela-  
 tionships of the Florideae and the As-  
 comycetes, 157  
*Dodonaea angustifolia*, 303  
*Doryanthites cretacea*, 298  
 Douglas Lake, Michigan, The introduced  
 vegetation in the vicinity of, 511  
*Douglasia montana*, 101, 463, 464;  
*nivalis*, 101, 465  
*Draba*, 462; *alpina*, 102; *andina*, 96, 99,  
 462, 463; *aurea*, 463; *aureiformis*, 464;  
*chrysantha*, 464; *crassa*, 464; *crassifolia*,  
 464; *densiflora*, 462, 463; *fladnizensis*,  
 93, 467; *glacialis*, 94, 96; *lonchocarpa*,  
 98, 468; *nivalis*, 98, 102, 468; *oligo-*  
*sperma*, 96, 462, 463; *Parryi*, 468; *pec-*  
*tinata*, 99; *saximontana*, 464; *strepto-*  
*carpa*, 464, 470  
*Drosera filiformis Tracyi*, 560, 563, 567  
*Dryas*, 483; *Drummondii*, 462, 464, 483,  
 484; *integrifolia*, 483; *integrifolia can-*  
*escens*, 483; *integrifolia intermedia*,  
 483; *octopetala*, 462, 463, 483, 484,  
 490; *octopetala intermedia*, 483; *octo-*  
*petala argentea*, 483, 484; *octopetala*  
*hirsuta*, 483; *octopetala minor*, 483;  
*tomentosa*, 483  
*Drymocallis agrimonioides*, 485; *Con-*  
*vallaria*, 339; *glandulosa*, 101; *pseudo-*  
*rupestris*, 99, 471; *pumila*, 101; *rupe-*  
*stris*, 99  
*Drymoglossum*, 397  
*Dudresnaya*, 167, 176, 177, 194, 195,  
 196; *coccinea*, 173, 195; *purpurifera*,  
 195  
*Eatonia nitida*, 30, 35  
*Eichhornia*, 225  
*Elaeodendron marylandicum*, 298  
*Elaphomyces*, 182  
*Elephantella*, 472; *groenlandica*, 471, 472  
*Elettaria Cardamomum*, 107, 127  
*Elymus canadense*, 356  
*Endogone*, 157, 192  
*Epigaea repens*, 28, 33, 35, 414  
*Epilobium adenocaulon*, 76; *angusti-*  
*folium*, 517, 519; *coloratum*, 76;  
*hirsutum*, 75; *lineare*, 75, 76; *palustre*,  
 75; *palustre labradoricum*, 75; *palustre*  
*monticola*, 75; *strictum*, 76  
*Epipactis*, 143, 223, 224, 225, 231;  
*pubescens*, 230  
*Equisetum arvense*, 356  
*Erechtites hieracifolia*, 517  
*Erica cinerea*, 418; *Tetralix*, 416, 417  
 Ericaceae, 413  
*Erifonum flavum*, 100; *xanthum*, 100  
*Erigeron alpinum*, 94; *annuus*, 360;  
*canadensis*, 360, 517; *compositus*, 97,  
 462, 463; *expansus*, 15; *glabellus*, 470;  
*grandiflorus*, 102; *lanatus*, 102; *melano-*  
*cephalus*, 96; *multifidus*, 97, 99, 462,  
 463; *pedatus*, 99; *pinnatisectus*, 462,  
 464; *ramosus*, 354, 356; *simplex*, 96,  
 462, 463; *speciosus*, 339; *trifidus*, 97,  
 462, 463; *unalaschensis*, 102; *uniflorus*,  
 96  
*Eriocaulon decangulare*, 560, 566, 567  
*Eriogonum compositum*, 341; *flavum*,  
 100; *heracleoides*, 341; *niveum*, 341,  
 342; *tomentosum*, 563; *xanthum*, 100,  
 464  
*Eriophorum gracile*, 471; *polystachyum*,  
 471  
*Eriophyllum lanatum*, 341, 342  
*Eritrichium argenteum*, 99, 462, 464;  
*elongatum*, 99, 463, 464; *nanum*, 99;  
*villosum*, 99  
*Ernodea*, 12; *littoralis*, 12  
*Eryngium*, 359; *yuccifolium*, 356, 357, 359  
*Erysimum asperum*, 340  
*Erythrina Crista-galli*, 224; *flabelliformis*,  
 303  
*Erythrocoma*, 490, 491, 492; *affinis*, 492;  
*aliena*, 492; *arizonica*, 492; *australis*,  
 492; *canescens*, 493; *ciliata*, 490; *cin-*  
*erascens*, 492, 493; *companulata*, 491;  
*grisea*, 492; *tridentata*, 492  
*Erythronium grandiflorum*, 339  
*Erythrophyllum*, 173, 178, 194, 197;  
*delesserioides*, 173  
*Erythroxyllum Coca*, 107, 126  
*Eucalyptus attenuata*, 298; *Geinitzi*, 298;  
*latifolia*, 298; *Wardiana*, 298



- Eujungermannia*, 588  
*Eupatorium aromaticum*, 28, 32, 35;  
*capillifolium*, 560, 563; *coelestinum*,  
 28, 33, 35; *compositifolium*, 560, 563;  
*perfoliatum*, 358, 359; *purpureum*, 560;  
*rotundifolium*, 28, 32, 35, 560  
*Euphorbia*, 223, 230; *corollata*, 355, 357;  
*cyparissias*, 514; *hirsuta*, 512; *maculata*,  
 512; *palustris*, 224, 230; *procera*, 224,  
 230; *virgata*, 229  
*Euthamia grandiflora*, 340  
*Euvittaria*, 394, 395  
*Euxolus emarginatus*, 509  
 EVANS, A. W. Report on the Hepaticae  
 of Alaska, 577  
*Exoascus*, 170  
  
*Fagus grandifolia*, 213, 216, 219, 512, 559  
*Fallugia*, 496; *acuminata*, 496; *mexicana*,  
 496; *micrantha*, 496; *paradoxa*, 496  
 FARWELL, O. A. The correct name for  
 the hemlock spruce, 621  
*Fatsia japonica*, 222  
*Fegatella conica*, 585  
 Ferns and flowering plants of Nantucket,  
 The—XII, 71;—XIII, 411  
*Festuca brachyphylla*, 99, 463; *ingrata*,  
 469; *minutiflora*, 99, 464; *ovina*, 93, 96;  
*rubra*, 93, 469; *saximontana*, 96, 463,  
 469; *supina*, 93, 463, 464; *Thurberi*,  
 469, 470  
*Ficus Cecilensis*, 298; *crassipes*, 298;  
*daphnogenoides*, 298; *Krausiana*, 298;  
*ovatifolia*, 297  
*Fimbriaria tenella*, 613  
 FISHER, G. C. Seed development in the  
 genus *Peperomia*, 137, 221  
*Foeniculum vulgare*, 107, 126, 127  
*Fontainea grandifolia*, 297  
*Fragaria platypetala*, 339; *virginiana*, 356  
*Fraxinus americana*, 213, 219; *nigra*, 29,  
 36; *quadrangulata*, 28, 36  
*Frullania chilcootiensis*, 613, 615; *fran-*  
*ciscana*, 612, 615; *nisquallensis*, 590,  
 607, 612, 614, 615; *Tamarisci*, 614  
*Fucus*, 229  
  
*Gaillardia aristata*, 342  
*Galactinia*, 158; *succosa*, 170  
*Galega officinalis*, 107  
*Galium Aparine*, 339; *boreale*, 339; *sp.*  
 357; *uniflorum*, 214  
*Garcinia*, 222  
*Gaultheria procumbens*, 28, 33, 34, 36, 414  
*Gaylussacia baccata*, 419; *dumosa*, 212,  
 419, 421; *dumosa Bigeloviana*, 419;  
*frondosa*, 419  
*Geinitzia formosa*, 298  
*Gelsemium sempervirens*, 212  
*Geocalyx graveolens*, 595  
*Geoglossum*, 171, 180  
*Gentiana Andrewsii*, 359; *crinita*, 29, 36;  
*lutea*, 126; *oregana*, 339  
*Geranium viscosissimum*, 339  
*Geum*, 484, 490, 491, 494; *agrimoni-*  
*oides*, 484, 485; *album*, 485, 486;  
*album flavum*, 486; *aleppicum*, 488;  
*auranthacum*, 489; *calthifolium*, 494;  
*camporum*, 484; *canadense*, 484, 485,  
 486; *cercocarpoides*, 496; *ciliatum*,  
 491; *decurrens*, 486; *flavum*, 486;  
*florum*, 486; *geniculatum*, 488; *Gra-*  
*hami*, 492; *hirsutum*, 486; *intermedium*,  
 488; *laciniatum*, 484; *macrophyllum*,  
 487, 488; *macrophyllum* × *oregonense*,  
 489; *macrophyllum* × *rivale*, 489;  
*macrophyllum* × *strictum*, 489; *mexi-*  
*canum*, 488; *Meyerianum*, 484, 485,  
 486; *nutans*, 488; *oregonense*, 487;  
*oregonense* × *strictum*, 489; *perin-*  
*cisus*, 487; *pulchrum*, 489; *Rafi-*  
*nesquianum*, 488; *rivale*, 484, 488,  
 489, 490; *rivale* × *strictum*, 489;  
*rotundifolium*, 494; *scopulorum*, 487;  
*strictum*, 363, 486, 487, 488, 489;  
*triflorum*, 491; *urbanum*, 487, 488, 489;  
*vernum*, 484; *virginianum*, 484  
*Gigartina*, 173, 178  
*Ginkgo biloba*, 90  
 GLEASON, H. A., and McFARLAND, F. T.  
 The introduced vegetation in the vicin-  
 ity of Douglas Lake, Michigan, 511  
*Gleichenia delawarensis*, 297; *Saundersii*,  
 297; *Zippei*, 297  
*Gloiosiphonia*, 176, 177, 194  
*Glyceria nervata*, 358, 359, 360  
*Glycyrrhiza glabra*, 126  
*Gnomonia*, 158, 171; *erythrostroma*, 159  
*Gonianthes Lindeniana*, 23; *Sagraeana*, 23  
*Gormaniana debilis*, 101, 464  
*Graphis elegans*, 164  
*Griffithsia Bornetiana*, 167  
 GRIGGS, R. F. Observations on the  
 behavior of some species at the edges  
 of their ranges, 25; Observations on the  
 edge of the forest in the Kodiak region  
 of Alaska, 381  
*Grimaldia fragrans*, 612  
*Grindelia robusta*, 127  
*Grossularia hirtella*, 415  
*Gunnera*, 137, 138, 223; *macrophylla*, 137  
*Gymnadenia*, 149, 150; *conopsea*, 149  
*Gymnoascus*, 171, 193; *candida*, 159  
*Gymnocladus dioica*, 29, 35  
*Gymnomitrium concinatum*, 612; *coral-*  
*lioides*, 612; *crenulatum*, 612, 615;  
*obtusum*, 586, 615  
*Gyrostachys gracilis*, 33  
*Gyrothyra Underwoodiana*, 587, 615  
  
*Habenaria nivea*, 561  
*Halesia diptera*, 219  
 Haloragidaceae, 82  
*Hamamelis virginiana*, 214  
*Haplopappus marginatus*, 14  
*Haplopteris*, 393, 394, 395



- HARPER, R. M. The "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession, 209; A superficial study of the pine-barren vegetation of Mississippi, 551
- Harrimanella hypnoides, 467
- HARRIS, J. A. On the relationship between the number of ovules formed and the number of seeds developing in *Cercis*, 243; Further observations, 533
- Harveyella, 173, 174, 194, 197; mirabilis, 167, 172
- Havardia, 8
- Hecistopteris, 400; minima, 398; Werckleana, 399
- Hedera cecilensis, 298; cretacea, 298; Helix, 367, 368, 370, 371
- Hedyosmum, 232
- Helenium tenuifolium, 560
- Helianthus, 363; angustifolius, 561; annuus, 512; decapetalus, 362; divaricatus, 362; grosse-serratus, 358, 360; Maximiliani, 355; occidentalis, 355; scaberrimus, 355
- Heliopsis scabra, 355
- Helminthora, 167
- Helotium citrinum, 190
- Helvella, 179
- Hemlock spruce, The correct name for the, 621
- Hepaticae of Alaska, Report on the, 577
- Heracleum lanatum, 85, 86, 339
- Herberta adunca, 597, 601, 615
- Heteromallae, 592
- Heuchera cylindrica, 339; Hallii, 465; hispida, 356; parvifolia, 463
- Hibiscus aculeatus, 561
- Hicoria alba, 216, 219, 559; glabra, 211, 213
- Hieracium albiflorum, 339; paniculatum, 28, 35; Scouleri, 339; venosum, 28, 33, 35
- Hoffmannia aphylla, 56
- Hordeum jubatum, 512
- Houttuynia, 232
- HOWE, R. H., JR. The nomenclature of the genus *Usnea*, 373
- Hulsea carnosae, 465, 466
- Humaria granulata, 159; rutilans, 171
- Humulus Lupulus, 512
- Hydrangea arborescens, 28, 35
- Hydrastis canadensis, 109
- Hydnocystis, 182
- Hydrocotyle umbellata, 83
- Hyoscyamus muticus, 126; niger, 107, 125, 444; orientalis, 125
- Hypericum Drummondii, 29, 32, 35; fasciculatum, 560; sp. 359
- Hypocopra, 161, 183
- Hypopitys americana, 412; insignata, 413; lanuginosa, 412
- Hypoxis hirsuta, 358
- Ichmadophila aeruginosa, 159
- Ilex coriacea, 216; fastigiata, 414; glabra, 559, 567; myrtifolia, 560, 563, 567; opaca, 214, 216, 219, 559; severnensis, 298
- Illicium, 148; deletoides, 298
- Impatiens biflora, 339
- Inga Hystrix, 4; obovalis, 5
- Introduced vegetation in the vicinity of Douglas Lake, Michigan, The, 511
- Ionactis linariifolius, 212
- Iris, 149; cristata, 29, 35, 36; sibirica, 149; verna, 212; versicolor, 359
- Isnardia palustris, 74
- Isoetes Bolanderi, 474; paupercula, 474
- Isopyrum biternatum, 28, 35
- Isotria verticillata, 29, 34
- Iva xanthifolia, 512, 514
- Jacobinia jamaicensis, 16
- Jeffersonia diphylla, 109
- Juglans, 231
- Juncoides arcticum, 102, 471; arcuatum, 102, 471; hyperboreum, 102, 471; parviflorum, 470; saltuensis, 28, 32, 35; spicatum, 93, 94, 467, 470
- Juncus, 466; biglumis, 102, 471; castaneus, 93, 467, 470; Drummondii, 467, 470; Parryi, 467, 470; Roemerianus, 560, 563; sp. 357; triglumis, 93, 467, 470
- Jungermannia, 588; albicans, 602; albicans taxifolia, 602; atrovirens, 587; caespiticia, 613, 615; cochleariformis, 610; conchaefolia, 611; cordifolia, 587; gigantea, 611; lanceolata, 613; minuta, 588; nemorosa, 606; orcadensis, 588; purpurea, 610; saxicola, 613; setiformis, 613; sphaerocarpa, 613; trichophylla, 601; ventricosa, 613
- Jungermanniaceae, 586, 612
- Juniperus australis, 11; hypnoides, 298; lucayana, 11; scopulorum, 343
- Kalmia, 467; angustifolia, 414; glauca, 97; latifolia, 28, 33, 35, 214, 216, 413; microphylla, 97, 472, 473
- Kantia Trichomanis, 596
- Kerria, 331; japonica, 367, 370
- Kieseria, 20; cubensis, 19
- Kneiffia pumila, 82
- Koeleria cristata, 354, 356
- Koellia incana, 28, 35
- Krigia amplexicaulis, 356
- Kuhnistera pinnata, 212, 563
- KUNKEL, L. O. Physical and chemical factors influencing the toxicity of inorganic salts to *Monilia sitophila* (Mont.) Sacc., 265
- Kuntzia, 496, 497; tridentata, 495
- Laboulbenia chaetophora, 159
- Lachemilla, 319, 320, 321; Bourgeau,



- 321; domingensis, 321; ocreata, 321; orbiculata, 320, 321; orizabensis, 321; Pringlei, 321; procumbens, 321; Schiedeana, 321; venusta, 320
- Lachnea, 169, 180, 186; abundans, 163, 165, 189, 193; cretea, 159, 160, 165, 167, 172, 189, 193; leucotricha, 189; melaloma, 166, 193; scutellata, 159, 165, 171, 181, 185, 186, 189, 193, 194; stercorea, 159, 164, 181, 185, 186, 189, 192, 193
- Lacistema, 232
- Lactuca canadensis, 360
- Lappula ciliata, 341; deflexa, 512, 514, 515, 518
- Larix, 153; sibirica, 222
- Lasiobolus, 195; equinus, 159, 160, 193, 194; pulcherrimus, 193, 194
- Lasiocroton Fawcettii, 16; **Harrisii**, 16
- Lathyrus palustris, 356
- Laurus Cinnamomum, 126; Hollickii, 297; plutonia, 297; proteaefolia, 297
- Laurophyllum angustifolium, 297; elegans, 297
- Lecanora subfusca, 166
- Lechea racemulosa, 28, 36
- Ledum glandulosum, 467, 472, 473
- Leguminosites canavalioides, 297; coronilloides, 297; omphalobioides, 297
- Lejolisia, 160
- Lemna, 231
- Leotia, 171; chlorocephala, 159
- Lepachys pinnata, 355, 357, 360
- Lepidium apetalum, 512; virginicum, 512, 514, 515, 516, 517, 518, 520
- Lepidozia, 599, 600; filamentosa, 598, 600, 615; Pearsoni, 601; reptans, 598, 600; sandvicensis, 598, 599, 600, 601, 614, 615; setacea, 601, 614
- Leptandra virginica, 109
- Leptasea austromontana, 96, 466; bronchialis, 96, 99; chrysantha, 98, 468; flagellaris, 467; Hirculus, 98, 468, 469; Van Bruntiae, 99, 469
- Leptilon canadense, 561
- Leptinae, 377
- Lespedeza capitata, 355, 360
- Levisticum officinale, 126
- Liagora, 167
- Liatris scariosa, 354, 361; spicata, 358, 359, 360
- Lichen articulatus, 376, 377; barbatus, 376, 377; floridus, 374; hirtus, 374, 375; plicatus, 375
- Ligusticum Porteri, 472; scoticum, 85
- Lilium, 229, 231; canadense, 356
- Linum floridanum, 561; intercursum, 415
- Liquidambar Styraciflua, 219, 559, 563
- Liriodendron Tulipifera, 41, 46, 216, 219, 559
- Liriodendropsis constricta, 297
- Lithospermum canescens, 355; ruderale, 341
- Lloydia serotina, 90, 93, 95, 470
- Lobelia inflata, 107, 127; leptostachys, 29, 36; puberula, 29, 35; spicata, 356; syphilitica, 359
- Lomatium Grayi, 341; triternatum, 340
- Lonicera japonica, 367
- Lophiola aurea, 560, 563, 566
- Lophocolea cuspidata, 595, 615
- Lophozia, 588, 589; attenuata, 613; Floerkei, 587; guttulata, 613; heterocolpa, 613; incisa, 587; inflata, 587; lycopodioides, 613; minuta, 588; obtusa, 613, 615; porphyroleuca, 587; quadriloba, 613; quinquedentata, 588; ventricosa, 613
- Ludwigia alternifolia, 74; pilosa, 561
- Lupinus albus, 267; microcarpus, 343; Piperi, 341
- Lychnis alba, 514, 518
- Lycium carolinianum, 12; halimifolium, 367, 368, 369
- Lyopodiales, 51
- Lycopodiaceae, 51
- Lycopodium, 51, 55; alopecuroides, 561; arbuscula, 58; capillaceum, 54; cernuum, 51, 53; clavatum, 29, 32, 35, 36, 38, 51; compactum, 53; complanatum, 29, 33, 35, 36, 37; crassifolium, 54; curvatum, 53; digitatum, 57; erubescens, 51, 52, 53; Haleakalae, 51, 53; javanicum, 52; lucidulum, 28, 33, 35, 36, lucidulum porophilum, 28, 34, 36; macrostachys, 55; Menziesii, 58; nudum, 56; nutans, 51, 54; obscurum, 29, 35, 36, 38; pachystachyon, 54; pachystachyon phyllanthon, 54; pennigerum, 58; Phlegmaria, 51, 53; phyllanthum, 51, 54, 55; polytrichoides, 52, 56; Sabinae-facie, 57; sargassifolium, 52; selaginoides, 57; serratum, 51, 52, 58; serratum dentatum, 52; serratum subintegrum, 52; squarrosum, 54; suberectum, 53; sulcinervium, 52; varium, 52; venustum, 52, 55; venustum herpeticum, 55; volubile, 52, 55
- Lysias orbiculata, 30
- Lysimachia quadrifolia, 28, 34
- Lythraceae, 73
- Lythrum Salicaria, 73; Salicaria tomentosum, 73
- Machaeranthera canescens, 342; Pattersoni, 465
- Macronema Lyallii, 465; pygmeum, 464
- Madotheca navicularis, 611; platyphylla, 613
- Magnolia acuminata, 219; Boulayana, 298; capellinii, 298; glauca, 216, 559;



- grandiflora*, 213, 216, 219, 559, 563; *Hollicki*, 298; *Lacoeana*, 298; *longipes*, 298; *macrophylla*, 219, 559, 563, 566; *obtusata*, 298; *pyramidata*, 219; *tenuifolia*, 298  
*Mairania alpina*, 102  
*Malva rotundifolia*, 514, 516  
*Marchantia*, 333; *polymorpha*, 585, 615  
*Marchantiaceae*, 585  
*Marsupella emarginata*, 586; *sphacelata*, 612  
Maryland, Contributions to the Mesozoic flora of the Atlantic coastal plain, —X., 295  
*Mastigobryum Didrichsenii*, 597; *Pearsoni*, 596; *deflexum*, 598  
*Maytenus phyllanthoides*, 12  
McFARLAND, F. T., GLEASON, H. A., and, Introduced vegetation in the vicinity of Douglas Lake, Michigan, The, 511  
Mechanical tissue development in certain North American vines, 365  
Medicinal plants, The propagation of, 105  
*Meibomia angustifolia*, 19; *Cowellii*, 19  
*Melampyrum lineare*, 29, 32, 35  
*Melanospora*, 161, 183, 184  
*Melastomaceae*, 74  
*Melilotus alba*, 360  
*Mentha canadensis borealis*, 339  
*Mentzelia integrifolia*, 342; *laevicaulis*, 342  
*Mertensia alpina*, 466, 467, 471; *Bakeri*, 100, 468; *brevistyla*, 468, 471; *Drummondii*, 102; *lanceolata*, 100; *lateriflora*, 100, 468; *nivalis*, 100; *oblongifolia*, 339; *Parryi*, 100, 468; *viridula*, 100, 468  
*Mesinae*, 374  
Mesozoic flora of the Atlantic coastal plain, Contributions to the, X.—Maryland, 295  
*Mesophylla orcadensis*, 588  
*Metzgeriaceae*, 585  
*Metzgeria conjugata* 586, 590, 593, 607; *hamata*, 612, 614, 615; *pubescens*, 586  
*Micranthes arnoglosa*, 98, 468; *brachypus*, 468; *crenatifolia*, 98, 469; *foliolosa*, 102; *hieracifolia*, 94, 98, 469; *nivalis*, 94, 98, 102; *rhomboidea*, 98, 467; *Rydbergii*, 98, 468; *stellaris*, 468; *Vreelandii*, 468, 469  
*Microglossum*, 180  
*Microlepidozia*, 614  
MILLER, F. A. The propagation of medicinal plants, 105  
*Mimosa arborea*, 7; *biuncifera*, 303; *circinalis*, 3; *filicifolia*, 7; *Saman*, 8; *Unguis-cati*, 3  
*Mitchella repens*, 214  
*Mitrulea*, 180  
*Monarda*, 109; *mollis*, 356, 363  
*Monilia sitophila* (Mont.) Sacc., Physical and chemical factors influencing the toxicity of inorganic salts to, 265  
*Monilia sitophila*, 266, 268, 269, 272, 275, 277, 281, 283, 284, 286, 289  
*Monotropaceae*, 412  
*Monotropa*, 149, 150; *Hypopitys*, 149; *uniflora*, 214, 215, 412  
*Morchella*, 169  
*Moriconia americana*, 298  
Morphological relationships of the Florideae and the Ascomycetes, The, 157  
*Morus*, 148, 149, 150; *alba*, 146, 147, 148  
Mosaic disease of tobacco, A review of investigations of the, together with a bibliography of the more important contributions, 435  
*Mucor*, 179; *Mucedo*, 286, 290  
*Muscaria adscendens*, 93, 467; *caespitosa*, 98, 102, 468; *delicatula*, 98, 468; *micropetala*, 98, 468; *monticola*, 98, 469  
*Muscus clavatus*, 57  
*Mylia anomala*, 595; *Taylori*, 595  
*Myosotis alpestris*, 93, 466, 467  
*Myrica cerifera*, 560; *inodora*, 566; *longa*, 298; *pumila*, 560  
*Myriophyllum humile*, 82; *tenellum*, 82  
*Myrsine borealis*, 298; *Gaudini*, 298  
Nantucket, The ferns and flowering plants of,—XII, 71; XIII, 411  
*Napaea dioica*, 29, 34, 38  
*Nardia compressa*, 613, 615; *Geoscyphus*, 613, 615; *haematosticta*, 613; *obovata*, 613, 615; *scalaris*, 587  
*Nelumbites primaeva*, 297  
*Nemalion*, 167, 171, 172, 174, 194, 195  
*Nepeta Cataria*, 514, 515, 516, 518, 519  
New or notable species of *Amaranthus*, 505  
*Nicandra physaloides*, 125  
Nomenclature of the genus *Usnea*, The, 373  
North American ferns, Notes on two, 307  
Notes on Rosaceae—VII, 319; VIII, 483  
Notes on two North American ferns, 307  
*Nyssa biflora*, 559, 560; *Ogeche*, 563; *sylvatica*, 87, 211, 219, 559, 563; *uniflora*, 559, 563  
Observations on the behavior of some species at the edges of their ranges, 25  
Observations on the edge of the forest in the Kodiak region of Alaska, 381  
*Oedocephalum albidum*, 290  
*Oedogonium*, 167  
*Oenothera*, 229, 366, 371; *albida*, 81; *biennis*, 76, 77, 78, 80, 355; *biennis parviflora*, 79; *canovirens*, 78; *cruciata*, 80; *Lamarckiana*, 80, 81, 366; *muricata*,



- 76, 77, 80; Oakesiana, 78, 80; rubrinervis, 366; *stenopetala*, 79, 80; *strigosa*, 77; *subulifera*, 78
- Oetosis, 395, 396, 397
- Onagraceae, 74
- Onoclea inquirenda, 297; *sensibilis*, 618; *Struthiopteris*, 617
- Onoclea sensibilis L., Branched cells in the prothallium of, 617
- Onosmodium, 497
- On the relationship between the number of ovules formed and the number of seeds developing in *Cercis*, 243; Further observations, 533
- Opulaster pauciflorus, 339
- Opuntia, 71, 72; *Opuntia*, 72; *polyacantha borealis*, 343; *vulgaris*, 72, 212, 214
- Orchis, 150; *latifolia*, 149; *Morio*, 149
- Oreobroma pygmaea, 463
- Oreocarya sericea, 342
- Oreochrysum Parryi, 468, 471
- Oreoxis alpina, 101, 464; *Bakeri*, 101, 464; *humilis*, 101, 464
- Origin of the alpine flora. Phytogeographical notes on the Rocky Mountain region, II, 89
- Ornithogalum, 229
- Osmanthus americana, 212, 214, 216
- Osmunda cinnamomea, 561; *delawarensis*, 297
- Ostrya virginiana, 214, 219
- Oxalis stricta, 358
- Oxycoccus, 472; *macrocarpus*, 426; *Oxycoccus*, 426
- Oxydendrum arboreum, 28, 33, 35, 37, 214, 219, 559, 562, 563
- Oxypolis filiformis, 560, 567; *rigidior*, 356, 359, 363
- Oxyria digyna, 93, 465, 466, 467
- Pallavicinia Flotowiana, 586, 615; *hiberica*, 586
- Panicularia acutiflora, 30; *elongata*, 30, 36; *pallida*, 30
- Panicum capillare, 512; *dichotomum*, 561; *nitidum*, 357; *polyanthes*, 28, 35; *Scribnerianum*, 356; *sp.*, 214, 357; *stipitatum*, 30, 35; *virgatum*, 354
- Papaver somniferum, 107
- Parnassia caroliniana, 29, 36
- Paronychia pulvinata, 101, 464
- Parrya macrocarpa, 98; *platycarpa*, 98, 464
- Parthenium integrifolium, 356, 357, 359
- Passiflora incarnata, 107; *lutea*, 29, 34, 38
- Pastinaca sativa, 85
- Pedicularis canadensis, 356; *flammea*, 102; *lanata*, 102; *lanceolata*, 29, 35; *Oederi*, 102; *Parryi*, 470; *racemosa*, 470
- Pellaea ternifolia, 308
- Pellia endiviaefolia, 612; *epiphylla*, 612; *Fabroniana*, 612; *Neesiana*, 586
- Penaea, 223
- Penicillium, 170, 173, 178; *crustaceum*, 289; *glaucum*, 290
- Pentstemon confertus, 339; *Hallii*, 464, 465; *Harbourii*, 465; *stenosepalum*, 468
- Peperomia, Seed development in the genus, 137, 221
- Peperomia, 137, 138, 140, 141, 146, 148, 150, 151, 152, 154, 156, 221, 222, 223, 224, 225, 226, 229, 230, 231, 232, 233, 234; *arifolia*, 140, 143, 223, 224; *blanda*, 138, 139, 154, 225; *Fraseri*, 153; *Fraseri resediflora*, 138, 139, 153, 225; *galioides*, 138, 139, 155, 225; *hispidula*, 137, 142, 223; *humilis*, 139; *ionophylla*, 140; *Langsdorffii*, 138, 139, 155, 225; *metallica*, 138, 139, 152, 153; *Ottoniana*, 223; *pellucida*, 137, 138, 142, 144, 223; *pulchella*, 145; *reflexa*, 138, 139, 145, 146, 150, 151, 152, 154, 155, 225; *resedaeflora*, 139, 153; *scandens*, 138, 150, 151, 225; *Sintenisii*, 143, 223, 224; *urocarpa*, 140; *verticillata*, 138, 139, 145, 147, 148, 149, 151, 152, 154, 225
- Peronospora, 160
- Persea Borbonia, 214
- Pertusaria communis, 159
- Petalostemum purpureum, 355
- Petrocelis, 176
- Petroselinum hortense, 84
- Petunia nyctaginifolia, 444
- Phacelia alpina, 100, 464, 471; *ciliosa*, 470; *dubia*, 29, 32, 35; *heterophylla*, 100, 342; *Lyallii*, 99, 465; *sericea*, 99, 464, 470
- Phallus, 179
- Phaseolus, 256, 548; *multiflorus*, 224; *vulgaris*, 243, 548
- Philadelphus Lewisii, 341
- Phippsia algida, 97, 474
- Phleum alpinum, 93, 94, 469, 471; *pratense*, 360, 514, 515, 516, 518, 519, 520
- Phlox, 462; *caespitosa*, 100, 462, 463; *condensata*, 100, 462, 464; *glaberrima*, 356; *pilosa*, 356, 358; *stolonifera*, 29, 32, 34, 36, 38
- Phoradendron flavescens, 560
- Phragmites communis, 359
- Phycomyces nitens, 286
- Phyllactinia corylea, 159
- Phyllanthus, 230
- Phyllodoce, 467; *coerulea*, 98; *empetiformis*, 98, 472, 473; *glanduliflora*, 98, 472, 473
- Physalis virginiana, 354
- Physaria Geyeri, 342
- Physical and chemical factors influencing the toxicity of inorganic salts to *Monilia sitophila* (Mont.) Sacc., 265
- Physiotium cochleariforme, 610
- Physostegia virginiana, 358



- Physma compactum*, 192  
 Phytogeographical notes on the Rocky Mountain region, II. Origin of the alpine flora, 89; III. Formations in the alpine zone, 459  
*Picea alba*, 628; *balsamea*, 628; *canadensis*, 621, 628, 629; *mariana*, 628; *nigra*, 628; *sitchensis*, 381, 580  
*Pimpinella Anisum*, 107, 127  
 Pine-barren vegetation of Mississippi, A, superficial study of, 551  
*Pinus*, 153; *alba*, 628; *americana*, 628; *balsamea*, 623, 624, 625, 626, 627, 628; *canadensis*, 621, 622, 623, 625, 626, 627, 628, 629; *contorta*, 343; *echinata*, 211, 559, 563; *Elliottii*, 559, 563, 564; *glabra*, 219, 559, 563, 565; *mariana*, 628; *nigra*, 628; *palustris*, 211, 551, 559, 561; *ponderosa*, 342; *rigida*, 29, 32, 33, 35; *serotina*, 209, 563; *Taeda*, 219, 559, 563, 565; *virginiana*, 29, 33, 35  
*Piper*, 137, 138, 140, 141, 153, 155, 156, 229, 231, 232; *Betle monoicum*, 156; *medium*, 156; *nigrum*, 126; *tuberculatum*, 138, 155, 156, 233; *umbellata*, 156  
*Pistia Nordenskioldi*, 298  
*Pitcheria galactioides*, 212  
*Pithecolobium*, 2; *arboreum*, 3, 7; *asplenifolium*, 3, 6; *bahamense*, 2, 4; *Berterianum*, 3, 8; *brevifolium*, 8; *calliandrifolium*, 4; *circinale*, 2, 3; *discolor*, 2, 4; *filicifolium*, 7; *guadalupense*, 2, 4; *guantanamense*, 3, 7; *Hystrix*, 2, 4; *latifolium*, 8; *mucronatum*, 3; *nipense*, 3, 6; *obovale*, 2, 5; *pinetorum*, 2, 6; *prehensile*, 3, 8; *Saman*, 3, 8; *savannarum*, 2, 4; *tortum*, 3, 8; *trinitense*, 3, 7; *truncatum*, 2, 5; *Unguis-cati*, 2, 3; *vincentis*, 8  
*Plagiochila*, 589, 591, 594; *alaskana*, 590, 591, 592, 594, 595, 615; *asplenioides*, 590; *fragilis*, 592, 593; *Fryei*, 593, 594, 595, 615; *oxyphylla*, 592, 593; *pachyloma*, 592, 593; *renitens*, 591, 592; *trapezoidea*, 591, 592  
*Plantago lanceolata*, 514, 515; *major*, 512, 514, 515, 516, 518, 519  
*Platanus*, 297; *Heerii*, 297  
*Pleuroschisma Pearsoni*, 596  
*Pleurozia*, 610; *cochleariformis*, 610; *conchaefolia*, 611; *gigantea*, 611; *purpurea*, 610, 611, 614, 615, 616  
*Poa*, 469; *alpicola*, 470; *alpina*, 93, 94, 467; *annua*, 515; *arctica*, 96, 99, 467; *Buckleyana*, 469; *cenisia*, 93, 96, 467; *compressa*, 356, 357, 363, 514, 515, 516, 518, 520; *crocata*, 100, 101, 463; *epilis*, 464, 469; *Grayana*, 470; *leptocoma*, 469, 471; *Lettermannii*, 101, 463, 464; *longiligula*, 469; *Pattersonii*, 100, 463, 464; *pratensis*, 360, 512, 514, 515, 516, 518, 519, 520, 521; *pudica*, 99, 470; *reflexa*, 471; *rupicola*, 101, 463; *Sheldoni*, 470  
 "Pocosin" of Pike County, Alabama, and its bearing on certain problems of succession, The, 209  
*Podostemon*, 229  
*Podozamites Knowltoni*, 297; *lanceolatus*, 296; *marginatus*, 296  
*Polemonium*, 466; *Brandegei*, 101, 468; *confertum*, 101, 465, 468, 470; *delicatum*, 99, 466; *Grayanum*, 101; *humile*, 96; *mellitum*, 101, 470; *micranthum*, 343; *parviflorum*, 99, 469; *pulcherrimum*, 96, 99, 466, 467; *speciosum*, 101, 465, 470; *viscosum*, 101, 466, 468, 471  
*Polygala cruciata*, 561; *cymosa*, 560, 566; *ramosa*, 560, 567  
*Polygonatum biflorum*, 214  
*Polygonum amphibium Hartwrightii*, 360; *arifolium*, 32, 35; *aviculare*, 512, 514, 515, 518, 520; *convolvulus*, 514, 515, 517, 518, 519; *erectum*, 512; *Persicaria*, 514, 515, 518; sp. 356  
*Polyides*, 167, 173, 176  
*Polypodium*, 391; *polypodioides*, 212, 214  
*Polysiphonia*, 167, 174  
*Polystigma*, 158, 171, 191  
*Populus balsamifera*, 381, 580; *deltoides*, 359; *grandidentata*, 511; *stygia*, 298; *tremuloides*, 29, 36; *trichocarpa*, 338, 340  
*Porella*, 608; *navicularis*, 611, 615; *platyphylla*, 613; *rivularis*, 612; *Roellii*, 612, 615  
*Poronia punctata*, 159  
*Porteranthus stipulatus*, 29, 35  
*Portlandia*, 21; *coccinea*, 21, 23; *coriacea*, 23; *daphnoides*, 21, 23, 24; *domingensis*, 21, 24; *elliptica*, 21, 22; *grandiflora*, 21, 22; *gypsophila*, 23; *Harrisii*, 21, 22; *involuta*, 21, 22; *Lindeniana*, 21, 23; *longiflora*, 23; *nitens*, 21, 22; *pendula*, 21, 23; *sessilifolia*, 21; *uliginosa*, 21, 22  
*Portulaca oleracea*, 517  
*Potamogeton alpinus*, 474  
*Potentilla*, 92, 495; *arguta*, 485; *decurrens*, 100; *diversifolia*, 100, 470; *emarginata*, 102; *glaucophylla*, 470; *Macounii*, 464; *minutiflora*, 101; *minutifolia*, 464; *modesta*, 98; *nipharga*, 96, 464; *nivea*, 90, 92, 93, 96, 98, 464; *paucijuga*, 464; *perdissecta*, 100; *quinquefolia*, 96, 98, 462, 463; *Robbinsiana*, 92; *rubripes*, 470; *saximontana*, 101; *tenerrima*, 101, 464; *uniflora*, 93, 102; *villosa*, 93, 102  
*Poteridium*, 322; *annuum*, 322, 323; *occidentalis*, 323  
*Poterium*, 323; *annuum*, 323; *Sanguisorba*, 323; *spinosum*, 323



- Preissia hemisphaerica*, 585; *quadrata*, 585  
*Primula angustifolia*, 100, 467, 470; *Broadheadae*, 100; *farinosa*, 90; *Parryi*, 465, 470, 472  
*Prionitis*, 194, 197; *Lyallii*, 174  
 Propagation of medicinal plants, The, 105  
*Proserpinaca palustris*, 82  
*Prosopis velutina*, 303  
*Protophylocladus lobatus*, 297; *sub-integrifolius*, 297  
*Protophyllum*, 296, 297; *multinerve*, 297; *Sternbergii*, 297  
*Prunus americana*, 362; *caroliniana*, 214; *demissa*, 340; *serotina*, 213; *umbellata*, 214  
*Psedera quinquefolia*, 363, 366, 369  
*Pseudocymopterus montanus*, 100; *purpureus*, 471; *Tidestromii*, 100, 464  
*Pseudopteryxia anisata*, 465; *Hendersonii*, 466  
*Pseudotsuga taxifolia* in arid parts of Washington, Slope exposure as a factor in the distribution of, 337  
*Pseudotsuga taxifolia*, 337, 338, 339, 340, 343, 344  
*Psilotaceae*, 56  
*Psilotum*, 56; *complanatum*, 56, 57; *nudum*, 56; *oahuensis*, 56; *triquetrum*, 56  
*Psoralea Onobrychis*, 29, 36  
*Psychotria*, 11; *ligustrifolia*, 11; *pulverulenta*, 11; *Sulzneri*, 11; *undata*, 11  
*Pteridium aquilinum*, 212  
*Pteridophyta* of the Hawaiian Islands, A taxonomic study of the,—IV, 51  
*Pteris*, 395, 396, 397; *lanceolata*, 397; *lineata*, 393, 394, 395, 397; *piloselloides*, 397; *scolopendrina*, 394  
*Pteropsis*, 397  
*Ptilidium californicum*, 601, 615; *ciliare*, 602; *pulcherrimum*, 602  
*Ptilimnium capillaceum*, 84  
*Ptiloria exigua*, 342  
*Puccinia Helianthi*, 267  
*Pulsatilla*, 490  
*Purshia*, 331, 496, 497  
*Pustularia vesiculosa*, 169  
*Pycnanthemum virginianum*, 356, 363  
*Pyrenula*, 191  
*Pyrethrum cinerarifolium*, 126  
*Pyrola americana*, 411, 415; *chlorantha*, 411, 415; *elliptica*, 29, 33, 34; *rotundifolia*, 29, 32, 34; *uliginosa*, 472  
*Pyrolaceae*, 411  
*Pyronema*, 158, 160, 161, 163, 164, 166, 167, 169, 171, 179, 180, 181, 184, 186, 188, 190, 192, 193, 194, 196; *confluens*, 159, 190  
*Pyrus coronaria*, 362  
*Quamasia hyacinthina*, 29, 35  
*Quercus alba*, 213, 219; *aquatica*, 214; *arkansana*, 214; *Catesbaei*, 211, 559, 563, 566; *cinerea*, 211, 559, 563; *falcata*, 559; *geminata*, 559, 563; *laurifolia*, 213, 559; *Margaretta*, 211, 214; *marylandica*, 211, 214, 559, 563; *Michauxii*, 559; *microcarya*, 214; *minor*, 29, 34, 38; *Morrisoniana*, 298; *myrtifolia*, 214; *nigra*, 214, 219, 559; *oblongifolia*, 303; *Phellos*, 559; *Prinus*, 29, 33, 35; *pumila*, 563, 566; *rubra*, 219; *severnensis*, 298; *sp.* 214; *stellata*, 211, 559; *velutina*, 213; *virginiana*, 559  
*Quillaja Saponaria*, 126  
*Radiovittaria*, 391, 393, 397, 400  
*Radula arctica*, 606, 607, 613, 615; *Bolanderi*, 606, 607, 609, 615; *cochleariformis*, 610; *complanata*, 613; *Krausei*, 613; **polyclada**, 607, 608, 609, 610, 615; *prolifera*, 609, 610; *spicata*, 607  
*Ramona incana*, 341  
*Ranunculus*, 466; *adoneus*, 101, 473; *affinis*, 96, 472; *alismaefolius*, 473; *eximius*, 473; *glaberrimus*, 339; *hyperboreus*, 97, 467; *Macauleyi*, 98, 468; *nivalis*, 98; *pedatifidus*, 96; *pygmaeus*, 93, 467; *saxicola*, 468; *stenolobus*, 101, 472, 473  
*Raritania gracilis*, 298  
 Relationship between the number of ovules formed and the number of seeds developing in *Cercis*, On the, 243; Further observations, 533  
 Report on the Hepaticae of Alaska, 577  
 Review of investigations of the mosaic disease of tobacco, together with a bibliography of the more important contributions, A, 435  
 Revision of the genus *Vittaria* J. E. Smith, A. I. The species of the subgenus *Radiovittaria*, 391  
*Rhamnites apiculatus*, 298  
*Rhexia Alifanus*, 560, 565, 567; *glabella*, 567; *lutea*, 561; *virginica*, 74  
*Rhodiola*, 466; *integrifolia*, 96, 99, 467; *polygama*, 99, 468; *rosea*, 96  
*Rhododendron maximum*, 28, 29, 30, 32, 35, 41  
*Rhodotypus*, 331  
*Rhus copallina*, 560, 563; *glabra*, 363, 560, 563; *glabra occidentalis*, 341; *mollis*, 303; *radicans*, 214; *Toxicodendron*, 341, 363; *Toxicodendron radicans*, 366, 368  
*Ribes aureum*, 340; *montigenum*, 465; *parvulum*, 465, 466  
*Riccardia*, 599, 601; *latifrons*, 585; *major*, 612, 615; *multifida*, 586, 615  
*Riccia crystallina*, 333; *Frostii*, 333; *natans*, 333



- Ricciocarpus natans* (L.) Corda, The appearance of polar bodies in the spermatogenous tissue of, 333  
*Ricciocarpus natans*, 333, 335  
*Ricinus*, 230; *communis*, 107  
*Robinia*, 548  
 ROBINSON, W. J. A taxonomic study of the Pteridophyta of the Hawaiian Islands—IV, 51  
*Roripa Nasturtium*, 339  
 Rosaceae, Notes on, VII, 319; VIII, 483  
*Rosa humilis*, 354, 357, 363; *polyantha*, 367, 370  
*Rubus idaeus aculeatissimus*, 517; *nigrobaccus*, 560; *occidentalis*, 363, 367, 370; *odoratus*, 29, 34, 38; sp. 363  
*Rudbeckia hirta*, 355, 366, 367, 512  
*Rumex Acetosella*, 515, 516, 518, 519, 520  
*elongatus*, 514, 515, 516, 518  
 RYDBERG, P. A. Notes on Rosaceae—VII, 319; VIII, 483; Phytogeographical notes on the Rocky Mountain region, II. Origin of the alpine flora, 89; III. Formations in the alpine zone, 459  
*Rydbergia Brandegei*, 101; *grandiflora*, 101, 469, 470  
*Rynchospora axillaris*, 561; *Baldwinii*, 561; *Chapmani*, 560; *corniculata*, 561; *cymosa*, 1; *elongata*, 2; *glomerata*, 30, 36; *jamaicensis*, 1; *polyphylla*, 2; *semiplumosa*, 561  
*Sabalites magothiensis*, 298  
*Sabbatia angularis*, 561; *campanulata*, 560; *decandra*, 567; *gentianoides*, 567; *macrophylla*, 560, 563, 567  
*Saccobolus*, 193  
*Sagina nivalis*, 97, 468; *saginooides*, 467  
*Sagittaria lancifolia*, 561  
*Salix*, 231, 472; *alexensis*, 102, 473; *amygdaloides*, 29, 35; *anglorum*, 99; *arbusculoides*, 102, 473; *arctica*, 99; *Barrattiana*, 102, 473; *cascadensis*, 99, 467, 468; *chlorophylla*, 95, 472; *Dodgeana*, 99, 467, 469; *Drummondiana*, 102, 473; *flexuosa*, 298; *glaucophylla*, 230; *glauca*, 95; *glaucops*, 95, 99, 472; *Lesquereuxii*, 296, 298; *longifolia*, 359; *monticola*, 472; *nigra*, 559; *nivalis*, 98, 467, 468; *petrophila*, 467; *phyllicifolia*, 95; *pseudolapponum*, 99, 468; *reticulata*, 93, 98; *retusa*, 99; *saximontana*, 98, 467, 472; *Scouleriana*, 338  
*Salsola Kali tenuifolia*, 517  
*Sambucus canadensis*, 362; *glauca*, 339; *pubens*, 29, 34; *racemosa*, 517  
*Sanguinaria*, 548  
*Sanguisorba*, 322, 323; *canadensis*, 322; *latifolia*, 322; *media*, 322; *Menziesii*, 322; *microcephala*, 322; *officinalis*, 322; *sitchensis*, 322  
*Sanicula canadensis*, 83; *marylandica*, 83; sp. 214  
*Santalum album*, 126  
*Sapotacites Knowltoni*, 298  
*Saprolegnia mixta*, 290  
*Sarcocolla*, 223  
*Sarcopoterium*, 323  
*Sarcoscyphus sphacelatus*, 613  
*Sarracenia flava*, 563, 566; *psittacina*, 561, 563, *rubra*, 566; *Sledgei*, 560, 563, 566  
*Sassafras acutilobum*, 296, 297; *varifolium*, 560, 563  
*Satureja Acinos*, 516  
*Sauteria alpina*, 612  
*Saururus*, 141, 229, 232; *cernuus*, 561  
*Saxifraga*, 466; *cernua*, 94, 98, 467; *debilis*, 98, 468; *pennsylvanica*, 29, 35; *rivularis*, 98, 102, 468; *simulata*, 98; *virginiensis*, 29, 33, 35  
*Scapania albescens*, 603; *Bolanderi*, 602, 615; *cordifolia*, 577, 603, 604, 605, 615; *curta*, 613; *dentata*, 603, 604, 605; *imbricata*, 613; *irrigua*, 606; *nemorosa*, 606, 615; *paludosa* 605; *paludosa papillosa*, 603, 605; *planifolia*, 616; *uliginosa*, 605, 606, 615; *umbrosa*, 606, 615; *undulata*, 603, 606  
*Schizonotus discolor*, 339  
*Schoenocaulon officinale*, 107, 127  
*Scilla*, 224; *maritima*, 126  
*Scinaia*, 177  
*Scirpus caespitosus*, 472; *cubensis*, 1; *lineatus*, 359; *pauciflorus*, 472  
*Scleria Baldwinii*, 561  
*Scleroderma*, 179  
*Scutellaria galericulata*, 29, 35; *grandiflora*, 341, 342; *lateriflora*, 107, 339  
*Sebastiania ligustrina*, 214  
*Secale cereale*, 516, 518, 520  
*Securinega*, 230  
*Sedum acre*, 514; *stenoperalum*, 339, 462, 463  
 Seed development in the genus *Peperomia*, 137, 221  
*Selaginella*, 55, 57; *arbuscula*, 58, 59; *deflexa*, 57, 58; *densa*, 465, 466; *flabellata*, 58, 59; *Menziesii*, 58, 59; *parvula*, 59; *Springii*, 58, 59  
 Selaginellaceae, 57  
*Senecio*, 466; *amplectens*, 471; *atratus*, 472; *aurens*, 97; *Balsamitae*, 358, 359; *carthamoides*, 465; *crocatius*, 468; *cymbalarioides*, 97, 467; *Fremontii*, 465, 466; *Harbourii*, 464; *Holmii*, 101, 468; *hydrophilus*, 339; *invenustus*, 465; *lugens*, 102; *Nelsonii*, 464; *petrocallis*, 101, 464, 466; *pseudaureus*, 470; *Porteri*, 101; *Purshianus*, 463; *Soldanella*, 101, 468; *taraxacoides*, 101, 468  
*Sequoia ambigua*, 298; *heterophylla*, 298; *Reichenbachii*, 298



- Serenoa*, 563; *serrulata*, 559, 566  
*Sericocarpus asteroides*, 29, 33, 35  
*Setaria viridis*, 514, 515, 516  
*Sibbaldia procumbens*, 321, 466, 467  
*Sidalcea candida*, 470  
*Sieversia*, 489, 490, 494; *anemonoides*, 489, 490, 491; *brevifolia*, 491, 493; *calthifolia*, 490, 493, 494; *calthifolia congesta*, 493; *campanulata*, 491; *canescens*, 491, 492, 493; *ciliata*, 339, 343, 370, 490, 491, 492, 493; *flavula*, 491, 493; *glacialis*, 491; *grisea*, 491, 492, 493; *macrantha*, 494; *montana*, 490, 493; *Peckii*, 92, 490, 493; *pentapetala*, 490, 491; *radiata*, 493; *radicata*, 490; *rosea*, 492; *triflora*, 491, 492, 493  
*Silene acaulis*, 93, 463, 463; *Douglasii multicaulis*, 339; *noctiflora*, 514, 515, 517, 518; *rotundifolia*, 29, 30, 32, 35, 44, 45  
*Silphium*, 358, 359; *integrifolium*, 355, 356; *laciniatum*, 354, 355, 363, 512; *terebinthaceum*, 356, 357, 359, 363, 512  
*Siphonychia* sp., 212  
*Sisymbrium altissimum*, 514, 515, 518; *officinale leiocarpum*, 514, 515  
*Sisyrinchium* sp., 357  
*Sium cicutaefolium*, 84  
 Slope exposure as a factor in the distribution of *Pseudotsuga taxifolia* in arid parts of Washington, 337  
 SLOSSON, M. Notes on two North American ferns, 307  
*Smelowskia americana*, 96, 462, 463; *calycina*, 96  
*Smilacina*, 223, 231; *stellata*, 223, 224, 225  
*Smilax echirrata*, 29, 36; *laurifolia*, 560; *pumila*, 214, 216  
*Solanum Dulcamara*, 124, 339; *nigrum*, 514, 517, 519; *tuberosum*, 444  
*Solidago bicolor*, 33; *canadensis*, 354, 357; *ciliosa*, 101, 470; *decumbens*, 101, 470; *erecta*, 30, 35; *juncea*, 29, 35; *nemorialis*, 354; *odora*, 212, 214; *ohioensis*, 359; *oreophila*, 101, 470; *Riddellii*, 359; *rigida*, 354, 356, 357; *scopulorum*, 101; *serotina*, 354  
*Sonchus alpinus*, 624; *asper*, 517  
*Sorghastrum nutans*, 354, 357, 360; *secundum*, 212  
*Sparganium angustifolium*, 474; *minimum*, 474  
*Spartina Michauxiana*, 358, 359; *polystachya*, 561  
*Spathularia*, 180; *stellaris*, 98; *Vreelandii*, 98  
*Spermacoce floridana*, 13; *keyense*, 13  
*Sphaeralcea rivularis*, 340  
*Sphaerites raritanensis*, 297  
*Sphaerosoma*, 189  
*Sphaerotheca*, 170, 182, 192, 193, 194; *Castagnei*, 159  
*Sphenolobus exsectus*, 588; *minutus*, 588; *saxicola*, 613  
*Sphenopholis obtusata*, 308  
*Spiraea corymbosa*, 339  
*Spiranthes cernua*, 356  
*Spirogyra*, 267; *communis*, 290  
*Sporobolus heterolepis*, 354, 356, 357, 360  
*Sporodinia grandis*, 286  
*Stachys cordata*, 29, 35; *palustris*, 339, 358  
 STANDLEY, P. C. New or notable species of *Amaranthus*, 505  
*Staphylea*, 548  
*Stenophyllus ciliatifolius*, 212  
*Stenostomum myrtifolium*, 12  
*Steironema ciliatum*, 339, 340  
*Sterculia cliffwoodensis*, 298; *minima*, 298  
*Sterigmatocystis nigra*, 290  
*Stigmatomyces Baeri*, 161  
*Stipa spartea*, 354, 356, 357  
*Stokesia laevis*, 560, 563, 567  
*Strophanthus hispidus*, 127; *Kombe*, 127; sp., 127  
*Strychnos Nuxvomica*, 107, 126  
 Studies of West Indian plants—V, 1  
*Stylopus*, 484; *vernus*, 484  
*Stylosanthes biflora*, 29, 34, 38  
*Sullivantia Sullivantii*, 29, 32, 35  
 Superficial study of the pine-barren vegetation of Mississippi, A, 551  
*Swertia palustris*, 96, 472; *perennis*, 96  
*Symplocos tinctoria*, 216, 219  
*Syntheris plantaginea*, 465  
*Synthyris rubra*, 339  
  
*Taeniopsis*, 394  
*Taeniopteris*, 394, 395  
*Taraxacum*, 148, 149; *arcticum*, 98; *officinale*, 514, 515, 516, 517, 518, 519, 520, 521; *scopulorum*, 98, 466, 467  
*Taxodium ascendens*, 565; *distichum*, 90, 559, 563, 565; *imbricarium*, 559, 563, 565  
 Taxonomic study of the Pteridophyta of the Hawaiian Islands—IV, A, 51  
*Tecoma radicans*, 367, 369, 370; *stans*, 303  
*Teichospora*, 196  
*Telesonix heucheriformis*, 101, 465, 466; *Jamesii*, 101, 465  
*Tellima parviflora*, 339; *tenella*, 339  
*Temnoma setiforme*, 613  
*Tephrosia virginiana*, 355  
*Thalictrum alpinum*, 93, 470, 472; *dasycarpum*, 358, 359, 363  
*Thaspium aureum*, 359  
*Thecotheus*, 160, 190, 193; *Pelletieri*, 159, 192, 193  
*Thelebolus*, 170, 179, 190, 194, 196; *stercorarius*, 159

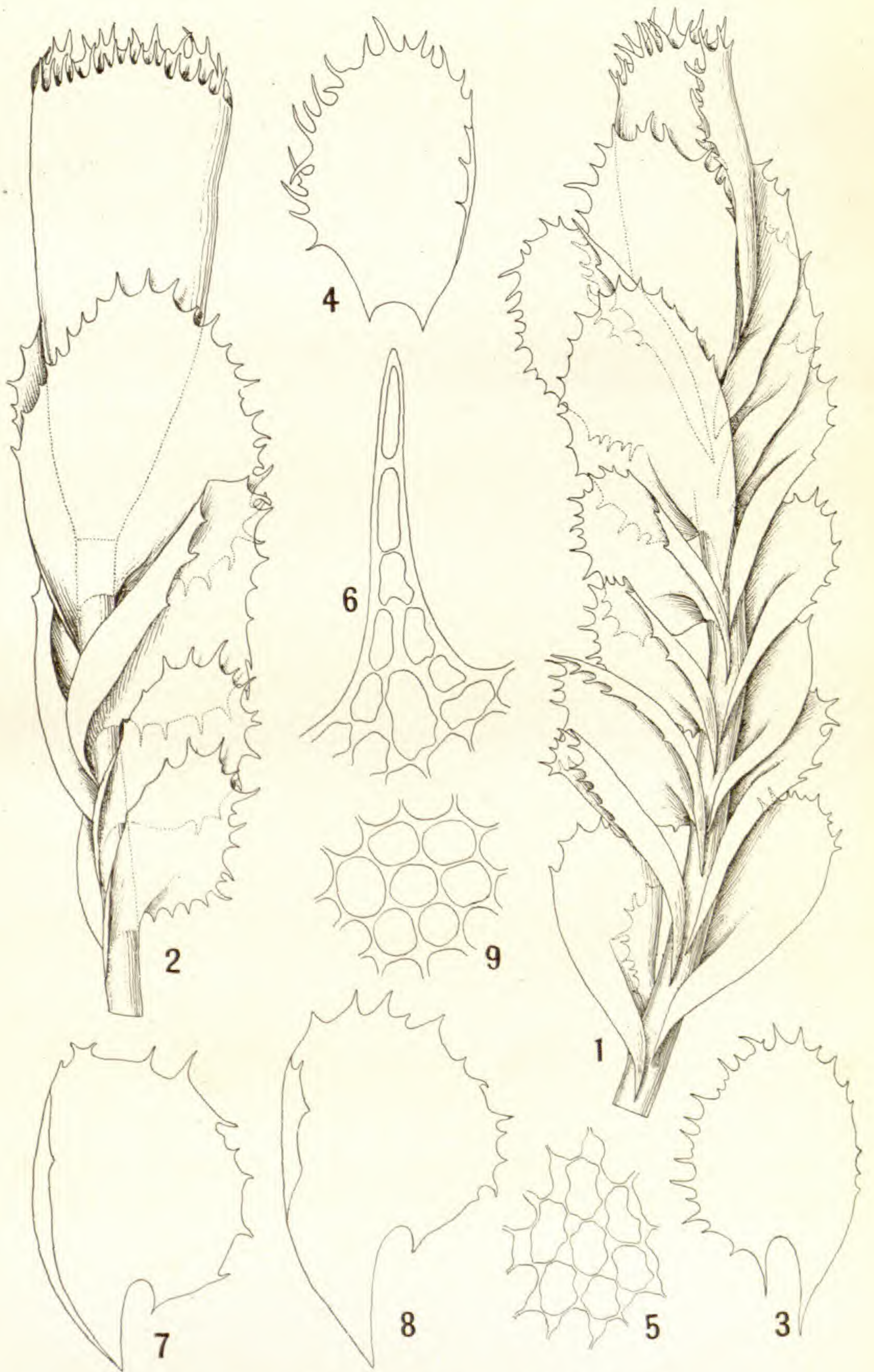


- Theobroma Cacao*, 127  
*Thlaspi alpestre*, 100; *coloradense*, 100, 462, 464; *glaucum*, 100; *purpurascens* 100, 462, 464  
*Thrinax microcarpa*, 11  
*Thuidium* sp. 214, 216  
*Thuja cretacea*, 298; *occidentalis*, 512; *plicata*, 343  
*Thurberia thespesioides*, 301, 302, 303, 304, 305  
*Tigarea*, 496  
*Tilia heterophylla*, 212, 219  
*Tillandsia usneoides*, 212, 214, 560  
*Tium alpinum*, 470  
 Tobacco, A review of investigations of the mosaic disease of, together with a bibliography of the more important contributions, 435  
*Tofieldia coccinea*, 102; *palustris*, 95, 471; *racemosa*, 560  
*Tonestus Lyallii*, 101; *pygmaeus*, 101, 468  
*Tradescantia reflexa*, 356  
*Tremella*, 179  
*Trichomanes hymenoides*, 307; *Krausii*, 307; *Petersii*, 307; *punctatum*, 307  
*Trichostema dichotomum*, 29, 35  
*Trifolium attenuatum*, 101, 468; *bracteolatum*, 101, 468; *Brandegei*, 101, 467, 468; *dasyphyllum*, 101, 462, 463, 468; *Haydeni*, 471; *hybridum*, 514, 515, 516, 518, 519, 520; *lividum*, 101, 468; *montanense*, 101; *nanum*, 101, 470; *Parryi*, 101, 467, 470; *pratense*, 360, 514, 515, 516, 517, 518, 520; *reflexum*, 30; *repens*, 360, 514, 515, 516, 518, 519, 520; *salictorum*, 101; *stenolobum*, 101, 468  
*Trilisa odoratissima*, 561  
*Trillium Hugerii*, 214; *petiolatum*, 339  
*Triplasis americana*, 212  
*Trisetum majus*, 469; *subspicatum*, 93, 94, 463, 469  
*Trollius laxus*, 30  
*Tsuga americana*, 629; *canadensis*, 29, 33, 35, 45, 512, 621, 622, 629; *heterophylla*, 580; *Mertensiana*, 580  
*Tuber*, 169, 179; *excavatum*, 182; *puberulum*, 182  
 TURESSON, G. Slope exposure as a factor in the distribution of *Pseudotsuga taxifolia* in arid parts of Washington, 337  
*Typha*, 231; *latifolia*, 359  
  
 Umbelliferae, 83  
*Unifolium canadense*, 29, 34, 36, 38  
*Usnea*, The nomenclature of the genus, 373  
*Usnea*, 169, 373; *articulata*, 374, 376, 377; *barbata*, 159, 373, 374, 376, 377; *barbata articulata*, 373; *barbata cera*; *tina*, 373; *barbata dasypoga*, 373a; *barbata florida*, 373; *barbata florida* *hirta*, 373; *barbata florida rubiginea*, 373; *barbata florida strigosa*, 373; *barbata hirta*, 373; *barbata intermedia*, 378; *barbata plicata*, 373; *barbata rubiginea*, 373; *barbata stricta*, 378; *californica*, 376; *ceratina*, 374, 375, 376, 377, 378; *coralloides*, 376; *dasypoga*, 374, 376; *dasypoga plicata*, 374, 377; *florida*, 374, 375, 377; *florida hirta*, 375; *plicata*, 374, 375, 377; *plicata barbata*, 374; *plicata dasypoga*, 377  
*Utricularia vulgaris*, 474  
  
 Vacciniaceae, 419  
*Vaccinium*, 423; *amoenum*, 423; *angustifolium*, 420, 421, 422, 423, 424; *angustifolium* × *corymbosum*, 424; *atlanticum*, 422, 423; *atrococcum*, 425, 426; *australe*, 424; *Brittonii*, 420, 421, 422; *caesariense*, 424; *caespitosum*, 97, 467; *canadense*, 421; *corymbosum*, 420, 423, 424, 425, 426; *corymbosum amoenum*, 423; *corymbosum glabrum*, 424; *disomorphum*, 425; *Dobbini*, 422; *fuscatum*, 426; *Myrtillus*, 96; *nigrum*, 420; *oreophilum*, 96, 470, 472; *pennsylvanicum*, 420, 421; *pennsylvanicum nigrum*, 420, 421; *scoparium*, 470; *vacillans*, 420, 422; *vicinum*, 425; *virgatum*, 423  
*Vagnera amplexicaulis*, 339; *stellata*, 415  
*Valeriana acutiloba*, 470; *edulis*, 359; *officinalis*, 127; *pauciflora*, 29, 35; *septentrionalis*, 471  
*Valerianella macrocera*, 339  
*Varronia clarendonensis*, 16  
*Vaucheria*, 167  
*Vauquelinia californica*, 303  
*Veratrum album*, 126; *nigrum*, 126; *viride*, 126; *Woodii*, 30  
*Verbascum Thapsus*, 514, 515, 516, 517, 518, 519, 520, 521  
*Verbena bracteosa*, 512; *stricta*, 354  
*Verbesina*, 362  
*Veronica virginica*, 358, 363; *Wormskjoldi*, 472  
 VESTAL, A. G. Black-soil prairie station in northeastern Illinois, A, 351  
*Viburnum dentatum*, 29; *molle*, 29; *nudum*, 560; *rufidulum*, 214  
*Vicia americana*, 339  
*Viola adunca*, 339; *biflora*, 90; *hirsutula*, 29, 32, 35; *papilionacea*, 358; *pedatifida*, 356, 357; *retroscabra*, 339; *rostrata*, 29, 35; *rotundifolia*, 29, 32, 35; sp. 214  
*Vitis aestivalis*, 560; *rotundifolia*, 214; *vinifera*, 367, 369; *vulpina*, 362, 363  
 Vittaria J. E. Smith, A revision of the genus, I. The species of the subgenus *Radiovittaria*, 391  
*Vittaria*, 391, 392, 393, 394, 395, 399, 400, 404, 406; *Bommeri*, 401, 407;



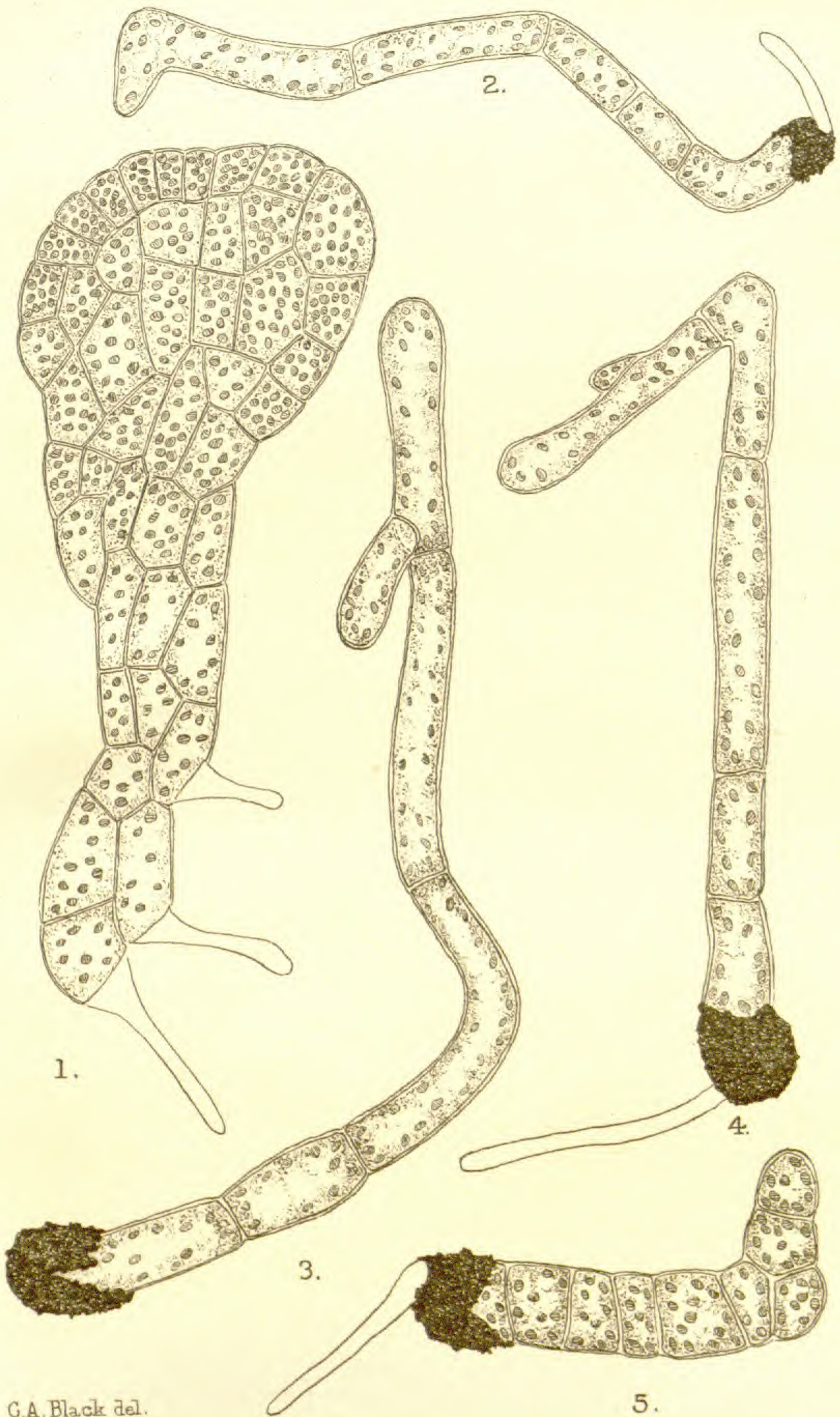
- elongata, 394; Forbsei, 394; Gardneriana, 398, 400, 401, 404, 407; gracilis, 400, 401; Karsteniana, 400, 401; **latifolia**, 398, 403, 404, 407; lineata, 394, 395, 397, 404; longipes, 405, 406; minima, 398, 399, 400; Moritziana, 405, 406; Orbignyana, 405, 406; remotota, 398, 401, 402, 403, 404; Ruiziana, 398, 405; scolopendrina, 394, 395; sikkimensis, 395, 399; stipitata, 398, 404, 406; **Williamsii**, 398, 407
- Waldsteinia, 331; Doniana, 331, 332; Fragarioides, 331, 332; idahoensis, 332; lobata, 332; parviflora, 332
- Warea cuneifolia, 212
- West Indian plants, Studies of,—V., 1
- Widdringtonites Reichii, 298
- Wild cotton plant (Thurberia thespesioides) in Arizona, The, 301
- Williamsonia delawarensis, 297; marylandica, 297
- Wisteria frutescens, 367, 368
- Wrangelia, 173, 178
- Xolisma ligustrina, 414
- Xylaria, 170; tentaculata, 159
- Xylorrhiza Brandegei, 101, 464; coloradensis, 101, 464
- Xyris flexuosa, 561; sp. 561
- Zodiomyces vorticellarius, 161
- Zygalchemilla, 319, 321
- Zygia, 8; arborescens, 8





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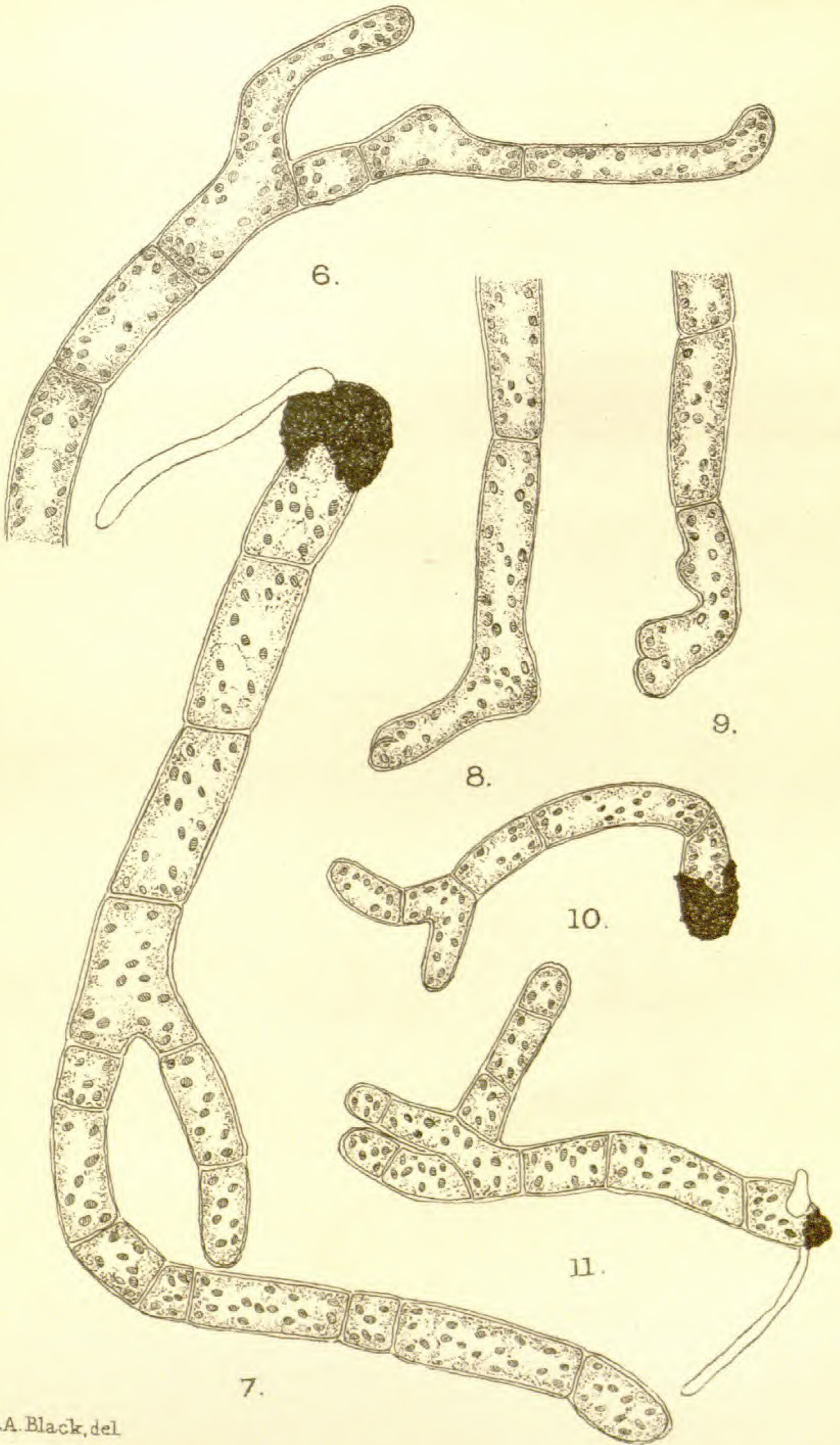




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