JOURNAL

OF THE

ARNOLD ARBORETUM

HARVARD UNIVERSITY

ALFRED REHDER
EDITOR

JOSEPH H. FAULL AND CLARENCE E. KOBUSKI
ASSOCIATE EDITORS

VOLUME XVI

JAMAICA PLAIN, MASS.
1935

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Arnold Arboretum of Harvard University
KRAUS REPRINT CORPORATION
New York
1968

DATES OF ISSUE

No. 1, (pp. 1-143, pl. 119-128) issued January 25, 1935.
No. 2, (pp. 145-271, pl. 129-139) issued April 24, 1935.
No. 3, (pp. 273-365, pl. 140-154) issued July 10, 1935.
No. 4, (pp. 367-483, pl. 155-165) issued October 25, 1935.

Printed in U.S.A.

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JOURNAL
OF THE
ARNOLD ARBORETUM

VOLUME XVI | JANUARY, 1935 | NUMBER 1

STUDIES IN BORAGINACEAE, X
THE BORAGINACEAE OF NORTHEASTERN SOUTH AMERICA

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THE present paper is a critical account of the Boraginaceae known from British, Dutch and French Guiana and the adjoining portions of Brazil, north and east of, the Amazon and the Rio Negro. A general account, it is preliminary to a treatment of the Dutch Guianan species of the family which Prof. A. A. Pulle has invited me to prepare for his "Flora of Surinam."

The borages of the Guianas have been long neglected. Such fragmentary work as has been done on them has been restricted to the narrow political boundaries. Though various species of the group have been described from the Guianas, some of them among the first based upon South American material, the identity of the types has remained obscure, and material in herbaria has continued to be named largely by guess or has been left to accumulate unidentified. The great reference works, such as DeCandolle's Prodromus, or Martius's Flora Brasiliensis, resolve little of the confusion that seems always to have enveloped our knowledge of the Guianan Boraginaceae. They added little to the observations all ready long available in the writings of Lamarck and Poiret. Indeed, so little known and confused were the Guianan species of *Cordia* and *Tournefortia,* that a few years ago, during my studies of the Brazilian species of these genera, Contr. Gray Herb. **92:** 1–89 (1930), I was forced to pass over, undiscussed, the very evident relations existing between the species of the Guianas and those of northern Brazil, and forced to admit that certain of the obscure species (several of them not even listed in the Index Kewensis) might be identical and older than the ones I was forced to accept. A careful study of the Guianan Boraginaceae has been long needed.

The conspicuous relationship evident among the Guianan Boraginaceae is that with Brazil, most of the species extending into and about the Amazon Basin or having their immediate relatives there. The affinities westward in Venezuela are not so numerous nor so pronounced. Except for Trinidad (which after all is floristically close to that of eastern Venezuela) direct relations to the northward are negligible. Among the Guianan Boraginaceae only the group *Cordia* § *Pilicordia* has developed any number of local species. The relations of these local endemics are in the Amazon Basin where the species of this group are not local but widely distributed. The Guianas are a marked endemic center for *Pilicordia* comparable with the centers of that group found in southeastern Brazil, northern Venezuela and adjacent Colombia, and the West Indies.

I have treated in this paper all the borages known north and east of the Amazon, the Rio Negro and the eastern boundary of Venezuela. The monotypic *Lepidocordia* is endemic to this area. Of the 38 species definitely known from this large area only two, *Cordia multispicata* and *Cordia naidophila* are at present unknown from British, Dutch or French Guiana. Several other species approach our area, reaching the Orinoco Valley from the westward. Among these species those which may eventually be found in northwestern British Guiana are *Cordia globosa* (Jacq.) HBK., *Cordia alba* Jacq. and *Bourreria cumanensis* (Loefl.) O. E. Schulz. The writings of Schomburgk, Aublet and others have listed various West Indian species from the Guianas. Some of these records are evidently based upon misidentifications, others, however, I am convinced, are simply unfortunate guesses as to what the authors believed might be found there. Most of these questionable records relate to species common and widespread at low altitudes in the Antilles. This group of plants is poorly represented on the Guianan coastal area, probably because of adverse winds and currents and the unfavorably humid conditions.

In the preparation of this report I have examined practically all the types concerned and have studied most of the large or important Guianan collections in Europe and United States. Studies have been made at Kew, London, Leiden, Utrecht, Copenhagen, Berlin, Munich, Geneva and Paris. Large loans of critical material have been obligingly sent for further, more leisurely study at the Arnold Arboretum and the Gray Herbarium from Kew, London, Leiden, Utrecht, Berlin, Paris and New York. Particular mention, however, is to be made of the large loan from the Botanical Museum at Utrecht. This material, assembled through the inspiration of Prof. Pulle and kindly made available to me by him, consists of numerous series of copious specimens collected over a number of years, at different seasons, from various numbered individual trees or shrubs, in the Forest Reserves of Dutch Guiana. Through the examination of this remarkable record of seasonal variation I have been able to establish unquestionably the specific identity of certain seasonal forms heretofore troublesome to identify. Of great help in the preparation of this report the collections have been generally instructive to me personally. It has been a privilege to have such a convincing demonstration of the nature and extent of seasonal variation in individual trees and shrubs of the Tropics.

The following abbreviations have been used in designating the source of the material cited. B. W. — collections by the Forest Service (Boschwezen) of Dutch Guiana; AA — Arnold Arboretum; BD — Botanical Museum at Berlin; BM — British Museum of Natural History; DC — Prodromus Herbarium of DeCandolle at Geneva; Del — Delessert Herbarium at Geneva; G — Gray Herbarium; K — herbarium at Kew; Leid — herbarium at Leiden; NY — New York Botanical Garden; US — U. S. National Herbarium; Utr — Utrecht Herbarium.

KEY TO THE GENERA

Stigmas 2 or 4, simple; inflorescence cymose-paniculate or spicate or globose, the branches not distinctly scorpioid; erect broad-leaved trees and shrubs.

Stigmas 4, capitate or clavate, borne on a conspicuous slender, twice lobed or cleft style ....1. *Cordia*, p. 3.

Stigmas 2, conic, sessile on the apex of the ovary, short and inconspicuous ....2. *Lepidocordia*, p. 45.

Stigma 1, consisting of an anulate fertile base and a more or less developed sterile frequently bifid apical portion; inflorescence with distinctly scorpioid branches or the flowers cauline and solitary in the internodes.

Fruit baccate; clambering shrubs ....3. *Tournefortia*, p. 46.

Fruit dry; herbs or small suffrutescent plants ..4. *Heliotropium*, p. 57.

1. Cordia [Plumier] Linnaeus, Gen. 87 (1754).

Trees or shrubs, usually with broad leaves. Inflorescence a loosely paniculate or glomerate or capitate or spicate cyme. Calyx usually 5-toothed or 5–10-lobed, usually persistent. Corolla white, yellow or reddish, small to conspicuous, usually 5-merous, rarely 6–15-merous, salverform or subrotate to funnelform or subtubular. Stamens as many as the corolla-lobes, exserted or included, filaments short or long. Ovary 4-celled, ovules 1–4. Style terminal, well developed, 2-lobed or 2-parted, the branches each 2-lobed. Stigmas 4, capitate or clavate, small. Fruit unlobed, a drupe with a bony pit and mucilaginous or dry exocarp, or the walls dry and papery, 1–4-celled. Endosperm none. Cotyledons plicate.

A very large genus of diverse habit and structures; widely distributed throughout the Tropics. Centering in America. Type Species: *C. sebestena* L.

On the grounds that the original *"Cordia"* of Plumier, Nov. Pl. Amer. Gen. 13, tab. 14 (1703), which was accepted and validated by Linnaeus, is not a member of the Boraginaceae, the generic name *Cordia* has been recently discarded for the present concept by Dr. von Friesen, Bull. Soc. Bot. Genève, sér. 2, **24**: 131–4 (1933). With this I can not agree. It is pointed out by von Friesen that Plumier's illustration shows a 2-celled ovary and a simply bifid style and that the generic description of *Cordia* (based upon Plumier's plate and description) given by Linnaeus in the Genera Plantarum of 1754, pg. 87, also calls for these structures. Dr. von Friesen believes they are structures of some genus outside of the Boraginaceae. I believe they are structures of *Cordia sebestena* faultily described from inaccurate drawings.

I have had the privilege of studying, in the library of the Natural History Museum at Paris, the amazing series of volumes of plates and manuscripts accumulated by Plumier during his visits (1689–97) to the West Indies. In one of these volumes of manuscript, **6**: tab. 64–66, are found fine drawings labeled *"Cordia nucis iuglandis folio, flore purpureo."* The best of these original drawings, made in the West Indies by Plumier, fills a folio page and shows a characteristic branch of *Cordia sebestena* bearing leaves, flowers and fruit. In the corner of the page are the details of flower and fruit, differing only in arrangement from those printed in Plumier's Genera. The structures of style and ovary are quite alike in both. This may be verified by a comparison of the small plate in Plumier's Genera and the good copy of the original folio plate published in Burmann's edition of Plumier's Plantarum Americanarum, fasc. 5, tab. 105 (1757). The later plate is identified as *C. sebestena* by Urban, Rep. Spec. Nov. Beiheft **5**: 60 (1920). Von Friesen, l. c. 135, however, believes that only the leafy, flower-bearing branch is *C. sebestena* and that the disputed unattached analytic details belong to some other genus. Since, however, the disputed details are an integral part of the original drawing of Plumier, which consists mainly of a flowering and fruiting branch unquestionably of *C. sebestena,* and since the details, as far as one can compare them, are quite like homologous structures shown growing attached to the flowering and fruiting branch of *C. sebestena,* I feel there is every reason for believing that, however inaccurate, they were intended to show the structures of that species.

It is to be recalled that Plumier's drawings were made long before the work of Linnaeus on the Sexual System directed particular attention and gave special importance to the number and structure of the internal parts of the flower and fruit. Plumier, and Linnaeus who copied from him, may have given erroneous descriptions of the fruit and style of *Cordia sebestena* but since they were trying to describe that species I believe we should retain their name for the genus containing it.

Plumier's drawing was made on the island of St. Thomas. The following quotation from his manuscript gives the type-locality of *C. sebestena* in some detail. "Martio plantarum florentem frutusque maturos ferentem adinveni apud insulam Sancti Thomae, juxta Littus quoddam La Baye du nord vocitatum, sinum scilicet ad septenttrionalem plagam ipsi Arci oppositum."

Key to the Species

Corolla marcescent; fruit cylindrical, dry, with a fibrous chartaceous coat, not bony, closely invested by the tube of the persistent corolla and the strongly ribbed cylindrical calyx, at maturity flower disarticulating from the inflorescence and the calyx and corolla and the enclosed fruit falling away together, with the spreading corolla-lobes acting as a parachute; pubescence stellate; axis of inflorescence usually tunnelled or inflated and inhabited by ants ....1. *C. alliodora.*

Corolla withering after anthesis and soon deciduous; fruit usually baccate, with a bony ovoid or globose stone; pubescence simple.

Corolla red or orange, large; calyx becoming fleshy and completely enveloping the dry fruit and even adnate to it ....2. *C. sebestena.*

Corolla white or yellow; fruit juicy, not adnate to the dry calyx.

Corolla-lobes longer than broad; calyx explanate at maturity; inflorescence usually large and loosely branched; trees or shrubs with usually horizontal branches and flat tops.

Petioles of well developed leaves 15–40 (usually 20–30) mm. long; ovary and fruit glabrous; inflorescences terminating leafy branchlets.

Leaves glabrous and lustrous above, 15–40 cm. long; calyx ca. 5 mm. long; stone obliquely ovoid, ca. 18 mm. long; explanate calyx 10–13 mm. broad ....3. *C. fallax.*

Leaves strigose and rather dull above, 10–27 cm. long; calyx 2.5–3.5 mm. long; stone transversely compressed-ovoid, ca. 10 mm. long; explanate calyx 5–7 mm. broad ....4. *C. tetrandra.*

Petioles of well developed leaves 3–15 (usually 5–10) mm. long; inflorescence usually borne at the forks of the dichotomous stems.

Ovary and style hairy; fruit mostly pubescent.

Leaves glabrous above or practically so; veins less conspicuously rebranched than in next; calyx usually apiculate, opening somewhat irregularly.

Stems with conspicuous subnodal swellings that serve as ant-domatia; calyx tending to disintegrate at maturity and showing a fibrous structure; plant usually conspicuously bristly ....5. *C. nodosa.*

Stems without subnodal swellings, not myrmecophilous; calyx not with fibrous structure; plant not bristly.

Fruit glabrous; calyx with a fine minute strigose-puberulence; lower leaf-surfaces glabrous or practically so ....6. *C. laevifrons.*

Fruit strigose; calyx strigose; lower leaf-surfaces pubescent.

Lower surfaces of leaves evidently bearing numerous erect slender hairs; inflorescence stiffish but loose and open...7. *C. Sprucei.*

Lower surfaces of leaves apparently glabrous, but really bearing scattered minute inconspicuous very short ascending hairs; inflorescence dense with short rigid crowded branches ....8. *C. nervosa.*

Leaves abundantly hairy above, veins repeatedly rebranched; calyx opening by 5 triangular lobes.

Calyx prominently and regularly 10-ribbed, 4–5 mm. long; fruit velvety, stone transversely ovoid ....9. *C. fulva.*

Calyx not ribbed, 2–4 mm. long.

Upper surface of leaves velvety, with very abundant slender erect or ascending hairs; leaves usually strongly dimorphic about the stem-forks (the normal elongate leaves usually opposed by much smaller suborbicular ones); fruit clothed with abundant slender appressed usually tawny hairs; stone ascending, ovoid ....10. *C. toquevo.*

Upper surface of leaves simply strigose or minutely scabrous; leaves homomorphic.

Lower surface of leaves green (drying brown), scabrid with very short sparse hairs; leaves lanceolate; fruit minutely strigose; stone ascending ovoid ....11. *C. scabrifolia.*

Lower surface of leaves pallid, with a felty covering of abundant appressed slender hairs; leaves broadly lanceolate to ovate; fruit glabrescent; stone transversely ovoid .... 12. *C. bicolor.*

Ovary, style, and fruit glabrous.

Lower surface of leaves pallid with a felty covering of abundant slender appressed hairs ...... 12. *C. bicolor.*

Lower surface of leaves not felty with a pallid indument.

Stone globose or depressed globose, quite rugose; calyx with abundant long slender hairs on the inner surface which project beyond the edge of the calyx-lobes and appear as a dense pale ciliation on their margins.

Calyx outside covered with abundant slender silky hairs; leaves rather thin, more or less dimorphic at the stem-forks, lower surface much paler than the upper .... 13. *C. sericicalyx.*

Calyx sparsely strigose outside; leaves rigid, homomorphic, lower surface scarcely paler than upper .... 14. *C. panicularis.*

Stone ovoid or ellipsoid, smooth, erect, elongate; calyx strigose on the inner surface, the hairs projecting beyond the calyx-lobes sparse and dark if present.

Hairs on lower leaf-surface erect.

Lower leaf-surface somewhat scabrid with minute stout hairs; leaves large, 15–28 cm. long, with evidently falcate midrib; branchlets with short erect hairs ... 15. *C. Sagotii.*

Lower leaf-surface velvety with long slender hairs; leaves moderate-sized, 8–18 cm. long, midrib weakly falcate; branchlets brownish hirsute .... 16. *C. hirta.*

Hairs on lower leaf-surface appressed.

Flower-buds elongate, obovoid, 4–5 mm. long; leaves 8–20 cm. long; inflorescence large and stiffish; Lower Amazon and the Guianas.

Leaf-blades broadest at or above middle, drying olivaceous or muddy brown .... 17. *C. exaltata.*

Leaf-blades broadest at or below the middle drying a bright warm brown .... 17a. var. *melanoneura.*

Flower buds subglobose, 2–3 mm. long; leaves 6–11 cm. long; inflorescence slender and usually small; Upper Amazon ... 18. *C. naidophila.*

Corolla-lobes distinctly broader than long; calyx cupulate or cylindrical at maturity; inflorescence dense, globose or spicate, or exceptionally a small loose cyme; shrubs with erect or ascending branches, frequently subscandent.

Corolla very large, 35–50 mm. long, the slender tube abruptly and much expanded into a coarse cylindrical throat; inflorescence capitate; tip of calyx-lobes conspicuously long-attenuate ....19. *C. grandiflora.*

Corolla small, about 5 mm. long or less, tube and throat weakly differentiated.

Inflorescence glomerate or cymose ....20. *C. polycephala.*

Inflorescence distinctly spicate.

Leaves not hairy above, merely more or less verrucose or muriculate, elongate; spikes terminal; petioles not decurrent on the peduncles ....21. *C. macrostachya.*

Leaves hairy above, strigose or velvety, broad; spikes axillary with the base of the petiole apparently decurrent on the subtended peduncle.

Calyx-lobes in bud lacking free tips; inflorescence becoming quite loosely flowered and elongate; upper surface of leaves strigose, somewhat lustrous ....22. *C. Schomburgkii.*

Calyx-lobes in the bud with projecting free tips; inflorescence dense and stout; upper surface of leaves with stiff erect or ascending hairs which arise from bulbous bases, surface not lustrous.

Calyx hairy all over, lobes narrowly triangular, long acuminate ....23. *C. tomentosa.*

Calyx with tube nearly glabrous, lobes broadly triangular, short acuminate .....24. *C. multispicata.*

1. **Cordia alliodora** (R. & P.) Chamisso ex DeCandolle, Prodr. **9:** 472 (1845); Johnston, Contr. Gray Herb. **92:** 13 (1930). *Cerdana alliodora* Ruiz & Pavon, Fl. Peruv. **2:** 47, tab. 184 (1799). *Cordia trichotoma* sensu Sandwith, Kew Bull. **1933:** 335 (1933).

Tree up to 20 m. tall; branchlets sparingly to densely stellate-pubescent; leaves oblong or lanceolate to elliptic, usually broadest at or above the middle, 3–8 cm. broad, 1–2 dm. long, base acute or obtuse, apex acuminate, margin entire, upper surface stellate-pubescent or glabrate, lower surface paler, stellate-tomentose or glabrescent, 5–7 pairs of veins, petiole 1–3 cm. long; inflorescence terminal, loosely and widely branched, 1–3 dm. thick, the flowers crowded on the branches, the axis commonly inflated, gall-like, irregular, usually serving as an ant-domatium; calyx cylindrical, with ten prominent ribs, densely stellate-tomentose, 4–6 mm. long, 2–2.5 mm. thick, lobes 5, inconspicuous; corolla white, drying brown, marcescent, lobes oblong, 5–7 mm. long, 1.5–3.5 mm. broad, spreading; fruit sausage-shaped with fibrous chartaceous wall, ca. 5 mm. long, completely enveloped by the tube of the persistent corolla and by the ensheathing calyx-tube and falling away enclosed by them.

Headwaters of the Rio Branco in northern Brazil and adjacent southern British Guiana; northern Venezuela and Colombia and southward along the Andes and northward in Central America and the West Indies.

British Guiana: north side of Kanuku Mts., ca. 10 miles east of the Takutu River, ca. 135 m. alt., small tree, 4.5 m. tall, trunk ca. 8 cm. thick, in secondary forest near edge of savanna, fl. pure white, Oct. 10, 1931, *Forest Dept. Brit. Guiana D230/2221* (K); Pirara (Marakanata), Rupununi Savannas, ca. 120 m. alt., tree ca. 20 m. tall, trunk 11 m. to fork, 4 dm. thick, in sandy soil on patch of savanna-forest on top of ridge, Oct. 21, 1931, *Forest Dept. Brit. Guiana D195/2186* (K).

Brazil: Mniam, tributary of Suruma River, Nov. 1909, *Ule 8290* (K, BD, Del); Limão, lower Cotinga River, Sept. 1927, *Tate 140* (NY).

Although previously I have cited one of the above collections as *C. trichotoma*, Contr. Gray Herb. **92:** 15 (1930), I am now of the opinion that all the material from the upper Rio Branco watershed is more closely related to *C. alliodora*. The corolla-lobes in our plants are 3–3.5 mm. broad. The stems are simply tunneled by ants. There are no distorted, gall-like thickenings in the axis of the inflorescence. Compared with large series of *C. trichotoma* and *C. alliodora* our plants seem most like the latter species in gross aspect. The colony on the Rio Branco was probably derived from northern Venezuela where only *C. alliodora* is known. Strangely *C. alliodora* seems to be rare or absent in the Orinoco Valley and in the other parts of the wet tropical forests of northeastern South America.

Previously I have attempted to maintain the Argentine, Paraguayan and Brazilian plant, ranging to the east and south of the Amazon Basin, as a species distinct from *C. alliodora*. I am now of the belief that this plant, called *C. trichotoma* in my treatment of the Brazilian species, is distinguished from *C. alliodora* only by its larger flowers, and that it had best be classified as a variety of that latter species. The correct trinomial for the large-flowered Brazilian form is *Cordia alliodora* var. *tomentosa* A. DC.

2. **Cordia sebestena** Linnaeus, Sp. Pl. 190 (1753). *Cordia speciosa* Salisbury, Prodr. 111 (1796); DeCandolle, Prodr. **9:** 476 (1845); Pulle, Enum. Pl. Surinam 397 (1906).

Tree or shrub 1–7 m. tall; branchlets with a fine soft curly pubescence and scattered much coarser appressed hairs; leaves ovate to elliptic or subcordate, 9–16 cm. long, 5–14 cm. broad, broadest below the middle, base obtuse or rounded or subcordate, apex obtuse to coarsely short-acuminate, margin entire, upper surface with scattered short stiff appressed hairs, the hairs usually arising from minute pustulate disks, lower surface glabrescent or sparsely strigose, with 5–6 pairs of veins; petiole slender, 1–4 cm. long; inflorescence corymbose, usually terminal, ascendingly branched; calyx firm, strigose and densely brown puberulent, elongate in the bud, 12–15 mm. long, 3–5 mm. thick, opening by several unequal teeth ca. 2–3 mm. long, at maturity becoming much expanded by the enlarging fruit which it encloses, 3–4 cm. long; corolla orange or scarlet, funnelform, tube twice length of the cylindrical calyx; fruit bony, dry, ovoid, pointed, 1–2 cm. long, completely and tightly invested by the juicy white accrescent calyx.

Native on the islands of the Caribbean and probably also along the coasts of Venezuela, Colombia and Central America; frequently cultivated in the Tropics.

BRITISH GUIANA: Botanic Gardens, Georgetown, cultivated, Aug. 1905, *collector not given 7976/6915* (BD).

DUTCH GUIANA: Surinam, cultivated, tree 6–9 m., fl. red, Dec. 1837, *Splitgerber 312* (Leid); Cottica district near Plant. Alliance, Aug. 1901, *Went 280* (Utr); Paramaribo, *Focke 1371* (Utr).

FRENCH GUIANA: indefinite, 1802, *Gabriel* (Del).

3. **Cordia fallax**, sp. nov. *Cordia guianensis* Klotzsch ex Schomburgk, Fauna u. Fl. Brit. Guian. 960 (1848), nomen; not *C. gujanensis* (Desv.) R. & S. (1819), nor *C. guianensis* R. & S. ex DC. (1845).

Arbor 5–10 m. alta; ramulis brunnescentibus cum pilis abundantibus brevibus erectis velutinis; foliis homomorphis ellipticis vel obovato-oblongis 15–40 cm. longis 6–18 cm. latis ad medium vel paullo supra medium latioribus minute glanduloso-punctulatis, basi rotundis vel subcordatis ad obtusis vel late acutis, apice breviter acuminatis, margine integerrimis vel rariter leviter sinuatis, supra lucentibus in costa et nervis primariis pilos inconspicuos gerentibus ceteris glabris vel subglabris, subtus pilis plus minusve abundantibus gracillimis ascendentibus molliter vestitis, nervis 7–8-jugatis, costa falcato-curvatis, petiolis 15–30 mm. longis; cymis ramulos foliatos terminantibus laxissime ramosis ad 3 dm. diametro; calyce in alabastro obovoideo extus indumento brunnescente velutino molli vestito, intus glaberrimo, ad anthesin ca. 5 mm. longo (lobis deltoideis 5), fructifero explanato 10–14 mm. lato; corolla 1 cm. longa, lobis obovatis extus glabris, filamentis basim versus pilosis; ovario et stylo glaberrimo; fructu glabro; nuce valde rugoso oblique ovoideo acuminato ca. 18 mm. longo.

Endemic to British Guiana.

BRITISH GUIANA: Issorora, Aruka River, wet forest, tree 9 m. tall, Jan.

1920, *Hitchcock 17563* (TYPE, Gray Herb.; isotype, NY); upper Rupununi River near Dadanawa, ca. lat. 2° 45′ N., tree 5 m. tall, June 10, 1922, *La Cruz 1484* (NY); indefinite, 1844, *Schomburgk 875/1510b* (K); indefinite, 1841, *Schomburgk 875* (BD, Del, P); indefinite, *Schomburgk 1510* (BD, TYPE of *C. guianensis*; G).

Although bearing various numbers and different data, the material from Schomburgk cited above agrees so completely in details of maturity, pressing, etc., that one may recognize it as consisting of parts of a single collection. The material at Berlin bears Klotzsch's binomial. This, however, has never been associated with a description and is further invalid by reason of being a homonym. Schomburgk, l. c., reported *C. guianensis* Kl. only from the banks of the Barama River and there is every reason for believing that this is indeed the source of the Schomburgk material mentioned.

The species has been confused with *C. tetrandra,* although it is readily distinguished from that species by having glabrous upper leaf-surfaces and in being noticeably larger in all its parts. Its relations are with that group of species of Venezuela and Colombia which is exemplified by *C. bogotensis* Benth. Its very large leaves, hairy beneath, quickly distinguish it from these much more westerly species.

4. **Cordia tetrandra** Aublet, Hist. Pl. Guian. Fr. **1:** *222*, tab. 87 (1775); Poiret, Encyc. **7:** 42 (1806); Pulle, Enum. Pl. Surinam 397 (1906); Johnston, Contr. Gray Herb. **92:** 55 (1930). *Lithocardium tetrandrum* (Aubl.) Kuntze, Rev. Gen. **2:** 976 (1891). *Cordia cordifolia* Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. **3:** 70 (1818); DeCandolle, Prodr. **9:** 483 (1845). *Lithocardium cordifolium* (HBK.) Kuntze, Rev. Gen. **2:** 976 (1891). *Cordia muneco* Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. **7:** 207 (1825); DeCandolle, Prodr. **9:** 486 (1845). *Lithocardium muneco* (HBK.) Kuntze, Rev. Gen. **2:** 977 (1891). *Borellia asper* Rafinesque, Sylva Tellur. 41 (1838). *Cordia umbraculifera* DeCandolle, Prodr. **9:** 484 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 960 (1848); Fresenius in Martius, Fl. Bras. **8**[1]**:** 16 (1857). *Lithocardium umbraculiferum* (DC.) Kuntze, Rev. Gen. **2:** 977 (1891).

Tree, 3–12 m. tall; branchlets pallid, tomentose with abundant curved spreading short hairs; leaves homomorphic, ovate to elliptic or oblong or lance-ovate, broadest either below or just above the middle (usually the latter), 1–1.7 dm. long, 5–14 cm. broad, base more or less oblique, obtuse or rounded or subcordate, apex obtusish to acute, the very tip blunted (not acuminate), under surface green, sparsely strigose, secondary venation obscure, lower surface much paler, more or less brownish with rather abundant short slender curved hairs which spring from the much rebranched veins, usually velvety, with 7–10 pairs of veins; petioles well developed, 2–5 cm. long; cymes usually terminating leafy branchlets, loosely branched, 1–3 dm. broad; calyx obovoid in bud, densely covered with fine appressed hairs, inside sparsely strigose or hispidulous; calyx at anthesis 2.5–3.5 mm. long, with 4–5 more or less equal deltoid lobes, in fruit explanate and 5–7 mm. broad; corolla white, prevailingly 5-merous, 4–5 mm. long, glabrous, lobes elongate, filaments exserted, hairy at base; ovary and style glabrous; fruit glabrous; stone very rugose, transversely compressed-ovoid, ca. 1 cm. long, pulp white and mucilaginous.

Northeastern coast of Brazil (Maranhão and Pará), northern South America and southward along the Andes to Bolivia; frequently cultivated.

British Guiana: Rockstone, banks of the Essequibo, 1921, *Gleason 865* (K); Demerara River, May 1889, *Jenman 4878* (K); Demerara, *Parker* (K, DC); Platburg Creek, Canje River, fruit glutinous, yellowish green, 1914, *Hohenkerk 631* (K); indefinite, large tree, flowers yellowish white, 1837, *Schomburgk 408* (DC, type of *C. umbraculifera*; isotypes, G, K, BD, P).

Dutch Guiana: upper Nickerie River, Feb. 1915, *B. W. 1074* (Utr); near Paramaribo, 1910, *native collector* (Utr); near Paramaribo, tree, fl. white, 1844, *Kappler, ed. Hohenacker 1619* (Utr, P); Plant. Jagtlust, 5 m. tall, 1913, *Soeprato 6E* (Utr); Plant. Osembo-Onverwacht, 1913, *B. W. 6229* (Utr); Plant. Slootwijk, tree 5 m. tall, *Soeprato 10H* (Utr); Watramiri, tree no. 1568, fruit edible, mucilaginous, June 4, 1916, *B. W. 1836* (Utr); Watramiri, tree no. 1568, Feb. 7, 1917, *B. W. 2659* (Utr); Watramiri, tree no. 1568, Feb. 18, 1920, *B. W. 4551* (Utr); Watramiri, tree no. 1568, Dec. 7, 1920, *B. W. 4974* (Utr); Surinam, tree 9–12 m. tall with broad horizontal branches, usually cultivated, fl. white, Nov. 1837, *Splitgerber 123* (Leid); Surinam, 1841, *Berthoud-Coulon 553* (BM); Surinam, *Hostmann 355* (K, BM, BD, Del, P); Surinam, *Hostmann* (Utr).

French Guiana: Mana, March 1854, *Mélinon 215* (P); Mana, 1857, *Sagot* (P); Iles du Salut, fruit white, glutinous, 1854, *Sagot 445* (K, BM, P); Ile de Cayenne, 1851, *Sagot* (P); Cayenne, *Aublet* (BM, type of *C. tetrandra*); Mahoury near Cayenne, *Sagot* (P); indefinite, *Martin ex herb. Rudge* (BM), *LePrieur 252* (Del, P), *Perrottet* (P), *Gabriel* (Del) and *Poiteau* (K).

Aublet reports *C. tetrandra* from the Ile de Cayenne and from the mainland of French Guiana. I have examined specimens from his personal herbarium, now at the British Museum, as well as a duplicate from it now in the Swartz herbarium at Stockholm. His description, his illustration, and the two specimens, leave no doubt as to the exact identity of *C. tetrandra*. Aublet's name is inapt, the species is practically always pentandrous.

The species appears to be indigeneous only in a broad band of wet tropical forest about the northern margin of South America, where it seems to be most common at low altitudes on the coastal plain. On the east base of the Andes it is known from Peru and Bolivia. I have seen no material from the dryer portions of Brazil to the south of the Amazon Basin that is indubitably from wild plants. Brade, Bol. Mus. Nac. Rio Janeiro **8**: 35 (1932), however, has recently reported it from Manáos. The collections by Spruce from the mouth of the Rio Negro, reported (sub *C. umbraculifera*) in the Flora Brasiliensis, **8**[1]: 16 (1857), is not *C. tetrandra,* but the material subsequently made the type of *C. Sprucei* Mez. I have reported, Contr. Gray Herb. **92**: 55 (1930), *C. tetrandra* from Ceará and Pernambuco. This was incorrect and is the result of a bad clerical error. The specimens actually represent *C. toqueve*. I am indebted to Mr. Killip, *in lit.,* and to Mr. Brade, l. c. 34, for the correction of this unfortunate error.

The wood of *C. tetrandra* has been described by Pfeiffer, De Houtsoort. v. Surinam. **1**: 444 (1926). In the herbarium at Utrecht the collection, cited above, from the Plantation of Osembo-Onverwacht bears the annotation, "Pfeiffers Woods of Surinam no. 59."

Aublet states that the species is called "Bois Margarite" and "Arbre à parasol." The following vernacular names are associated with the specimens cited above, Kakuru or Clammy Cherry—*Hohenkerk 631;* Kakhoro' (Arow.), Tafrabom (Nig. Eng.) and Alatoeloeka (Kar.)—*B. W. 1074;* Tafelboom—*B. W. 6229* and *Splitgerber 123;* Tafelboom (Sur. Dutch), Tafraboom (Nig. Eng.), Boggi lobbi (Saram.), Toenbalobbi (Saram.), Kakhoro (Arow.), Araatroekoe (Kar.)—*Watramiri tree no. 1568;* Bois parasol—*Sagot 445;* Roqueí—*Sagot at Cayenne and Mahoury.*

5. **Cordia nodosa** Lamarck, Tab. Encyc. **1**: 422 (1791); Poiret, Encyc. **7**: 43 (1806); Schomburgk, Fauna u. Fl. Brit. Guian. 960 1848); Fresenius in Martius, Fl. Bras. **8**[1]: 16, tab. 5 (1857); Bailey, Bot. Gaz. **77**: 32–49, tab. 6–7 (1924); Johnston, Contr. Gray Herb. **92**: 46 (1930). *Lithocardium nodosum* (Lam.) Kuntze, Rev. Gen. **2**: 977 (1891). *Cordia hirsuta* Willdenow, Sp. Pl. **1**: 1076 (1798); Meyer, Prim. Fl. Esseq. 114 (1818). *Firensia hirsuta* (Willd.) Rafinesque, Sylva Tellur. 40 (1838). *Cordia formicarum* Hoffmannsegg ex Roemer & Schultes, Syst. **4**: 800 (1819). *Cordia miranda* DeCandolle, Prodr. **9**: 475 (1845). *Lithocardium mirandum* (DC.) Kuntze, Rev. Gen. **2**: 977 (1891). *Cordia hispidissima* DeCandolle, Prodr. **9**: 475 (1845). *Lithocardium hispidissimum* (DC.) Kuntze, Rev. Gen. **2**: 977 (1891). *Cordia nodosa* var. *hispidissima* (DC.) Fresenius in

Martius, Fl. Bras. **8**[1]**:** 17 (1857). *Cordia nodosa* var. *angustifolia* Fresenius in Martius, Fl. Bras. **8**[1]**:** 17 (1857). *Cordia umbrosa* Spruce ex Rusby, Bull. Torr. Bot. Cl. **26:** 147 (1899). *Cordia volubilis* Pittier, (Explor. Bot. Cuenca de Maracaibo p. 41) Bol. Comer. e Indust. **4:** ? (1923); Jour. Wash. Acad. Sci. **19:** 184 (1929). *Cordia collococa* sensu Aublet, Hist. Pl. Guian. Fr. **1:** 219, tab. 86 (1775).

Shrub or tree, 2–11 m. tall; stems bearing stiff spreading brownish bristles which are usually abundant but may be sparse or nearly absent; the stems below each fork abruptly and asymmetrically enlarged and containing a cavity usually serving as an ant-domatium; leaves usually subopposite or whorled, more or less heteromorphic, somewhat lustrous on both surfaces, lanceolate to nearly elliptic, broadest near the middle, 10–35 cm. long, 3–28 cm. broad, base obtuse, apex acuminate, margin entire, upper surface with impressed veins, more or less bullate, with a few hairs along the midrib, lower surface paler, with very scattered bristles on the veins, with 6–10 pairs of veins, these repeatedly rebranched and anastomosing, petiole 2–5 mm. long, bristly; inflorescence cymose-paniculate, loose or dense, 2–10 cm. in diameter, bristly and usually also with minute curly brownish pubescence, borne at the forks of the stem; calyx usually somewhat puberulent and strigose, more or less bristly especially about the apiculate apex, papery in texture and very obscurely ribbed, opening irregularly to form several very irregular lobes, frequently persisting and eventually breaking up into fibers; calyx in the bud ovoid or ellipsoid, ca. 5 mm. long; corolla white, tube 4–6 mm. long, lobes 2–3 mm. long, filaments hairy at base, 3–4 mm. long; style and ovary hairy; fruit usually more or less bristly; stone transversely ovoid, 13–17 mm. long.

In British, Dutch and French Guiana and widely distributed in the Amazon Basin; also in the headwaters of the Orinoco (in southern Venezuela and eastern Colombia) and in northwestern Venezuela.

British Guiana: Amakura River, 5 m. tall, March 1923, *La Cruz 3430* (G); Barima River, March 1896, *Jenman 7055* (K); Kamakusa, upper Mazaruni, ca. long. 59° 50', 1922–23, *La Cruz 2887* and *4231* (G); Macouria River, Nov. 1886, *Jenman 2391* and *2392* (K); Tumatumari, dense upland forest, shrub 2.5–6 m. tall, 1921, *Gleason 311* (K); Kaieteur Falls, Potaro River, 1923, *La Cruz 4407* (G); island in Cuyuni River below Kamaria Falls, 18 dm. tall, 1920, *Bailey 40* (G); Kartabo region, second growth forests, 1920, *Bailey 29, 41* and *42* (G); Bonasika Creek, at sea-level, *Anderson 66* (K); Moraballi Creek, small tree up to 6 m. tall, in low brush and clearings in mixed forest, fl. white, fruit bristly, becoming pale red, Aug. 15, 1929, *Sandwith 12* (K, BD); Rockstone, dense upland forest, 2.5–3 m. tall, 1921, *Gleason 583* (K); Blue Mts., Demerara, fruit red, hairy, sweet and clammy, an expectorant, *Parker 272* (K); Demerara

River, May 1889, *Jenman 4924* (K); Malaroo Creek, Corantyne River, small tree, 3–6 m. tall, Oct. 1879, *im Thurn* (K, P); indefinite, *Schomburgk 904* (K) and *984* (K, BM, BD, P).

DUTCH GUIANA: Kaboeri Reserve, Corantyne River, tree no. 684, Nov. 1920 and Aug. 1922, *B. W. 4835* and *5986* (Utr); mouth of Lucie River, Corantyne River, 1910, *Hulk 315* (Utr); way to Kwatta, Paramaribo, June 1916, *Samuels 237* (G, Leid, BD, P); Station at Groningen, forest, May 1916, *Samuels 123* (G, K, Leid, BD, P); Watramiri reserve, Saramacca River, June 1918, *B. W. 3864* (Utr); Watramiri reserve, tree no. 1652, mature fruit yellow, soft and sweet, Dec. 1916, *B. W. 2488* (Utr); Watramiri, tree no. 1652, used for tea, May, 1916, *B. W. 1911* (Utr); Watramiri reserve, tree no. 1652, April 1917, Oct. 1917, July 1918, and Feb. 1920, *B. W. nos. 2756, 3309, 3872* and *4541* (Utr); Watramiri reserve, tree no. 1652, fl. white, *B. W. 4012* (Utr); Watramiri reserve, tree no. 1652, March 1919, ripe fruit sordid white, *B. W. 4301* (Utr); Sectie O. reserve, upper Para River, tree no. 800, fl. light green, leaves used for tea, Aug. 1916, *B. W. 2306* (Utr); woods near Poelebantji, tree 4–6 m. tall, Feb. 1845, *Kegel 691* (Utr); Brownsberg, Surinam River, tree 10 m. tall, trunk 1 dm. thick, fl. sordid white, Sept. 1915, *B. W. 727* (Utr); Brownsberg reserve, tree no. 1174, fl. white, dried leaves used as a substitute for tea, fruit yellow, globose, soft and juicy, Nov. 1916, *B. W. 2498* (Utr); Brownsberg reserve, tree no. 1174, fl. white, Sept. 1918, *B. W. 4002* (Utr); Brownsberg reserve, tree no. 1174, March 1917, Feb. 1919 and March 1921, *B. W. nos. 2721, 4265* and *5075* (Utr); Brownsberg reserve, tree no. 1174, fl. sordid white, with strong odor, Sept. 1923, *B. W. 6227* (Utr); Brownsberg reserve, tree no. 1174, fl. sordid white, odor strong, Nov. 1924, *B. W. 6684* (Utr); Brownsberg summit, July 1924, fl. white, *B. W. nos. 6634* and *6722* (Utr); woods near Raleigh Falls, Coppename River, hispid tree, fl. yellowish white, fruit white, hispid, Sept. 11, 1933, *Lanjouw 788* (Utr).

FRENCH GUIANA: Maroni, 1864, *Mélinon* (G, Del, P); Ile Portal, Maroni River, *Sagot* (P); Ile Portal, fruit white, soft, size of a grape, June 1857, *Sagot 446* (P); Acarouani, tree, corolla pale yellowish, sepals 4, stamens 4, Oct. 1854, *Sagot 446* (P); Acarouani, 1854, *Sagot* (P); Acarouani, fruit red, April 1858, *Sagot 446* (P); Acarouani, 1859, *Sagot* (P); Acarouani, fruit pale yellow, 1854, *Sagot 446* (P); Godebert, *Wachenheim 410* (P); in loco Macaya ad praedicem Patuis, *Richard* (P) vicinity of Cayenne, hill above Grant's Road, Montabo, shrub, 1921, *Broadway 543* (G, K); Cayenne, *Martin* (BM, BD, P); Cayenne, March 1859, *Sagot* (P); Cayenne, *Patris* (BM, Del); indefinite, 1850, *Leprieur* (BM, P); indefinite, *Aublet* (BM, TYPE of *C. nodosa*); indefinite, *Perrottet 214* (Del, DC) and *Poiteau* (K, BD, P).

BRAZIL: Carmo, Rio Branco, Sept. 1, 1924, *Bequaert* (G); Surumu, Serra do Mairary, Rio Branco, tree or shrub 2–8 m. tall, fl. white, Nov. 1909, *Ule 8456* (K, BD); Rio Negro below mouth of Xibarú, betw. Barcellos and São Gabriel, Dec. 1854 *Spruce 3790* (NY, K, Del); Rio Cuminá, *Sampaio 5136* and *5148* (BD); near Montalegre, Nov. 24, 1873, *Traill 561* (K); Prainha, Dec. 17, 1873, *Traill 562* (K).

VENEZUELA: Casiquiari, in shade along streams, fl. white, tree 6 m. tall, Jan. 1853, *Spruce 3281* (G).

This is a classic ant-plant. The results of an anatomical study and a review of the more important literature on this plant have been published recently by I. W. Bailey, Bot. Gaz. **77**: 32–49, tab. 6–7 (1924). According to this author the peculiar subnodal structures serving as ant-domatia are "formed by an invagination of epidermal, cortical, and fibrovascular tissues which originate in the axil of one of the leaves of the false verticil, and which develops into the interior of a more or less symmetrical or unilateral, subnodal enlargement of the cauline axis."

The attention drawn by the complex ant-domatia has, I believe, blinded students to the evident relationships of this remarkable plant. The flowers and fruit are very similar to those found in *C. Sprucei* and its relatives. The apiculate, papery, irregularly disrupted calyx, the hairy ovary and style, and the transversely ovoid stone, not to mention the glabrous upper leaf-surfaces, comparatively stiff and contracted inflorescence, etc., all indicate close relations with that group of upper Amazon and Guianan species. *Cordia nodosa* has only three notable peculiarities, its subnodal swellings, its bristly indument, and its fibrous calyx. In the past the species has been placed in a special section, ***Physoclada,*** of the genus *Cordia*. I have become so impressed with its obvious relations with *C. Sprucei* and allies, however, that I now am quite content to associate it with these species in the section *Pilicordia*.

The species is very variable both in the size and shape of its leaves, and in the abundance of the bristles on its herbage. This variation seems to be ecological in origin. In any case I can find no evidence that it is in any way geographically correlated. It should be noted that collectors have given the fruit in British Guiana as red. In Dutch and French Guiana the fruit is given as white or whitish in numerous cases, and once as yellow.

Aublet gives the Carib name for the plant as "Achira-mourou." The following vernacular names are associated with specimens cited: Courabelli ants plant—*Anderson 66;* Ylŭrĭ-hee-lĕvĭ-koŭ—*Parker 272;* Hurneyreyroko—*Sandwith 12;* Awelemoeloe (Kar.)—*B. W. 727;* Marribonsoehoedoe (Neg. Eng.), Horowejoreroko (Arow.), Arreuonoe (Kar.)—*Tree no. 1652 at Watramiri;* Mattoe toenbalobbi (Sar.), Horowé, joee lokko, Hoereuereroko (Arow.), and Awali emoeloe, Aloeko uonoré (Kar.)—*Tree 800 at Sectie O.*

6. **Cordia laevifrons,** sp. nov.

Arbor minor vel frutex, dichotome ramosus; ramulis fuscis, apicem versus dense puberulis mox glabrescentibus; foliis vix crassis ellipticis ad lanceolato-oblongis vel oblongo-obovatis 12–25 cm. longis 6–14 cm. latis saepe ad medium vel supra medium latioribus, basi obtusis vel plus minusve rotundis vel late acutis, apice saepe abrupte acuminatis, supra lucentibus saepe in costa pilos paucos adpressos gerentibus ceteris glaberrimis, subtus pallidioribus glabris vel sparsissime minutissimeque ascendenter adpresseque pubescentibus, nervis primariis 6–8-jugatis, nervis tertiariis obscuris, petiolis 5–18 mm. longis; cymis saepissime in furcis ramulorum ortis, laxe graciliterque ramosis 3–15 cm. diametro, pedunculo gracili; corolla alba glabra, tubo 6 mm. longo calycem superante, lobis 2 mm. longis rotundis latis, filamentis 4 mm. longis longe exsertis basim versus pilosis; calyce in alabastro anguste obovato 4–5 mm. longo extus dense puberulento (intus subglabro) obscure lateque 10-costato, apice plus minusve apiculato ad anthesin in lobos irregulares lacerulatos disrupto, fructifero explanato; stylo et apice ovarii sparse minuteque hispidulo; fructu glaberrimo; nuce transverse ovoideo 10–14 mm. longo.

Endemic to French and Dutch Guiana.

DUTCH GUIANA: Lucie River, a small tree 6 m. tall, fl. white, April 12, 1926, *B. W. 6999* (Utr); forest near Abontjeman, May 1910, *native collector 236* (TYPE, Utrecht).

FRENCH GUIANA: Maroni River, 130 km. upstream, fruit edible, 1877, *Crevaux* (P); along the Maroni, 1861, *Mélinon 16, 59, 254* and *271* (P); along the Maroni, 1863, *Mélinon 283* (P); Maroni, along road to St. Laurent, clearings, 15 dm. tall, fl. white, Oct. 1876, *Mélinon 225* (P); St. Jean, 2 m. tall, fl. white, May 16, 1914, *Benoist 1230* (P).

A relative of *C. Sprucei* notable chiefly for its rather thin, nearly glabrous leaves, puberulent obscurely ribbed calyces, and quite glabrous fruits. As with other relatives of *C. Sprucei* the veins of the leaves are not so finely rebranched as is common in this section of the genus. Crevaux gives the bush-negro name of the plant as "Tiki Topichi."

7. **Cordia Sprucei** Mez, Bot. Jahrb. **12**: 549 (1890); Johnston, Contr. Gray Herb. **92**: 53 (1930). *Lithocardium Sprucei* (Mez) Kuntze, Rev. Gen. **2**: 977 (1891).

Tree 4–5 m. tall, branching dichotomous; branchlets dark, sparsely short-hirsute or with short incurved hairs; leaves drying brown, subhomomorphic, elliptic or oblong-obovate, 12–23 cm. long, 6–11.5 cm. broad, broadest at or above the middle, apex acuminate, base acute to truncate, upper surface somewhat lustrous, hairy along the midrib and with scattered hairs along the principal veins but otherwise glabrous, lower surface with rather abundant short soft erect hairs, petiole 5–10 mm. long, veins in 6–9 pairs, tertiary veins tending to be obscure; inflorescence rather loosely though rigidly branched, ca. 1 dm. thick, usually borne at the forks of the stem, rarely terminal; calyx well covered with short incurving tawny hairs, obscurely ribbed, obovate in the bud and apiculate, 4–5 mm. long, ca. 2.5 mm. thick, bursting rather irregularly at the apex into 2–5 broad rather thin teeth; corolla white, tube 4–5 mm. long, lobes broad ca. 1.5 mm. long, filaments hairy at base, 4 mm. long; ovary densely hairy above the middle; fruit yellow, strigose; stone transversely ellipsoid, 1–1.5 cm. long.

Known only from the Rio Negro of Brazil and from French Guiana.

FRENCH GUIANA: "in Sylvis doeciduis Fluvii Kourou, ad casam indi Felix," Nov., *Richard* (P).

BRAZIL: Barra do Rio Negro, 1850–51, *Spruce 1019* (Munich, TYPE; BD, frag; G, photo.); vicinity of Barra, 1850–51, *Spruce* (G, K, BM); Barra to Matiriho, Jan. 1851, *Spruce 1234* (K, BM); Barra, fruit yellow, transversely oblong, April 1851, *Spruce 1234* (K, BM, Del); São Gabriel, Rio Negro, ca. 90 m. alt., 1930–31, *Holt & Blake 608* (G).

Richard's label gives the following field data concerning his collection from French Guiana,—"frutex 3–4 ped., ramis diffuse patentibus, dichotomis; fl. albidi; ramillis cymae recurvis et, inexpansis floribus, revolutis." The collections are remarkably similar to Spruce's material from the lower Rio Negro, except that in one of Richard's two sheets the branches of the inflorescence are somewhat tawny tomentulose.

Since discussing the type of *C. Sprucei*, l. c., I have examined the actual type-specimen at Munich. The specimen has the following familiar printed label reading, "In vicinibus Barra, Prov. Rio Negro, coll. R. Spruce, Dec.-March, 1850–51." The collector's number, in script, is "1019." The specimen is that cited under *C. umbraculifera* in the Flora Brasiliensis. It is evidently part of the same collection as the unnumbered specimens I have seen at the Gray Herbarium, at Kew, and at the British Museum.

This species not only has relatives in *C. nervosa* and *C. laevifrons* of the Guianas but also in undescribed trees of the Putumayo and the Huallaga of eastern Peru. The glabrous upper leaf-surfaces and the somewhat papery irregularly disrupted apiculate calyces are characters of this group of species.

8. **Cordia nervosa** Lamarck, Tab. Encyc. **1**: 422 (1791); Poiret, Encyc. **7**: 47 (1806); DeCandolle, Prodr. **9**: 484 (1845). *Lithocardium nervosum* (Lam.) Kuntze, Rev. Gen. **2**: 977 (1891). *Cordia calophylla* Vahl, Ecolog. **3**: 5 (1807); DeCandolle, Prodr. **9**: 486 (1845). *Lithocardium calophyllum* (Vahl) Kuntze, Rev. Gen. **2**: 976 (1891).

Shrub or small tree, up to 5 m. tall; branchlets closely and antrorsely strigose; leaves homomorphic, stiff and coriaceous, with an arcuate midrib, broadly lanceolate to elliptic or lance-oblong, 10–25 cm. long, 4–10 cm. broad, margin weakly recurved, apex acuminate, base rounded to acute and usually more or less oblique and asymmetrical, upper surface glossy, smooth and quite glabrous, lower surface drying brown, dull, somewhat scabrous with abundant short inconspicuous hairs, with 8–10 pairs of primary veins, these connected by simple branches, the secondary branches of the veins absent or very obscure; petiole canaliculate, stiff, 5–10 mm. long; inflorescence small and compact, 1–4 cm. long, peduncles very short or none, branches slender, strictly forked, bearing flowers on only one side and in age studded with the elevated pedicellar flower-attachments, becoming rigid and woody in age and more or less spreading or deflexed, persistent long after the falling of the fruit; calyx obovoid in bud, 4–5 mm. long, minutely short-strigose, more or less apiculate, not at all ribbed, sparsely strigose inside, bursting apically and the lobes torn and irregular, in fruit explanate; corolla white, tube ca. 5 mm. long, lobes broad, ca. 3 mm. long, filaments very hairy; ovary glabrous or sparsely hairy towards the apex; style usually sparsely hairy; fruit minutely and abundantly strigose, pulp bright red, glutinous, insipid; stone transversely ovoid, 10–13 mm. long.

French Guiana and adjacent Brazil; British Guiana.

British Guiana: Kaieteur Savanna, spreading shrub 18 dm. tall, 1881, *Jenman 1062* (K).

French Guiana: Cayenne, 1857, *Mélinon* (P); Gourdonville, Kourou River, shrub, fl. white, Sept. 25, 1914, *Benoist 1618* (P); in umbrosis sylvis praedii Dm. [?] Patuis, *Richard* (P); indefinite, *herb. Lamarck* (Paris, TYPE of *C. nervosa*); indefinite, *von Rohr 152* (herb. Vahl, TYPE of *C. calophylla;* BM, isotype); indefinite, 1859, *Leprieur* (Del); indefinite, 1819–21, *Poiteau* (K, Del).

Brazil: Counany, Oct. 13, 1895, "Chapeo del Sol," *Huber 1032* (Boiss).

The type of *C. nervosa* in the Lamarck herbarium is so very similar to the material collected by Richard (in the General Herbarium at Paris) that I believe they are parts of a single collection or, in other words, that the type of *C. nervosa* was collected by Richard. Unfortunately, I have been unable to identify Richard's locality with any degree of confidence. At Paris I found on the label of a very different species the following more explicit mention of the probable locality, i. e. "in loco Dm. [spelling?] Macaya ad praedicem Dm. [?] Patuis." There was formerly a sugar plantation called Macaya on the Ile de Cayenne several kilometers east of Matoury. This may have been that referred to by Richard, for he is known to have collected extensively about the Island of Cayenne as well as over most of the French Guianan coastal region.

It is interesting to note that Richard has appended to his specimen a manuscript name, under *Collococcus*, in which the same specific epithet is used as was subsequently published by Vahl. Richard and von Rohr were both in the Guianas about 1785. These facts naturally make one wonder if there may not have been some meeting or some exchange of material between these two botanists and possibly if Vahl's type may not have had the same source as that of Lamarck.

The species is an unusually distinct one, being notable because of its suppressed tertiary leaf-veins and small dense subsessile inflorescence. Its closest relations are with *C. Sprucei* and *C. laevifrons* which have similar somewhat papery, irregularly dehiscent apiculate calyces. In *C. Sprucei* the veins are more repeatedly branched than in *C. nervosa*, though generally less so than in other species of the section *Pilicordia*.

9. **Cordia fulva**, sp. nov.

Arbor vel frutex, dichotome ramosus; ramulis brunneis cum pilis brevibus divergentibus abundantissimis velutinis; foliis subhomomorphis crassiusculis ellipticis vel ovatis 10–22 cm. longis 7–11 cm. latis saepe ad medium vel supra medium latioribus, basi obtusis vel rotundis vel rariter acutis, apice breviter acuminatis, supra scabris pilis brevibus rigidusculis ascendentibus vestitis, subtus saepe brunnescentibus velutinis in nervis et nervulis elevatis et numerosis pilos graciles erectos abundantes gerentibus, nervis 5–7-jugatis, petiolis brevibus; cymis in furcis ramulorum ortis vel rariter terminalibus, rigidis brunneo-velutinis laxe ramosis, floribus in ramulis plus minusve congestis; calyce in alabastro obovato 4–5 mm. longo 2–3 mm. crasso evidenter 10-costato extus brunneo-velutino intus supra medium strigoso; lobis 5 deltoideis; corolla alba, tubo 5 mm. longo, lobis ca. 2.5 mm. longis et latis, filamentis 4–5 mm. longis basim versus pilosis; ovario apicem versus dense longeque pilosis; fructu evidenter velutino; nuce transverse ovoideo 1–1.5 cm. longo.

Known only from northern Dutch Guiana and adjacent French Guiana.

DUTCH GUIANA: near Abontjeman, in forest, May 1910, *native collector 227* (Utr); near Gold Placers, April 14, 1910, *native collector 103* (Utr).

FRENCH GUIANA: Maroni, shrub 3 m. tall, in clearings, fl. white, branches horizontal, 1877, *Mélinon 137* (TYPE, Gray Herb.; isotype, Paris); Maroni, *Mélinon 455* (G, P); Maroni, *Wachenheim 75* (G, P); indefinite, 1862, *Mélinon 82* (P); indefinite, 1821, *Perrottet* (P).

Related to *C. trichoclada* DC. and *C. Chamissoniana* Don, of eastern Brazil, this species differs from the former in its velvety rather than bristly stems, more softly hairy scarcely bullate leaves, looser less stiffly branched larger inflorescences and slightly smaller calyces, and from *C. Chamissoniana* in its more hairy leaves and conspicuously ribbed, more tawny calyces.

10. **Cordia toqueve** Aublet, Hist. Pl. Guian. Fr. **1:** 228, tab. 90 (1775); Poiret, Encyc. **7:** 44 (1806); DeCandolle, Prodr. **9:** 488 (1845); Johnston, Contr. Gray Herb. **92:** 52 (1930). *Lithocardium toqueve* (Aubl.) Kuntze, Rev. Gen. **2:** 977 (1891). *Cordia heterophylla* Poiret, Dict. Sci. Nat. **10:** 409 (1818); Willdenow ex Roemer & Schultes, Syst. **4:** 800 (1819); Chamisso, Linnaea **4:** 480 (1829); DeCandolle, Prodr. **9:** 487 (1845). *Lithocardium heterophyllum* (Poir.) Kuntze, Rev. Gen. **2:** 977 (1891). *Cordia pubescens* Willdenow ex Roemer & Schultes, Syst. **4:** 800 (1819). *Lithocardium pubescens* (Willd.) Kuntze, Rev. Gen. **2:** 977 (1891). *Toquera tomentosa* Rafinesque, Sylva Tellur. 40 (1838). *Cordia hebecarpa* DeCandolle, Prodr. **9:** 488 (1845). *Lithocardium hebecarpum* (DC.) Kuntze, Rev. Gen. **2:** 977 (1891).

Tree; branchlets velvety with abundant soft more or less curled brown hairs; leaves strongly dimorphic, upper surface with rather abundant short straight ascending hairs, lower surface velvety with curved soft slender spreading hairs from the prominent and numerous veins and veinlets; larger principal leaves very broadly lanceolate to lance-ovate, broadest towards the base, 1–3 dm. long, 6–15 cm. broad, above the middle contracted to an acute or acuminate apex, base obtuse to rounded, somewhat oblique; smaller sort of leaves more or less orbicular, 5–12 cm. long, 5–11 cm. broad, broadly obtuse or even subcordate at base, rounded or acuminate at apex; inflorescence loosely and slenderly branched, 1–1.5 dm. broad; calyx obovoid in bud, 2.5–3 mm. long, opening by 5 triangular lobes, unribbed, strigose inside, outside covered with a dense indument of appressed slender curved hairs; calyx becoming somewhat cupulate at maturity, ca. 1.5 mm. deep; corolla white, tube 2.5 mm. long, lobes 1.5 mm. long, filaments 2 mm. long, hairy near base; ovary densely hairy at apex; fruit abundantly tawny-strigose, style-base forming a short eccentric beak; stone ovoid, strictly ascending, ca. 1 cm. long.

Confined to French Guiana and eastern Brazil.

French Guiana: vicinity of Cayenne, small tree, fruit yellowish, May 16, 1921, *Broadway 201* (G); near Cayenne, fl. yellow, 1897, *Soubiron* (P); near Cayenne, July 1841, *Mélinon 243* (Leid, P); Cayenne, Feb. 1859, *Sagot* (P); Cayenne, *Martin* (K); Cayenne, *Leblond, ex Mus. Paris 348* (BD, P); Cayenne, *ex Mus. Paris sine no.* (G, BD); Cayenne, *Herb. Willd. sub no. 4574* (BD, TYPE of *C. heterophylla* Willd.); Cayenne, *Herb. Poiret* (P, TYPE of *C. heterophylla* Poir.); indefinite, *Aublet* (BM, TYPE of *C. toqueve*); indefinite, *Poiteau* (K); indefinite, 1859, *Leprieur* (Del).

The original material of this species was collected by Aublet in clearings made by the Caribs about 15 leagues up the Sinnamary River. The tree was called "Toquévé" by these inhabitants of French Guiana. I have seen Aublet's specimen at the British Museum. This material, taken in conjunction with Aublet's illustration and lengthy description, leaves no doubt as to the correctness of the present application of the name.

At Paris among Poiret's specimens (in the Cosson collections) there is a fragmentary specimen of the present species accompanied by a label in Poiret's script reading, *Cordia heterophylla,* folia altera majora et minora, rami asperi, hirti. Caienne. Added to the label in another, and unrecognized hand is "dict. des Sc. nat. herb. Poiret." Poiret stated that *Cordia heterophylla* was seen in the Desfontaines herbarium. The specimen in the Poiret collections at Paris is, I believe, a fragment of the type of *C. heterophylla* Poir., now probably conserved at Florence.

The binomial *"C. heterophylla"* is found on a specimen of *C. toqueve* in Willdenow's herbarium at Berlin and was published by Roemer & Schultes a year after Poiret's published use of the name. The specimen is also given as from "Cayenne" and may be a duplicate of the specimen described by Poiret.

Cordia toqueve is readily distinguished among the South American species by its tawny velvety indument, strikingly dimorphic leaves, and conspicuously hairy fruit. It is known only from Bahia, Ceará and Pernambuco in Brazil, and from near Cayenne in French Guiana. The Brazilian plant, which is quite like that from the Guianas, has been described as *C. hebecarpa* DC.

11. **Cordia scabrifolia** A. DeCandolle, Prodr. **9:** 485 (1845); Johnston, Contr. Gray Herb. **92:** 53 (1930); Brade, Bol. Mus. Nac. Rio Janeiro **8:** 34 (1932).

Tree or shrub up to 15 m. tall, branching dichotomous; branchlets dark, abundantly and minutely antrorse-strigose; leaves homomorphic, ovate- to oblong-lanceolate, 11–18 cm. long, 4–7 cm. broad, broadest near the middle, apex acuminate, base acute to somewhat rounded; upper surface drying dark, abundantly and very minutely antrorse-strigose, lower surface drying light, bearing numerous very minute very short appressed hairs on the abundant veins and veinlets, the hairs tending to be directed centripetally towards the middle of the veinlet-areoles, petiole 4–9 mm. long, veins in 5–8 pairs, repeatedly rebranched; inflorescence usually borne at the forks of the stems, pedunculate, slender, loosely branched, 4–10 cm. broad; calyx obovoid in the bud, ca. 3 mm. long, densely strigose, opening by 5 subequal triangular lobes, strigose inside, base substipitate; corolla white, tube ca. 3 mm. long, lobes ovate, ca. 2 mm. long, filaments exserted, hairy at base; style and at least the apex of the ovary hairy; fruit densely and minutely strigose; stone ovoid, ascending, ca. 1 cm. long.

Probably restricted to the Amazon Basin; doubtfully reported from British Guiana.

British Guiana: indefinite, *Schomburgk 911* (Boiss, type; isotypes, K, BM, BD, P).

Brazil: Prainha, Nov. 1873, *Traill 563* (K); Rio Cuminá, Oct.-Nov. 1928, *Sampaio 5367, 5505* and *5510* (BD); Rio Negro-gapó above Cabuquena, Dec. 1851, *Spruce 1942* (K, BM).

Except for the type-collection, *Schomburgk 911,* which is given as from British Guiana, all known collections of *C. scabrifolia* come only from within the Amazon Basin. I suspect that the type also came from the Amazon watershed and from what is now Brazil. Schomburgk, Fauna u. Fl. Brit. Guiana 960 (1848), reports the species from the upper Essequibo. It is significant, however, that no other collectors have found it in British Guiana and that, in the notes of Robert Schomburgk, plant no. 911, which certainly seems to apply to this species, refers to a collection almost certainly from the Rio Negro watershed. In the list no. 911 has no locality indicated but the adjacent numbers, where the locality is indicated in several instances, all do come from Barcellos on the Rio Negro.

12. **Cordia bicolor** A. DeCandolle, Prodr. **9:** 485 (1845); Pulle, Enum. Pl. Surinam 397 (1906). *Lithocardium bicolor* (A. DC.) Kuntze, Rev. Gen. **2:** 976 (1891). *Cordia dichotoma* Klotzsch ex Schomburgk, Fauna u. Fl. Brit. Guiana 1084 (1848), nomen; not Forst. (1797). *Lithocardium Lockartii* Kuntze, Rev. Gen. **2:** 438 (1891). *Cordia Lockartii* Kuntze, Rev. Gen. **2:** 438 (1891), in synonymy. *Cordia trichostyla* Pittier, Contr. U. S. Nat. Herb. **18:** 252, fig. 102 (1920). *Cordia carnosa* Rusby, Three Hundred N. Sp. So. Amer. Pl. 104 (1920). *Cordia coriacea* Killip, Jour. Wash. Acad. Sci. **17:** 329 (1927). *Cordia sericicalyx* sensu Johnston, Contr. Gray Herb. **92:** 54 (1930).

Shrub or small tree up to 6 m. tall, branching dichotomous; branchlets angulate, velvety with very abundant spreading usually tawny short hairs; leaves homomorphic, ovate to more or less broadly lanceolate, broadest at or below the middle, 8–16 cm. long, 2.5–7 cm. broad, apex acuminate, base acute to rounded, upper surface dark, finely strigose, lower surface very pale, covered by appressed slender hairs that are borne on the veins and veinlets and which converge over and cover the veinlet-areoles; veins in 5–7 pairs, repeatedly rebranched; petiole 5–10 mm. long; inflorescence usually at the forks of the stem, loosely branched; calyx in bud ca. 4 mm. long, obovoid, clothed with abundant short appressed more or less tawny hairs, inner surface with numerous appressed longer white hairs, opening by 5 subequal triangular lobes; corolla white, tube ca. 3 mm. long, lobes ca. 2.5 mm. long, filaments hairy near base; style and upper part of ovary hairy or these exceptionally glabrous; fruit glabrescent; stone transversely ovoid, over 1 cm. long.

Occurring in the Amazon headwaters of Bolivia; east and south of the Amazon Basin in Brazil; and across northern South America from Dutch Guiana to eastern Colombia; apparently very sporadic in occurrence, widely distributed but not common. Also in Central America and in the southern-most West Indies.

BRITISH GUIANA: Oreala, Corantyne River, Oct. 1879, *Jenman 7* (K); indefinite, *Schomburgk "109"* (K); indefinite, *Schomburgk 601* (BM).

DUTCH GUIANA: indefinite, *Hostmann 406* (DC, TYPE of *C. bicolor*; isotypes, K, BD, Del, P); indefinite, *Hostmann & Kappler 406* (Munich); indefinite, *Kappler 406* (P).

BRAZIL: Roraima, 1200 m. alt., corolla white, Feb. 1910, *Ule 8748* (K, BD); Roraima, 1842–43, *Schomburgk 678* (Del, P); indefinite, *Schomburgk 678/1032* (K); indefinite, Nov. 1842, *Schomburgk 1032* (BD, TYPE of *C. dichotoma*).

VENEZUELA: Lower Orinoco, 1896, *Rusby & Squires 418* (NY, TYPE of *C. carnosa*).

In my paper on the Brazilian cordias I quite incorrectly applied the name *C. sericicalyx* to this present species. The type of *C. sericicalyx* is *Schomburgk 109*. There is material of *C. bicolor* at Kew and the British Museum, however, which bears Schomburgk's no. 109. Mr. Killip has suggested to me that this may have resulted from inverting no. 601. Reexamination of the specimens makes me believe this suggestion is correct, especially since one finds in Robert Schomburgk's notes (for nos. 589–700 incl.), which were forwarded from Curasscuraka (on the Rupununi at the base of the Annai Hills) on Feb. 1838, that no. 601 bears the following appropriate data, "a shrub with brown bark growing like the table tree, leaves green, below silvery, calyx light green, petals white, filaments and anthers cream-colored." No locality for no. 601 is given, but it is certain that the gamut of numbers to which it belongs was collected either during the exploration south to the Akarai Mts., on the Brazilian border, or about the Annai savannas.

Schomburgk's nos. 678 and 1032 appear on printed labels as from "Roraima." Schomburgk approached the base of that mountain from the south (Brazilian territory) along the Kukenam River. It will be noted that Schomburgk, Fauna u. Fl. Brit. Guiana 1084 (1848), reports *C. dichotoma* only from the banks of that Brazilian stream.

13. **Cordia sericicalyx** A. DeCandolle, Prodr. **9:** 485 (1845); Pulle, Enum. Pl. Surinam 397 (1906); not Johnston, Contr. Gray Herb. **92:** 54 (1930). *Lithocardium sericicalyx* (A. DC.) Kuntze, Rev. Gen. **2:** 977 (1891). *Cordia sericicalyx* var. *latifolia* Miquel, Stirp. Surinam. 140 (1850). *Cordia ierensis* Britton, Bull. Torr. Bot. Cl. **50:** 54 (1923).

Tree 3–6 m. tall, branching dichotomous; branchlets slender, finely strigose; leaves conspicuously heteromorphic, firm but rather thin and smooth, much paler beneath, finely strigose on both surfaces, veins repeatedly branched and anastomosing; larger leaves oblong to broadly lanceolate, 11–25 cm. long, 5–12 cm. broad, usually broadest below the middle, base obtuse or broadly acute, midrib somewhat arcuate, veins in 7–11 pairs, petiole densely strigose, 5–20 mm. long; smaller leaves elliptic to orbicular-ovate, 6–8 cm. long, 3–7.5 cm. broad; cymes loose, 5–20 cm. broad, branches slender, usually borne at the forks of the stems; calyx sessile, 5-toothed, outside completely covered with minute appressed silky hairs, inside above the middle densely villous-strigose with the hairs projecting a little beyond the edge of the calyx and so appearing as ciliate margins of the lobes; calyx at anthesis 3–4 mm. long, 1.5–2.5 mm. broad, unribbed, in fruit becoming explanate; corolla ca. 5 mm. long, glabrous, lobes obovate, filaments exserted, pilose near base; ovary and style glabrous; fruit glabrous; stone very rough, depressed, weakly asymmetric 8–10 mm. broad.

Ranging from Dutch Guiana westward to the Orinoco and apparently to Trinidad.

British Guiana: indefinite, *Schomburgk 109* (DC, type of *C. sericicalyx;* isotypes BD, P).

Dutch Guiana: Wayombo River near Cornelis Kondre, tall tree, fl. greenish white, Jan. 23, 1915, *B. W. 824* (Utr); Para District, in forest, Feb.-April, 1844, *Kappler 1510* (Utr, type of var. *latifolia;* isotypes, Leid, BD, Del, P).

Venezuela: lower Orinoco, 1896, *Rusby & Squires 282* (NY, K) and *259* (K).

In my paper on the Brazilian species of *Cordia* I incorrectly applied the name *C. sericicalyx* to the concept properly called *C. bicolor*. Some of the details of this confusion will be found discussed under *C. bicolor* in the present paper.

The type of *C. sericicalyx* is *Schomburgk 109,* given merely as from British Guiana. The species is not listed in Schomburgk's "Fauna und Flora von Britisch Guiana," although possibly it may be the basis for the otherwise unintelligible report of *C. heterophylla,* l. c. 960 (1848), which is listed as on the Demerara and Essequibo. Of all the cordias collected by the Schomburgks, *Cordia sericicalyx* has the most pronounced dimorphic leaves and hence is the one most apt to be associated with the appropriate but incorrect name, *C. heterophylla*.

The type of *C. sericicalyx* var. *latifolia* Miquel has been examined. It is not separable from the typical form of the species. Miquel gives the type of his variety as "*Kappler 1500*." The type-specimen, however, is clearly numbered "*1510*"!

In defining *C. sericicalyx* I have excluded a very closely related form which seems to replace our Guianan plant across the northern parts of Venezuela and Colombia. This form, called *C. opaca* Rusby, is a more slender plant with more elongate, frequently more or less ribbed, fulvous calyces, very sparsely hairy, short filaments, and firmer, usually more lanceolate leaf-blades.

The specimen of *C. sericicalyx* from Cornelis Kondre is associated with two vernacular names. These are Omosé (Kar.) and Kakóro (Arow.).

14. **Cordia panicularis** Rudge, Pl. Rar. Guian. 30, tab. 46 (1805). *Lithocardium paniculare* (Rudge) Kuntze, Rev. Gen. **2:** 976 (1891).

Shrub or large tree, 3–20 m. tall, dichotomous or trichotomous; branchlets drying dark, sparsely strigose, loosely branched; leaves subhomomorphic, lucent, elliptic to lance-elliptic or broadly lanceolate, 1–2 dm. long, 4–7.5 cm. broad, broadest at or just below the middle, mature leaves usually drying quite brown, apex long-acuminate, base obtuse, both surfaces sparsely strigose or beset with minute very short ascending hairs arising from inconspicuous pustulate bases, lower surface slightly the paler; veins in 5–6 pairs, evident, repeatedly rebranched; petiole 5–10 mm.; cymes loose, 5–30 cm. broad, borne at the forks of the stem; calyx sessile, 5-toothed, 4–5 mm. long, subcylindric or obconic-cylindric, terete or very obscurely angulate, outside rather sparsely strigose, inside densely villous-strigose, becoming explanate in fruit; corolla glabrous, ca. 8 mm. long, lobes obovate to oblong, 2–3 mm. long, filaments hairy near base; ovary and style glabrous; fruit glabrous; stone very rugose, depressed, weakly asymmetric, 8–10 mm. broad.

Known only from the Guianas.

British Guiana: Potaro Landing, clearings and roadsides, shrub 3–4.5 m. tall, 1921, *Gleason 259* (NY, K); Tumatumari, dense upland forest, tall shrub, almost vine-like, 1921, *Gleason 156* (NY, K); Bootooba, sand-hill in forest, Oct. 1924, *Persaud 184* (BD, NY).

Dutch Guiana: near Patricksavanna, in forest, May 1910, *native collector 182* (Utr); Brownsberg Summit, June 1924, tree 20 m. tall, *B. W 6513* and *6519* (Utr.).

French Guiana: Acarouani, fl. white, 1857, *Sagot 448* (K, P); Acarouani, 1854, *Sagot 448* (P); Acarouani, medium-sized tree or shrub, Oct. 1856, *Sagot* (K, P); Cayenne, *Martin ex herb. Rudge* (BM, type); Cayenne, *Martin* (K, P); Cayenne, *Martin 151* (P).

The type of *C. panicularis* is a young flowering branch bearing leaves not yet stiff and somewhat coriaceous as they become in the mature state. Sagot has distributed under an unpublished name, sub no. 448, collections of this species made over several years which show both the young and the mature foliage. Although quite different in appearance I am confident that *C. panicularis* and *C. sericicalyx* are close relatives. The rough depressed glabrous fruits in these species are notably similar. The specimen from Brownsberg Summit is given as called "Berg Tafraboom."

15. **Cordia Sagotii,** sp. nov. *Cordia coriacea* Sagot ex Benoist, Archives Bot. 5, Mem. **1**: 257 (1933), not Killip (1927).

Frutex vel arbor 5–10 m. alta, dichotome ramosa; ramulis scabridis pilos minutos numerosos erectos vel ascendentes e basi incrassatos gerentibus; foliis homomorphis ellipticis vel late lanceolatis vel oblongis rigide coriaceis 15–30 cm. longis 7–14 cm. latis medium versus latioribus, basi rotundis vel obtusis vel acutis aliquantum obliquis, apice breviter acuminatis, supra sparse inconspicueque brevi-strigosis, subtus pilis numerosis brevissimis erectis asperatis, nervis 6–8-jugatis abundanter ramosis; petiolis 5–10 mm. longis; cymis saepe in furcis ramulorum ortis sed rariter ut videtur lateralibus, laxissime ramosis 1–3 dm. crassis; calyce in alabastro obovoideo ca. 3 mm. longo sparse striguloso, lobis triangularibus 5; corolla alba fragrante, tubo 4–5 mm. longo, lobis 1.5–2 mm. longis, filamentis 5–6 mm. longis basim versus pilosis; ovario et stylo glaberrimis; fructu glabro flavo; nuce anguste ovoideo erecto ca. 15 mm. longo laevi.

Known only from northeastern Dutch Guiana and northwestern French Guiana.

Dutch Guiana: Sectie O. Reserve, fl. white, Nov. 14, 1917, *B. W. 3414* (Utr); Sectie O. Reserve, tree no. 505, Oct. 23, 1916, *B. W. 1194* (Utr); Sectie O. Reserve, tree no. 506, fruit yellow, April 30, 1915, *B. W. 345* (Utr); Zanderij I. Reserve, tree 176, flower white, fragrant, Nov.

1915, Oct. 1917, Nov. 1919, April 1920, Jan. 1921 and Nov. 1921, *B. W. 1137, 3357, 4433, 4631, 5037* and *5565* (Utr); Zanderij I. Reserve, tree no. 230, fl. white, fragrant, Feb. 1, 1917, Feb. 14, 1917, July 1917, Oct. 1917, and Nov. 1918, *B. W. 2679, 2673, 3026, 3372* and *4067* (Utr.)

FRENCH GUIANA: banks of the Maroni, 1861, *Mélinon 243* (P); Godebert, 1920–21, *Wachenheim 81* and *207* (P); Charvein, fl. white fragrant, shrub 10 m. tall, Dec. 9, 1913, *Benoist 318* (P); Acarouani, medium-sized tree, mature leaves very coriaceous fl. white, fragrant, Dec. 1856, *Sagot 447* (TYPE of *C. coriacea* Sagot and *C. Sagotii*, Paris); Acarouani, 1856, *Sagot 447* (K, P); Acarouani, tall shrub, fl. white, fragrant, mature leaves very coriaceous, 1857, *Sagot 447* (K, BD, P); Acarouani, 1855, *Sagot 447* (K); indefinite, 1863, *Mélinon 63/96;* indefinite, 1862, *Mélinon 412* (P); indefinite, 1802, *Gabriel* (Del).

This species is represented in many herbaria of Europe by various collections of Sagot (all numbered 447). These are all determined as *C. coriacea* Sagot, a name unpublished until Benoist recently used it in his work on the timbers of French Guiana. Benoist has given an adequate botanical description (in French) of Sagot's species. The lengthy description of the wood-structures and the vernacular name, given by him, however, are based upon *Mélinon 88* which represents *Cordia hirta*. Since Benoist's formal botanical description is evidently based upon Sagot's collections and since his binomial was also evidently derived from them, I am content to accept Sagot's species as formally established by Benoist's description, especially since the description was not drawn to include Mélinon's herbarium specimen. Among the several collections of Sagot, obtained in various states of maturity over several years (but all distributed under the same collection-number) I have selected the specimen at Paris collected in Dec. 1856 as the type of *C. coriacea* Sagot. Unfortunately the name *C. coriacea* Sagot is a homonym of an earlier published name. Furthermore its publication by Benoist, because of the lack of a Latin diagnosis, is invalid. For these reasons the plant is described as a new species, *C. Sagotii*. The type is the same as that selected for *C. coriacea* Sagot.

The species is readily recognized by its very large rigid coriaceous leaves which have the midrib markedly bowed and the lower surface scabrous with minute short erect hairs. The glabrous fruit is erectly ovoid and yellow when mature.

The following vernacular names have been found on the labels accompanying specimens from Dutch Guiana—Tafraboom (Surinam Dutch), Kakóro (Arow.), Anoemalatti (Nig. Eng.), Danlieba (Sar.), Dokoa or Dokka (Arow.) and Anaakara (Kar.)—*B. W. 345;* Tafrabom, Arowtroeka (Arow.) and Kokoro konokodikoro (Kar.)—*B. W. 1194;* Tafelboom (Surinam. Dut.), Tafraboom (Nig. Eng.), Boggi lobbi and

Toenba lobbi (Sar.), Kakoro (Arow.) and Aratroeka (Kar.)—*Tree 176 at Zanderij I.*

16. **Cordia hirta,** sp. nov.

Arbor summum ad 20 m. alta, dicho- vel trichotome ramosa; ramulis brunneis saepe fulvo-hirsutis; foliis subhomomorphis ellipticis vel oblongo-oblanceolatis ad medium vel supra medium latioribus 8–18 cm. longis 3.5–7 cm. latis, basi acutis vel obtusis vel plus minusve rotundis, apice abrupte breviterque acuminatis, supra plus minusve scabris pilis abundantibus brevibus rigidis ascendentibus vestitis, subtus plus minusve velutinis pilis gracilioribus erectioribus ornatis, nervis 7–9-jugatis, petiolis hirsutis 4–9 mm. longis; cymis in furcis ramulorum ortis laxe ramosis 1–3 dm. crassis pilis rigidis erectis brunneis vestitis; calyce sessili in alabastro obovoideo 3–4 mm. longo vix costato extus brunneo-hispido intus sparse strigoso, lobis 5 triangularibus erectis; calyce fructifero explanato; corolla 5–6 mm. longa, lobis ca. 1.5 mm. longis rotundis recurvatis, filamentis exsertis basim versus pilosis; ovario et stylo glaberrimo; fructu glaberrimo; nuce anguste ellipsoidea valde ascendente 15–18 mm. longa vix rugosa.

French Guiana to eastern Venezuela, apparently in the mountains back from the coast.

Dutch Guiana: forest near Raleigh Falls, Coppename River, tree 20 m. tall, Aug. 26, 1920, *Pulle 317* (Utr); Raleigh Falls, July 29, 1923, *B. W. 6149* (Utr).

French Guiana: indefinite, 1863, *Mélinon 88* (P); indefinite, 1863, *Mélinon 113* (P).

Venezuela: Arabopo, slopes of Roraima, ¾ mile above Arabopo Swamp, 1260 m. alt., Jan. 1, 1928, *Tate 259* (type, New York); (??) Arabopo, slopes of Roraima, Jan. 1, 1928, *Tate 255* (NY).

This plant evidently frequents the hills. No locality is given for Mélinon's collections but his vernacular names, "Bois Calalon de montagne" and "Cèdre Calalon de serre basse" suggest that the specimens may have come from high ground up the Maroni where he is known to have collected. It is to be noted that the wood sample accompanying *Mélinon 88* is that described by Benoist, Arch. Bot. 5, Mem. **1:** 267 (1933), under the incorrect name of *C. coriacea* Sagot (= *C. Sagotii*). The species is a well marked one with its closest relation probably in *C. Sagotii*, from which it is quickly separable by its smaller leaves, and more copious longer brown pubescence.

17. **Cordia exaltata** Lamarck, Tab. Encyc. **1:** 422 (1791); Poiret, Encyc. **7:** 47 (1806); DeCandolle, Prodr. **9:** 484 (1845). *Lithocardium exaltatum* (Lam.) *Kuntze,* Rev. Gen. **2:** 977 (1841). *Cordia*

mucronata Poiret, Dict. Sci. Nat. **10:** 410 (1818). *Cordia scabrida* Martius ex Fresenius in Martius, Fl. Bras. **8**[1]**:** 11, tab. 9, fig. 12 (1857); Johnston, Contr. Gray Herb. **92:** 62 (1930). *Lithocardium scabridum* (Mart.) Kuntze, Rev. Gen. **2:** 439 (1891).

Shrub or tree, 2–24 m. tall, branching dichotomous; branchlets dark, sparsely strigose; leaves somewhat scabrid, sparsely strigose on both surfaces, commonly more or less heteromorphic, usually drying olivaceous or muddy brown, tertiary veinlets evident; smaller leaves ovate to orbicular, 4–9 cm. long; larger leaves elliptic to broadly oblanceolate, broadest at or above the middle, 8–20 cm. long, 4–10 cm. broad, apex abruptly short-acuminate, base acute to somewhat rounded, veins in 6–8 pairs, petiole 5–10 mm. long, inflorescence borne at forks of stem, loosely branched, 1–2 dm. broad, somewhat scabrous, sparsely strigose or finely hirsute; calyx sessile, sparsely strigose outside, strigose inside the tube, pubescent on the inner face of the 5 regular triangular teeth, in the bud elongate, 4–5 mm. long, 1.5–2 mm. thick, apex rounded, not ribbed, in fruit explanate; corolla white, tube 5–7 mm. long, lobes ca. 2 mm. long, ovate; filaments long exserted, hairy at base; ovary and style glabrous; fruit glabrous, orange-yellow or red; stone ellipsoid, erect or nearly so, 1–1.5 cm. long, not irregularly roughened.

Lower Amazon Valley and along the coast into French Guiana.

FRENCH GUIANA: Cayenne, *Martin* (P); "Cayenne, *Martin*" (herb. Poiret, TYPE of *C. mucronata*); Cayenne, *Perrottet* (Del, P); indefinite, *Leprieur sine no.* (K, Del, DC) and *164* (K, P); indefinite, *Poiteau* (K, Del); indefinite, *Richard* (K, Del); indefinite, *ex Richard* (herb. Lamarck, TYPE of *C. exaltata*).

17a. **Cordia exaltata** var. **melanoneura** [Klotzsch], var. nov. *Cordia melanoneura* Klotzsch ex Schomburgk, Fauna u. Fl. Brit. Guiana 960 (1848), nomen.

A forma typica differt foliis ellipticis vel oblongo-ovatis medio vel infra medium latissimis in sicco plus minusve spadiceis apice longe acuminatis; inflorescentia saepe lata et laxa.

Known only from middle and western British Guiana.

BRITISH GUIANA: Gravee Creek, Kaituma River, N.W. Dist., fairly high tree, Oct. 28, 1908, *Anderson 103* (K); Assakatta, lat. 7° 45′ N., long. 59° 5′ W., Sept. 1923, *La Cruz 4322* (G); Waini River, lat. 8° 20′ N., long. 59° 40′ W., tree 6 m. tall, April 1923, *La Cruz 3855* (G); Santa Rosa, Moruka River, Pomeroon Dist., tree 9 m. tall, fl. white, Aug. 1921, *La Cruz 1015* (G); Moruka River, July 1927, *La Cruz 4522* (G); Waramuri Mission, Moruka River, 9 m. tall, fl. white, Oct. 1922, *La Cruz 2399* (G); Tabla, Pomeroon Dist., fl. white, Sept. 1921, *La Cruz 1224* (G); banks of the Pomeroon, Aug. 1843, *Schomburgk 1398* (BD, TYPE of *C. melanoneura*); Mazaruni River, Aug. 1889, *Jenman 5475* (NY, K, BM); opposite Bartica, April 1887, *Jenman 3625* (K, NY); Moraballi Creek near Bartica, tree 24 m. tall, trunk 25 cm. thick, fl. white, Aug. 26, 1929, *Sandwith 118* (K); Essequibo River, Aug. 1889, *Jenman 5817* (K); indefinite, *Schomburgk 842/1398b* (K), *842* (Del) and *840* (P).

The type of *Cordia exaltata* is said to have come from Richard. In the General Herbarium at Paris there are two good specimens of this species collected by Richard, one bearing mature, and the other very young fruit. Neither collection is provided with exact geographical data though they are provided with the collector's detailed field-notes. The specimen with young fruit, of which Lamarck's type may be a duplicate, is given as "arbor 12–25 pedalis, trunco recto cortice griseo laevissimo, ramis expansis." The other specimen has the following (abbreviated) field-notes, Arbor 20–40 pedalis, ramis patentibus ramosis saepius ternatis, divaricatis; folia sparsa pulchre viridia; bacca elliptica, laevissima, glabra, nitens, flavescens; pulpa glutinosa viscosa; in sylvis variis; dec. fructus maturant.

Poiret's material of his *C. mucronata* consists of two small fragmentary specimens which are so much alike that I believe they are parts of a single collection. Leaves, flowers, and fruit are represented. The material is undoubtedly conspecific with the type of *C. exaltata.* Martin probably collected it about La Gabrielle to the southeast of Cayenne. The species enters French Guiana from the coastal area of Brazil and probably does not extend much northwest of Cayenne.

Cordia scabrida, which has been repeatedly collected in the area about the city of Pará and also about Santarem further up the Amazon, is evidently conspecific with the plant of French Guiana. Exploration will no doubt show that it is present along the north bank of the lower Amazon and in the coastal forests of Brazil towards the Guianan border.

The characters I am able to give for the plant of British Guiana, which I call *Cordia exaltata* var. *melanoneura,* do not separate it sharply from typical *C. exaltata,* but I am of the opinion that the British Guianan plant merits at least varietal and possibly even specific rank. Geographically, it is separated from *C. exaltata* by half of French, half of British, and all of Dutch Guiana. The leaves usually differ in shape and in the characteristic warm brown they assume in drying. Most of the material of the species and variety can be sorted rapidly and accurately merely on the basis of differences in gross aspect. The species *C. melanoneura* first appeared in Schomburgk's book, l. c., where it is said to grow on the banks of the Pomeroon River. This is in the very region in which the var. *melanoneura* has been most collected. The following vernacular names appear on herbarium specimens of the variety, Table Tree—*Sandwith 118;* Yowanarow and Iguana Tree—*Anderson 103.*

18. **Cordia naidophila,** sp. nov.

Arbor minor dichotome ramosa; ramulis fuscatis dense adpresseque cinereo-hirsutulis; foliis homomorphis ovatis vel elliptico-ovatis 6–11 cm. longis 4–5 cm. latis medium versus vel infra medium latioribus, basi acutis vel rotundis, apice graciliter acuminatis, utrinque scabris pilis abundantibus brevibus rigidis antrorse adpressis asperatis, nervis 5–8-jugatis, nervulis abundanter ramosis, petiolis ca. 5 mm. longis; cymis in furcis ramulorum ortis laxe graciliterque ramosis; calyce strigo in alabastro 2–3 mm. longo 2 mm. crasso subgloboso intus supra medium strigoso, lobis 5 triangularibus; corolla alba tubo 2–3 mm. longa, lobis ca. 2 mm. longis, filamentis ca. 2.5 mm. longis basim versus pilosis; ovario et stylo glaberrimo; fructu glabro; nuce obovoideo erecto ca. 12 mm. longo.

In the upper Amazon Basin, particularly in the drainage of the Rio Negro, Brazil.

VENEZUELA: near San Carlos, headwaters of the Rio Negro, 1853–54, *Spruce 2960* (G).

BRAZIL: Manáos, Agricultural Experiment Station, tree 2.5–3 m. tall, corolla creamy white, Oct. 13, 1929, *Killip & Smith 30008* (TYPE, Gray Herb.); Barra, Oct. 1819, *Martius* (BD); Marary Juruá, Sept. 1900, *Ule 5191* (BD).

This plant of the upper Amazon Basin has been confused with *C. silvestris* Fresen., of the coastal states of southeastern Brazil, but differs in having the upper leaf-surfaces, dull rather than more or less glossy and abundantly rather than very sparsely hairy. The lower surface of the leaves in *C. naidophila* is regularly strigose in a manner quite like the upper surfaces. In true *C. silvestris* the lower face of the leaves is very finely strigose and usually coarsely hairy as well; the upper face is sparsely hairy or nearly glabrous. Specimens of *C. naidophila* have been referred to *C. silvestris* by Fresenius in Martius, Fl. Bras. 8^1: 13 (1857) and by Johnston, Contr. Gray Herb. **92**: 61 (1930).

19. **Cordia grandiflora** (Desv.) Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. **3**: 77 (1818); Fresenius in Martius, Fl. Bras. 8^1: 21 (1857); Johnston, Contr. Gray Herb. **92**: 21 (1930). *Varronia grandiflora* Desvaux, Jour. de Bot. **1**: 273 (1809); Poiret, Encyc. Suppl. **3**: 730 (1814); von Friesen, Bull. Soc. Bot. Genève, sér. 2, **24**: 170, fig. 8 (1933). *Lithocardium grandiflorum* (Desv.) Kuntze, Rev. Gen. **2**: 977 (1891). *Varronia lantanoides* Willdenow ex Chamisso, Linnaea **4**: 492 (1829), in synonymy. *Cordia rufa* Klotzsch in Schomburgk, Fauna u.

Fl. Brit. Guiana 960 (1848), nomen. *Varronia grandiflora* var. *glabrata* von Friesen, Bull. Soc. Bot. Genève sér. 2, **24:** 171, fig. 8e (1933). *Varronia grandiflora* var. *Sprucei* von Friesen, Bull. Soc. Bot. Genève sér. 2, **24:** 148 (1933), nomen.

Shrub, 1–3.5 m. tall; stems clothed with slender appressed hairs; leaves triangular-ovate to lanceolate, with rather conspicuous veins, 4–10 cm. long, 1.5–5 cm. broad, base quite obtuse, margin conspicuously crenate-dentate, upper surface with slender appressed or ascending hairs, usually strigose, lower surface with shorter and more slender hairs, petioles 1–2 cm. long; inflorescence capitate, terminal, 1.5–2 cm. thick, peduncle 5–15 cm. long; calyx coarsely strigose, 7–10 mm. long, lobes long attenuate, the tips linear and free (ca. 2 mm. long) in the bud; corolla white, very large, 3.5–5 cm. long, tube 5–9 mm. long and 2 mm. thick, abruptly expanded into the coarse cylindrical throat (9–14 mm. thick); fruit ca. 9 mm. long, elongate, invested by calyx nearly to its apex.

British Guiana to central Venezuela and southward into the Amazon Valley.

British Guiana: Essequibo, Jan. 1842, *Schomburgk 358* (BD, type of *C. rufa*); Essequibo, *Appun 2514* (K); Mamette, Rupununi River, Oct. 1889, *Jenman 5533* (K).

Venezuela: Ciudad Bolivar, ca. 35 m. alt., June 1931, *Holt & Blake 740* (G); Paloma, lower Orinoco, March 1896, *Rusby & Squires 14* (G, BM, BD); Angostura, *Moritz* (BD).

Brazil: Rio Trombetas, vicinity of Obidos, shrub ca. 25 dm. tall, growing into the water, corolla white, Dec. 1849, *Spruce 515* (G, K, BM); Rio Branco, herbaceous, growing by side of river, corolla white, Sept. 1858, *Schomburgk 817* (K, BM, Del).

This remarkable species was first collected by Humboldt & Bonpland near San Fernando de Apure, Venezuela, just west of the great bend of the Orinoco. The material collected was described as *Varronia grandiflora* by Desvaux. *Cordia rufa* Klotzsch is a name based upon a collection made by Schomburgk (no. 358) on the Essequibo in British Guiana. It has never been described. Schomburgk in his catalogue mentions it only from the upper Essequibo. The Schomburgk brothers, however, made two collections of this species. A study of Robert Schomburgk's field-notes at Kew shows that his collection no. 817, labeled and distributed as from British Guiana, is in fact from Brazil, from the Rio Branco almost certainly between São Joaquin and Pirara.

20. **Cordia polycephala** (Lam.), comb. nov. *Varronia polycephala* Lamarck, Tab. Encyc. **1:** 418 (1791). *Lantana corymbosa* Linnaeus, Sp. Pl. 628 (1753), not *C. corymbosa* Willd. ex R. & S. (1819). *Var-*

ronia monosperma Jacquin, Pl. Rar. Hort. Schoenbr. **1:** 18, tab. 39 (1797). *Cordia monosperma* (Jacq.) Roemer & Schultes, Syst. **4:** 463 (1819). *Varronia dichotoma* Ruiz & Pavon, Fl. Peruv. **2:** 23, tab. 146 (1799), not *C. dichotoma* Forst. (1786). *Varronia ulmifolia* Jussieu ex Dumont-Courset, Le Bot. Cult. ed. 1, **2:** 148 (1802), nomen. *Cordia ulmifolia* (Juss.) DeCandolle, Prodr. **9:** 494 (1845), not *C. ulmifolia* Spreng. (1825). *Varronia corymbosa* Desvaux, Jour. de Bot. **1:** 275 (1809), not "*V. corymbosa* L." ex Desf. (1804), nomen. *Cordia corymbosa* (Desv.) Don, Gen. Syst. **4:** 383 (1838), not *C. corymbosa* Willd. ex R. & S. (1819). *Cordia bifurcata* Roemer & Schultes, Syst. **4:** 466 (1819). *Cordia corymbosa* of Urban, Symb. Ant. **4:** 519 (1910), and most subsequent authors; Johnston, Contr. Gray Herb. **92:** 30 (1930). *Cordia patens* sensu Pulle, Enum. Pl. Surinam 398 (1906). — *Periclymenum rectum, salviae foliis majoribus, etc.*, Sloane, Nat. Hist. Jamaica **2:** 83, tab. 194, fig. 3 (1725). *Ulmi angustifoliae facie Baccifera Jamaicensis etc.*, Plukenet, Phytogr. tab. 328, fig. 5 (1691) and Almag. Bot. 393 (1694).

Slender shrub, 1–5 m. tall, frequently subscandent; stems with appressed or somewhat spreading indument of intermixed short and long hairs; leaves ovate to lanceolate, 2–12 cm. long, 1–5 cm. broad, base acute to obtuse or nearly rounded, apex acute, margin toothed or subentire, upper surface bearing numerous minute limy tuberculations, very sparsely strigose, under surface usually brown, commonly finely and densely tomentulose, on the veins bearing slender appressed or ascending coarser hairs; petiole slender, 3–10 mm. long, decurrent 1–3 mm. on the subtended branchlet and peduncle; cymes usually densely glomerate, subglobose, 5–15 mm. thick, rarely expanding and becoming loosely flowered and the branches more or less evidently dichasial and scorpioid; peduncles axillary and terminal; calyx strigose, 2–3 mm. long, lobes broad, the tips not free in the bud, at maturity calyx tightly investing the fruit nearly to the apex; corolla white, 4–5 mm. long; fruit red, stone 4–5 mm. long, ovoid or subglobose.

Very widely distributed in the warm parts of America.

British Guiana: Pirara, Jan. 1842, *Schomburgk 601* (BD); savannas, shrub 3–4 m. tall, fl. white, *Schomburgk 382* (K, BM, Leid, BD, DC, P); Nigate, Nealu, Corantyne River, a few feet tall, Oct. 1879, *Jenman 367* (K); indefinite, *Schomburgk 384* (BM).

Dutch Guiana: Matappi, Corantyne River, June 18, 1916, *B. W. 2153* and *2174* (Utr); common on backlands of Paramaribo Gardens, 2–2.5 m. tall, June 1910, *Stockdale 8823* (K); near Paramaribo, frequent, shrub 2.5–3 m. tall, fl. white, Nov. 1837, *Splitgerber 72* (Leid); near Paramaribo, *Focke 755* and *1132* (Utr); near Paramaribo, shrub 2 m. tall, *Kuy-*

per 20 (Utr); near Paramaribo, 1910, *native collector no. 117* (Utr); near Paramaribo, *Kegel 109* (P); edge of forest near Paramaribo, fl. yellow, 1844, *Kappler ed. Hohenacker 1570* (P); Plant. Liberté, edge of forest, fl. white, shrub 2.5 m. tall, 1933, *Lanjouw 223* (Utr); Plant. Rust en Werk, Aug. 5, 1913, shrub 4 m. tall, *Soeprato 60* (Utr); Slootwijk, Commewyne River, roadside shrub 1 m. tall, July 1913, *Soeprato 29G* (Utr); Bloemendal Boite, June 4, 1913, 2 m. tall, *Soeprato 25A* (Utr); Leonsberg, Aug. 8, 1913, *Soeprato 127* (Utr); near Plant. Jagtlust, Aug. 1901, *Went 64* (Utr); Para District, 1919, *Kuyper 20* (Utr); lower Commewyne River near Plant. Maasstroom, *Focke 1358* (Utr); indefinite, *Hostmann 292* (K, BD, P), *Hostmann sine no.* (Leid), *Focke 1355* (G, Utr), and *Leschenault* (P); indefinite, 1841, *Berthoud-Coulon 551* (BM).

Brazil: Rio Negro, Jan. 11, 1887, *Moura 568* (BD); between mouth of Rio Negro and the Capoenas, shrub 2.5 m. tall, July 1851, *Spruce 1695* (K, BM); Igarape Burete, Pracuá, Rio Surumu, Feb. 1909, *Ule 7962* (BD).

Venezuela: lower Orinoco, 1896, *Rusby & Squires 309* (G).

This is the most widely distributed species of *Cordia* in America and, in many regions, one of the commonest. Its nomenclatorial history is involved. Its list of synonyms is a long one. Above I have given merely the oldest names, those published down to and including the Systema by Roemer & Schultes, vol. 4, in 1819. Since 1845 the plant has been called either *C. ulmifolia* or *C. corymbosa*. A study of these names proves them to be illegitimate on several grounds.

The name *C. ulmifolia* was sponsored by DeCandolle, Prodr. **9**: 494 (1845). Those who followed him cited the name "*Cordia ulmifolia* Juss. in Dum. Cour., Bot. Cult. **2**: 148 (1802)." A study of the work cited, however, shows that the name was actually published under *Varronia* and that no description was provided. It is a mere garden name! *Varronia ulmifolia* Juss. was accepted by no one until DeCandolle took it up and transferred it to *Cordia*. Previously, however, Sprengel, Syst. **1**: 653 (1825), had applied the binomial *Cordia ulmifolia* to another concept. *Cordia ulmifolia* (Juss.) DC. is hence a late homonym, besides being based upon a mere garden name.

The name *C. corymbosa* seems to have been introduced by Urban, Symb. Ant. **4**: 519 (1910). It has been universally accepted in recent years. The basic synonymy given by Urban and repeated by subsequent authors is as follows,—*Cordia corymbosa* (L.) Don, Gen. Syst. **4**: 383 (1838) and *Lantana corymbosa* L. Sp. Pl. 628 (1753). The name-bringing synonym is based upon several pre-Linnaean references all of which refer to our concept. *Cordia corymbosa* Don, however, is not based upon *Lantana corymbosa* but upon *Varronia corymbosa* Desvaux, Jour. de Bot. **1**: 275 (1809). This latter name is expressly a renaming of *C. monosperma* Jacq. Both Desvaux l. c. 277 and Don, l. c. 385, cite *Lan-*

tana corymbosa L. among the synonyms of *Varronia* (or *Cordia*) *lineata!!* The name *Cordia corymbosa* Don, can not be used for our plant in any case. It is antedated by *Cordia corymbosa* Willd. ex R. & S., Syst. **4**: 801 (1819). Hence, since the name *Cordia corymbosa* Don is not based upon *Lantana corymbosa* L., and since it is invalid through being a later homonym, it must be rejected.

Although it is the oldest name applied to our plant, *Lantana corymbosa* L. can not be transferred to *Cordia* because of two earlier published homonyms. The next oldest name used for our plant is *Varronia polycephala* Lam., which is based upon a phrase-name and illustration given by Plukenet. Transferred to *Cordia* Lamarck's name becomes the correct one for the present concept.

Various names cited by me in my formal list of synonyms have, at one time or another, been involved with binomials which I would refer to other species. The most important of these are *Varronia lineata* L. and *V. humilis* Jacq. Since these two names seem primarily based upon the notes and description given by Browne, Nat. Hist. Jamaica 172, tab. 13, fig. 1 (1759), I identify them with the plant current as *C. globosa* (Jacq.) HBK. Browne's plant has the short pedunculate, terminal, globose flower-heads and the subulate calyx-lobes of that common West Indian species.

The Guianan plants represent the typical West Indian form of *Cordia polycephala*, which is characterized by having the lower surfaces of the leaves densely and finely tomentulose. In South America, the typical form is found in our area, and in the country south along the Andes. One collection from Dutch Guiana, according to the label, is called, "Man blala oema" (*native collector 117*).

21. **Cordia macrostachya** (Jacq.) Roemer & Schultes, Syst. **4**: 461 (1819). *Varronia macrostachya* Jacquin, Enum. Pl. Insul. Carib. 14 (1760) and (*C. macrostachia*) Select. Stirp. Amer. 41 (1763); Desvaux, Jour. de Bot. **1**: 272 (1809). *Varronia guianensis* Desvaux, Jour. de Bot. **1**: 270 (1809). *Cordia gujanensis* (Desv.) Roemer & Schultes, Syst. **4**: 460 (1819); (*C. guianensis*) Meyer, Nov. Acta Acad. Caes.-Leop. Car. **12**^{2}: 778 (1825). *Montjolya guianensis* (Desv.) von Friesen, Bull. Soc. Bot. Genève sér. 2, **24**: 181 (1933). *Cordia interrupta* DeCandolle, Prodr. **9**: 491 (1845). *Cordia oxyphylla* DeCandolle, Prodr. **9**: 492 (1845). *Lithocardium oxyphyllum* Kuntze, Rev. Gen. **2**: 977 (1891). *Cordia graveolens* Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. **3**: 74 (1818); Miquel, Stirp. Surinam. 141 (1850); Pulle, Enum. Pl. Surinam 398 (1906). *Varonia martinicensis* sensu Aublet, Hist. Pl. Guian. Fr. **1**: 232 (1775); of Poiret, Encyc.

4: 264 (1797), as to *Leblond 370.* ? *Cordia cylindrostachya* sensu Schomburgk, Fauna u. Fl. Brit. Guian. 960 (1848). ? *C. salicina* sensu Garcke, Linnaea **22:** 68 (1849). *Varronia cylindrostachya* sensu Graham, Ann. Carnegie Mus. **22:** 240 (1934).

Shrub 1–2.5 m. tall, younger parts bearing minute resinous granules; stems more or less strigose or with stiff incurved hairs; leaves lanceolate to oblong-ovate, elongate, 5–10 (–20) cm. long, 1–3 (–10) cm. broad, base obtuse or acute, contracted into a petiole 5–20 (–30) mm. long, apex obtuse to acute, margin denticulate to evidently dentate or sinuate-dentate, upper surface smooth to scabrous and characteristically glabrous, bearing small limy tuberculations or murications which are low or somewhat prominent (rarely each bears a very short erect hair), lower surface pale, with soft curved hairs on the veins and veinlets; peduncles terminal, distinct from the petioles, 2–10 cm. long, slender; spikes 5–10 cm. long, becoming rather loosely flowered at maturity; calyx granulate and usually somewhat strigose, ca. 3 mm. long at anthesis, the tips of the triangular lobes not free in the bud; corolla white, ca. 5 mm. long; fruit red, invested to beyond the middle by the cupulate calyx; stone broadly ovoid, 4–5 mm. long.

Northern South America and northward into Central America and the West Indies.

British Guiana: Frechal, dry savanna, shrub, fl. white, fruit red, Sept. 6, 1927, *Tate 37* (NY); Pomeroon River, 25 dm. tall, 1922–23, *La Cruz 3041–3145* (G); Demerara, coastal region, 12 dm. tall, 1881, *Jenman 1501* (K, P); vicinity of Demerara, 1824, *Parker* (DC, type of *C. interrupta*); Georgetown, wild land in the Botanic Garden, fl. white, Oct. 1919, *Hitchcock 16535* (G, NY); coast lands, June 1889, *Jenman 5206* (NY).

Dutch Guiana: Corantyne River, 1911, *Hulk 99* (Utr); near Paramaribo, 1910, *native collector 41* (Utr); near Paramaribo, 2–3 m. tall, *Essed 120* (Utr); near Paramaribo, 1904, *Essed 120* (Utr); Paramaribo, Aug. 1901, *Went 305* (Utr); Paramaribo, June 1903, *Versteeg 464* (Utr); Paramaribo, Jan. 1901, *Went 570* (Utr); Paramaribo, shrub 1–2 m. tall, *Kuyper 34* (Utr); near Paramaribo, shrub 2–2.5 m. tall, fl. white, fruit red, Nov. 1837, *Splitgerber 44* (Utr); Paramaribo near Agricultural Experiment Station, marshy land, fl. white, shrub ca. 1 m. tall, 1933, *Lanjouw 65* (Utr); near Paramaribo on road to Plant. Leonsberg, Aug. 1920, *Pulle H48* (Utr); Leonsberg, 1913, *Soeprato 135* (Utr); between Kwatta and Paramaribo, Feb. 28, 1900, *Tulleken 67* (Leid); Div. Q, forest of Agric. Experim. Station, Paramaribo, 1916, *Samuels 60* (G, K, Leid, BD, P); La Liberté, 1 m. tall, 1913, *Soeprato 235* (Utr); Post Sommelsdijk, lower Commewyne River, July 1913, *Soeprato 37* (Utr); Plant. Domburg near Surinam River, Aug. 23, 1900, *Tulleken 265* (Leid); Para District, in woods, shrub, fl. white, April 1838, *Splitgerber 1160* (Leid); Matappica, Dec., *Focke 279* (Utr); Lawa River, Oct. 1903, *Versteeg 298* (Utr); upper

Commewyne River, in forest, *Focke 213* (Utr); indefinite, *Focke 282* and *446* (Utr), *Tulleken 17* (Leid), *Hostmann sine no.* (Leid) and *Hostmann 323* (K, BM, BD, Del, P); indefinite, 1823–24, *Leschenault* (Leid, P).

French Guiana: Acarouani, cultivated, "var. inodora," 1856, *Sagot* (P); Mana, shrub, leaves fragrant, 1857, *Sagot 444* (K, P); Mana, shrubby, leaves fragrant, fl. white, *Sagot 444* (P); Iles du Salut, shrub 5–15 dm. tall, fragrant, fruit red, March 1856, *Sagot* (P); Iles du Salut, shrub with fragrant leaves, 1854, *Sagot 444* (K, BM, P); Cayenne, *von Rohr* (BM); Cayenne, 1853, *Rothery 202* (K, BM) and *sine no.* (BM); near Cayenne in savannas, shrub, fl. white, fruit rose-colored, June 1921, *Broadway 573* (G, NY, K); Cayenne, aromatic shrub, fl. white, fruit red, April 1897, *Soubiron* (P); Cayenne, very common about town, *Richard* (Paris, TYPE of *V. guianensis*); near Cayenne, shrub near sea, fl. white, fruit red, April 1921, *Broadway 49* (G); indefinite, 1820, *Perrottet 212* (DC, TYPE of *C. interrupta*); indefinite, 1792, *Leblond 370* (Del, Lamarck).

The type of *Varronia macrostachya* Jacq. comes from Cartagena. It is briefly described, and then largely through comparison with *V. curassavica* Jacq., but with little doubt is evidently conspecific with our common Guianan shrub. Our plants are remarkably similar to some I have seen from Cartagena. Among the spicate varronias of the coastal area of northern South America *C. macrostachya* is characterized by its glabrous upper leaf-surfaces, usually large leaves, and elongate slender terminal spikes. In dry localities the leaves tend to become smaller and the spikes short. In these phases the plant is distinguished from *C. curassavica* Jacq. only by the absence of hairs on the upper side of the leaves.

Desvaux's *Varronia guianensis* evidently applies to this plant. The vernacular name, "Montjoly," and Aublet's discussion which are mentioned by Desvaux, both apply to our plant. There is a sheet from the Desvaux collections at Paris which is determined as *V. guianensis* by Desvaux. The specimen is labeled merely as from South America, except that it is given as a shrub, no other data concerning it is given on the accompanying label. The specimen, however, is almost certainly a duplicate of one, also at Paris, collected by Richard and labeled as "frequentissima in suburbanis, Cayenne." This information as to locality is that given by Desvaux as the source of his species. I consider the specimens as types of the species.

The type of *C. interrupta* was collected by Perrottet. It is given merely as from French Guiana and it consists of a leaf of *C. tomentosa* and a branch of *C. macrostachya*. A comparison of this type-material in the Prodromus Herbarium with other Perrottet material in the Delessert collections, at Geneva, shows such a close agreement in details of discoloration, etc., etc., that we may well believe them parts of one collection. The material in the Delessert Herbarium is labeled as from "Mana, 1820, *Perrottet*."

Humboldt and Bonpland collected material near Angostura on the Orinoco which seems to be good *C. macrostachya*. The material, however, was described as a new species, *Cordia graveolens* HBK. Further up the Orinoco, perhaps in very shaded humid locations, there have been collected plants evidently related to *C. graveolens*, though differing in having the upper leaf-surfaces quite smooth and bearing only minute very scattered microscopic limy disks and resinous granulations. This form was described as *Cordia polystachys* HBK. and *C. canescens* Willd., from the Mapure. Spruce (no. 3012) has collected a quite similar plant near the Brazil-Venezuela border. The type of another species, *C. spicata* Willd., given as from Angostura, seems to be an essentially similar form.

The material given as collected by Richard in Cayenne by Poiret, Encyc. **4**: 264 (1797), under the name *Varronia curassavica,* differs from all Guianan plants and is, I believe, West Indian. Desvaux, Jour. de Bot. **1**: 271 (1808), and later Poiret, Encyc. Suppl. **3**: 728–29 (1814), associate this specimen with *V. angustifolia* West. of the island of St. Croix. This is probably correct.

In the Lamarck herbarium there are only two sheets labelled *V. martinicensis*. This material belongs to Leblond no. 370 and is the basis of the description of *V. martinicensis* by Poiret, Encyc. **4**: 264 (1797). Desvaux referred the plant to *V. curassavica,* but I consider it quite representative of *C. macrostachya.*

It should be noted that plants of eastern Brazil (from Ceará southward to Rio Grande do Sul), which I have treated as *Cordia verbenacea* DC., cf. Johnston, Contr. Gray Herb. **92**: 25 (1930), is verly closely related to *C. macrostachya* and perhaps should be accepted as a form of it.

The present species seems to be well known in French Guiana under the name "Montjoly." In several collections from Dutch Guiana the plant is given as called "Blaka oema."

22. **Cordia Schomburgkii** DeCandolle, Prodr. **9**: 490 (1845); Schomburgk, Fauna u. Fl. Brit. Guiana 960 (1848); Garcke, Linnaea **22**: 68 (1849); Pulle, Enum. Pl. Surinam 397 (1906). *Lithocardium Schomburgkii* (DC.) Kuntze, Rev. Gen. **2**: 977 (1891). *Cordia lucida* Splitgerber ex Pulle, Enum. Pl. Surinam 397 (1906), nomen sub *C. Aubletii*. *Cordia tobagensis* Urban in Fedde, Rep. Spec. Nov. **16**: 39 (1919). *Cordia tobagensis* var. *Broadwayi* Urban in Fedde, Rep. Spec.

Nov. **16**: 40 (1919). (?) *Cordia Aubletii* sensu Schomburgk, Fauna u. Fl. Brit. Guiana 960 (1848). *Cordia polystachya* sensu Schomburgk, Fauna u. Fl. Brit. Guiana 1151 (1848). *Cordia patens* var. *polycephala* sensu Miquel, Stirp. Surinam. 140 (1850). *Cordia Aubletii* sensu Pulle, Enum. Pl. Surinam 397 (1906). *Varronia guianensis* sensu Graham, Ann. Carnegie Mus. **22**: 239 (1934).

Shrub 1–4 m. tall; stems with a thin indument of fine curved pubescence and intermixed short coarse curved bristles; leaves ovate to elliptic or lance-elliptic, 5–10 cm. long, 2–7 cm. broad, base obtuse or nearly rounded, apex acute, margin entire to sharply dentate, upper surface drying brown, usually somewhat lustrous, distinctly and simply strigose, lower surface pale, covered with a fine minute curved puberulence, petiole slender 6–9 mm. long, decurrent 5–8 mm. on the subtended branchlet or peduncle; peduncles axillary, slender, ascending, up to 9 cm. long; spikes elongate and loosely flowered, 5–15 cm. long; calyx nearly glabrous, bearing numerous resinous granules, with a few bristles about the apex, the tips of the deltoid lobes not free in the bud, calyx at anthesis or when sterile vase-shaped or funnel-form and 3–4 mm. long, at maturity expanded by the enlarging fruit; corolla white, ca. 4 mm. long; fruit red, tightly ensheathed by the calyx; stone ovoid 4–5 mm. long.

Known only from British, Dutch and French Guiana and from Trinidad and Tobago.

British Guiana: banks of the Barama, Oct. 1843, *Schomburgk 1510* (BD); Tumatumari, Potaro River, along trail in forest, shrub 2.5–3 m. tall, fl. white, Jan. 1920, *Hitchcock 17382* (G, NY); Penal Settlement, 1911, *Hitchcock 17150* (K); upper Mazaruni River, long. 60° 10′ W., fl. yellow, 8–12 dm. tall, Sept. 1922, *La Cruz 2343* and *2260* (G, NY); Mazaruni, *Appun 293* (K); Kamakusa, upper Mazaruni, long. 59° 50′ W., Nov. 1922, *La Cruz 2882* (G, NY); Kyk-over-all, near Kartabo, bushy shrub 3 m. tall, July 1924, *Graham 215* (NY); Kartabo, large shrub in clearing, Aug. 11, 1920, *Bailey 170* (G); Kalacoon, shrub in clearing, fruit red, Aug. 23, 1920, *Bailey 170* (G); Kalacoon, shrub 15 dm. tall, along creek, June 1924, *Graham 133* (NY); banks of Rupununi, May 1843, *Schomburgk 1304* (BD, as *C. polystachya*, det. Kl.); Demerara, *Parker* (K); Kamuni Creek, Demerara River, March 1889, *Jenman 4919* (K); Malali, Demerara River, lat. 5° 35′ N., 1922, *La Cruz 2678* (G, NY); Christianburg, Demerara River, 1910, *Anderson 553* (K); Vryheid, Demerara River, fl. white, Feb. 15, 1924, *Linder 61* (G, NY); between Demerara and Berbice rivers, ca. lat. 5° 50′ N., 18 dm. tall, fl. white, *La Cruz 1594* (G, NY); Berbice, 1837, *Schomburgk 406* (Del); indefinite, 1838, *Schomburgk 406* (DC, TYPE of *C. Schomburgkii*; isotypes, K, BM, Leid, BD, P); Canje Creek, Aug. 1908, *Bartlett* (NY).

Dutch Guiana: upper Nickerie River, Feb. 24, 1915, *B. W. 1035*

(Utr); Saramacca River, Dec. 1902 and Jan. 1903, *Pulle 125* and *417* (Utr); Heidoti, Saramacca River, 1920, *B. W. 4621* (Utr); road near Paramaribo, 1842, *Focke 816* and *760* (Utr); near Paramaribo, shrub 2.5–3.5 m. tall, fl. white, Dec. 1837, *Splitgerber 206* (Leiden, TYPE of *C. lucida*); Plant. Liberté, lower Surinam, edge of forest, shrub 2–3 m. tall, fl. white, 1933, *Lanjouw 224* (Utr); Para District, forest, fl. white, April 1838, *Splitgerber 1161* (Leid); Para District, June 1904, *Versteeg 507* (Utr); Plant. Guineesche Vriendschap, 1915, *Soeprato 313* (Utr); Carolina Creek, Para River, May 1921, *B. W. 5123* (Utr); near Guyana placer mines, Oct. 1909, *Boldingh 3918H* (Utr); Kadjoe, Surinam River, May 1910, *native collector* (Utr); Koemba Rapids, upper Surinam River, July 1908, *Tresling 232* (Utr, BD); indefinite, *Hostmann* (Leid), *Hostmann 295* (Utr, P), *Hostmann 877* (G, K, BM, Utr, BD, Munich, Del, P), *Kappler 877* (P) and *Focke* (K).

FRENCH GUIANA: St. Laurent du Maroni, shrub 2–3 m. tall, fl. white, Jan. 15, 1914, *Benoist 604* (P); St. Jean, shrub 2 m. tall, fl. white, May 16, 1914, *Benoist 1223* (P); Mana, fl. white, 1858, *Sagot 1169* (K, BM, P); Godebert, Jan. 1920, *Wachenheim 79* (K, BM, P), *101* (G, K, BM, P) and *352* (P).

The species is most nearly related to *C. Poeppigii* DC., of eastern Peru and to *C. ferruginea* (Lam.) R. & S. of the northern Andes and Central America. It is readily recognized by its peculiar calyx. This, when not distorted by the enlarging fruit, is funnel-form or vase-shaped and is abruptly expanded from a short tube (ca. 1–1.5 mm. thick and 1–2 mm. long) or even from the narrow base. The calyx-tube is covered with numerous minute resinous granules. The ascending, more or less deltoid, lobes are somewhat strigose outside especially towards their apices.

The following vernacular names have been found on the labels of the specimens indicated. Black sage—*Anderson 553;* Waijanaka erepaloe—*B. W. 4621;* Baka Oema—*Tresling 232;* Blakka hoema—*B. W. 5123* and Makoeja pipá (Kar.), Kaboejakoro diamaroe (Arow.) and Blakka wintje (Nig. Eng.)—*B. W. 1035.*

23. **Cordia tomentosa** Lamarck ex Roemer & Schultes, Syst. **4**: 459 (1819). *Varronia tomentosa* Lamarck, Tab. Encyc. **1**: 419 (1791); Poiret, Encyc. **4**: 264 (1797); Desvaux, Jour. de Bot. **1**: 268 (1808). *Lithocardium tomentosum* (Lam.) Kuntze, Rev. Gen. **2**: 977 (1891). *Montjolya tomentosa* (Lam.) von Friesen, Bull. Soc. Bot. Genève sér. 2, **24**: 183 (1933). *Cordia Aubletii* DeCandolle, Prodr. **9**: 490 (1845). *Lithocardium Aubletii* (DC.) Kuntze, Rev. Gen. **2**: 976 (1891).

Shrub, 1–4 m. tall; stems clothed with a mixture of curved ascending coarse and slender hairs; leaves lanceolate to ovate-lanceolate or ovate, 7–15 cm. long, 2.5–7 cm. broad, base obtuse or somewhat rounded, apex acute or somewhat acuminate, margin irregularly dentate, upper surface dull, scabrous, with numerous stiff ascending bristles which arise from more or less bulbous bases, lower surfaces pallid, more or less tomentose with abundant fine short interlaced hairs; petioles 5–10 cm. long, decurrent 2–6 mm. on the subtended branchlet or peduncle; peduncles axillary, ascending, 2–10 cm. long; spike broadly clavate, very dense, 1.5–4 cm. long, at anthesis ca. 7 mm. thick, increasing to about twice that thickness in fruit; calyx densely hairy or tomentose with intermixed resinous granules, ca. 5 mm. long at anthesis, much accrescent in maturity, the tips of the lobes evidently free in the bud, calyx-lobes narrowly triangular, very elongate, acuminate; corolla white; fruit tightly invested by the calyx at maturity; stone ca. 4 mm. long.

Known only from French and Dutch Guiana.

DUTCH GUIANA: Voltz Mts., open formation, small shrub 2 m. tall, fl. white, Aug. 22, 1920, *Pulle 252* (Utr).

FRENCH GUIANA: Cayenne, open ground near Baduel, July 10, 1921, *Broadway 720* (G); Cayenne, shrub 4.5 m. tall, fl. white, Feb. 1859, *Sagot* (P); Cayenne, S. Marca savanna near Mt. Baduel, 1867, *Jelski* (BD); Cayenne, 1859, *Sagot 1315* (K, BM, P); Cayenne, *Martin* (K), *Lepricur* (K, Del, P) and *Aublet* (BM); indefinite, *Martin ex herb. Rudge* (BM); indefinite, *Poiteau* (K, BD, Del); indefinite, 1820, *Perrottet 211* (DC).

The present species is most closely related to *C. multispicata* Cham. of eastern Brazil, from which it differs in having the calyx coarsely strigose or tomentose all over, rather than nearly or quite glabrous. The type of *Varronia tomentosa* in the Lamarck Herbarium is labeled as coming from Jussieu and is devoid of any geographic data. It consists of a leaf and a fragment of inflorescence. These, however, evidently represent the much collected plant of the vicinity of Cayenne which is treated here.

There must remain some question as to the proper disposition of the name *Cordia Aubletii* DC. The plant actually described by DeCandolle is Perrottet (no. 211), which represents *C. tomentosa*. The reference by DeCandolle to "*Varronia Martinicensis* Aubl. guian. 232 non Jacq.", which might stand as the basis for the name chosen by him, is quite ambiguous. Aublet quoted a name and a descriptive phrase from Jacquin which apply to a West Indian species. The several lines of discussion by Aublet, concerning the fragrance of the herbage, the color of the fruit, the vernacular name and the local uses of the plant, in fact all the original data, all apply to *C. macrostachya* Jacq. Consequently if the name *C. Aubletii* is taken as founded upon the reference to Aublet's work, the species justly should become a synonym of *C. macrostachya*. I have preferred, however, to associate the name *C. Aubletii* with DeCandolle's specimen from Perrottet and the description of that specimen published in the Prodromus. It may be further noted that the specimen of *Hostmann 877,* which the younger DeCandolle, in a foot-note, cited as representing *C. Aubletii,* is in fact representative of *C. Schomburgkii.*

In the British Museum there is a collection of *C. tomentosa* made by Aublet. Among his manuscripts I have seen a good description of the species mentioned. It is possible that Aublet identified the plant as *Varronia globosa* and that the report of *V. globosa* in his book, l. c. **1:** 232 (1775), may be based upon his collection of *C. tomentosa.*

24. **Cordia multispicata** Chamisso, Linnaea **4:** 490 (1829); Fresenius in Martius, Fl. Bras. **8**[1]**:** 17, tab. 6 (1857); Johnston, Contr. Gray Herb. **92:** 29 (1930). *Lithocardium multispicatum* (Cham.) Kuntze, Rev. Gen. **2:** 977 (1891). *Cordia bahiensis* DeCandolle, Prodr. **9:** 489 (1845). *Varronia spicata* Salzmann ex DeCandolle, Prodr. **9:** 489 (1845), as synonym.

Shrub becoming subscandent, 1–3 m. tall; stems clothed with a mixture of curved ascending coarse and slender hairs; leaves ovate to ovate-lanceolate, 4–10 cm. long, 2.5–6 cm. broad, base obtuse to rounded, apex acute to somewhat acuminate, margin crenate or dentate, upper surface not lustrous, scabrous, bearing numerous coarse short ascending hairs from bulbous bases, lower surface pale, bearing slender soft curved hairs on the nervation; petioles slender, 4–10 mm. long, decurrent 2–5 mm. on the subtended peduncle or branchlet; peduncle axillary, 1–6 cm. long, ascending; spike broadly clavate to nearly subcylindrical, 1–7 cm. long, short and dense to rather loose and elongate, 7–10 mm. thick; calyx hairy on the lobes, the tube practically glabrous, bearing numerous resinous granules, tip of lobes short but free in the bud, lobes broadly triangular and short acuminate; calyx ca. 3 mm. long at anthesis, accrescent; corolla white, 4–5 mm. long; fruit ensheathed by the calyx at maturity; stone ca. 4 mm. long.

Brazilian, from the mouth of the Amazon southward to Rio Janeiro.

Brazil: beach at Prainha, Nov. 26, 1873, *Traill 561* (K).

This species which has been much collected about the mouth of the Amazon, particularly in the vicinity of Pará, is clearly related to *C. tomentosa* of French and Dutch Guiana. Collecting on the Brazilian coast north of the Amazon will no doubt reveal the presence of the species in that region and possibly may produce forms transitional to *C. tomentosa* as well. *Cordia multispicata* seems to differ from *C. tomentosa* chiefly in its calyx which tends to be entirely glabrous and evidently resinous-granulate below the shorter nearly deltoid lobes. In *C. tomen-*

tosa the calyx-lobes are distinctly more elongate, being narrowly triangular, and have more elongate tips. The calyx-tube in the Guianan plant is hairy all over. In fact, except for the free lobe-tips of the calyx, *C. multispicata* is more suggestive of *C. Schomburgkii* than of *C. tomentosa*.

Doubtful and excluded Species

Cordia flavescens Aublet, Hist. Pl. Guian. Fr. **1:** 226, tab. 89 (1775); Poiret, Encyc. **7:** 43 (1806); Schomburgk, Fauna u. Fl. Brit. Guiana 960 (1848); Johnston, Contr. Gray Herb. **92:** 63 (1930). *Lithocardium flavescens* (Aubl.) Kuntze, Rev. Gen. **2:** 977 (1891). *Cordia sarmentosa* Lamarck, Tab. Encyc. **1:** 422 (1791). *Cordia echitioides* Lamarck ex Dietrich, Synop. **1:** 612 (1839), in synonymy. *Firensia* Scopoli, Intr. 157 (1777).

According to Aublet, l. c. 227, the original material of this species was collected on the Ile de Cayenne and on the adjacent mainland of French Guiana near Tonnegrande. The species is based upon mixed material consisting of (1) flowers of some species of *Cordia,* and (2) fruiting branches of *Ocotea commutata* Nees, of the Lauraceae. Since the species is based upon two entirely discordant elements it must be rejected under article 51 of the International Rules of Nomenclature. At the British Museum and at the museum in Stockholm there are specimens of this species collected by Aublet. These specimens represent only the *Ocotea*.

Cordia lutea Lamarck, Tab. Encyc. **1:** 421 (1791).

A specimen of this species in the Delessert Herbarium is labeled as collected in Cayenne by Perrottet. The species is known only from the semi-arid regions of western Peru and Ecuador and is not even to be expected from the wet Guianan coast. The data on the specimen at Geneva are obviously incorrect. I have had previous occasions to question the accuracy of the geographic data associated with the Perrottet collections in the Delessert Herbarium.

Cordia scandens Poiret, Dict. Sci. Nat. **10:** 410 (1818).

This species is given as collected by Martin in Cayenne. I have seen the fragmentary type in Poiret's herbarium and ample specimens of evidently the same collection in the General Herbarium, also at Paris. A search in the herbarium proved that this authentic material is referrable to *Dichapetalum vestitum* Baill., var. *scandens* [Benth.] Baillon in Martius, Fl. Bras. **12**^{1}**:** 372 (1886). The correct name for that plant, consequently, is **Dichapetalum scandens** (Poir.), comb. nov.

Cordia tetraphylla Aublet, Hist. Pl. Guian. Fr. **1:** 224, tab. 88 (1775); Poiret, Encyc. **7:** 42 (1806); Schomburgk, Fauna u. Fl. Brit.

Guian. 1151 (1848); Fresenius in Martius, Fl. Bras. **8**[1]: 13 (1857); Pulle, Enum. Pl. Surinam 397 (1906); Johnston, Contr. Gray Herb. **92:** 64 (1930). *Lithocardium tetraphyllum* (Aubl.) Kuntze, Rev. Gen. **2:** 977 (1891). *Firensia lutea* Rafinesque, Sylva Tellur. 40 (1838).

Aublet, l. c. 226, states that this shrub is very common on the sand near Kourou and westward along the French Guiana coast to Sinnamary. The description given by Aublet is a mixture, based partly upon the flowers of some species of *Cordia* and partly upon a leafy fruiting branch of *Buchenavia capitata* (Vahl) Eichl. of the Combretaceae. The name based upon entirely discordant elements must be discarded.

Cordia Myxa sensu Schomburgk, Fauna u. Fl. Brit. Guiana 830 (1848).

Cordia curassavica sensu Schomburgk, Fauna u. Fl. Brit. Guiana 830 (1848).

Cordia martinicensis sensu Schomburgk, Fauna u. Fl. Brit. Guiana 830 (1848).

The three names above cited are listed by Schomburgk in his catalogue of the plants of British Guiana. The first two are given as cultivated. The last is given as growing wild on plantations and in ditches in the coastal region. I suspect that all three names represent misdeterminations.

2. **Lepidocordia** Ducke, Archiv. Jard. Bot. Rio Janeiro **4:** 170 (1925).

Large tree with broad leaves. Inflorescence a dichotomously branched corymbose panicle. Calyx 5-lobed, persistent. Corolla white, small, 5-merous, with short tube and spreading lobes. Stamens 5, short-exserted. Ovary 4-celled. Stigmas 2, conic, sessile on the apex of the ovary. Fruit unlobed, a drupe, breaking up into 2 flattened bony 2-seeded nutlets. Endosperm present. Cotyledons flat.

A monotype endemic to our area. Its immediate relationships are obscure.

1. **Lepidocordia punctata** Ducke, Archiv. Jard. Bot. Rio Janeiro **4:** 171, tab. 22 (1925); Sandwith, Kew Bull. **1933:** 335 (1933).

Tree 15–30 m. tall, trunk irregularly and very deeply fluted; leaves oblong-lanceolate, broadest at or above the middle, 1–2 dm. long, 2–7 cm. broad, with 6–9 pairs of veins, base obtuse to acute, apex acuminate, upper surface with inconspicuous short erect hairs on the veins and veinlets, minutely and abundantly white-pustulate, lower surface darker with ascending or appressed hairs on the principal veins, petiole 1–2 cm. long; inflorescence stiff, 5–10 cm. broad, flowers crowded at the ends of the branches, not scorpioid; calyx 2–3 mm. long at anthesis, in fruit twice as large and persistent, lobes lance-ovate, acuminate; corolla white, 2–2.5 mm. long, lobes ovate and about as long as the tube; filaments flattened, glabrous, ca. 1 mm. long, inserted in the middle of the corolla tube; anthers small; ovary glabrous; fruit erect, narrowly obovoid or ellipsoid, glabrous, lustrous, red, 5–7 mm. long, ca. 3 mm. thick.

British Guiana: right bank of the Rewa River, ca. 14 miles SSE. of mouth, ca. 90 m. alt. tree 6 dm. in diameter, over 30 m. tall, trunk deeply fluted, growing in Malata (*Mimusops*) Forest on a low hill with red clayey soil, Oct. 7, 1931, *Forest Dept. Brit. Guiana, Field No. D91, record no. 2082* (K).

Brazil: Rio Branco de Obidos, northeast of Obidos in the forest called "Repartimento," State of Pará, non-flooded forest, medium-sized tree with fluted trunk, fl. white, Dec. 15, 1913, *Ducke, Jard. Bot. Rio Jan. no. 17864* & *Herb. Amaz. Mus. Pará no. 15152* (K, BD, isotypes); hills near the Rio Branquinho, a tributary of the Rio Branco de Obidos, large tree with trunk excavated and sulcate, fl. white, fruit red, Jan. 27, 1918, *Ducke, Jard. Bot. Rio Jan. no. 17863* & *Herb. Amaz. Mus. Pará no. 16958* (K, BD); forest on Rio Branco de Obidos, elevated place near mouth of Rio Branquinho, large tree with white flowers, Nov. 1, 1919, *Ducke, Jard. Bot. Rio Jan. no. 11406* (BD).

This remarkable tree is known only from the collections cited. Ducke found it on a minor tributary of the Amazon, just to the northeast of Obidos, State of Pará, Brazil. He has made several collections at this type-locality. Members of the Forest Service of British Guiana recently discovered a second locality on the Rewa (or Illiwa) River, between the Rupununi River and the upper Essequibo between 3° and 4° N. lat. This new station is about 650 km. east-northeast of the type-station near the Amazon, and separated from it by the basin of the Rio Trombetas and the headwaters of the Essequibo River. There is every reason to believe that *Lepidocordia* will be found in the intervening region when it is reasonably well explored.

3. **Tournefortia** Linnaeus, Gen. 68 (1754).

Shrubs or woody vines with broad leaves. Inflorescence consisting of scorpioid racemes or spikes borne in dichotomous panicles. Calyx persistent, usually 5-lobed. Corolla white or yellowish, small, usually 5-merous, with cylindrical tube and spreading limb. Stamens usually 5, borne on the corolla-tube, included; filaments short. Ovary 4-celled, style terminal and solitary. Stigma sessile or borne on a distinct style, peltate or conic, fertile on the sides, apex usually bifid. Fruit a drupe, lobed or unlobed at maturity breaking up into 2–4 bony nutlets. Nutlets 1–2-seeded, frequently with 1–2 empty cavities. Endosperm thin. Cotyledons flat.

A genus of about 100 variable and ill-defined species; widespread in the Tropics but evidently centering in America. Type Species, *T. hirsutissima* L.

KEY TO THE SPECIES

Fruit deeply 4-lobed; embryos curved; corolla-lobes linear or long acuminate. § *Cyphocyema.*
  Corolla-tubes short, 1.5–2.3 mm. long, constricted at the throat, lobes linear, nearly as long as the tube; fruit white; plant very slender .... 1. *T. volubilis.*
  Corolla-tube elongate, 3–8 mm. long, not constricted at throat; lobes broadened below middle, half length of tube or less; fruit yellowish.
    Herbage sparsely and inconspicuously short-strigose or glabrous, even when young .... 2. *T. syringaefolia.*
    Herbage evidently and usually abundantly hairy, especially when young .... 3. *T. paniculata.*
Fruit obscurely if at all lobed; embryos straight; corolla-lobes broad and rounded. § *Eutournefortia.*
  Style well developed, 2–3 mm. long, evident even on the mature fruit; throat of corolla inflated; fruiting calyces frequently pedicellate .... 4. *T. Ulei.*
  Style short, the stigma apparently sessile on the mature fruit; throat of corolla constricted; calyx sessile even in fruit.
    Stems with pale short curving appressed hairs or glabrous; corolla-tube 4–5 mm. long .... 5. *T. bicolor.*
    Stems with spreading brown or tawny bristles; corolla-tube 5–8 mm. long.
      Leaves dull, with abundant long slender hairs; stems with abundant bristles 2–4 mm. long .... 6. *T. cuspidata.*
      Leaves glossy, with only scattered hairs along the veins, practically glabrous; stems with only scattered short bristles 1–2 mm. long .... 7. *T. melanochaeta.*

1. **Tournefortia volubilis** Linnaeus, Sp. Pl. 140 (1753). *T. floribunda* sensu Schomburgk, Fauna u. Fl. Brit. Guian. 1084 (1848).

Slender vine, densely clothed with slender curved hairs; branchlets slender; leaves lanceolate to ovate-lanceolate, 2–10 cm. long, 1–5 cm. broad, base rounded or obtuse, apex acuminate, surface densely strigose or velvety-tomentose, pale or tawny; inflorescence very slender and loosely branched, the spikes becoming 2–10 cm. long; calyx 1–2 mm. long, weakly accrescent, lobes subulate, reaching to beyond middle of corolla-tube; corolla white, tube 1.5–2.3 mm. long, strigose, throat constricted, lobes linear, 1–2 mm. long, spreading; fruit white with black dots, 4-lobed, the lobes subglobose, breaking up into single-seeded nutlets; style developed.

Eastern British Guiana, Venezuela, Colombia and Ecuador, and northward in the West Indies and Central America.

BRAZIL: Roraima, 1842–3, *Schomburgk 732* (BM, P); indefinite, *Schomburgk 732/1110b* (K); indefinite, Jan. 1843, *Schomburgk 1110* (BD).

I believe that the three above cited specimens are parts of a single collection and the basis upon which Schomburgk, l. c. 1084, reported *T. floribunda* from the southern slopes of Roraima. Part of the south slope of Roraima belongs to Venezuela, and it is quite possible that Schomburgk's specimens may have come from within Venezuelan rather than Brazilian territory.

Schomburgk, op. cit. pg. 830, reports *T. volubilis* as occurring about abandoned plantations near the coast of British Guiana, and Aublet, Hist. Pl. Guian. Fr. **1:** 117 (1775), lists it as occurring in French Guiana. I have seen no specimens to substantiate either of these two records. I consider the accuracy of both records extremely questionable.

2. **Tournefortia syringaefolia** Vahl, Symb. **3:** 23 (1794). *Messerschmidia syringifolia* (Vahl) Roemer & Schules, Syst. **4:** 543 (1819); Don, Gen. Syst. **4:** 370 (1838). *T. peruviana* Poiret, Encyc. Suppl. **4:** 425 (1816); Urban, Symb. Ant. **4:** 524 (1910); Johnston, Contr. Gray Herb. **92:** 78 (1930). *T. surinamensis* A. DeCandolle, Prodr. **9:** 526 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 961 and 1151 (1848); Miquel, Stirp. Surinam. 138 (1850); Pulle, Enum. Pl. Surinam. 398 (1906). *T. Hostmanni* Klotzsch ex Schomburgk, Fauna u. Fl. Brit. Guian. 1151 (1848), nomen. *T. maculata* sensu Lamarck, Tab. Encyc. **1:** 416 (1791) and Poiret, Encyc. **5:** 357 (1804), as to plants in Herb. Lam. *T. laurifolia* sensu DeCandolle, Prodr. **9:** 522, adnot. (1845). *T. foetidissima* sensu De Vriese, Nederl. Kruidkund. Arch. **1:** 347 (1848).

Shrubby vine; branchlets inconspicuously short-pubescent; leaves ovate to lance-elliptic or broadly lanceolate, 4–10(–15) cm. long, 2–5(–8) cm. broad, base acute to rounded, apex acuminate, lower face paler than upper, both faces very sparsely and very inconspicuously short-strigose (even when immature), usually abundantly and very minutely tuberculate, petioles 7–15 mm. long; inflorescence slender, loosely branched, terminal, 5–15 cm. broad, spikes usually less than 5 cm. long even in fruit; calyx 1–1.5 mm. long, weakly accrescent, lobes subulate to ovate; pedicels 0–1 mm. long at anthesis, in fruit becoming 1–5 mm. long and usually much thickened; corolla greenish white, tube 3–4 or even 8 mm. long, limb 3–4 or even 5 mm. broad, lobes 1–1.3 or even 2.5 mm. long, spreading, broad below the middle and above coarsely long-acuminate; fruit yellow or yellowish, usually spotted with black, conspicuously 4-lobed, the lobes subglobose, breaking up into 4 single-seeded nutlets; style developed.

From northern Brazil and Peru northward into the West Indies and Central America.

British Guiana: Berbice, Jan. 1896, *Jenman 6925* (K).

Dutch Guiana: Plant. Jagtlust, 1913, *Soeprato 38E* (Utr); Para District, scandent shrub, corolla somewhat greenish white, April 1838, *Splitgerber 1159* (Leid, P); Brownsberg Summit, liana with greenish flowers, 1924, *B. W. 6650* (Utr); banks of lower Commewyne River, Dec. 1842, flowers greenish, *Focke 750* (Utr); indefinite, *Hostmann 289* (BD, type of *T. Hostmanni* Kl.; K, BM, P), *Hostmann 951* (Boiss, type of *T. surinamensis*; G, K, BM, Utr, BD, Deles, P), *Hostmann ed. Hohenacker 1721* (P), *Kappler 951* (P), *Kappler 1721* (Utr) and *Focke 180* (Leid).

French Guiana: Cayenne, *von Rohr* (Copenhagen, type of *T. syringaefolia*, BM, isotype); Cayenne, *Martin* (K); Cayenne, *Rudge* (BM); near Cayenne, Feb. 12, 1845, *Rothery 207* (K), *sine no.* (BM); Montabo, Cayenne, 1866, *Jelski* (BD).

I have seen the types of all the species listed above. Vahl's species evidently belongs here and is notable chiefly for having the leaf-blade ovate (in accord with its name) rather than lance-oblong as is usually common in this plant. The common form of the species in the Guianas and in northwestern South America is well exemplified by the types of *T. Hostmanni* and *T. surinamensis*. All the material from French Guiana, including the type of *T. syringaefolia*, has corolla-tubes a few millimeters longer than in other South American plants. Similar elongate corolla-tubes, however, are found in the West Indian plants that have been classified, along with all South American forms, as *T. peruviana*. Possibly the difference in corolla-length may merit some nomenclatorial recognition, particularly as both the Cayenne and West Indian forms with elongate corollas also tend to have more ample leaf-blades than the short-tubed plants.

3. **Tournefortia paniculata** Cham. var. **spigeliaeflora** (A. DC.), comb. nov. *Tournefortia spigeliaeflora* A. DeCandolle, Prodr. **9**: 525 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 1151 (1848); Johnston, Contr. Gray Herb. **92**: 81 (1930).

Similar to *T. syringaefolia* Vahl, differing only in the more abundant and usually more slender and tawny hairs on the herbage, particularly on the immature leaves.

About the margins of the Amazon Basin in southwestern British Guiana, Colombia and Peru; also in Costa Rica.

British Guiana: Rupununi near Pirara, Feb. 1842, *Schomburgk 669* (BD); Pirara, etc., *Schomburgk 427* (BM, Deles, P); near Pirara, 1838, *Schomburgk 749* (K, BM, Leid, BD, Deles; DC, type); indefinite, *Schomburgk 427/669b* (K).

The elusiveness and scarcity of characters separating the many recognizable species of *Tournefortia* are well exemplified by the case of *T. paniculata*. This plant, centering in Brazil and having a distribution generally to the south and east of its close relative, *T. syringaefolia*, is separated from its relative only by quantity of pubescence. This difference is usually very real and tangible. When not, it at least gives to the two forms a perceptible though almost intangible difference in aspect, which coupled with their distinctly natural and credible wide geographic range, leads one inevitably to the conviction that two large genetic entities are concerned. These two species would be united by a stern judge of species-behavior. In his treatment of *Tournefortia*, however, he would be forced to create specific aggregations so large as to be all inclusive and indefinite, or to assemble under his aggregates such an array of subspecific categories as to be cumbersome and impractical. Difficulties in defining and describing species are encountered repeatedly in *Tournefortia* and force the student of the genus to abandon rigid and preconceived notions concerning species values. Testing the subjective matters of plant aspect by the facts of geographic distribution, he must gropingly work out natural concepts of the incipient and unfortunately not yet sharply definable species. The test of the resulting classification of the species of *Tournefortia* is not the imposing number and decisiveness of the key-characters, but the objectivity of the concept judged by one studying masses of material of it and of the group to which it belongs. A study of material of *T. paniculata* and *T. syringaefolia* does justify these two concepts and, as in many other similar cases in *Tournefortia* (e. g. *T. hirsutissima* and *T. bicolor*), does lend support to the universal recognition of these weak but practicable concepts.

The present variety is that race of *T. paniculata*, with tawny somewhat shaggy pubescence, long corolla-tubes and long acuminate corolla-lobes, which occurs about the head-waters of the Amazon and is geographically separated from the typical form of *T. paniculata*, of eastern Brazil and Paraguay, by the great tracts of the Amazon Basin. It is a weak variety but certainly worthy of some recognition. The extreme form is well exemplified by the type-collection of *T. spigeliaeflora*, collected by Schomburgk and labeled as from Pirara. In Robert Schomburgk's notes at Kew the type-number (749) appears in a list of plants (nos. 701–769) sent out to the coast from Pirara on June 25, 1838. In this list only six numbers are provided with definite localities, these all being given as from Pirara. Richard Schomburgk in his published catalogue, l. c. 1151, lists *T. spigeliaeflora* only from the "vicinity of Pirara at the edge of the oasis." This locality is on the margin of the Rio Branco watershed.

4. **Tournefortia Ulei** Vaupel, Notizbl. Bot. Gart. Berlin **6:** 186 (1914); Johnston, Contr. Gray Herb. **92:** 70 (1930). *T. Miquelii* Macbride, Proc. Amer. Acad. **51:** 541 (1916). *T. syringaefolia* of most authors, e. g. Miquel, Stirp. Surinam. 137, tab. 41 (1850); Pulle, Enum. Pl. Surinam 398 (1906), excl. of *Splitgerber 841.*

Shrub or liana; branchlets puberulent; leaves rather thin, ovate or ovate-elliptic or rarely broadly lanceolate, 6–17 cm. long, 3–8 cm. broad, base obtuse, apex acuminate, surfaces glabrous except for inconspicuous puberulence on the veins beneath, frequently with numerous scattered minute usually pale tuberculations; inflorescence loosely branched, the racemes loosely flowered and becoming 2–10 cm. long; calyx 1.5–2 mm. long, weakly accrescent, with triangular or subulate lobes, sessile or shortly and distinctly pedicellate; corolla 7–8 mm. long, greenish white, tube 3–4 mm. long, throat 1–1.5 mm. long, inflated, limb 2–3 mm. broad, lobes ovate ca. 1 mm. long; fruit glabrous, 4–5 mm. thick, not quite so long, broadest below middle; style well developed, becoming 2–3 mm. long, usually persistent; stigma clavate.

Known from the Guianas and in the head-waters of the Amazon south to Bolivia.

British Guiana: Arawak Matope, Cuyuni River, Oct. 1904, *Bartlett 8333* (K); upper Demerara River, Sept. 1887, *Jenman 4117* (K, NY).

Dutch Guiana: Surinam River near Bergendal, *Focke 1308* (Utr, type of *T. Miquelii*); road near Brownsberg, 1910, *native collector 170* (Utr); Commewyne River, *Focke* (K); Surinam, *Focke 121* (Leid).

French Guiana: Maroni River near Apatou, Oct. 1901, *Went 458* (Utr); Ile Portal, Maroni River, May 1857, *Sagot 1011* (K, P); St. Jean, fl. greenish, May 18, 1914, *Benoist 1247* (P); Charvein, fl. green, Jan. 20, 1914, *Benoist 648* (P); Roura, 1858, *Sagot* (P); Cayenne, 1859, *Sagot* (P); indefinite, *Poiteau* (K, BD).

In the Guianas this plant has been generally misdetermined as *T. syringaefolia*, a name properly applicable to the very different plant that has been called *T. peruviana*. The first name for our very distinct species is *T. Ulei*, based upon material collected by Ule in extreme southwestern Brazil. The name *T. Miquelii* Macbr., is based upon a plate published by Miquel, l. c. Since this is evidently drawn from the specimen at Utrecht collected at Bergendal by Focke (no. 1308), that specimen may be considered as the type of *T. Miquelii*. It is quite like *T. Ulei.*

5. **Tournefortia bicolor** Swartz, Prodr. 40 (1788) and Fl. Ind. Occ. **1:** 344 (1797); Johnston, Contr. Gray Herb. **92:** 69 (1930). *T. laevigata* Lamarck, Tab. Encyc. **1:** 416 (1791); Fresenius in Martius, Fl. Bras. 8^1: 49 (1857). *T. laevigata* var. *latifolia* DeCandolle, Prodr.

9: 519 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 1151 (1848). *T. glabra* Aublet, Hist. Pl. Guian. Fr. **1:** 118 (1775), not Linn. (1753). *T. Aubletii* Macbride, Proc. Amer. Acad. **51:** 541 (1916).

Shrub 1–5 m. tall, becoming subscandent; branchlets with weak short usually sparse ascending appressed hairs, rarely glabrous or puberulent; leaves ovate to elliptic or lance-ovate, 5–14 cm. long, 3–9 cm. broad, subcoriaceous, base obtuse to rounded, apex acute, upper surface slightly lustrous, bearing a few scattered weak short appressed hairs, smooth or bearing very minute inconspicuous papillae, lower surface slightly more hairy than upper; petioles 5–15 mm. long; inflorescence dense, branched, 5–20 cm. broad, racemes becoming 1–4 cm. long; calyx sparsely strigose at anthesis with lobes lanceolate or ovate, 1–2.5 mm. long, weakly accrescent, usually sessile; corolla white, tube 4–5 mm. long, strigose outside, about twice length of calyx, limb 6–7 mm. broad; fruit white, very fleshy, ca. 8 mm. long, glabrous; stigma subsessile.

Widely distributed in the American Tropics.

British Guiana: Barima River, 2.5–3.5 m. tall, fl. white, March 1923, *La Cruz 3372* and *3373* (G); Issorora, Aruka River, wet forest, tree 10 m., Jan. 1923, *Hitchcock 17560* (G, NY); Arawak Matope, Cuyuni River, fl. white, Oct. 1904, *Bartlett 8333* (K); near Pirara, Feb. 1842, *Schomburgk* (BD).

Dutch Guiana: Coppename River, fl. white Sept. 1901, *Boon 1112* (Utr); banks of Surinam River below Kabel, liana, fl. white, 1933, *Lanjouw 1231* (Utr); Brownsberg, tree no. 66, *B. W. 3243* (Utr); Brownsberg Summit, 1924, *B. W. 6513* and *6714* (Utr); Brownsberg, 1915, *B. W. 711* (Utr); Tapanahoni River, scandent shrub, fl. white, Oct., *Kappler ed. Hohenacker 2094* (BD); Maroni River, shrub 4–5 m., July 1904, *Versteeg 714* (Utr); indefinite, 1862, *Kappler 137* (Leid).

French Guiana: La Mana, 1823–24, *Leschenault* (P); Cayenne, 1786–91, *von Rohr* (BM); indefinite, 1820, *Perrottet* (Deles).

5a. **Tournefortia bicolor** var. **calycosa** Donn. Smith, Bot. Gaz. **14:** 27 (1889); Johnston, Contr. Gray Herb. **92:** 70 (1930). *T. Schomburgkii* DeCandolle, Prodr. **9:** 517 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 961 (1848). *T. alba* Splitgerber ex DeVriese, Nederl. Kruidkund. Arch. **1:** 347 (1848); Schomburgk, Fauna u. Fl. Brit. Guian. 1151 (1848). (?) *T. coriacea* Vaupel, Bot. Jahrb. 54, Beibl. **119:** 3 (1916).

Calyx 3–4 mm. long, the lobes linear or lanceolate; plant tending to be slightly more pubescent than in the species.

Dutch and British Guiana and southwestward across the Amazon Basin to Peru and Ecuador; also in Guatemala and Honduras.

British Guiana: Rockstone, bank of Essequibo, July 31, 1921, *Gleason 897* (NY, K); bank of Corantyne River, shrub 2.5–3 m. tall, Sept. 1878, *im Thurn* (K, P); Oreala, Corantyne River, trailing over bushes, Nov. 1879, *Jenman 120* (P); Epira, Corantyne River, trailing over bushes, Nov. 1879, *Jenman 65* (P); Berbice, 1837, *Schomburgk 70* (Deles); indefinite, *Schomburgk 70* (DC, TYPE of *T. Schomburgkii;* BM, Leid, BD, P); indefinite, ligneous twiner, fl. white, *Schomburgk 70* (K).

DUTCH GUIANA: Apoera Island, Corantyne River, fl. white, June 22, 1916, *B. W. 2043* (Utr); Wilhelmina Range, Peak no. 1200, June 9, 1926, *B. W. 7060* (Utr); near Plant. Catharina Sophia, Saramacca River, shrub 1–2.5 dm. high, in shade, fl. white, April 1838, *Splitgerber 841* (Leid, TYPE of *T. alba;* isotype, P).

BRAZIL: Rio Negro near confluence with Rio Solimöes, May 1851, *Spruce 1491* (G, K, BM).

The widely distributed "*T. bicolor* Sw." is reported by Schomburgk, l. c. 830, as cultivated as a decorative shrub in the coastal regions of British Guiana. *Tournefortia glabra* Aubl. is based entirely upon an unpublished plate by Plumier, (manuscripts at Paris vol. 6, tab. 53). This plate represents *T. bicolor* and is drawn from specimens obtained at Léogane in Haiti. The name *T. Aubletii* Macbr., is a mere renaming of *T. glabra* Aubl., because of an earlier Linnaean homonym. In a strict sense, therefore, both *T. glabra* Aubl. and *T. Aubletii* Macbr. are really West Indian plants.

The var. *calycosa* is based upon material from Guatemala. In Central America it appears to be rare and restricted to eastern Guatemala and adjacent Honduras where it is found in the same regions as *T. bicolor* and *T. hirsutissima.* In South America it occurs in the region to the east and south of the Orinoco Basin and hence far separated from *T. hirsutissima* L., which in South America is known only from northern Venezuela and Colombia. While the var. *calycosa* is not known to grow with *T. bicolor* in South America, it does occur in Ecuador, Peru and the Guianas where the species has been much collected. The variety seems to be a plant of more wet forests than those usually selected by *T. bicolor*. A study of *T. bicolor* from all parts of its very extensive range shows it to be remarkably uniform in the size of its calyx. The uniformly and evidently more elongate calyx-lobes of the var. *calycosa* merit some nomenclatorial recognition particularly since this variation seems to be geographically localized.

The variety has been frequently confused with *T. hirsutissima,* but that species may be readily distinguished from both *T. bicolor* and the var. *calycosa* by its more abundant, more spreading hairs on the herbage, and particularly by the stiff erect or ascending hairs (usually from a somewhat bulbose base) that according to abundance give a hirsute to velvety covering to the upper surfaces of the leaves. The fruit in *T. hirsutissima,* furthermore, is usually hairy. In *T. bicolor* and variety the somewhat glossy upper leaf-surfaces have weak scattered and commonly inconspicuous appressed hairs. The fruit is glabrous. The stems are usually sparsely hairy or glabrous. The calyx of *T. hirsutissima* is very variable in length. It may be short to elongate in the various parts of the range of the species. The two species, *T. bicolor* and *T. hirsutissima,* are very closely related and the differences separating them are almost exclusively those of pubescence mentioned. The difference seems to be decisive, however, and the resulting concepts natural and practicable.

The type of *T. alba* is the common form of the var. *calycosa,* it has the pubescence, particularly on the stems, sparse and scarcely, if at all, more abundant than is commonly found in *T. bicolor*. The type of *T. Schomburgkii* agrees with other collections from British Guiana in having conspicuously and rather densely hairy stems. In this regard it tends to suggest *T. hirsutissima* with which it has been confused. Schomburgk's original collection of *T. Schomburgkii* (no. 70), was distributed labeled as from "British Guiana" or from Berbice. In his catalogue, l. c. 961, he states that it grows on the banks of the Essequibo and makes no mention of Berbice. In closing it may be added that the type of *T. alba, Splitgerber 841,* was incorrectly cited under *T. syringaefolia* (equals *T. Ulei*) by Pulle, Enum. Pl. Surinam 398 (1906).

6. **Tournefortia cuspidata** Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. **3:** 83 (1818). *T. obscura* A. DeCandolle, Prodr. **9:** 517 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 961 (1848); Fresenius in Martius, Fl. Bras. **8**[1]**:** 49, adnot. (1857); Johnston, Contr. Gray Herb. **92:** 68 (1930). *T. setifera* Urban & Ekman, Ark. Bot. **22A,** no. **17:** pg. 94 (1929). *T. hirsutissima* sensu Pulle, Enum. Pl. Surinam 398 (1906).

Shrub or liana; branchlets pubescent, also conspicuously shaggy with abundant slender spreading brown hairs 2–4 mm. long; leaves lance-ovate to lanceolate, 7–15 cm. long, 3–6 cm. broad, base rounded or obtuse, apex acuminate, both surfaces with abundant appressed slender elongate hairs; petioles 5–13 mm. long; inflorescence stiffly and loosely branched, the spikes becoming 1–3 cm. long and crowded at the ends of the elongate branches; calyx-lobes subulate or linear, 7–9 mm. long at anthesis, weakly accrescent, sparsely long-hairy and short-strigose; corolla white, tube 5–8 mm. long, densely strigose outside, limb 4–6 mm. broad, lobes broad; fruit white, fleshy, compressed ovoid, probably ca. 8 mm. long, glabrous, more or less verrucose; stigma sessile.

Northern South America (Dutch Guiana to Colombia) and southward, in the upper reaches of the Amazon Basin, to Bolivia, doubtfully from eastern Brazil; Central America; West Indies.

British Guiana: Barima, March 1896, *Jenman 7118* (K); banks of the Quitaro, 1837, *Schomburgk 571* (DC, type of *T. obscura;* G, K, BM, Leid, BD); Berbice, June 1889, *Waby ex Jenman 5157* (K, BM); Berbice, *Burmann* (Deles); Demerara, *Parker* (K).

Dutch Guiana: Matappi, Corantyne River, liana, fl. white, June 18, 1916, *B. W. 2168* (Utr); Brownsberg Summit, liana, fl. white, July 3, 1924, *B. W. 6570* (Utr); Goddo, upper Surinam River, Jan. 29, 1926, *Stahel 134* (Utr); Pikien River, fl. white, July 1908, *Tresling 203* (Utr); Maroni River near Armina Falls, small shrub, fl. white, 1933, *Lanjouw 526* (Utr); indefinite, *Hostmann 227* (K, BM, Utr, BD, Deles, P).

I have examined the types of the species above cited. They are evidently conspecific! The type of *T. obscura* is *Schomburgk 571,* labeled as from the banks of the Quitaro. The specimen was collected by Robert Schomburgk. A study of his manuscript list at Kew shows that no. 571 falls within the gamut (no. 511–588) of numbered collections sent out from Curassawaka (on the Essequibo) in Dec. 1837. According to the list these numbers apply to specimens from "the Quitaro in November and to a few on the River Rewa, but the greater part of the high numbers from the mountains of Attarypou [Kanuku Mts.]." Only one number is provided with a definite locality, no. 581 being given as from the "mountains of Attarypou." The list gives the following field-notes for no. 571, "A ligneous twiner growing by river side, leaves light-green, a shade lighter below, calyx light green, petals and organs of fructification pure white, fruit a white berry." In Richard Schomburgk's published catalogue, l. c. 961, *T. obscura* is reported from the banks of the Rupununi, Rewa and Quitaro rivers.

In my paper on the Brazilian species of *Tournefortia* I reported this species, sub *T. obscura,* doubtfully from eastern Brazil. At Paris I have since seen a collection by Glaziou (no. 9981) labeled as from "São João da Barra" on Feb. 8, 1876. This locality is at the mouth of the Parahyba River in the northeastern section of the State of Rio Janeiro. The same number is cited by Glaziou, Bull. Soc. Bot. France **57,** Mem. **3e:** 478 (1910), under the name *"T. Salzmanni"* and as from "São João, près Campos." At Kew this collection by Glaziou, no. 9981, is labeled as cultivated at Rio Janeiro. The species has evidently been collected in eastern Brazil but whether or not from cultivated plants is still to be settled.

7. **Tournefortia melanochaeta** DeCandolle, Prodr. **9:** 520 (1845).

Shrub or liana; branchlets with scattered spreading brown hairs 1–2 mm. long; leaves lance-ovate, 9–11 cm. long, 5–6 cm. broad, base obtuse to rounded, apex acuminate, both surfaces lustrous and glabrous except for a very few slender appressed hairs along the midrib and veins, petioles 10–13 mm. long; inflorescence stiffly and loosely branched, spikes becoming 10–15 mm. long and crowded at the ends of the elongate branches; calyx-lobes glabrous, lanceolate to linear, 4–7 mm. long, weakly accrescent; corolla white, tube 5–7 mm. long, densely strigose outside, limb 4–5 mm. broad, lobes broad; stigma sessile; fruit unknown but probably as in *T. cuspidata.*

Known only from French Guiana.

FRENCH GUIANA: "Cayenne ou Guyane française," *Museum de Paris, 1821* (DC, TYPE); Cayenne (*Martin*) ex Museo Horti Paris, 1819 (BD); Cayenne, *Martin* (G, P).

The material cited is evidently all part of one large collection by Martin. It seems to be scarcely more than a glabrescent phase of *T. cuspidata,* a species which extends, from the westward, to the borders of French Guiana, though it is not as yet known to have been collected within that colony.

DOUBTFUL AND EXCLUDED SPECIES

Tournefortia gnaphalodes (Linn.) R. Brown ex Roemer & Schultes, Syst. **4:** 538 (1819).

Schomburgk, Fauna u. Fl. Brit. Guian. 830 (1848), reports this plant from the coasts of British Guiana, while Lamarck, Encyc. **3:** 94 (1789), and Aublet, Hist. Pl. Guian. Fr. **1:** 117 (1775) under the name *Heliotropium gnaphalodes,* indicate its occurrence in French Guiana. The plant is widely distributed in the West Indies but does not reach south to Trinidad. I have seen no material of it from the Guianan coast and, furthermore, do not believe that it is native in the region.

Tournefortia foetidissima Linnaeus, Sp. Pl. 140 (1753).

Tournefortia hirsutissima Linnaeus, Sp. Pl. 140 (1753).

Tournefortia cymosa Linnaeus, Sp. Pl. ed. 2, 202 (1762).

The above three species are listed by Aublet, Hist. Pl. Guian. Fr. **1:** 117–118 (1775), as occurring in French Guiana. They are West Indian species not known from the Guianas and, furthermore, not to be expected there.

Tournefortia incana (Meyer) Don, Gen. Syst. **4:** 368 (1838), not Lamarck (1791).

Tournefortia Meyeri DeCandolle, Prodr. **9:** 530 (1845).

The above two names are based upon *Messerschmidia incana* Meyer from the mouth of the Essequibo. The plant seems to be a species of *Heliotropium.*

4. **Heliotropium** [Tournef.] Linnaeus, Gen. 63 (1754).

Mostly low herbaceous or suffrutescent plants, rarely shrubs; leaves small to large. Inflorescence of solitary, geminate or ternate scorpioid spikes or racemes or the flowers solitary cauline and internodal. Calyx persistent or deciduous, with 5 teeth or lobes. Corolla yellow, white or blue, small, 5-merous, tube cylindrical, limb spreading. Stamens 5, borne in the corolla-tube, included, filaments short. Ovary 4-celled; style terminal, solitary; stigma sessile or on a distinct style, peltate or conic, fertile on the side, apex bearing a conic or cylindrical sterile appendage that is usually bifid or bidentate. Fruit dry, lobed or unlobed, at maturity breaking up into 2–4 bony nutlets. Nutlets 1–2-seeded, frequently with 1–2 sterile cavities. Endosperm developed.

A large genus widely distributed in the warmer regions of the world. Type Species, *H. europaeum* L.

KEY TO THE SPECIES

Plant distinctly succulent, entirely glabrous, frequently somewhat glaucous . . . . 1. *H. curassavicum.*
Plant not succulent, more or less pubescent, not glaucous.
  Flowers borne singly along the leafy stems; fruit contracted into a conic apex . . . . 2. *H. lagoense.*
  Flowers borne in well developed scorpioid spikes or racemes.
    Corolla blue or purple; fruit glabrous, ribbed, angulate, deeply 2-lobed with the lobes horizontally divergent; plant coarse, erect, more or less hirsute with large evidently veined leaves 3–10 cm. broad . . . . 3. *H. indicum.*
    Corolla white; fruit strigose, rounded, weakly 4-lobed vertically; plant rather slender, erect or decumbent; leaves with appressed pubescence, very obscurely veined, less than 2 cm. broad.
      Leaf-blades elliptic to broadly oblanceolate, 5–20 mm. broad, petiole 4–15 mm. long; racemes mostly geminate or ternate, bractless . . . . 4. *H. procumbens.*
      Leaf-blades linear to oblanceolate, 1–8 mm. broad, petiole 1–2 mm. long; racemes always single, bearing small lanceolate bracts 1–2 mm. long.
        Corolla 4–6 mm. long, anthers joined at their apices; stigma borne on a short but evident style; stems comparatively coarse and stiff; leaves drying rather light colored . . . . 5. *H. ternatum.*
        Corolla 2–2.5 mm. long, anthers not joined apically; stigma sessile on the fruit; stems wiry, very slender, leaves usually drying dark colored. . . . . . 6. *H. filiforme.*

1. **Heliotropium curassavicum** Linnaeus, Sp. Pl. **1:** 130 (1753); Schomburgk, Fauna u. Fl. Brit. Guian. 961 (1848); Johnston, Contr. Gray Herb. **81:** 14 (1928).

Annual or short-lived perennial, succulent, glabrous; stems prostrate or decumbent, 1–3 dm. long, ascendingly branched; leaves narrowly to broadly oblanceolate, 2–4 cm. long, 3–10 mm. broad, fleshy, frequently somewhat glaucous; flowers borne in bractless single or geminate scorpioid spikes 1–10 cm. long; calyx ca. 1.5 mm. long at anthesis, over 2 mm. long at maturity, sessile or subsessile, lobes broadly cuneate to triangular-ovate; corolla white, 2–3 mm. long, lobes ca. 1 mm. long, tube shorter than calyx; anthers 0.6–1 mm. long, sagittate, apex with acuminate appendage, not joined together; fruit weakly 4-lobed, epicarp slightly fleshy and wrinkled in drying; style sessile, disk of stigma broad; nutlets 4, equal, oblong, 2–2.5 mm. long, 1-celled, 1-seeded.

From the coast of British Guiana, Venezuela and Colombia southward along the west coast of South America to central Chile and Patagonia, and northward through the West Indies and in Central America to southern-most United States.

BRITISH GUIANA: Georgetown, *Hitchcock 16572* (G, NY); indefinite, seashore, June, 1889, *Jenman 5471* (US, BM); indefinite, *Jenman 2165* and *4466* (NY).

The species is listed as occurring in French Guiana by Aublet, Hist. Pl. Guian. Fr. **1**: 117 (1775). I consider this record very questionable. It may be noted that I have examined and made dissections of the type of *H. Lehmannianum* Bruns, Mitt. Inst. Allg. Bot. Hamburg, **8**: 69, fig. 10 (1929), recently described from the coast of southern Peru. My study has shown the type to be quite ordinary *H. curassavicum*. Bruns described and illustrated remarkable developments in corolla-lobing and in anther-shape. In the various dissections made on the type I could find no suggestion of remarkable structures, the corolla and the anthers agreeing perfectly with the familiar typical West Indian *H. curassavicum*.

2. **Heliotropium lagoense** (Warm.) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. **3a**: 97 (1893); Johnston, Contr. Gray Herb. **81**: 49 (1928). *Schleidenia lagoensis* Warming, Kjoeb. Vidensk. Meddel. **1867**: 15 (1868). *Heliotropium trinitense* Urban, Symb. Ant. **7**: 350 (1912).

Annual herb with scattered slender appressed hairs; stems slender, prostrate, 5–30 cm. long, ascendingly branched; leaves oblanceolate, 0.5–1.5 cm. long; flowers borne singly along the leafy stems, extra-axillary; calyx of 5 unequal lanceolate or cuneate lobes, at anthesis 1.5–2 mm. long, becoming about twice as long in fruit; pedicels 1–3 mm. long, ascending; corolla white, 3–4 mm. long, funnelform; lobes ovate, 1–1.5 mm. long; sinus rounded, plaited, occasionally with a minute lobule; anthers oblong, bearing an obese hairy apical appendage nearly as large as the anther proper, anthers joined together by their appendages; fruit glabrous or nearly so, subterete, base rounded, from at or below middle contracted upwardly into a broad conic or short-rostrate apex; nutlets 4, ca. 1.5–2 mm. long, single seeded.

Northern Dutch Guiana, Trinidad, northern Venezuela, eastern Bolivia, and eastern and western Brazil; not common and apparently local and erratic in distribution.

Dutch Guiana: "Suriname," Jan. 1885, *Suringar* (Leid).

This species is frequently confused with *H. filiforme,* which it resembles in its wiry stems and slender leaves, but it is readily distinguished from that plant by its conic fruit and its cauline internodal flowers. Although Suringar's collection has no definite locality it is to be supposed that it is from the vicinity of Paramaribo where Suringar is known to have done most of his collecting in Dutch Guiana.

3. **Heliotropium indicum** Linnaeus, Sp. Pl. 130 (1753); Aublet, Hist. Pl. Guian. Fr. **1:** 117 (1775); Pulle, Enum. Pl. Surinam 399 (1906); Johnston, Contr. Gray Herb. **81:** 19 (1928). *Heliophytum indicum* (Linn.) DeCandolle, Prodr. **9:** 556 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 831 and 961 (1848).

An erect coarse weedy annual herb, usually more or less pale-hirsute, 1–10 dm. tall, mostly branched above the middle; leaves ovate or elliptic to broadly lanceolate, herbaceous, veined, 5–15 cm. long, 3–10 cm. broad, margin repand or undulate, apex acute, base obliquely acute to subcordate, petioles 4–10 cm. long, winged just below the leaf-blade; flowers borne in bractless single scorpioid spikes becoming 5–30 cm. long; calyx with subulate or cuneate lobes 2–2.5 mm. long, somewhat accrescent in fruit; corolla blue or violet or exceptionally white, salverform, tube 2.5–4.5 mm. long, evidently surpassing the calyx, limb 2–4 mm. broad; anthers elongate, the apices not united; style short and slender; fruit glabrous, strongly ribbed, deeply 2-lobed (the lobes spreading) and breaking up into 4 angulate nutlets 2–3 mm. long.

A Pan-Tropic weed, probably of American origin.

British Guiana: Comaca, Moruka River, *La Cruz 1058* (NY, US); Waranuri Mission, Moruka River, Oct. 1922, *La Cruz 2600* (G, NY, US); Kamakusa, upper Mazaruni River, Nov. 1922, *La Cruz 2748* (G, NY); Tumatumari, *Gleason 370* (NY); Hyde Park, east bank of Demerara River, *Dahlgren* (FM); Demerara, *Parker* (K); Georgetown, weed along canal, fl. white, 1919, *Hitchcock 16684* (G, NY, US); Epira, banks of Corantyne River, Nov. 1879, *Jenman 54* (K); Corantyne River, Oct. 1879, *im Thurn* (P); indefinite, *Schomburgk 206* (BD) and *600* (K).

Dutch Guiana: bank of Corantyne River, 1911, *Hulk 33* (Utr); sand near Maripaston, Saramacca River, Nov. 1902, *Pulle 4* (Utr); Paramaribo, fl. bluish, *Kuyper 25* (Utr); near Paramaribo, fl. blue, Dec. 1837, *Splitgerber 338* (Leid, P); Combee, Paramaribo, Aug. 1901, *Went 319* and *332* (Utr); Plant. Rust en Werk, 1913, *Soeprato 57* (Utr); upper Surinam River near Saida, 1908, *Tresling 346* (Utr); Plant. Slootwijk, Commewyne River, 1913, *Soeprato 151* (Utr); beach facing Cottica Mt., Lawa River, fl. white with yellowish throat, light lilac when young, Oct. 1903, *Versteeg 289* (Utr); Cottica River near Moengo, marshy ground, fl. light blue, 1933, *Lanjouw 403* (Utr); indefinite, *Focke 1370* (Utr).

French Guiana: Maroni, *Wachenheim 287* and *290* (P), *291* (BM); St. Jean, fl. pale blue, April 26, 1914, *Benoist* (P); St. Jean, fl. pale blue with yellowish center, March 8, 1914, *Benoist 1154* (P); St. Laurent du Maroni, Jan. 1908, attractive to butterflies, *LeMoult* (P); Acarouani 1855, about dwellings, fl. bluish, *Sagot 449* (P); vicinity of Cayenne, fl. purple, May 6, 1921, *Broadway 118* (K); Cayenne, Feb. 18, 1845, *Rothery 165* (BD); Iles du Salut, 1854, fl. pale bluish, *Sagot 449* (BM, P).

Brazil: Obidos, *Spruce 476* (K); Monte Alegre, 1873, *Traill* (K).

Venezuela: Ciudad Bolivar, 1931, *Holt & Blake 838* (G); Las Batillas, *Passarge & Selwyn 301* (BD); Puerto Ayacucho, 1931, *Holt & Blake 834* (G).

In Dutch Guiana this species is called "Kaha Kankay" (*Tresling no. 346*) and "Kokorrode" (*Pulle no. 4*) and is given as being used with salt as a cure for gas on the stomach (*Versteeg no. 289*). According to Aublet, l. c., it is called "Cret-de-Coq" in French Guiana and an infusion of the flowers used "pour arrêter les pertes de sang chez les femmes."

4. **Heliotropium procumbens** Miller, Dict. ed. 8, no. 10 (1768); Johnston, Contr. Gray Herb. **81**: 52 (1928). *Heliotropium inundatum* Swartz, Prodr. 40 (1788).

Annual herb with more or less abundant slender appressed hairs, plant usually cinereous; stems erect or decumbent, 1–5 dm. long, ascendingly branched; leaves with elliptic, obovate or broadly oblanceolate blades, 1–4 cm. long, 5–20 mm. broad, petioles slender 4–15 mm. long; flowers borne in slender scorpioid racemes, racemes mostly geminate or ternate, bractless, elongating, becoming 2–10 cm. long, peduncles 1–4 cm. long; calyx with 5 unequal lanceolate or linear lobes, at anthesis 0.5–1 mm. long, becoming 1–2.5 mm. long in fruit, pedicels ca. 0.5 mm. long; corolla white 1–5 mm. long, lobes ovate, short, with rounded sinus; anthers ovate, contracted apically into short narrow appendages, anthers not joined apically; fruit depressed globose, 4-lobed, strigose; stigma sessile; nutlets strigose, 0.5–1 mm. long.

Northern Argentina northward through Tropical America to southern United States; rare in the very wet regions.

British Guiana: indefinite: *Appun 1762* (K), *Schomburgk 1024* (K, BD) and *1026* (K).

Brazil: Prainha, *Traill* (K); Alemquer, *Spruce* (K).

5. **Heliotropium ternatum** Vahl, Symb. Bot. **3:** 21 (1794); Johnston, Contr. Gray Herb. **81:** 69 (1928). *Heliophytum passerinoides* Klotzsch ex Schomburgk, Fauna u. Fl. Brit. Guian. 1152 (1848), nomen. *Schleidenia Fumana* Fresenius in Martius, Fl. Bras. 8[1]: 40 (1857). *Heliotropium Fumana* (Fresen.) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. **3a:** 97 (1893); Johnston, Contr. Gray Herb. **81:** 71 (1928). *Heliotropium* sp., Oliver, Trans. Linn. Soc. London, Bot. **2:** 279 (1887). *Heliotropium strictissimum* sensu N. E. Brown, Trans. Linn. Soc. London, Bot. **6:** 51 (1901). *Heliotropium fruticosum* of authors, not Linnaeus.

Suffrutescent, with abundant ascending or appressed hairs; stems erect or decumbent, 1–5 dm. long, ascending branched; leaves lanceolate to linear, revolute, 1–3 cm. long, 1–8 mm. broad, with slender petiole 1–2 mm. long; flowers borne in stiff scorpioid racemes; racemes single, elongating and becoming 2–15 cm. long, bearing scattered lanceolate bracts 2–3 mm. long; calyx at anthesis 2–3 mm. long, consisting of 5 more or less unequal lanceolate lobes, becoming twice as large in maturity; pedicels 0.5–1 mm. long; corolla white, 4–6 mm. long, lobes ovate, sinus rounded and plicate; anthers ovate with short obtuse hairy apical appendages which are apically joined to one another; fruit depressed globose, 4-lobed, strigose; style short but evident; nutlets 1–1.5 mm. long.

Central America and the West Indies, northern Colombia and Venezuela, southern British Guiana and eastern Brazil; chiefly in open places or in dry thickets.

British Guiana: Kamakot, Ireng River, 1884–85, *Jenman 3* (US); Konkarmo, Ireng Valley, Nov. 16, 1884, *im Thurn 3* (K, BM); Ireng Valley, *Quelch & McConnell 220* (K, BM) and *302* (K); Rupununi, *Appun 2203* (K); Rupununi, May 1842, *Schomburgk 573* (BD, type of *H. passerinoides*); Pirara, etc., 1841–42, *Schomburgk 282* (P); indefinite, gravelly savanna, leaves appear farinaceous, fl. white, 1836, *Schomburgk* (K).

In and about the West Indies *H. ternatum* is generally recognized as a variable species in habit, pubescence and leaf-shape. The typical and most common form of it has loosely revolute leaves 3–5 mm. broad and a loosely appressed indument of slender hairs. This plant appears to be rare or absent in our area. In the Guianas the species seems to be represented only by a form found in the savannas near the Brazilian border. This has linear leaves 1–3 mm. broad and is silky strigose. It is quite like plants from eastern Brazil that have been described as *H. Fumana*. In my monograph, l. c. **81:** 69–71 (1928), *H. Fumana* was treated as doubtfully distinct from *H. ternatum*. Subsequent consideration of its relation with *H. ternatum,* in the light of new material, has led me to the belief that it is only a pronounced form, possibly a savanna-ecad of that species. Much of the material from the dry eastern corner of Brazil, which formerly I placed in *H. Fumana* (and even some that I placed in *H. salicoides* Cham.) I now refer unhesitatingly to *H. ternatum*. Only the material with narrow sublinear leaves and distinctly silky strigose indument should be placed under *H. Fumana*. This form comes from more interior, more moist localities than those in which *H. ternatum* is usually found. Transitional forms are common. If the linear-leaved, silky-strigose form of the savannas needs to be recognized, it may be called **Heliotropium ternatum** var. **Fumana** (Fresen.), comb. nov.

Both *H. ternatum* and the variety may be distinguished from *H. salicoides* by having white rather than bright yellow corollas. The leaves also dry much lighter in color in *H. ternatum* and the pubescence of the herbage is not so strongly spreading and so coarse as in *H. salicoides*. Warming's *Schleidenia subracemosa,* which I placed under *H. salicoides,* I now refer to *H. ternatum*. *Schleidenia dasycarpa* Fresen. is also based upon material referable to *H. ternatum*. I have recently examined the types of these Brazilian species.

The only Guianan specimen of this species at Berlin that was collected by Schomburgk (no. 573) is labeled as from the Rupununi. It bears Klotzsch's name, *Heliophytum passerinoides,* and is evidently the type of that undescribed species. Schomburgk, in his published list, however, gives *H. passerinoides* Kl. only from the savannas near the Takutu River. That stream joins the Ireng not far west of Pirara which in its turn is even a shorter distance west of the Rupununi. All of Schomburgk's specimens, under their various labels, probably came from the general region to the west of Pirara. From this region *H. ternatum* var. *Fumana* extends up the Ireng where others have collected it.

The typical form of the species is either very rare or absent in the coastal region of the Guianas. Possibly the region is too wet. The description of the puzzling *Messerschmidia incana* Meyer, from the mouth of the Essequibo, suggests *H. ternatum* in all except the fruit. The doubt surrounding Meyer's plant, however, forces me to leave it unplaced.

6. **Heliotropium filiforme** Lehmann, Götting. Gel. Anzeigen **1817:** 1515 (1817) and Asperif. **1:** 37 (1818); DeCandolle, Prodr. **9:** 545 (1845); Pulle, Enum. Pl. Surinam 399 (1906); Johnston, Contr. Gray Herb. **81:** 61 (1928). *Schleidenia filiformis* (Lehm.) Fresenius in Mar-

tius, Fl. Bras. 8^1: 40 (1857). *Heliotropium helophilum* Martius, Flora Regensb. 21^2, Beibl. 4: 85 (1838) and Herb. Fl. Bras. p. 165, no. 267 (1841); DeCandolle, Prodr. 9: 544 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 961 (1848); Miquel, Stirp. Surinam. 136, tab. 40 (1850).

Annual herb, sparingly strigose; stems slender, erect or decumbent, 1–4 dm. long, ascendingly branched; leaves 1–2.5 cm. long, 1.5–3.5 mm. broad, oblanceolate, petiole very slender, 1–2 mm. long; inflorescence consisting of very slender scorpioid racemes, these solitary, elongating, becoming 2–15 cm. long, bearing minute scattered lanceolate bracts, 1–2 mm. long; flowers 1–3 mm. distant, strict, numerous; calyx of 5 unequal lanceolate or lance-ovate lobes, at anthesis 1.5–2 mm. long, becoming about twice as long in fruit, pedicels becoming 0.5–1 mm. long in fruit; corolla white, funnelform, 2–2.5 mm. long; lobes ovate with broad open sinus, ca. 1 mm. long; anthers each contracted into a short puberulent apical appendage, not coherent; fruit depressed globose, obscurely 4-lobed, strigose; stigma sessile or subsessile; nutlets almost 1 mm. long.

Eastern Bolivia and Paraguay northward through Brazil to Venezuela and the Guianas; also in Trinidad and British Honduras; growing in sand, usually near water.

British Guiana: Essequibo River, Demerara, 1881, *Jenman 1095* (K, P); Essequibo, Jan. 1842, *Schomburgk 321* (BD); upper Rupununi, *Appun 2394* (K); Pirara, 1845, *Schomburgk 228* (BD, P); Berbice, sandy soil, 1837, *Schomburgk 351* (K, BD, P); indefinite, *Schomburgk 228/321b* (K).

Dutch Guiana: Corantyne River, sandy places near Wonotobo, 1916, *B. W. 2866* (Utr); Avanavero Rapids, Kabalebo River, in sand, 1920, *B. W. 4653* (Utr); island in Lucie River, sandy soil, 1910, *Hulk 398* (Utr); lower Saramacca River, in sand, Nov. 1902, *Pulle 69* (Utr); lower Surinam River, April 1846, *Kappler, ed. Hohenacker 1810* (Utr, BD); Maroni River, rocks at Armina Falls, 1901, *Went 467* (Utr); Maroni River near Bonnidoro, in sand, fl. white, *Kappler, ed. Hohenacker 2095* (BD); Lawa River, sandy flat, Oct. 1903, *Versteeg 277* (Utr); indefinite, 1862, *Kappler 158* (Leid).

French Guiana: Maroni, 1862, *Rech* (P); Cayenne, *Martin* (P); Cayenne, 1853, *Rothery 209* (Cambr.); Oyapock, Oct. 1844, *collector not given, no. 269* (K).

Brazil: Monte Alegre, *Traill 570* (K); middle Rio Cuminá, Dec. 24, 1928, *Sampaio 5906* (BD); Rio Cuminá, Cataract of Tronca, Sept. 18, 1928, *Sampaio 5011* (BD); Rio Trombetas, Lag. Caypurú, *Traill 568* (K); Barra Rio Negro, *Spruce 1115* (G, K).

Venezuela: Angostura, 1864, *Grosoudy* (P); Puerto de Tablas, Canton de Upata, 1864, *Grosoudy* (P); Tigrito, *Passarge & Selwyn 515* (BD); Las Botillas, *Passarge & Selwyn 302* (BD).

Doubtful and Excluded Species

Heliotropium fruticosum L. ex Aublet, Hist. Pl. Guian. Fr. **1:** 117 (1775).

Although listed by Aublet I believe that this species does not occur in French Guiana. The binomial was applied to *H. ternatum* in many of the older books. But neither this latter species nor the one properly called *H. fruticosum* is known or even to be expected in French Guiana.

Heliotropium latifolium Willd. ex Schomburgk, Fauna u. Fl. Brit. Guian. 961 (1848).

Listed by Schomburgk as distributed through the forests in the northern parts of British Guiana. The species (and the cited synonym, *H. scorpioides* HBK.) is a synonym of *H. angiospermum* Murray (= *H. parviflorum* L.). Although this plant is known from eastern Brazil and from northern Venezuela, no specimens have been seen from the Guianas.

Messerschmidia incana Meyer, Prim. Fl. Esseq. 92 (1818). *Tournefortia incana* Don, Gen. Syst. **4:** 368 (1838), not Lamarck (1791). *Tournefortia Meyeri* DeCandolle, Prodr. **9:** 530 (1845); Schomburgk, Fauna u. Fl. Brit. Guian. 1151 (1848).

The description given by Meyer makes it evident that this plant must be a *Heliotropium,* rather than a *Tournefortia*, if indeed it really is a member of the Boraginaceae at all. The original description strongly suggests *H. ternatum* Vahl in all but the fruit, which is given as consisting of two biovulate sub-trilocular nutlets. The type was collected on the west bank of the Essequibo River near its mouth, where it is given as growing in dry places. Until the type (probably at Goettingen) is examined the species must remain very puzzling and unplaced.

Herbarium, Arnold Arboretum,
Harvard University.

HANDELIODENDRON, A NEW GENUS OF SAPINDACEAE

Alfred Rehder

With plate 119 and one text figure

Handeliodendron, gen. nov.

Flores ut videntur hermaphroditi, symmetrici, satis parvi, albescentes; sepala 5, libera, imbricata, ovato-oblonga vel oblonga, obtusiuscula, uninervia, ciliolata, extus intusque puberula, basin versus ut pedicellus squamulis patelliformibus obsita; petala 4 vel interdum 5, sepalis duplo longiora, imbricata, oblonga, obtusiuscula, basin versus sensim in unguem attenuata, supra basin lamellis 2 elevatis instructa, extus adpresse pubescentia, intus glabra, ciliolata, medio reflexa; discus lateralis pulvinaris, irregulariter lobulatus, latere staminibus opposito concavus, fere aeque latus quam altus; stamina 7, raro 8, inaequalia, longiora petalis subaequilonga, sed ob petala recurvata manifeste exserta, filamentis leviter sursum curvatis, apice excepto villoso-pilosis, antheris late ovalibus mucronulatis, infra medium dorsum affixis; ovarium late fusiforme, longiuscule stipitatum, in stylum brevem apice stigmatibus 3 brevissimis conicis coronatum attenuatum, triloculare; ovula in quoque loculo 2, alterum erectum, alterum pendulum. Capsula piriformis, leviter 3-loba vel abortu 2-loba vel simplex, stipitata, loculicida, pericarpio coriaceo brunneo lenticellis albidis consperso; semina in quaque capsula 1–4, ovoidea, testa crustaceo-coriacea, atra, nitida, hilo brunneo parvo elliptico, arillo albido duplici circiter semen medium tegente, e trichomatibus cohaerentibus constituto, exteriore hilum cingente ab interiore annulo incrassato separato. Embryo vix curvatus, cotyledonibus plano-convexis fere rectis, basi tantum curvatus et in radiculam dorsalem gracilem in plica testae immersam et fere ad micropylem descendentem contractus.

Arbor alta, cortice griseo, ramulis hornotinis brunneis glabris, annotinis lenticellatis spadiceis. Folia opposita, glabra, digitata, foliolis 5 inaequalibus petiolulatis ellipticis vel elliptico-obovatis, abrupte in acumen caudatum productis, bais late cuneatis in petiolulum decurrentibus, supra laete viridibus subtus pallidioribus et glandulis scutellatis initio fusco-rubris demum nigrescentibus sparse vel sparsissime conspersis, pinnatinerviis, nervis utrinsecus 9–12 patentibus arcuatis supra levissime subtus magis elevatis margine anastomosantibus, costa supra elevata sed in canaliculo plus minusve immersa subtus manifeste elevata; petiolis gracilibus teretibus basi tantum leviter sulcatis estipulatis. Panicula terminalis, plus minusve longe pedunculata, pyramidalis, laxa, multiflora, pedicellis squamulosis exceptis glabra, ramulis oppositis, in dichasia pluraque triflora exeuntibus, pedicellis gracilibus squamulosis bracteis bracteolisque deciduis instructis; alabastra ovoidea.

Species unica Chinae provinciae Kweichou incola.

Handeliodendron Bodinieri (Lévl.), comb. nov.

Sideroxylon Bodinieri Léveillé, Fl. Kouy-Tchéou, 384 (1915).

Character generis.

Petiolus 4–11 cm. longus; foliola basalia terminali saepe duplo minora, 3–12 cm. longa et 1.5–6.5 cm. lata, petiolulis 1–15 mm. longis; panicula pedunculo 3–5 cm. longo excluso circa 10 cm. longa et lata, pedicellis 2–5 mm. longis; sepala 2–3 mm. longa; petala 9 mm. longa et 2 mm. lata; stamina 5–9 mm. longa, antheris 0.75 mm. longis; ovarium stylo brevissimo incluso 1.25 mm. longum, stipite 1.5 mm. longo. Capsula stipite circiter 1 cm. longo incluso 3.2 cm. longa; semina circa 1 cm. longa.

CHINA. Kweichou: district de Ly-po, *J. Cavalerie* in herb. Bodinier, no. 2626, Sept. 1898 (fruit), May 11, 1899 "grand arbre" (holotype of *Sideroxylon Bodinieri* in herb. Léveillé, Bot. Gard. Edinb.); Mapo, Pingchow, alt. 500 m., common in light woods, *Y. Tsiang*, no. 6813, Aug. 30, 1930, "tree, bark dark gray, branchlets lenticellate, fruit reddish, seeds black" (in Herb. Nat.-hist. Mus. Wien ex Herb. Metrop. Mus. Nat. Hist. Acad. Sin. Nanking).

Though *Handeliodendron* resembles in its opposite digitately 5-foliolate leaves the Hippocastanaceae, it shows in its other characters a closer affinity with the Sapindaceae and is best placed with the tribe Harpullieae on account of the 2-ovuled locules, the symmetrical flower, the dehiscent fruit, the not spirally curved embryo and the presence of a terminal leaflet. The genus exhibits a number of characters unusual or rare in the family, as the opposite digitate leaves, flowers with 7 stamens, stipitate ovary and a unilateral disk, and seeds with a double arillus and straight embryo. Opposite leaves are very rare in the family, they occur in *Valenzuela* and some species of *Matayba*, digitately 5-foliolate leaves are still rarer and are only found in a few species of *Allophylus* as in *A. dimorphophyllus* Radlk., though ternate leaves occur in a number of genera as *Delavaya, Hypelate, Llagunoa, Thouinia,* and *Allophylus;* also the double arillus is very rare. The wood, but not the bark and other parts of the plant, contains saponin according to Dr. Handel-Mazzetti.

The solitary flowering specimen I have seen has only the terminal

SIDEROXYLON BODINIERI (Lévl.) Rehd.

flowers of the dichasia at the end of the branches fully open, all the other flowers are in bud. The open flowers as well as the flowers still in bud seem to have normal ovaries and normal anthers; all the open flowers have 4 petals, while in at least some of the flowers in bud I counted 5 petals; in one flower I found 8 stamens. The description of the seeds is based on notes and on drawings kindly furnished me by Dr. Handel-Mazzetti, since I did not feel at liberty to dissect the solitary fruit of the type specimen. He had identified Tsiang's no. 6813 which

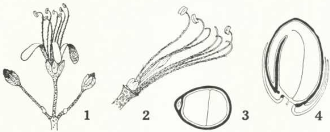


FIGURE 1. HANDELIODENDRON BODINIERI (Lévl.) Rehd. 1. Flower (× 2). 2. Flower with sepals and petals removed (× 4). 3. Cross-section of seed (× 3). 4. Longitudinal section of seed, showing the double arillus, the inner one interrupted above the micropyle (× 3).

is in fruit as belonging to the same species as Bodinier's flowering specimen, after I had sent him a photograph of the type of *Sideroxylon Bodinieri* Lévl. with a detached flower. A photograph of Tsiang no. 6813 kindly sent me with a detached fruit by Dr. Handel-Mazzetti confirmed the identity of the two specimens.

I take pleasure in naming this interesting and distinct new genus in honor of Dr. H. Handel-Mazzetti, who has collected extensively for several years in China and whose critical account of the plants of his and other collections in his Symbolae Sinicae is one of the most important contributions to our knowledge of the flora of China.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

NOTES ON SOME OF THE EBENACEAE AND VERBENACEAE OF THE SOLOMON ISLANDS COLLECTED ON THE ARNOLD ARBORETUM EXPEDITION, 1930–1932[1]

R. C. BAKHUIZEN VAN DEN BRINK

With plates 120–122

EBENACEAE

Diospyros ellipticifolia (Stokes) Bakhuizen, Enum. Mal. Eben. in Gard. Bull. Str. Settl. **7**(2): 162 (1933).

Maba elliptica J. R. et G. Forster, Char. Gen. Pl. 122, tab. 6 (1776).

Y s a b e l I s l a n d: Tiratoña, alt. 600 m., *Brass* 3318, ♂, flor., Dec. 8, 1932. — Vernacular name "Gaitutunu."

Diospyros ferrea (Willd.) Bakhuizen, Enum. Mal. Eben. in Gard. Bull. Str. Settl. **7**(2): 162 (1933).

Maba buxifolia (Rottb.) A. L. Jussieu in Ann. Mus. Hist. Nat. **5**: 418 (1804).

Diospyros ferrea var. **salomonensis** Bakhuizen, var. nova.

Subsimilis D. ellipticifoliae, sed staminibus 9, foliis submajoribus differt.

Ramuli teretes, rugosi, dense tuberculatim lenticellati. Folia elliptica vel oblongo-lanceolata, basi obtusa vel rotundata, apice obtusa vel breviter obtuse acuminata, 5–20 cm. longa, 3–7 cm. lata, chartacea vel tenuiter coriacea, supra atro-viridia, nitida vel statu sicco subopaca, subtus pallidora, primum subtus appresse pubescentia, denique costa excepta utrinque glabra, nervis lateralibus utrinsecus 7–10 vel pluribus, utrinque subinconspicuis, venis reticulatis laxis utrinque subprominulis invisibilibus; petiolus semiteres, appresse rufo-pubescens, glabrescens, 0.3–0.5 cm. longus. Flores masculi sessiles, 3–5-ni, cymosi vel in

[1] In the latter part of 1930 Mr. S. F. Kajewski, in continuation of his botanical work on behalf of the Arnold Arboretum in the New Hebrides and North Queensland, left Brisbane for Bougainville Island and the British Solomon Islands. He resigned in June 1931 and in July 1932 his place was taken by Mr. L. J. Brass, who remained there until December 1932 when he returned to Brisbane, and after a few weeks left for Papua as botanist to the Archbold Expedition of the American Museum of Natural History, New York. Mr. C. T. White, Brisbane, to whom the collections have been entrusted for arrangement, advises that they have now been roughly sorted into families. Several of these have been sent to specialists for critical examination, and we have already received determinations of the Ebenaceae and Verbenaceae from Dr. R. C. Bakhuizen van den Brink. The descriptions of the new species, new varieties and of one new combination are offered herewith. The list of other determinations will be included in the general account of the Bougainville and Solomon Islands collection to be published at a later date.—Ed.

pseudo-racemis dispositi; calyx urceolatus, 3-dentatus, in anthesi saepius rumpens, intus versus apicem appresse rufo-pubescens; corolla albida, versus lobos purpurascens; stamina 9, sublibera, glabra. Fructus ellipsoideus vel subglobosus, primum appresse pubescens, maturitate glabrescens, flavescens, 1.5–2 cm. longus, 1.5–1.75 cm. diam.; calyx fructifer subpatelliformis, marginibus reflexus, extus sparse appresse pubescens, glabrescens, rugulosus, intus toto superficie sericeus, 1–1.2 cm. diam.; semina oblonga, triquetra, utrinque acuta, facie recta, dorso convexa, a latere compressa, rugulosa, nigra, 1.2–1.5 cm. longa, 0.5–0.7 cm. lata, 0.5 cm. crassa; albumen aequabile.

Ulawa Island: *Brass* 2958, ♀, fruct., Oct. 5, 1932. Ysabel Island: Jaukau, *Brass* 3152, ♂, flor., Nov. 19, 1932. — Vernacular names "Aibul" (under no. 2958) and "Gno-gno-finete" (under no. 3152).

Diospyros insularis Bakhuizen, Enum. Mal. Eben. in Gard. Bull. Str. Settl. **7**(2): 173 (1933). PLATE 120, 121

Arbuscula. Folia elliptico-oblonga, basi cordata, apice breviter obtuse acuminata, supra atro-viridia, statu sicco olivacea, subopaca, nervis lateralibus 7–12 distantibus, secus marginem non vel indistincte anastomosantibus, utrinque prominentibus; petiolus subteres vel apicem versus subdepressus. Fructus axillaris, sessilis, plerumque solitarius, ellipsoideus vel subglobosus, utrinque rotundatus, primum sericeus, statu maturo glabratus, ruber, statu sicco niger, rugulosus, opacus, 2–2.5 cm. diam.; calyx fructifer viridis, valde accrescens, extus glaber, 3.5–4 cm. diam., tubo crasso, plano-cupuliforme, subquadrato, intus rufosericeo, rimo elevato, 2–2.5 cm. diam., lobis late ovatis obtusis vel suborbicularibus, coriaceis, patulo-recurvis vel reflexis, striato-nervosis, utrinque glabris, 1–1.5 cm. longis, basi 1.5–1.75 cm. latis; semina usque ad 8, oblongo-ellipsoidea, triquetra, dorso convexa, a latere compressa, ca. 1.5 cm. longa, 0.7 cm. lata, 0.4–0.5 cm. crassa; testa rugulosa, nigra; albumen aequabile.

Ysabel Island: Maringe, *Brass* 3166, ♀, fruct., Nov. 22, 1932.

Diospyros maritima Blume, Bijdr. Flor. Ned. Ind. 669 (1825).

Ysabel Island: Sigana, alt. 100 m., *Brass* 3450, ♀, fruct., Jan. 11, 1933. — Vernacular name "Gegila."

Diospyros samoensis A. Gray in Proc. Amer. Acad. **5**: 326 (1861).

San Christoval Island: Star Harbor, *Brass* 3073, ♂ flor., Oct. 18, 1932. Ngela Group: Nayotana Island, *Brass* 3240, ♀, fruct., Nov. 16, 1932.

VERBENACEAE

Avicennia marina (Forsk.) Vierhapper, Beitr. Kennt. Flor. Süd-arab. in Denkschr. Akad. Wiss. Wien, **71:** 435 (1907).

Avicennia marina var. **resinifera** (Forst.) Bakhuizen, Rev. Gen. Avic. in Bull. Jard. Bot. Buitenz., ser. **3**(2): 210, tab. 16 (1921).

Malaita Island: Quoimonapu, sea level, *Kajewski* 2344, Dec. 11, 1930. — Vernacular name "Bu-bula."

Callicarpa pedunculata R. Brown, Prod. Flor. Nov. Holl. 513 (1810).

Guadalcanal Island: Berande River, sea level, *Kajewski* 2420, Jan. 7, 1930. — Vernacular name "Bau."

Callicarpa pentandra Roxb., Flor. Ind. **1:** 409 (1820) var. **typica** (Schau.) Bakhuizen, forma **genuina** Bakhuizen in H. J. Lam. & Bakhuizen, Rev. Verb. in Bull. Jard. Bot. Buitenz., sér. 3, **3**(1): 12 (1921).

Bougainville Island: Kieta, sea level, *Kajewski* 1560, March 21, 1930; Kupei Gold Field, alt. 950 m., *Kajewski* 1643, April 7, 1930; Kugu-maru, Buin, alt. 150 m., *Kajewski* 1841, June 9, 1930. San Cristoval Island: Waimamura, alt. 200 m., *Brass* 2625, August 10, 1932. — Vernacular name "Sor-ku-ku" (under no. 1841).

Callicarpa pentandra var. **paloensis** (Elm.) Bakhuizen, forma **furfuracea** Bakhuizen in H. J. Lam & Bakhuizen, Rev. Verb. in Bull. Jard. Bot. Buitenz., sér. 3, **30:** 15 (1921).

Malaita Island: Quoimonapu, sea level, *Kajewski* 2340, Dec. 11, 1930. Guadalcanal Island: Ma-massa, Konga, alt. 400 m., *Kajewski* 2485, Feb. 12, 1931; Vulolo, Tutuve Mt., alt. 1200 m., *Kajewski* 2540, April 20, 1931. — Vernacular names, "Quoi-esa" (under no. 2340), "Kim-berri" (under no. 2485) and "Kimberi" (under no. 2540).

Clerodendron Buchanani (Roxb.) Walpers, Rep. Bot. Syst. **4:** 108 (1845).

Bougainville Island: *Kajewski* 1606, March 29, 1930; Karngu, Buin, sea level, *Kajewski* 2222, Oct. 6, 1930. San Cristoval Island: Waimamura, *Brass* 3140, Oct. 1932. Ysabel Island: Sigana, alt. 20 m., *Brass* 3465, Jan. 13, 1933. — Vernacular name "Arka-koo" (under no. 2222).

Clerodendron confusum Hallier f. in Meded. Rijks Herb. Leiden, **37:** 65 (1918).

Bougainville Island: Kupei Gold Field, alt. 900 m., *Kajewski* 1687, April 11, 1930; Kugu-maru, Buin, alt. 150 m., *Kajewski* 1925, August 4, 1930; same locality, *Kajewski* 1978, August 23, 1930. Malaita Island: Quoi-mon-apu, sea level, *Kajewski* 2341, Dec. 11, 1930. Guadalcanal Island: Vulolo, Tutuve Mt., alt. 1200 m., *Kajewski* 2502, April 14, 1931. San Cristoval Island: Hinuahaoro, alt. 900 m., *Brass* 2919, Sept. 22, 1932. Ysabel Island: Tiratoña, alt. 600 m., *Brass* 3403, Dec. 29, 1932. — Vernacular names "Koru-kopu" (under no. 1925), "E-yapapor" (under no. 1978), "Kaka-fair" (under no. 2341), "Ambus-gorle-le" (under no. 2502) and "Fuho" (under no. 3403).

This species is closely related to *C. buruanum* Miq. which differs in the much longer corolla-tube and also to *C. infortunatum* L., which has a glabrous corolla and a longer corolla-tube. Nevertheless all these species may perhaps be considered as only extreme forms of *C. infortunatum* L.

Clerodendron inerme (L.) Gaertner, Fruct. Sem. Plant. **1:** 271, tab. 75 (1788).

Bougainville Island: Karngu, Buin, sea level, *Kajewski* 2244, Oct. 12, 1930. Guadalcanal Island: Berande, sea level, *Kajewski* 2407, Jan. 5, 1931. — Vernacular names "Pumbarg-aru" (under no. 2244) and "A-la-loi-alugi" (under no. 2407).

Faradaya amicorum (Seem.) Seemann in Jour. Bot. **3:** 258 (1865).
Clerodendron amicorum Seemann in Bonplandia, **10:** 249 (1862).

Faradaya amicorum var. **salomonensis** Bakhuizen, var. nova.

Frutex flexuosus plerumque scandens, primum appresse pubescens, denique glabrescens, in ramulis florigeris cinereo-subsericeus. Folia valde variabilia, lanceolata-oblonga vel obovata, utrinque attenuata, basi acute vel obtuse cuneata, apice breviter subacute acuminata, utrinque glabra, 7–20 cm. longa, 3.5–10 cm. lata, nervis lateralibus distantibus, utrinsecus 5–7. Inflorescentiae axillares vel in paniculis speciosis terminalibus dispositae, multiflorae, cymis subinde trichotomis, basi conspicue bracteolatis; bracteolae oblongo-ellipticae vel sublanceolatae, utrinque sericeae, 1–2.5 cm. longae, 0.3–1 cm. latae. Flores subparvi, in alabastro globosi, pedicellati; pedicelli teretes, graciles, cinereo-sericei, basi bracteolati, 0.5–1.5 cm. longi; calyx primum subclausus vel apice poro dehiscens, denique truncatus vel margine undatus, vel dentatus vel etiam distincte lobatus, 0.5–0.6 cm. longus, 0.7–1 cm. diam., fructifer accrescens, saepius irregulariter ruptus, extus sparse pubescens, basi excepta glabrescens; corolla alba, hypocrateriformis, utrinque glabra, tubo variabili, 1–1.5 cm. longo, lobis ovatis vel suborbicularibus, glabris, margine ciliatis; stamina longe exserta, glabra; ovarium quadrangulare vel 4-lobatum, glabrum; stylus filiformis, teres, glaber, usque ad 3 cm. longus. Fructus submagnus, abortu 1-pyrenus; pyrena elongata, nucleis reductis appendiculiformibus basi suffulta, monosperma, glabra, 3–4 cm. longa, 1.5–2 cm. diam.

San Cristoval Island: Waimamura, alt. 50 m., *Brass* 2635, August 11, 1932. Ysabel Island: Tiratoña, alt. 600 m., *Brass* 3399, Dec. 29, 1932. — Vernacular name "Naosokoño."

Perhaps this is not really different from the typical form, but it has a glabrous corolla.

Gmelina moluccana (Bl.) Backer in Heyne, Nutt. Plant. Ned. Ind. **4**: 118 (1917); Bakhuizen in H. J. Lam & Bakhuizen, Rev. Verb. in Bull. Jard. Bot. Buitenz., sér. 3, **3**(1): 67 (1921).

San Cristoval Island: Waimamura, sea level, *Brass* 2860, Sept. 12, 1932.

Gmelina salomonensis Bakhuizen, spec. nova. PLATE 122

Arbor speciosa. Ramuli crassi, teretes, novelli rufo-tomentosi, vetustiores glabrescentes, sparse lenticellati. Folia opposita, longe petiolata, coriacea, ovata vel oblongo-elliptica, basi cordata vel subtruncata, apice acuminata, obtusa, integerrima, 15–35 cm. longa, 10–24 cm. lata, supra viridia, lucida, primum sparse pubescentia, denique costa et nervis exceptis glabra, subtus grisea, submolliter rufo-tomentosa, basi nonnullis glandulis parvis obsessa, costa supra leviter subtus valde prominente, utrinque glabrescente, nervis lateralibus utrinsecus 12–18 pallidis, supra prominulis glabris, subtus prominentibus rufo-tomentosis, venis reticulatis utrinque prominulis. Inflorescentiae terminales, elongatae, paniculiformes, dense ramosae, infra foliatae, rufo-tomentosae, bracteolatae, dense multiflorae, 20–30 cm. longae, 10–15 cm. diam.; bracteae parvae, lineari-oblongae, utrinque acuminatae acutae, utrinque tomentosae, mox deciduae. Flores minores, pedicellati; calyx cupuliformis, regulariter obtuseque 5-dentatus, extus rufo-tomentellus, glandulis 2–4 parvis vestitus, intus glaber, 0.3–0.4 cm. longus et diam., fructifer subaccrescens; corolla minor, inaequaliter 5-lobata, subbilabiata, utrinque pubescens, statu sicco ca. 1.5 cm. longa, tubo inferne angustato in faucem ventricosam ampliato, intus ad insertionem staminum longe hirsuto, superne glabrato, calyce multo longiore, 0.7–1 cm. longo; stamina 4, didynamia, vix exserta, statu sicco 0.5–1 cm. longa, filamentis glabris; ovarium subglobosum vel obovoideum, apice subtruncatum, glaberrimum; stylus filiformis, teres, sparse pilosus, vix exsertus, statu sicco ca. 1 cm. longus. Drupa minora, ovoideo-globosa, nitida, maturitate nigra, statu sicco 1.2–1.5 cm. diam.; calyx fructifer leviter excrescens, subapplanatus vel marginibus reflexis, quinatus, 0.5–0.7 cm. diam.

Y s a b e l I s l a n d: Tiratoña, alt. 600 m., *Brass* 3309, Dec. 8, 1932. — Vernacular name "Koko."

This plant is intermediate between *G. moluccana* (Bl.) Backer and *G. macrophylla* (R. Br.) Benth. and may be a hybrid of these species. From *G. moluccana* it differs in the tomentose under side of the leaves and the villous calyx; from *G. macrophylla* in the terete branches, the elevated nerves and veins on the upper side of leaves, somewhat in the form of panicles, but especially in the small and regular 5-toothed calyx.

Petraeovitex multiflora (Sm.) Merr. var. **salomonensis** Bakhuizen, var. nova.

Frutex scandens, gracilis; ramuli quadrangulares, primum tomentelli, glabrescentes. Folia opposita, ternata vel inaequaliter biternata; foliola 3–9, minora, sessilia, chartacea; foliola lateralia ovato-oblonga vel oblongo-elliptica, basi rotundata, apice obtuse acuminata, 1–4.5 cm. longa, 0.5–2.3 cm. lata, foliolum terminale oblongo-lanceolatum, utrinque attenuatum, basi decurrens, acute acuminatum, apice obtusiuscule acuminatum, 3.5–6 cm. longa, 1.5–2.5 cm. lata, omnia margine integra, supra glabra, subtus primo farinaceo-tomentosa, denique glabrescentia vel costa nervisque excepta glabra, nervis lateralibus 6–8 cum venis reticulatis utrinque prominulis; petiolus communis 2–3 cm. longus, petiolus lateralis 0.5–1 cm. longus, omnes superne canaliculati, cinereo-tomentelli. Inflorescentiae terminales, laxe paniculiformes, infra foliatae, multiflorae, 30–50 cm. longae, 20–40 cm. diam.; bracteae minutae lineares, tomentellae, 0.15–0.25 cm. longae; cymulae breviter pedunculatae vel superne subsessiles, 7–15-florae, tomentellae, 0.5–1 cm. diam., pedunculis 0–1 cm. longis. Flores parvi, subsessiles, albidi; calyx 5-dentatus, cinereo-tomentellus, 0.1–0.15 cm. diam.; corolla alba, extus minute pubescens vel glabrescens, in fauce albido-puberula, 5-lobata, lobis inaequalibus, reflexis; stamina 4, exserta, fauci inserta, glabra; stylus gracilis, exsertus, glaber, 0.3 cm. longus, stigmatibus bifidis; ovarium ovoideum, basi glabrum, apice cinereo-tomentellum.

B o u g a i n v i l l e I s l a n d: Kupei Gold Field, alt. 850 m., *Kajewski* 1686, April 11, 1930.

This variety much resembles *P. sumatrana* H. J. Lam, but it has sessile leaflets, a cinereous-tomentose calyx and a hairy ovary.

Premna integrifolia Linnaeus, Mant. **2:** 252 (1771) s. l.

Bougainville Island: Kieta, sea level, *Kajewski* 1566, March 30, 1930; Kugu-maru, Buin, alt. 150 m., *Kajewski* 1842. Malaita Island: Quoimonapu, alt. 50 m., *Kajewski* 2330, Dec. 10, 1930. Guadalcanal Island: Vulolo, Tutuve Mt., alt. 1200 m., *Kajewski* 2503, April 14, 1931. San Cristoval Island: Waimamura, alt. 200 m., *Brass* 2624, August 10, 1932 (f. *taitensis* Schau.); Kirakira, *Brass* 2768, August 30, 1932; Star Harbour, *Brass* 3132, Oct. 1932. — Vernacular names "Garlu" (under no. 1842), "Qua-eu" (under no. 2330) and "Arru-arru" (under no. 2503).

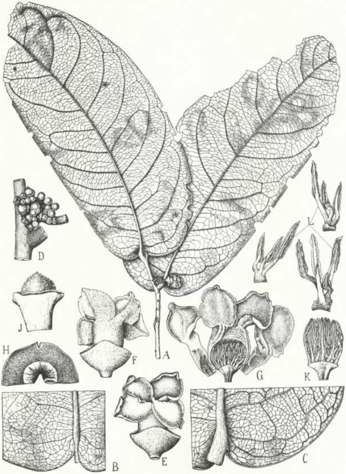
Teysmanniodendron Ahernianum (Merr.) Bakhuizen, comb. nov.
Vitex Aherniana Merrill in Bur. Gov. Lab. Bull. **6**: 18 (1903).

A large sized tree, up to 50 m. high; bark grey or brown; wood hard, brown; branchlets round, greyish, rufous-pubescent, glabrescent. Leaves 2–3-foliolate, short petioled; petiole terete, rufous-tomentose, especially at the base and in the insertion of the petiolules, 4–5 cm. long; petiolules in all leaves equal, furrowed above, thickened and rufous-tomentose at the base only, otherwise glabrous, 2–4 cm. long. Leaflets oblong, coriaceous, rather rigid, shining above, glabrous on both surfaces, except pubescent on the midrib beneath when young, 10–32 by 4–13 cm., reticulations of leaves very dense beneath. Cymes axillary, many-flowered, 15–30 cm. long; peduncles 1–2 in the axils, flattened, rufous-tomentose, 5–12 cm. long. Flowers rather small; calyx funnel-shaped, obscurely 5-dentate, rufous-sericeous, 0.4–0.5 cm. long, and wide; corolla with very short tube, glabrous at the base, otherwise sericeous, throat and base of the lip densely villous; ovary globose, glabrous, biloculate. Fruit oblong or pear-shaped, purple green when ripe, shining and striate when dry, 1.5–2 cm. long, 1–1.5 cm. diam., one-seeded; exocarp coriaceous, thin; seed oblong, 1 cm. long, 0.5–0.7 cm. diam.; fruiting calyx enlarged, cup-shaped, truncate, 0.5 cm. long, 0.5–0.8 cm. in diam.

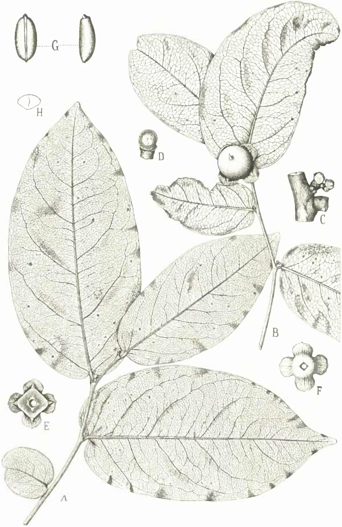
Ysabel Island: Tataba, alt. 50 m. *Brass* 3441, Jan. 5, 1933. Guadalcanal Island: Sorvorhio Basin, alt. 200 m., *Kajewski* 2715, Feb. 3, 1932. — Vernacular name "Seupa" (under no. 2715).

Vitex cofassus Reinwardt ex Blume, Bijdr. Flor. Ned. Ind. 813 (1826).

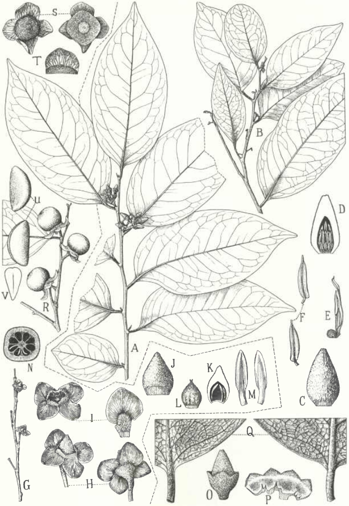
Bougainville Island: Kieta, sea level, *Kajewski* 1533, March 17, 1930; Kugu-maru, Buin, alt. 150 m., *Kajewski* 1843, May 28, 1930. Malaita Island: Quoimonapu, alt. 300 m., *Kajewski* 2381, Dec. 16, 1930. Guadalcanal Island: Berande River, *Kajewski* 2387, Dec. 24, 1930; Mamassa, Konga, alt. 400 m., *Kajewski* 2489, Feb. 13, 1931; Vulolo, Tutuve Mt., alt. 1200 m., *Kajewski* 2605, May 1, 1931. San Cristoval Island: Balego-



DIOSPYROS INSULARIS Bakh.



Diospyros insularis Bakh.



Diospyros samoënsis A. Gray

Nagonago, alt. 350 m., *Brass* 2821, Sept. 5, 1932. Y s a b e l I s l a n d : Maringe, *Brass* 3154, Nov. 19, 1932; Tasia, *Brass* 3272, Dec. 5, 1932. — Vernacular names "Moi-kewie" (under no. 1843), "Father" (under no. 2381), "Vada" (under no. 2387), "Vatha" (under no. 2489), "Vasa" (under no. 2605), "Hada" (under no. 2821), "Wara" (under no. 3154) and "Varha" (under no. 3272).

EXPLANATION OF PLATES

Plate 120

Diospyros insularis Bakh. (type G. Peekel 4 A from New Ireland, ♂). — A. Flowering branch (× ½). — B and C. Leaf base seen from above and from below (× 1½). — D. Inflorescence, flowers dropped (×2). — E–L. Male flowers with details: E–F. flowers from the inside and the outside (×2½); G. longitudinal section of flower, seen from the inside (× 2½); H. calyx, seen from the inside (× 2½); I. rudimentary ovary (× 10); K. androeceum (× 3½); L. stamens (× 5).

Plate 121

Diospyros insularis Bakh. (type Brass 3166 from the Solomon Islands, ♀). — A. Leafy branch (× ½). — B. Fruiting branch (× ½). — C. Axis of the fruiting branch (× 2½). — D. Peduncle of fruit at the apex (× 1½). — E–F. Fruiting calyx (× ½): E. from the inside; F. from the outside. — G–H. Seeds (× 1½): H. seed in transverse section.

Plate 122

Diospyros samoënsis A. Gray — A–B. Flowering branches of male plant (× ½). — C–F. Male flower bud with details: C. corolla bud (× 3); D. corolla bud cut lengthwise (× 3); E. stamens (× 5); F. anthers (× 10). — G. Flowering branch of female plant (× ½). — H–N. Female flower with details: H. flower buds from above and from below (× 2); I. calyx (× 2) and calyx-lobe, seen from the inside (× 2½); J. corolla bud (× 3); K. corolla bud cut lengthwise (× 3); L. ovary (× 3); M. anthers (× 15); N. ovary in transverse section (× 5). — R. Fruiting branch (× ½). — S–T. Fruiting calyx from the outside and from the inside (× 1); T. lobe of fruiting calyx from the outside (× 1½). — U. Seeds (× 1½). — V. Seed in cross section (× 2).

Botanic Gardens, Buitenzorg.
January 25, 1934.

AN ENDEMIC SOPHORA FROM RUMANIA

Edgar Anderson

With plates 123 and 124 and one text figure

One of the most interesting endemics of the Balkan peninsula is the *Sophora* discovered at Babadag by J. Prodan.[1] Through the kindness to visit this locality on September 4, 1934 and collected abundant fruit- of Dr. C. Georgescu of the Şcoală Politechnică at Bucarest I was able ing material. Subsequent comparison with Asiatic material of *Sophora alopecuroides* L. in the herbaria of the Royal Botanic Garden at Kew and of the Arnold Arboretum has convinced me that the Rumanian plant deserves to be described as a distinct species and I take pleasure in naming it after its discoverer.

Sophora Prodanii, sp. nov.

Herba suffruticosa, 5–7 dm. alta. Folia 5–10 cm. longa, imparipinnata; foliola 19–25, oblongo-elliptica, 12 mm. longa, 7 mm. lata, membranacea, supra glabra, subtus pilos sparsos appressos gerentia. Racemus densus. Flores ignoti, non visi. Legumen 5–7 cm. longum, glabrescens; semina 3–7, luteo-fusca, 5 mm. longa.

Known only from a single hilltop near Babadag, Rumania.

Şeremet, Babadag, Rumania, *Edgar Anderson* no. 85 (type), Sept. 4, 1934 (specimens deposited in the herbaria of the Arnold Arboretum, Royal Botanic Garden Kew and British Museum of Natural History).

An erect suffrutescent herb from an underground rootstalk; stems, erect, 5–7 dm. tall, slender, with ascending simple branches, subterete, dark green with fine, rather scattered, short, appressed hairs. Leaves alternate, imparipinnate, 5–10 cm. long; stipules wanting; leaflets 19–25, elliptic oblong to oblanceolate, up to 12 mm. long and 7 mm. wide when well developed, dark green, rather thin, becoming brittle when dry; apex rounded with a mucronate tip. Leaflets glabrous above, pubescent below with very scattered fine short appressed hairs; margin entire and somewhat revolute; midrib evident but veins weak and evident only beneath; petiolule about 1 mm. long. Inflorescence terminal, racemose, dense, sub-erect. Flowers not seen. Fruit terete, torose, wingless, indistinctly ribbed, indehiscent or tardily dehiscent,

[1] Mag. Bot. Lapok. **11**: 231, 235 (1912).

with sparse appressed hairs; pedicels in fruit 2–4 mm. long, strictly ascending. Seeds yellowish brown, 5 mm. long.

The species is of very restricted distribution. It is at present known only from this one locality, the summit of a small hill near the ancient town of Babadag. It occurs over a space of several acres in the edge of the forest and persists as a weed in an adjoining field. Prodan (loc. cit.) in his account of the plant from Babadag identified it with *S. alopecuroides* L. but pointed out that it was much more nearly glabrous.

Fig. 1. Distribution of Sophora alopecuroides and its Close Relatives

◎ = *Sophora Prodanii*
• = *S. alopecuroides*
○ = *S. alopecuroides* var. *tomentosa*
✤ = Intermediate form collected by Gilliat Smith

Sophora alopecuroides, sensu latiore, is a wide-spread species (see Fig. 1), extending from central Asia to northern Asia Minor and the vicinity of Constantinople (Istambul). From central Asia to Asia Minor there is a progressive transition in pubescence, leaf size, and leaf texture. If only the two ends of the series existed they could easily be maintained as two separate species, a small-leaved species with appressed silky hairs from northern Asia Minor and a coarser species with spreading tomentose pubescence from Central Asia. As early as 1850 Spach[1] had proposed the name *S. Jauberti* for the *Sophora* from Asia Minor and in 1894 Freyn and Sintenis[2] described *Goebelia reticulata* from northern Asia Minor, a name which was later transferred to *Sophora* by Hayek.[3] Aznavour[4] went so far as to advance the plants collected by him in the suburbs of Constantinople to the status of a variety, *Buxbaumii* of *Goebelia reticulata.*

It is certainly true that there is marked geographical differentiation in *S. alopecuroides,* sensu latiore, but when a large series of specimens is examined, these local and regional differences are found to intergrade. Particularly interesting are two collections made by Mr. B. Gilliat Smith (nos. 1904 and 1714) in the neighborhood of Tabriz, Persia, which can be assigned with certainty neither to the form from Central Asia nor to that from Asia Minor. Since Tabriz is in the region where these two forms come together, it seems best to follow Boissier[5] and Bornmüller[6] and treat the *Sophora* from Asia Minor as *S. alopecuroides* L. and that from Central Asia as *S. alopecuroides* L. var. *tomentosa* (Boiss.) Bornm. Further study will undoubtedly permit the separation of other geographical varieties. The specimens I have seen from N. W. China which have been referred to *S. alopecuroides* are certainly different from those collected in Afghanistan and Persia.

Taken as a whole, *S. alopecuroides* and *S. Prodanii* present a graded series in size and texture of leaflet, pubescence and color (Table I).

TABLE I. COMPARISON OF LEAF CHARACTERS

	S. Prodanii	*S. alopecuroides*	*S. alopecuroides* var. *tomentosa*
leaf texture	brittle when dry	tenuous	coriaceous
upper side of leaflets	glabrous	appressed silky pubescence	tomentose pubescence
under side of leaflets	scattered appressed hairs	appressed silky pubescence	spreading tomentose pubescence
color	dark green	greenish gray	yellowish green
size of leaflets	7 × 12 mm.	8 × 16 mm.	9 × 24 mm.

[1] Illustr. Plant. Orientalium, 4: 45, t. 330 (1850–1853).
[2] Oest. Bot. Zeit. 44: 66, 98 (1894).
[3] Prod. Fl. Pen. Balcan. 1: 770 in Fedde, Rep. Spec. Nov. Reg. Veg. Beih. 30: 770 (1926).
[4] Magyar Bot. Lapok, 12: 163 (1913).
[5] Fl. Or. 2: 628–629 (1872).
[6] Bot. Cent. Beih. 27: 347 (1910).

There is no more difference, if as much, between *S. Prodanii* and *S. alopecuroides* from the neighborhood of the Bosphorus as between *S. alopecuroides* from Asia Minor and *S. alopecuroides* var. *tomentosa* from Afghanistan. But in the latter case, there is a full set of intermediate forms from the intervening territory while in the former the intermediates which once undoubtedly existed have long since disappeared. In the 250 miles between Babadag and the Bosphorus no sophoras of this group have been collected. The differences between *S. alopecuroides* and *S. Prodanii,* though slight, include leaf texture and color as well as pubescence and general size. For this reason *S. Prodanii* is put forward as a distinct species rather than as a variety of *S. alopecuroides*.

Sophora Prodanii undoubtedly originated as a semi-glabrous variety on the westward edge of *S. alopecuroides*. A large number of Balkan species represent westward extensions of Asiatic species, or find their closest relatives in the Asiatic flora. "It is necessary to bear in mind . . . that the Hungarian and Roumanian plains were covered with the waters of the Sarmatic and Pontic seas and lakes until relatively recent geological times (and) that the Bosphorus is no wider than a broad river . . . It follows . . . that migration on a wide front between the lowlands of the Balkan Peninsula and those of the north has been possible for land plants only since the end of the Tertiary period and must for the most part have been in one direction—northwards—as the Sarmatic and Pontic waters dried up; that migration along the northern part of Asia Minor into the Balkan Peninsula is geographically feasible and has been even more so in past geological periods."[1]

The persistence of *S. Prodanii* in this one isolated station in the Dobrudja is to be explained by the geological history of the Babadag mountains. These low mountains (or hills) are of very great age and though low in elevation have persisted for a long time as a land mass, remaining above the waters of the Sarmatic and Pontic seas and lakes. "It is safe to assume that they formed a refuge for relatively old types of plants and to this fact is due the richness of the Dobrudja in Tertiary relicts." (Turrill. loc. cit.)

To the question as to whether *S. Prodanii* evolved its distinctive characteristics before or after its separation from the sophoras of Asia Minor, the present day differentiation within the latter suggests an answer. Not only is there a progressive reduction westwards in size and pubescence from Central Asia to the Bosphorus but the same tendency can be seen within Asia Minor itself. The specimens of *S. alopecuroides* which most closely resemble *S. Prodanii* are from northwestern Asia Minor. These

[1]Turrill, W. B. The Plant Life of the Balkan Pen. Oxford. 1929.

facts suggest that in Miocene times *S. Prodanii* was already a well marked variety of *S. alopecuroides*. The Sarmatic and Pontic waters (Upper Miocene or Pliocene) destroyed the intervening intermediates and reduced *S. Prodanii* to a dwindling remnant in the Babadag Mountains. Within the immediate past at any rate, it has been so reduced in numbers as to undergo severe inbreeding and further divergencies from the parental type would be expected to have accumulated through the random effects of inbreeding on a small population.

Most of the plants at Babadag seemed to be infected with some gall-producing organism. The characteristic "witches brooms" produced in this way are very conspicuous in the photograph of the type specimen. Similar growths are apparently common in *Sophora alopecuroides*. Dr. W. B. Turrill has very kindly supplied me with the following list of specimens in the Kew Herbarium which exhibit the phenomenon: Nestorian Mountains and Gawan, *Capt. Garden* in 1857; Caucasus, *Prescot* in 1828; Near Tabriz, Persia, *Gilliat-Smith* in 1926; Pamir and Thian Shan Journey, *H. Appleton 190* in 1906.

In Babadag, the seeds of *S. Prodanii* were reported to be extremely poisonous. While *S. alopecuroides* has never been listed as poisonous so far as I know, there are a number of references to the poisonous seeds of other species of *Sophora*. The seeds of *S. secundiflora* Lag. are used by Mexican Indians as an intoxicant; one seed is said to be sufficient to kill a man and a half a seed produces a stupor lasting two to three days.[1] *S. flavescens* Ait. contains poisons which are made use of as insecticides.[2] The seeds of *S. tomentosa* L. yield a poisonous alkaloid. They are a common native remedy in the Philippines for stomach disorders.[3]

EXPLANATION OF THE PLATES

PLATE 123

Sophora Prodanii E. Anderson. Type specimen.

PLATE 124

A. Leaflet of *Sophora alopecuroides* var. *tomentosa* (× 7). From Stapf, s. n., collected at Schiraz, Persia, Aug. 23, 1885.

B. Leaflet of *Sophora Prodanii* (× 7). From Anderson, no. 85 (type).

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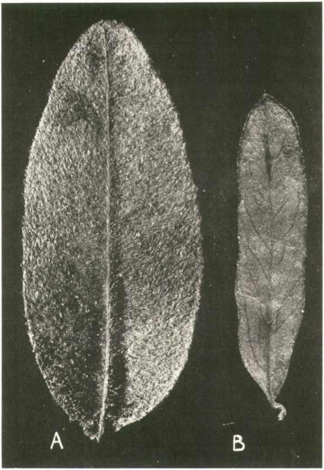
HARVARD UNIVERSITY.

[1]Kew Bull. **1892**: 216–217; **1896**: 231.
[2]Am. Jour. Pharm. **91**: 104 (1919).
[3]Contrib. U. S. Nat. Herb. **9**: 376 (1905).

Sophora Prodanii E. Anders.



A. Leaflet of Sophora alopecuroides var. tomentosa (Boiss.) Bornm.
B. Leaflet of Sophora Prodanii E. Anders.

SUPPLEMENT TO THE SPONTANEOUS FLORA OF THE ARNOLD ARBORETUM

ERNEST J. PALMER

SINCE THE PUBLICATION in 1930 of the list of plants growing spontaneously in the Arboretum[1] observation and collecting has been continued, and as a result so many additions have been made to the flora that it now seems desirable to publish a supplementary list.

In 1931 I had an opportunity for the first time to remain at the Arboretum throughout the spring months and to make a thorough exploration of the native and introduced plants at that season. As a result of this and of subsequent investigation a large number of plants not recorded in the first list have been found and additional information about some of the rarer species previously recorded has also been secured.

Of the 173 new species and varieties reported in this supplement 94, or nearly 55 percent, are plants native in the Boston area and presumably in the Arboretum, and the remaining 79, or 45 percent, are introduced. Seven plant families and 43 genera are added to the spontaneous flora in this supplementary list.

The grasses, sedges, and composites, as might be expected, furnish the largest number of additions. The really surprising thing about the present list is the relatively large number of native plants that have been found. Many of these are now quite scarce or rare in the Arboretum. Several of the introduced plants are probably recent introductions. Amongst the more interesting discoveries are: *Polystichum acrostichoides, Aristida dichotoma, A. gracilis, Carex communis, C. Goodenowii, C. longirostris, Erythronium americanum, Luzula nemorosa, Cypripedium acaule, ×Quercus Rehderi, Anemone quinquefolia, Potentilla canadensis* var. *villosissima, Polygala sanguinea, Lechea intermedia, L. tenuifolia, Viola pedata* var. *lineariloba, V. sagittata, Pyrola americana, Trientalis americana, Epifagus virginiana, Houstonia caerulea, Liatris scariosa, Aster acuminatus, Helenium nudiflorum, Senecio aureus, Hypochaeris radicata, Sonchus arvensis* var. *glabrescens, Hieracium florentinum,* and *H. vulgatum*.

A single weak plant of the Christmas fern was discovered in 1931 by Dr. Grant D. Darker on a wooded slope of the North Woods, where it had probably survived from a native colony. Later, sev-

[1] JOUR. ARNOLD ARB. 11: 63–119 (1930).

eral plants were found on the north side of Hemlock Hill. At a little lower level in the latter locality a small group of the stemless lady's slipper was found growing under the hemlock and pine trees. The star flower is also found here, as well as on the top of the hill and as a greater rarity along the base of a gravelly ridge in the North Woods. The little bluets or innocence grows sparingly among the laurels and other shrubs at the foot of the hill, and a little higher up is found the round-leaved wintergreen. As the hemlock grove on this rocky elevation is probably the only bit of practically virgin timber left in the Arboretum and as the native flora has been little disturbed even in a few spots along the base of the hill where there is an accumulation of richer soil, a number of interesting plants have been able to survive here that at present are not found elsewhere.

The March lily has not yet been seen flowering in the Arboretum, but a small colony of sterile plants comes up each year in a moist shady spot on the south side of Hemlock Hill. The plants apparently lack sufficient vitality to produce blossoms, probably due to the increased shade. A colony of plants blooming freely is found just outside the Arboretum area on a wooded bank in the grounds of the Adams Nervine Hospital, and only a few yards from the division fence. The wood anemone survives sparingly at the base of wooded hills and even on open banks that were cleared of native trees only in recent years. It has been found at the edge of the North Woods, on the slopes of Bussey Hill in the oak group, along a bank of Bussey Brook below the junipers, and in the South Woods near Peters Hill. The purple milkwort grows on an open grassy bank on the east side of Peters Hill, and near the same spot a single plant of the bird-foot violet was found. Several plants of the latter were also found in open rocky woods on the top of Hemlock Hill, but they are likely soon to be exterminated by careless picking and trampling. A specimen of the beech-drops was collected on the south side of Hemlock Hill, but it has not been observed elsewhere in the Arboretum. The hairy bush-clover and the pinweed (*Lechea tenuifolia*) grow together in dry gravelly or rocky soil at the edge of the Central Woods, on the north slope of Bussey Hill, and near a small abandoned quarry in the South Woods. *Lechea intermedia* is also found near the top of Peters Hill.

Amongst the native woody plants that have been added to the list the low juniper is one of the rarest. Two or three small plants of this are growing on conglomerate outcrops in the Central Woods, where they are probably indigenous. The scrub chestnut oak grows sparingly near the same spot as well as on top of Hemlock Hill, where a single plant was seen. At this locality in the Central Woods was also found the interesting natural hybrid between the bear oak and the black oak (*Quercus Rehderi*) growing with both of the parent species. The choke berry is another native shrub found in the Central Woods and a few plants of it have survived the repeated mowings of the grass on the northeast slope of Peters Hill. The spice-bush and high-bush blueberry grow in lower and richer ground at a few places on the borders of the woods.

It is gratifying to find evidence that a second species of thorn was native in the Arboretum. Specimens of *Crataegus rotundifolia* collected many years ago by Mr. C. E. Faxon and others in Bussey Wood and on Peters Hill were found in the herbarium, and sprouts of this species were found to be still growing at the latter locality. Mr. Faxon also collected specimens of the native blackberries and other plants in the Arboretum, some of which are preserved in this herbarium and others at the Gray Herbarium or in that of the New England Botanical Club.

It is interesting to note the introduction of new plants appearing spontaneously in the Arboretum and how they succeed and spread or fail to establish themselves and disappear after a single season or in a few years. Before the publication of the original list a few leaves of what appeared to be a sterile plant of *Senecio aureus* were seen between the Linden group and the bridle path. In 1931 a vigorous colony came up here and bloomed freely, making a conspicuous show. The following year only two or three plants remained and a search during the past summer failed to reveal any trace of it. A few plants of this species have also been found in the poplar group near Peters Hill. The king devil (*Hieracium florentinum*) has also recently appeared there, but in greater abundance farther up on the slopes of the hill among the thorns. This year it was also noted in the Celtis group near the North Woods. Fool's parsley has become more common at two localities, at the foot of the hills near the Leitneria group and along the base of Bussey bank near the Forsythia planting. A vigorous plant of the blue weed came up along the bridle path opposite the Horsechestnut group last year. It was blooming freely when cut down by the mowers, but this year no trace of it could be found. Two weedy grasses, *Eleusine indica* (the goose grass) and *Eragrostis cilianensis* have recently appeared on dumps and in waste ground at the old quarry along Bussey Street, and the latter also in the South Street nursery. The flower-of-an-hour, Japanese knotweed, four-o-clock, *Cyperus esculentus* and other cultivated and weedy things have also turned up here, and this and the South Street tract continue to be the chief sources for plants of this class. At the latter place, where a considerable tract of low fertile land surrounding the pond is still unoccupied and grown up with weeds, a real plant succession has been taking place. A number of plants that appeared here soon after the construction of the pond have already been crowded out by the more aggressive weeds but other immigrants arrive from time to time. Last year *Boltonia asteroides* and *Galium asprellum* were noted here for the first time, and the latter at least has become more abundant. Last year a large colony of the smooth form of the perennial sow-thistle made a conspicuous show with its large yellow flowers. The yellow Canada lily also sent up a number of tall spikes above the other weeds at one side of the tract. On and about the rubbish dumps here several other weeds as well as escapes from cultivation have appeared. Amongst them are the gourd and jimson weed, as well as another species of thorn-apple, *Datura Metel*.

A number of herbaceous plants, as well as a few shrubs and trees, persist in the Arboretum from the old gardens formerly planted here, and some of these appear to be holding their own or increasing in number. The Virginia spiderwort and ox-eye have spread into the meadow near the old Dawson House, and Scilla, tulips and crocuses of various colors spring up in the grass each year making a pretty display. A bank near the barn of the State Laboratory is also carpeted with the brilliant blue of the Scilla blossoms in spring, and it is found more sparingly in other localities. The star of Bethlehem, day lily, narcissus and European bellflower are all well established in different parts of the Arboretum. More restricted are the white-flowered form of *Campanula persicifolia,* which is growing along the lilac border and in the open ground on the east side of Bussey Hill, and the English violet, abundant but local along a bank near the Jamaica Plain gate. A few plants of a small perennial pea (*Lathyrus pannonicus* var. *versicolor*) come up and bloom each year on the east side of Bussey Hill below the Overlook, and *Corydalis bulbosa* is growing near the top of the bank below the Bussey greenhouses, where Dr. Edgar Anderson reports having seen it at least ten or twelve years ago.

Several plants reported in the first list have already disappeared from the Arboretum, or at least have not been seen again. Most of these were waifs escaped from cultivation, such as the cock's-comb, candytuft, sweet alyssum, beef-steak plant, sneeze weed, corn flower and *Nicotiana,* or weeds of chance introduction, such as the jointweed, small bindweed and *Bassia,* but amongst them are also the cardinal flower, blue lobelia, wild senna, beard-tongue and Venus' looking-glass. It is quite possible that some of these will be introduced again at some time. The European smoke-tree, mentioned as having formerly been seen on Hemlock Hill, has been rediscovered growing there amongst the rocks, and a specimen of the moth mullen was collected during the present summer among the lilacs at the foot of Bussey Hill. Hepatica has been reintroduced at the place where it formerly grew near the edge of the North Woods. A few plants of both *Hepatica americana* and of *H. acutiloba* have been set out and it is hoped they will survive. It is probable that it was the latter species that was formerly native here and not *H. americana* as reported on the list.

The presence of certain native plants persisting in places scarcely suitable to them at present offers some evidence as to former conditions in parts of the Arboretum and of the changes that have taken place, and this may have some value as a guide or check in future planting, since it affords a clue to both past and present soil and drainage conditions. Skunk cabbage continues to come up every year along what appears to be now a well-drained bank below the stone foot bridge over Bussey Brook and near the bald cypresses, as well as along the bridle path opposite the lindens, among the Chinese apples near Peters Hill, and at several other places. Sensitive fern, royal fern, and the lance-leaved violet coming up in the edge of the maple group, at the foot of the hills near the Ilex and Aesculus groups, along the Meadow Road by the laurels, and elsewhere, indicate former boggy areas and show that the water table even now is very near the surface in wet seasons. Along the edge of the path near a planting of *Aesculus parviflora* the water pennywort has even managed to survive and still sometimes to produce fruit. The persistence also of certain shade-loving plants in open sunny situations where they are gradually being exterminated furnishes evidence, in some case no longer available from records, that the protecting woods have not long been removed.

As the Arboretum has developed, the natural drainage has been modified or changed in many places. A brook formerly entered the Arboretum area from the west through a gap in the low hills near the Aesculus and Linden groups. A small tributary which drained the ponds near the Forest Hills gate joined it as it flowed across the level ground at the foot of the hills and into the low ground across the Meadow road. The water from this brook is now carried under ground and only a small fragment of the course of the smaller stream can be made out in the somewhat boggy area where the corkwood is now growing. The course of these streams is shown on old maps and their history helps to account for the presence here of such native plants as *Carex crinita, Scirpus rubrotinctus, Pilea pumila, Callitriche palustris, Ludvigia palustris, Hypericum majus, Hydrocotyle americana* and *Scutellaria lateriflora*, as well as suggesting the great changes that must have taken place in the character of the flora and the many plants that must have disappeared from the area since the time when these brooks flowed across the fields and into the low meadow and bog.

The course of Bussey Brook has also been diverted or straightened at several points, and the amount of water that it formerly received from seepage and springs has been greatly diminished by the clearing off or thinning of the forests on the hills and of thickets along its margins, the water now running off rapidly after a rain instead of sinking into the humus and soil. The diversion of its permanent water supply has also been made almost complete by the construction of ditches and sewers along its upper course beyond the Arboretum. It is evident from a study of the surviving native plants as well as from the topography that a small swamp or bog formerly occupied the low ground a little way above the stone foot bridge and between the base of Hemlock Hill and the slopes now occupied by the conifer groups. A spring and little rivulet carrying water except in the dryest seasons still feed the brook on the north side, and small areas are kept wet by seepage water here for a considerable part of the year. But even beyond these moist places some traces of the palustral flora still remain. Such plants as *Onoclea sensibilis, Lycopodium complanatum* var. *flabelliforme, Carex lurida,* and sprouts of *Salix pedicellaris, Alnus incana, Vaccinium corymbosum* and of an undetermined species of *Rhododendron* have been found here. On similar evidence it can be seen that certain parts of Bussey Hill and of Peters Hill were covered with forest until recent years. An early map of the Arboretum shows native woods extending over a large part of Bussey Hill, and Bussey Woods is mentioned on some of Mr. Faxon's plant labels, but I have seen no similar record in regard to Peters Hill. This hill was probably at one time covered with forest, but from the present composition of the flora it may be inferred that much of the surface was cleared and used for pasture or other purposes at an early day, but that remnants of the forest remained along the east and north sides until quite recently. Sprouts of a number of characteristic forest trees and shrubs continue to come up here in spite of annual mowing, and stumps of several large trees are still in evidence. A single large white oak survives on the east slope and in its protection a number of plants are growing that are not found in the open ground. Others still huddle rather pathetically about the decaying stumps or in the meager shade afforded by the small thorn trees. Several groups of sprouts of the trembling aspen and of the large-toothed aspen are found on the hillsides as well as scattered specimens of various species of oak, hickory, chestnut, birch, elm, wild-cherry and ash; and among shrubs are the bayberry, sweet fern, meadowsweet, dwarf juneberry (*Amelanchier oblongifolia*), choke-cherry, sheep laurel, panicled dogwood and several species of wild rose, blackberry, dewberry, raspberry and blueberry. A few depauperate plants of the ground pine still survive in one spot, and a large colony of false Solomon's seal (*Smilacina stellata*) is growing about one of the old stumps, with the wood aster, false lily of the valley and other plants that are evident relics of a woodland flora. The complete removal of the forest or thickets on rather steep slopes has resulted in the loss of the humus and in the leaching out and removal of the soil, which is reflected in the slow growth and poor condition of some of the Crataegus trees on this side of the hill.

The original native flora has almost entirely disappeared from most of the Arboretum, and increasing inroads upon such fragments of it as remain will necessarily be made as the planting of cultivated trees and shrubs continues and as they come to occupy the ground more fully, and as the surface and soil are further modified by drainage, grading, and the bringing in of outside soils and fertilizers. Such traces of it as still remain have considerable significance in a number of ways, and a record of it should be of increasing interest and value in the future. The introduction of weeds and other exotic plants from various sources is certain to continue, and specimens of them should be collected and records kept as they appear or are discovered, and it may be thought worth while to issue another supplement to the Spontaneous Flora at some time in the future.

I wish to express my thanks to the members of the staff and other friends who have shown an interest in the native and introduced plants of the Arboretum through the contribution of specimens and other assistance. Mr. Frederic W. Grigg has examined a number of the grasses, sedges, and other plants and has aided in their determination. I am also under obligation to Mr. C. A. Weatherby for assistance on points of nomenclature, and to Professor J. G. Jack and Professor Alfred Rehder of the Arboretum staff for information about early conditions in the Arboretum and for other suggestions, as well as to several others who have brought in specimens of plants found in the Arboretum.

ENUMERATION OF THE ADDITIONAL PLANTS COLLECTED[1]

Polystichum acrostichoides (Michx.) Schott. CHRISTMAS FERN. One plant found by Grant D. Darker on east slope of gravelly ridge, North Woods, probably surviving from a former native colony; also several plants on rocky wooded slopes on north side of Hemlock Hill. Nos. 40273, 42588. Rare.

Thelypteris spinulosa (O. F. Muell.) Nieuwland var. *intermedia* (Willd.) Nieuwland. SPINULOSE SHIELD FERN. Base of wooded hills, near Aesculus group. No. 39678.

[1]Introduced plants are marked by an asterisk (*).

Juniperus communis L. var. *depressa* Pursh. Low JUNIPER. Rocky ground, Central Woods. No. 36405. Rare.

Typha latifolia L. COMMON CAT-TAIL. Borders of ponds and brooks. No. 39605.

Sagittaria latifolia Willd. f. *gracilis* (Pursh) Robinson. Muddy margins of Pond, South Street tract. No. 40248.

Potamogeton epihydrus Raf. var. *Nuttallii* (Cham. & Schlecht.) Fernald. In shallow water along muddy margins of pond, South Street tract. No. 42723.

Panicum philadelphicum Bernh. Waste and cultivated ground, No. 39669. Uncommon.

Panicum dichotomiflorum Michx. Waste and cultivated ground. Nos. 38229, 39704.

Panicum depauperatum Muhl. var. *psilophyllum* Fernald. Rocky slopes and ledges. Nos. 25608, 25627.

Panicum linearifolium Scribn. Rocky ledges, conglomerate outcrops. No. 40172.

Panicum lanuginosum Ell. var. *Lindheimeri* (Nash) Fernald. (*P. Lindheimeri* Nash). Common in dry open woods and meadows. Nos. 39588, 39621, 39638, 42646.

Panicum lanuginosum var. *septentrionale* Fernald. Border of woods. No. 39635.

Panicum commutatum Schultes var. *Ashei* (Pearson) Fernald. Dry, open woods, South Street tract. No. 42675.

Panicum oligosanthes Schultes var. *Scribnerianum* (Nash) Fernald (*P. Scribnerianum* Nash). Dry gravelly banks between Shrub Collection and Arborway wall. Nos. 39627, 39694.

Panicum latifolium L. Edge of North Woods, near Celtis group. No. 39637. Rare.

**Echinochloa crusgalli* (L.) Beauv. f. *longiseta* (Trin.) Farwell. Cultivated and waste ground, with the typical form. No. 28102a.

Echinochloa muricata (Michx.) Fernald. Cultivated and waste ground. No. 42212.

Aristida dichotoma Michx. POVERTY GRASS. Sterile gravelly banks, between Shrub collection and Arborway wall, and also on conglomerate outcrops in Conifer group. Nos. 38190, 39742.

Aristida gracilis Ell. Sterile gravelly banks, between Shrub Collection and Arborway wall. No. 38191.

**Agrostis canina* L. BROWN BENT GRASS. Dry open ground, slopes of Bussey Hill. No. 39578.

**Eragrostis cilianensis* (All.) Link ex Lutati. (*E. megastachya* Link.)

Waste ground, old quarry near Bussey Street, and also as a weed in South Street nursery. Nos. 38197, 38227.

Eragrostis pectinacea (Michx.) Steud. Meadows and dry banks. Nos. 39687, 40234.

Glyceria septentrionalis Hitchc. Margins of Bussey Brook, near Conifer group. No. 39661.

Festuca ovina L. SHEEP'S FESCUE. Gravelly slopes, south side of Peters Hill. Nos. 36461, 36506.

Festuca rubra L. var. *commutata* Gaud. Open ground, border of Aesculus group. No. 40199.

**Cyperus esculentus* L. Rich waste ground, old quarry along Bussey Street. No. 42202.

Scirpus rubrotinctus Fernald. Along little brook, near Aesculus group. No. 36586.

Carex Crawfordii Fernald. Open banks and meadows. No. 40162.

Carex tenera Dewey (*C. straminea* of Gray's Man.). Dry ground, borders of woods and meadows. Nos. 42609, 42624.

Carex laxiflora Lam. var. *gracillima* Boott. Moist banks of pond, near Forest Hills gate. No. 36501.

Carex laxiflora var. *leptonervia* Fernald. Shaded banks and borders of woods. Nos. 39589, 42650.

Carex canescens L. var. *disjuncta* Fernald. Springy ground, near base of Peters Hill. No. 36531.

**Carex caryophyllea* Lat. Dry slopes and gravelly banks, Peters Hill, Bussey bank, and near Dawson House. Nos. 36455, 40132, 40165.

Carex angustior Mackenzie. (*C. stellulata* Good. var. *angustata* Carey). Local in boggy ground about spring, along southeast side of Peters Hill. Nos. 36532, 40128; also a specimen collected by *Mary E. Gilbreath,* June 6, 1892, in herb. of New England Botanical Club.

Carex panicea L. Grassy slopes of Peters Hill, in Crataegus group. Nos. 36423, 36460, 36529, 36558.

Carex pennsylvanica Lam. var. *lucorum* (Willd.) Fernald. Rocky banks, near top of Hemlock Hill. No. 36578.

Carex varia Muhl. Dry rocky ledges, south side of Hemlock Hill, and along base of hills, North Woods. Nos. 40029, 40279a, 40281a.

Carex Goodenowii J. Gay. Wet ground about spring, southeast side of Peters Hill, and also in low meadows near Administration Building. Nos. 40129, 40159, 40177.

Carex communis Bailey. Specimen in the herbarium of the New England Botanical Club, collected by *C. E. Faxon,* May 30, 1878; also found on Hemlock Hill. No. 36455.

Carex brevior (Dewey) Mackenzie. Dry open woods, Oak group. No. 42621.

Carex longirostris Torr. Shaded ground, at foot of Hemlock Hill, on south side. No. 40276.

Carex crinita Lam. var. *gynandra* (Schwein.) Schwein. & Torr. Wet rocky ground along Bussey Brook at foot of Hemlock Hill. No. 42622. Rare.

Carex lupulina Muhl. Margin of small pond west side of Bussey Hill. Nos. 40188, 40205.

**Tradescantia virginiana* L. VIRGINIA SPIDERWORT. Freely escaped into meadow, near Dawson House. Nos. 39646, 39675.

**Luzula nemorosa* (Poll.) Mey. Open grassy border, near Dawson nursery. No. 40185.

Erythronium americanum Ker. YELLOW ADDER'S-TONGUE. Under trees at base of Hemlock Hill, on southeast side, where leaves come up each year from a small colony, but it has not been found flowering. There is also a colony which flowers freely on a wooded hillside of the Adams Nervine Hospital grounds, only about 20 feet from the Arboretum boundary, where the flowering specimen was collected. Nos. 36387, 36415.

Allium canadense L. WILD GARLIC. Open wooded banks, South Street tract. No. 42620.

**Scilla sibirica* Andr. Well established on banks near State Laboratory barn, and at top of Bussey Bank. No. 36361.

Sisyrinchium angustifolium Mill. Dry open slopes of Peters Hill, in Crataegus group and on slopes of Bussey Hill. Nos. 36497, 40026, 40144.

Cypripedium acaule Ait. STEMLESS LADY'S SLIPPER. Under hemlocks and pines, near the base of Hemlock Hill, on the northeast side. No. 40272.

Salix lucida Muhl. SHINING WILLOW. Along small spring brook, Conifer group. No. 39604.

Salix pedicellaris Pursh. BOG WILLOW. In boggy ground about spring, southeast side of Peters Hill, and margins of Bussey Brook near Conifer group. Nos. 36384, 36418.

Salix humilis Marsh. PRAIRIE WILLOW. Open slopes of Peters Hill, in Crataegus group. Sprouts coming up after repeated mowing. No. 39706.

**Salix alba* L. var. *calva* G. F. W. Mey. Wet ground about spring, Poplar group. No. 36530.

**Salix fragilis* L. CRACK WILLOW. Slopes of Peters Hill; sprouts persisting after mowing. No. 39718.

**Salix pyrifolia* Anders. Waste ground near pond, South Street tract. No. 40250.

Populus tremuloides Michx. QUAKING ASPEN. Several large colonies of sprouts persistent after repeated mowings, on Peters Hill, in Crataegus group. No. 36413.

Carya ovalis (Wang.) Sarg. BROOM HICKORY. North Woods. No. 39651a.

Quercus prinoides Willd. SCRUB CHESTNUT OAK. Rocky banks near top of Hemlock Hill and on conglomerate outcrops, Central Woods. Nos. 36456, 39692. Rare as a native plant.

Quercus Rehderi Trelease. (*Q. ilicifolia* × *velutina*). Rocky slope, Central Woods. No. 39682. Rare.

**Quercus Leana* Nutt. (*Q. imbricaria* × *velutina*). Rocky slope, Central Woods; also sprouts that appear to be this hybrid coming up spontaneously in Oak group. No. 39683.

Polygonum Careyi Olney. Waste ground and cultivated beds, near State Laboratory barn. Nos. 42689, 42708.

Polygonum lapathifolium L. Moist waste ground and borders of ponds. Nos. 42693, 42709.

Polygonum punctatum Ell. var. *leptostachyum* (Meisn.) Small. No. 42711.

**Polygonum Sieboldii* De Vriese. Waste ground, old quarry near Bussey Street. No. 42201.

**Rumex crispus* × *obtusifolius*. Margins of small spring brook, Conifer group. Growing with the parent species. No. 40202.

**Mirabilis Jalapa* L. FOUR-O-CLOCK. Waste ground, as a waif, old quarry near Bussey Street. No. 39703.

**Aristolochia Kaempferi* Willd. JAPANESE BIRTHWORT. Open ground near Administration Building, and also along Meadow Road near rock spring. No. 42673. *Aristolochia Clematitis* included in the original list, without collection, was probably based on young sprouts of this species, and should therefore be dropped.

**Spergula arvensis* L. CORN SPURRY. In cultivated ground among laurels and other shrubs, near Hemlock Hill. Nos. 38171, 38190.

**Sagina decumbens* (Ell.) T. & G. PEARLWORT. Grassy borders and waste ground, old quarry and along Valley Road. Nos. 42633, 42660.

**Silene antirrhina* L. SLEEPY CATCHFLY. Waste and cultivated ground. Maple group. No. 32635.

**Silene Armeria* L. SWEET WILLIAM CATCHFLY. Grassy borders, near Administration Building. No. 42688.

**Saponaria officinalis* L. BOUNCING BET. Meadows and waste ground, near Dawson nursery. No. 39684.

**Ranunculus bulbosus* L. BULBOUS BUTTERCUP. Common in meadows. Omitted through oversight from first list. Nos. 36438, 36526, 36587.

Anemone quinquefolia L. WOOD ANEMONE. Local in open woods, North Woods, slopes of Bussey Hill, near Oak group, and South Woods, near Peters Hill. Nos. 36372, 36398, 36410.

**Clematis paniculata* Thunb. Escaped into meadows, in Tilia group, No. 40182.

**Aquilegia vulgaris* L. GARDEN COLUMBINE. Bussey bank, in partial shade. No. 42607.

**Liriodendron Tulipifera* L. TULIP TREE. There is a large tree of this species in the edge of the woods along the base of Hemlock Hill that appears to be spontaneous.

**Berberis Thunbergii* DC. Established in woods near top of Peters Hill, and also on Hemlock Hill. No. 36380.

Benzoin aestivale (L.) Nees. SPICE BUSH. Near base of gravelly ridge, North Woods. No. 36437.

**Corydalis bulbosa* DC. Shaded bank, near Bussey Greenhouse. No. 40005.

**Rorippa sylvestris* (L.) Bess. YELLOW CRESS. Waste ground and cultivated borders. Nos. 39562, 39657.

**Diplotaxis muralis* (L.) DC. Waste ground about pond, rich soil, South Street tract. No. 38233.

**Ribes sativum* Syme (*R. vulgare* Lam.) RED CURRANT. Wooded bank near Forest Hills gate, also in woods near top of Peters Hill. Nos. 36394, 36412a.

**Gillenia trifoliata* (L.) Moench. INDIAN PHYSIC. Open woods, edge of Oak group. No. 36602. Rare.

Aronia arbutifolia (L.) Ell. CHOKEBERRY. Rocky open woods, Central Woods, and also on north slope of Peters Hill. No. 36404.

**Malus baccata* Borkh. var. *mandshurica* Schneider. Northeast side of Peters Hill. No. 40017.

**Malus hupehensis* (Pamp.) Rehder (*M. theifera* Rehder). Northeast slopes of Peters Hill. No. 40253.

Amelanchier stolonifera Wiegand. Open woods, top of Hemlock Hill. No. 40265.

Crataegus rotundifolia Moench. Bussey Woods, *C. E. Faxon,* June 6, 1882; *Geo. Engelmann,* Aug. 27, 1882; Peters Hill, *C. E. Faxon,* Oct. 1, 1883, Sept. 21, 1889; *J. G. Jack,* May 23, 1900. Sprouts of this plant still persist in the edge of the woods near the top of Peters Hill.

Rubus Idaeus L. var. *strigosus* (Michx.) Maxim. Northeast slope of Peters Hill, in Crataegus group. No. 39725.

**Rubus parvifolius* L. Escaped and well established in Quercus group. No. 40203.

Rubus Jeckylanus Blanchard. *C. E. Faxon,* June 7, 1913.

Rubus allegheniensis Porter. Open woods and banks. Nos. 36564, 40145.

Rubus flagellaris Willd. DEWBERRY. Common in open rocky woods and on conglomerate outcrops. *C. E. Faxon,* July 19, 1909. Nos. 36451, 37689.

Rubus Randii (Bailey) Rydb. *C. E. Faxon,* July 21, 1912; July 31, 1912; July 7, 1913.

Potentilla canadensis* var. *villosissima* Fernald. Cultivated ground. No. 28014. (See Rhodora, **33: 187. 1931).

**Prunus Cerasus* L. MORELLO CHERRY. Rocky woods on Hemlock Hill, and in woods near top of Peters Hill. No. 36493.

**Prunus pumila* L. var. *susquehanae* Jaeg. SAND CHERRY. Open woods, Hickory group, and persisting as sprouts after repeated mowing on Peters Hill. Nos. 36493, 40259.

**Colutea media* Willd. BLADDER SENNA. Open banks near Arborway wall and on Overlook. *W. H. Judd,* July, 1931.

**Amorpha fruticosa* L. FALSE INDIGO. Borders of pond, near Forest Hills gate. No. 38240.

Lespedeza hirta (L.) Hornem. HAIRY BUSH-CLOVER. Rocky banks and borders of woods, Central Woods, near chestnuts, slopes of Bussey Hill and South Woods. Nos. 39653, 39735.

**Medicago hispida* Gaertn. BUR CLOVER. Waste ground, old quarry near Bussey Street. No. 38201.

Apios americana Med. (*A. tuberosa* Moench). GROUND NUT. Open grassy slopes, in Malus group, near foot of Peters Hill.

**Lathyrus pannonicus* (Kramer) Garcke var. *versicolor* (Gmel.) Maly. Open bank near small pond, on slope of Bussey Hill. Nos. 39660, 40008.

Oxalis europaea Jord. f. *villicaulis* Wiegand. Cultivated and waste ground, with the typical form. No. 39748.

Oxalis stricta L. Rocky open ground, South Woods. No. 38211.

Polygala sanguinea L. PURPLE MILKWORT. Open slopes of Peters Hill, in Crataegus group. No. 39655.

Callitriche palustris L. Moist banks and borders of ponds and brooks. Further study of more mature specimens show that plants reported in original list as *Callitriche heterophylla* Pursh are this species, and the latter should therefore be dropped from the list.

**Evonymus obovatus* Nutt. TRAILING STRAWBERRY BUSH. Moist ground at base of hills, North Woods. No. 36569.

**Celastrus orbiculatus* Thunb. Rocky slopes, south side of Hemlock Hill. No. 42591.

**Ampelopsis humulifolia* Bunge. Dumps and waste ground. South Street tract. No. 42694.

**Hibiscus Trionum* L. FLOWER-OF-AN-HOUR. Waste ground, old quarry near Bussey Street. No. 38199.

**Malva parviflora* L. Waste ground, old quarry, near Bussey Street. No. 38200.

**Malva verticillata* L. var. *crispa* L. CURLED MALLOW. Waste ground, old quarry south side of Bussey Street. No. 42794.

**Sida hermaphrodita* (L.) Rusby. VIRGINIA MALLOW. Rocky open ground, near Centre Street gate. No. 25893. This was incorrectly identified in original list as *Napaea dioica* L., a plant which it closely resembles.

Lechea tenuifolia Michx. PINWEED. Dry gravelly banks and borders of woods, Central Woods and South Woods. Nos. 39653, 40216.

Lechea intermedia Leggett. Gravelly banks, near top of Peters Hill. No. 42701.

Viola pedata L. var. *lineariloba* DC. BIRD-FOOT VIOLET. Rocky open woods, top of Hemlock Hill and a single plant found on east slope of Peters Hill. Nos. 36557, 40256.

Viola sororia Willd. Meadows, Aesculus group. No. 36477.

Viola latiuscula Greene. Common in meadows and on open banks. Nos. 36366, 36388.

Viola sagittata Ait. ARROW-LEAVED VIOLET. Moist grassy ground, near Arborway wall, in Maple group. Nos. 40268, 42670. Rare.

**Viola odorata* L. ENGLISH or SWEET VIOLET. Shaded bank, near Jamaica Plain gate. Nos. 36417, 39597, 40007.

Viola fimbriatula × *papilionacea*. Base of hills, near Leitneria group. No. 42682.

**Epilobium hirsutum* L. Low ground along brook, near Arborway wall and opposite Administration Building, *C. H. L. Gebfert*.

**Aralia hispida* Vent. BRISTLY SARSAPARILLA. Waste ground, old quarry along Bussey Street.

**Cornus stolonifera* Michx. RED OSIER. About small abandoned quarry, South Woods. Nos. 36513, 36524.

Pyrola americana Sweet. ROUND-LEAVED WINTERGREEN. Woods, north side of Hemlock Hill. Nos. 39565, 39591.

Vaccinium corymbosum L. HIGH BLUEBERRY. Open woods, Central Woods, slopes of Peters Hill, and along small brook near leitnerias. Nos. 39585, 39631, 40143.

Trientalis americana (Pers.) Pursh. STAR FLOWER. Woods, top and north slopes of Hemlock Hill, and base of hills, North Woods. Nos. 36454, 40030, 40271.

**Ligustrum vulgare* L. PRIVET. Escaped in thickets and open woods. Peters Hill and South Woods. No. 38184.

**Syringa vulgaris* L. COMMON LILAC. Persistent and spreading from cultivation in several places. *J. G. Jack.*

**Phlox paniculata* L. GARDEN PHLOX. Rich waste ground, South Street tract. Nos. 40242, 42676.

**Echium vulgare* L. BLUE WEED. Weedy and grassy border along bridle path, near Aesculus group. Nos. 40183, 40236.

Lycopus rubellus Moench. Wet meadow, between Administration Building and Arborway wall. No. 39691.

**Physalis heterophylla* Nees var. *nyctaginea* (Dunal) Rydb. Rich open ground, South Street tract. No. 28149.

**Datura Stramonium* L. JIMSON WEED. On dump, South Street tract. No. 38236.

**Datura Metel* L. THORN APPLE. On dump, South Street tract. No. 42208.

**Lycopersicon esculentum* Mill. TOMATO. Not rare in waste and cultivated ground and sometimes producing fruit and self-seeding. No. 39732.

Veronica peregrina L. NECKWEED. In waste and cultivated ground. Nos. 36442, 36516.

Epifagus virginiana (L.) Bart. BEECH DROPS. On superficial roots of beech trees, south side of Hemlock Hill. No. 38185.

Plantago major L. COMMON PLANTAIN. A common weed in waste ground. Nos. 39685, 39749, 40214.

**Galium asprellum* Michx. ROUGH BEDSTRAW. Moist weedy ground, South Street tract. Nos. 40251, 42678.

Houstonia caerulea L. BLUETS. Among shrubs and laurel bushes, foot of Hemlock Hill, northeast side, and also one plant collected amongst laurels near South Street gate. Nos. 40260, 40270.

Diervilla Lonicera Mill. BUSH HONEYSUCKLE. Rocky open woods and ledges, Central and South Woods and slopes of Hemlock Hill. No. 36571.

**Lonicera alpigena* L. Rocky ground, south slope of Hemlock Hill. No. 36452.

**Lonicera dioica* L. HONEYSUCKLE. Open woods, Oak group. No. 42216.

**Viburnum trilobum* Marsh. HIGH-BUSH CRANBERRY. Woods near top of Peters Hill. No. 38246.

**Lagenaria leucantha* (Duch.) Rusby. GOURD. On dump, South Street tract. No. 42209.

Liatris scariosa Willd. BLAZING STAR. Open woods, low hills, Maple group. No. 42204. Rare.

Solidago ulmifolia Muhl. Open woods, South Street tract. No. 42206. There is also a specimen of this species in the herbarium of the New England Botanical Club, collected by *C. E. Faxon*, on "Bussey Mountain," Sept. 4, 1887.

Solidago odora Ait. SWEET GOLDEN-ROD. Open woods, slopes of Bussey Hill near Oak group and in South Woods. Nos. 38213, 39736. Rare.

**Boltonia asteroides* (L.) L'Her. In low weedy ground, South Street tract. No. 42211.

Aster multiflorus Ait. Dry open slopes, near top of Peters Hill. No. 38721.

Aster linariifolius L. f. *leucactis* Benke. Slopes of Peters Hill, in Crataegus group. A form with smaller heads and white rays, growing with the species. No. 29730.

Aster acuminatus Michx. Under shade of apple trees, on hillside northwest of Administration Building. No. 42213. Rare.

Antennaria plantaginifolia (L.) Richards. Dry grassy slopes and meadows. Nos. 36362, 36386, 36444. Common.

Antennaria canadensis Greene. Grassy slopes, gravelly soil, between Arborway wall and Shrub Collection, and also on slopes of Peters Hill. Nos. 36393, 40014.

Antennaria neglecta Greene. Dry open slopes of Peters Hill. Nos. 40014a, 40014b.

**Heliopsis helianthoides* (L.) Sweet. OX-EYE. Spreading from cultivation into open ground, near Dawson House. No. 42681.

**Helenium nudiflorum* Nutt. SNEEZEWEED. Open grassy ground, near South Street gate and also near Administration Building. Nos. 42205, 42655, 42680.

**Chrysanthemum segetum* L. CORN MARIGOLD. Waste ground and dump, field near Dawson House.

Senecio aureus L. GOLDEN RAGWORT. Moist shaded ground between Tilia group and bridle path, and also in Poplar group near Peters Hill. Nos. 36476, 36511.

**Senecio viscosus* L. CLAMMY GROUNDSEL. Waste and cultivated ground, South Street tract and Conifer group. Nos. 38232, 39750.

**Hypochaeris radicata* L. CAT'S-EAR. Grassy open ground northwest of Administration Building. No. 42672.

**Sonchus arvensis* L. var. *glabrescens* Guenth. Wimm. & Grab. PERENNIAL SOW THISTLE. Rich waste ground, near pond, South Street tract. Nos. 42665, 42691, 42699.

**Sonchus asper* (L.) Hill. SOW THISTLE. Waste and cultivated ground. Nos. 35710, 35927. These numbers were listed through error as *Sonchus oleracea* in original list. Both species are found, and the latter has been collected under numbers 39739a and 40219.

**Crepis capillaris* (L.) Wallr. HAWK'S BEARD. Grassy open slopes near Administration Building and also along Meadow Road near Hemlock Hill. Nos. 42192, 42629, 42671.

**Lactuca scariola* L. PRICKLY LETTUCE. Waste ground, South Street tract. No. 40245.

**Lactuca sagittifolia* Ell. Waste ground, South Street tract. No. 40244.

**Lactuca spicata* (Lam.) Hitchc. var. *integrifolia* (Gray) Britton. Open woods, Carya group. No. 39648.

**Hieracium florentinum* All. KING DEVIL. Grassy slopes of Peters Hill in Crataegus group, near Roslindale Gate and in Celtis group. Nos. 36581, 39563, 40170, 40180.

**Hieracium vulgatum* Fries. Grassy open ground near Platanus nursery. No. 42795.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM FARL. AND THEIR RELATIVE SUSCEPTIBILITY

J. D. MacLachlan

With plates 125 to 128 and four text-figures

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I. INTRODUCTION

Gymnosporangium globosum Farl., a heteroecious rust, is restricted in its telial phase to a limited number of species and varieties of *Juniperus*. To the aecial phase, however, representatives of at least ten genera within the Pomoideae may serve as hosts; and certain of these genera, especially *Crataegus*, include a large number of species and varieties.

In spite of the number of hosts hitherto reported for *G. globosum*, very little information is available regarding the relative susceptibility of the hosts. This is a question of considerable importance because of the great damage done by the rust. A determination of the immune species and the comparative resistance of susceptible species within the various relevant host genera constitute the major part of this paper.

Concurrently with the investigations which led to a determination of the relative susceptibility of the hosts, the writer was enabled to compile a more nearly complete list of the known hosts, from which it appears that, instead of the approximately one hundred hosts hitherto reported, the number of hosts should be conservatively estimated at more than six hundred. This list constitutes the latter portion of the paper.

The work on the problems outlined above has been carried on at the Arnold Arboretum of Harvard University, where may be found one of the finest collections in the world of living representatives of species and varieties of *Juniperus* and of the Pomoideae.

II. RELATIVE SUSCEPTIBILITY OF HOSTS WITHIN GENERA OF THE POMOIDEAE

HISTORY

The earliest successful attempt to determine pomaceous hosts of *G. globosum* Farl. by means of cultures may be credited to Farlow (1880) who, in 1876–7, using teliospores from *Juniperus virginiana*, obtained spermogonia on *Crataegus tomentosa*. Farlow (1885) also made successful cultures on leaves of *Crataegus Douglasii*, *Crataegus Oxyacantha* and apple seedlings; but he obtained spermogonia only, because his experimental leaves molded before the aecial stage could develop. Thaxter (1887) obtained spermogonia on *Crataegus coccinea, Malus pumila, Sorbus americana,* and *Amelanchier canadensis;* and in 1887–8 (Thaxter, 1889) obtained spermogonia on *Sorbus americana* and *Cydonia oblonga* (= *Cydonia vulgaris*), and both spermogonia and aecia on *Crataegus coccinea* and *Malus pumila*. In a later report Thaxter (1891) confirmed the previous results on *Malus pumila* and records successful infections of *Crataegus crus-galli* and *Sorbus americana,* both resulting in aecial development. In 1906, cultures were made by Arthur (1907) on *Crataegus Pringlei* and *Sorbus americana* resulting in spermogonia and aecia, and on *Malus coronaria* giving spermogonia only. In 1908 Arthur (1909) confirmed his results on *Crataegus Pringlei,* and in 1909 (Arthur, 1910) those of Farlow on *Crataegus coccinea.*

Since Arthur's work more than one hundred suscepts have been added to the host list, mostly by observations made in the field. Authors who have contributed or made significant reference to this list include Clinton (1904 and 1934), Stewart (1910), Kern (1911), Stevens and Hall (1910), Arthur (1921, 1924, 1926 and 1927), Burnham and Latham (1917), Hesler and Whetzel (1917), Jackson (1921), Hunt (1926), Anonymous (1930), Thomas and Mills (1930), Sherbakoff (1932), and others. Bliss (1931), by culture, obtained abundant spermogonia and aecia on *Crataegus mollis,* but obtained only flecking on nine varieties of commercial apples.

These previous reports, together with the investigations made by the writer, warrant the conclusion that the genera involved as suscepts for the aecial phase of *G. globosum* are confined to the sub-family Pomoideae, and include *Amelanchier, Crataegus, Cydonia, Malus, Mespilus, Pyrus, Sorbus,* and the hybrid genera *Crataegomespilus, Sorbaronia* and *Sorbopyrus.*

METHODS USED TO DETERMINE SUSCEPTIBILITY

Two methods of approach were utilized in the determination of the various hosts and their relative susceptibility within each genus, namely, (1) quantitative observations on natural infection, and (2) serial artificial inoculations during the progressive development of the foliage to determine both the degree and the duration of the period of susceptibility. These methods of approach were especially applicable to *Crataegus* which is by far the largest genus susceptible to *G. globosum*. All cultures and observations were made on trees in the Arnold Arboretum.

CULTURAL TECHNIQUE

The cultural technique adopted was similar to that described by Crowell (1934). The inoculum was collected either the previous evening, or in the morning prior to inoculating, from *Juniperus virginiana*. Galls bearing abundant telial flanges were soaked in water until maximum swelling had taken place; then the gelatinous mass was crushed to form a thick aqueous suspension of teliospores. Fresh inoculum was prepared every two hours during inoculation in order to eliminate any possibility of crushing the promycelia emerging from the germinating teliospores, since microscopic examination revealed that the latter would germinate within that time. All inoculations were carried out in duplicate. For each test six to ten leaves on a twig were inoculated; the remainder of the tree served as a control. The spore suspension was painted on both sides of the leaves with a camel's hair brush; then a celluloid cylinder was slipped over the twig and the ends of the cylinder were plugged with moist sphagnum. Care was taken that the inoculation should not be exposed to direct rays of the sun; otherwise burning of the leaves within the cylinder might occur. The sphagnum-plugged cylinder formed an excellent moist chamber; on removal of the tube two days later the sphagnum was always found to be still wet, and both the inside of the tube and the surfaces of the leaves were moist. Thus, with a heavy sowing of spores, a moist atmosphere in the inoculation tube, and a temperature below 25°C. the conditions for optimum spore germination and infection exceeded any that might occur in nature. Plate 127 fig. 5 illustrates a type set-up.

RECORDING OF DATA OBTAINED FROM INOCULATIONS

In recording data the inoculated plants were classified according to four categories or degrees of susceptibility, based on the number of sori, their relative size, and the pathogenic effect on an average-sized leaf. They are designated and defined as follows:

0—Immune; no visible infection obtained.

1—Resistant; one to five lesions which are relatively small, which cause very little leaf killing and no leaf drop; with or without aecia. This is a type of infection which causes no material harm to the host.

2—Moderately Susceptible; five to twenty-five lesions per leaf with an intermediate pathogenic effect between categories 1 and 3; aecia always produced. This is a type of infection which, while reducing the photosynthetic leaf area and causing some leaf killing, does not result in defoliation.

3—VERY SUSCEPTIBLE; twenty-five or more lesions which are usually large or fuse to form large masses and which cause severe leaf killing and leaf drop; abundant aecial horns produced in each lesion. This is a type of infection which ruins the foliage.

While these definitions are, in general, applicable in allotting a suscept to any one category, they can not be considered as absolute criteria. Within the genus *Crataegus,* for example, as will be shown later in this paper, variation in susceptibility is for the most part not physiological but is dependent primarily upon a natural barrier, the cuticle; the probability that the basidiospore can produce infection varies inversely with the thickness of the foliar cuticle. Again, the amount of leaf killing is dependent upon whether infection takes place on main veins or elsewhere on the leaf. Consequently, for *Crataegus* at least, the actual number of lesions per average-sized leaf was given major significance. In other genera, the type of infection was accorded major consideration. In the genus *Pyrus*, for example, certain species exhibited very small lesions which died shortly after spermogonia appeared, while other species of this genus showed larger lesions producing aecia. In general, however, the foregoing definitions were employed as the bases for placing the various species within the different categories of susceptibility.

INVESTIGATIONS AND CONCLUSIONS WITH RESPECT TO THE VARIOUS GENERA CONSIDERED

For the sake of convenience the various host genera will be considered individually with respect to their relative susceptibility. All the known hosts within each genus will be listed at the end of the paper.

Crataegus

The Arnold Arboretum with almost one thousand trees comprising about five hundred and fifty named species and varieties, spread over twenty-four groups, afforded an excellent opportunity to study the relative susceptibility of the *Crataegi*. But, since the species of this genus hybridize so freely, and since the specific classification is still in an unstable condition, the time and labor involved in making inoculations for each of those species and varieties (especially in the large very susceptible groups where an abundance of natural infection was observed) would not justify the results that might be obtained; consequently typical representatives of each of the twenty-four groups were selected and the results were used as a basis of comparison by groups rather than by species. Likewise the data obtained on all the species and varieties by observations on natural infection were treated by groups rather than by species.

A. Presentation of Data Obtained by Observations on Natural Infection

In July, 1932, a general spread of *G. globosum* was observed throughout the entire plantation of *Crataegi* in the Arnold Arboretum.[1] Detailed observations were warranted by the fact that, within each group, the degree of infection was consistently uniform regardless of where the tree happened to be situated; likewise a sharp line of demarcation could be seen between the number of foliar lesions per tree in a relatively resistant group, such as the Crus-galli, and the number per tree in a more susceptible group, such as the Coccineae or Anomalae.

The amount of infection on any one tree while uniform was slight enough to allow fairly accurate counts to be made of the number of lesions per tree. While these data would hardly be adequate to permit comparison among species within any one group of *Crataegus*, they were sufficient for comparing the relative degree of susceptibility of the various groups represented in the Arboretum. As stated above, about one thousand trees were available for examination.

Observations were made at the spermogonial stage, and again at the aecial stage of the rust. In order that the amount of infection per tree might be fairly compared the trees were graded as to size, five size-classes being used.[1] Counts were made of the number of foliar lesions per tree at both stages of the rust; where the counts exceeded one hundred per tree, the degree of infection was termed "100+".[2] A collection of herbarium material was assembled for permanent reference.

In correlating the data obtained a method had to be devised by means of which a tree, for example size I, could be fairly compared with a tree, for example size V. The Coccineae, a group containing 46 species represented by 82 trees, exhibited the highest percentage of infection lesions per unit-sized tree. This group was classed as having severe infection, and the values obtained for this group were selected as a basis of com-

[1]This plantation is a pure, open stand situated on an exposed hillside; furthermore, the groups within the genus are arranged in contiguous blocks. Rust-infected cedars were so remote that there was undoubtedly a uniform distribution of inoculum over the *Crataegus* trees.

[1]The five size-classes were arbitrary gradings involving the relative amount of foliage as well as the actual tree size.

[2]A tree with "100+" lesions was considered as having 150 lesions. However, with the exception of those trees that were obviously very susceptible, such occurrences were so rare that deviation from this estimation would make no significant differences in the correlations.

parison for all the other groups. It was found that for the COCCINEAE:

Size I (9 trees) averaged 24.3 lesions per tree.
Size II (33 trees) averaged 51.7 lesions per tree.
Size III (35 trees) averaged 75.7 lesions per tree.
Size IV (5 trees) averaged 120.0 lesions per tree.
Size V (0 trees).[1]

If, for the sake of convenience, the ratio of the number of lesions per tree be changed from 24.3: 51.7: 75.7: 120.0: — to 25: 50: 75: 125: 200, for the respective tree sizes, and these values be considered as units for classifying a tree as having severe infection, then by taking arbitrary averages for the number of lesions required to class a tree as having moderate infection, mild infection, or no infection, the scheme as presented in Fig. 1 for classifying the trees of all the groups may be formulated.

	Number of lesions per tree within the respective tree sizes				
	I	II	III	IV	V
Severe infection .	25	50	75	125	200
	20	40	60	100	160
Moderate infection .	15	30	45	75	120
	10	20	30	50	80
Mild infection .	5	10	15	25	40
No infection .	0	0	0	0	0

FIG. 1. AN ARBITRARY SCHEME TO DETERMINE THE RELATIVE DEGREE OF INFECTION ON TREES OF DIFFERENT SIZES.

From this scheme any tree of any size with any number of lesions may be classified according to the relative amount of infection present. On a tree size I, for example, one to ten lesions would be classed as mild infection, ten to twenty as moderate infection, and more than twenty as severe infection. As may be noted in Fig. 1, the ratio of the average number of lesions for any sized tree for the four degrees of infection is 5: 3: 1: 0. If, then, we multiply the number of trees classed as having severe infection by 5, moderate infection by 3, mild infection by 1, and no infection by 0, take the total of these products and divide by the number of trees considered, a unit is obtained by which the relative susceptibility of any group may be fairly and quite accurately compared

[1]The COCCINEAE did not include any trees of size V; as a matter of fact there are only six trees of this size in the plantation. From actual measurements of the various tree sizes and from the table given above, it was estimated that a tree of size V must necessarily have at least 200 lesions to be classed as having severe infection.

with a similarly derived unit for any other group. To illustrate this, let us consider a moderately susceptible group, the Macracanthae, and a resistant group, the Crus-galli:

Macracanthae (see Table II):

Severe infection	..	7 trees	$\times$ 5	=	35
Moderate infection	..	10 trees	$\times$ 3	=	30
Mild infection	..	78 trees	$\times$ 1	=	78
No infection	..	4 trees	$\times$ 0	=	0
Total	..	99 trees			143

Susceptibility unit of comparison $\frac{143}{99} = \mathbf{1.44}$

Crus-galli (see Table II):

Severe infection	..	0 trees	$\times$ 5	=	0
Moderate infection	..	2 trees	$\times$ 3	=	6
Mild infection	..	46 trees	$\times$ 1	=	46
No infection	..	80 trees	$\times$ 0	=	0
Total	..	128 trees			52

Susceptibility unit of comparison $\frac{52}{128} = \mathbf{0.41}$

The groups of *Crataegus* examined, the number of species examined in each group and the number of trees representing these species, the numbers of trees classed according to the different degrees of infection, and finally the units of comparison, which may now be considered as the relative degrees of susceptibility as indicated by natural infection, are presented in Table II. These values for the degrees of susceptibility have been plotted in Fig. 4.

B. Presentation of Data Obtained by Serial Inoculations

Serial artificial inoculations were made at the following stages in the foliar development: (a) on April 23 and 24, 1934, at which time very little foliage was evident, a few buds had begun to unfurl, the majority were just breaking through the winter scales, while in many instances it was necessary to part the winter scales and insert the inoculum; (b) on May 7 and 8, 1932 and 1934, respectively, at which times (the foliar conditions being approximately the same in both years) the leaves in practically all cases were in an advanced stage of expansion but were still tender, exhibiting relatively little cuticular development; (c) on May 22 and 23, 1933 and 1934, respectively, at which times the leaf cuticle was fairly well developed and most of the trees were in an advanced stage of blossom;[1] (d) on June 28, 1934, when the foliage was, for all practical purposes, fully mature and certain of the groups exhibited a very heavy cuticle on the leaves.[2]

The number of species inoculated in each group and the percentage of these falling into the different classes of susceptibility for each of the four serial inoculations are presented in Table III. The correlation of these data will be found under sub-section D.

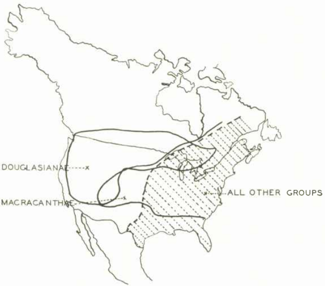

FIG. 2. DISTRIBUTION OF THE GENUS CRATAEGUS IN NORTH AMERICA.

[1]In certain groups, for example the CRUS-GALLI, differences could be observed in the type of foliage exhibited by two trees of the same species, in which case both were inoculated to determine if variation in susceptibility existed within a single species. Except in such instances totally different representatives were used in the respective years for inoculations (b) and (c).

[2]The inoculum for inoculations (c) and (d) had been kept in a refrigerator at 0°C., where, as will be shown in a subsequent publication, the teliospores will retain their viability to more than ninety percent germination for at least a year.

C. Factors Influencing the Relative Susceptibility of Crataegus

1. The geographical distribution of *Crataegus*

Of the twenty-nine groups as given by Rehder (1927), twenty-three are of American origin; the remainder have been introduced from Eurasia. With the exception of the Macracanthae, which extend into the middle west, and the Douglasianae, which are typically western, the American groups, as indicated by the dotted area in Fig. 2, are confined to the eastern part of North America. While certain of these groups are typically more northern than others they overlap to such an extent that no correlation could be made between the distribution and the relative susceptibility of the respective American groups. Although none of the Eurasian groups proved to be very susceptible, no differences from the type of infection produced on American groups could be observed. Consequently, the distribution of the genus gave no information that proved of value in determining the relative susceptibility of the various Crataegus groups.

2. The rôle of the foliar cuticle

By using herbarium material collected in the Arnold Arboretum from natural infection in 1932 a detailed comparison was made between one of the largest and most resistant groups, Crus-galli, and one of the largest and very susceptible groups, Tenuifoliae, in an attempt to correlate the susceptibility of the host plant with the mechanical structure of the leaf. As a check on the results obtained, the Coccineae, another very susceptible group, was examined in a similar manner. The following observations were made:

(a) Distribution of lesions on the leaf.
- i. Number of lesions primarily associated with mid and main lateral veins of the leaf.
- ii. Number of lesions on the chlorenchyma which, for present purposes, may be defined as the leaf area other than that occupied by the mid and main lateral veins.

(b) Spermogonial stage.
- i. Number of spermogonia per lesion.
- ii. Diameter of lesion.

(c) Aecial stage.
- i. Number of aecial horns per lesion.
- ii. Diameter of lesion producing aecia.
- iii. Length of mature aecial horns.
- iv. Number of lesions actually producing aecia.

(d) Detailed notes on thickness of foliar cuticle, degree of hypertrophy and amount of leaf-killing.

In addition to the above data separate measurements and counts were made for chlorenchyma and vein infections in the COCCINEAE. Table I gives the results obtained for these three groups.

TABLE I

PRESENTING DATA ON BIOMETRICS AS OBTAINED FROM HERBARIUM MATERIAL FOR THREE GROUPS OF THE CRATAEGI

Group	No. species	No. trees	No. leaves	No. lesions	% trees infected	% vein infections	Av. no. spermogonia per lesion	Av. diam. of lesion covered by spermogonia	Av. no. aecia per lesion	Av. diam. of lesion covered by aecia	Av. length of aecial horns	% of lesions bearing aecia
Crus-galli	76	121	2216	216	37	83	43	3.0	31	3.7	3.2	66
Tenuifoliae	83	183	1283	1361	96	47	25	2.0	21	3.0	2.5	90
Coccineae	42	75	638	717	97	31	16;33 25	1.7;2.7 2.[illegible]	18;32 25	2.2;3.8 3.0	2.3;2.5 2.4	100

Crus-galli – thick, coriaceous, waxy leaves. Tenuifoliae and Coccineae – thin, non-waxy leaves.

Within the COCCINEAE the pairs of values (separated by a semi-colon) refer to chlorenchyma and vein infections respectively; the averages are given below the pairs. All measurements were made to the nearest millimeter.

A comparison of these data brings out three significant facts:

(1) Practically all the CRUS-GALLI have thick coriaceous leaves with a very heavy cuticle. The TENUIFOLIAE and COCCINEAE, on the other hand, have thin leaves with little cuticle. This condition was checked for all the other groups, and while the thickness of the leaf itself did not show consistent correlation with the relative susceptibility of the respective groups, there was a surprisingly consistent correlation on the part of cuticular thickness. Groups that finally fell into the moderately susceptible class exhibited an intermediate deposition of cuticle, the degree of which varied somewhat in different species within the respective groups. All the species within the groups which were classed as resistant had consistently heavy cuticle and those classed as very susceptible had consistently little cuticle.

(2) The CRUS-GALLI leaves have more than eighty percent of the infections on veins, the TENUIFOLIAE approximately fifty percent and the COCCINEAE about thirty percent. By correlating these data with the relative susceptibility of the three groups, it appears that the degree of

susceptibility varies inversely as the percentage of infections primarily associated with the main veins.

(3) Although the Crus-galli exhibit the lowest percentage of trees infected, and thus would seem the most resistant, the individual lesions on the leaves of this group have the greatest diameter, and the largest number of spermogonia and aecia per lesion.

When these facts are fitted into the picture of the relative susceptibility of any host tree to the rust, they definitely indicate that the difference in susceptibility is purely mechanical, the cuticle being the deciding factor. The basidiospores of *G. globosum,* while able to produce infection from the lower surface of the leaf, germinate and gain entrance primarily through the upper side. Thus, spores carried by the wind and alighting on the smooth waxy surface of the Crus-galli leaf are not so liable to adhere, and if they do remain and germinate, a large percentage of the germ-tubes die before they can penetrate the heavy cuticle. Many instances illustrating this phenomenon occurred during investigations of the waxy-leaf types. Within the Crus-galli, for example, a much higher degree of susceptibility relative to the groups with non-waxy leaves was indicated by artificial inoculation where conditions were optimum for the infection process, than by natural infection where the basidiospores must necessarily withstand a certain amount of desiccation before infection can take place. Again, in many cases waxy leaves infected by natural inoculation were found on very low branches only, that is, branches almost touching the ground. Here the leaves were kept cool and moist for longer periods of time by the tall grass that happened to be growing around these trees; such an environment afforded a better opportunity for spore germination and germ-tube penetration.

The distribution of lesions on the leaves gives further evidence of the cuticle acting as a natural barrier. In the Crus-galli eighty-three percent of the lesions were primarily associated with the main veins. The little grooves over these veins afford lodging places for the basidiospores; moisture tends to remain longer along these areas, rendering a more favorable environment for the infection process. When making artificial inoculation by painting the leaves with an aqueous suspension of basidiospores, it was very difficult to get a film of the suspension to lie uniformly over waxy leaves. The water would form into droplets, and either roll off the leaf entirely or else remain in the little grooves over the veins. One can readily picture the same thing happening when the basidiospores are brought naturally. Inoculation usually takes place during wet weather, as it is then that the telial flanges on the galls swell and the teliospores germinate to produce basidiospores. The latter are then carried aerially, either directly to the Crataegus leaf by the wind, or else washed out of the air by falling rain onto the host leaf. Here, as in the case of artificial inoculation, the moisture necessary for spore germination accumulates in droplets and these either roll off the waxy leaf or remain in the grooves over the veins, carrying the basidiospores with them.

With a non-waxy leaf we have an altogether different picture. A film of water readily spreads over the surface of the leaf in a uniform layer, in which case the basidiospores are more apt to remain where they happen to alight on the leaf. Here the germinating basidiospores have no heavy cuticle with which to contend and can successfully penetrate the leaf surface almost as easily at any place over the chlorenchyma as over the veins. Since the area occupied by chlorenchyma far exceeds that occupied by the main veins, one can readily see why only thirty-one percent of the lesions on the COCCINEAE leaves were vein infections as compared with eighty-three percent on the CRUS-GALLI leaves.

The fact that within the CRUS-GALLI group the rust flourished even better than within the more susceptible groups, producing larger lesions with a larger number of spermogonia and aecia per lesion, can also be attributed to the relatively high percentage of vein infections. Regardless of leaf type the very large lesions, some seven to ten millimeters long, with more than one hundred spermogonia and fifty to one hundred aecia per lesion, were vein infections. In the COCCINEAE measurements of vein and chlorenchyma infections were kept separate, in order to obtain quantitative data on the relative size of the lesions and the number of spermogonia and aecia per lesion in the two types of infection. As may be seen from the foregoing table, the lesions are much larger in vein infections, producing almost twice as many spermogonia and aecia. All evidences indicate that *G. globosum* is capable of establishing a much more efficient nutritional regime when in direct contact with one of the veins. In the early spermogonial stage of even chlorenchyma infections one can see yellowish lines of fungal hyphae, radiating out along the vascular bundles from the centre of the lesion, as shown in Plate 125, Fig. 2. Again, in Plate 125, Fig. 1, the infection appears systemic, extending the entire length of a lateral vein. Plate 125, Fig. 3 shows a main lateral vein infection branching out along one of the sub-lateral veins. In fact, in every vein infection observed (eight hundred and eighteen), as may be seen in Plate 125, Fig. 4, the lesion was typically long and narrow, the long axis corresponding with that of the vein.

Vein infections appeared to produce aecia later in the season than chlorenchyma infections. Many cases were found among the former where the aecial horns were just emerging or else were very short when the leaves were collected, while nearly all the chlorenchyma lesions had fully developed aecia, with peridial cells ruptured and aeciospores emerging. It would seem, then, that the time of spore production is correlated with the availability of food supply. An infection not primarily associated with a main vein utilizes all the available nutrient and then produces spores. Vein infections, on the other hand, have a greater and more lasting nutrient supply from the host, develop more mycelium and, when they finally do sporulate, have a greater supply of reserve food to produce aecia. Thus chlorenchyma infections produce relatively smaller and fewer aecia over a smaller lesion and at an earlier date than vein infections. This fact would account for the higher percentage of the lesions within the Tenuifoliae and Coccineae actually producing aecia at the time the herbarium material was collected.

Severe leaf killing, where relatively few lesions per leaf were involved, was due in practically all cases to infections primarily associated with the main veins, the amount of leaf killing depending on how far back from the edge of the leaf the vein was attacked. Plate 126, Fig. 2 shows one lesion on the mid-vein resulting in the death of over half of the leaf. On the other hand, in Plate 126, Fig. 1, may be seen a chlorenchyma infection where leaf killing extends from the point of infection to the margin of the leaf but does not extend beyond the enclosing lateral veins. A purely chlorenchyma infection nearer the center of the leaf rarely causes killing beyond the area of actual infection.

If the degree of susceptibility is in any way physiological, one would necessarily expect that within the resistant groups the rust would have greater difficulty in establishing a satisfactory nutritional regime, and if once established would produce small lesions with relatively few fruiting bodies due to some antagonistic physiological reaction on the part of the host. Crowell (1934) found such to be the case when he determined the relative susceptibility of the genus *Malus* to *Gymnosporangium Juniperi-virginianae* Schw. In European species of *Malus* the lesions were very small, in some cases producing a few spermogonia but no aecia. Somewhat similar instances were found by the writer in determining the relative susceptibility of species of *Pyrus* to *G. globosum*. In the *Crataegi* a few rare instances were found that might suggest differential physiological antagonism on the part of the host. In Plate 126, Fig. 5 is shown a lesion that produced abundant spermogonia but died before any hypertrophy or production of aecia took place; the host tissue may have been hypersensitive to the rust mycelium, the latter taking such a heavy toll on the nutrient content of the leaf that the host tissue was killed and as a result the fungus died. Plate 126, Fig. 4 illustrates a case of leaf killing extending below the area of infection; this suggests the existence of a toxic agent secreted by the rust. In a few of the collections very small lesions not more than a millimeter in diameter that never produced even spermogonia were found. In Plate 126, Fig. 3 may be seen a small lesion that exhibits no hypertrophy and produced only one aecial horn. However, such instances as the foregoing were rare and not consistent even on a single host, and may be considered as insignificant factors in determining the relative susceptibility of the genus *Crataegus*. Indeed, from examination of the herbarium material the writer found the exact opposite to any physiological antagonism on the part of the host to be true; *G. globosum* is apparently able to establish itself more satisfactorily in the most resistant groups, due to the relatively high percentage of vein infections. This condition would indicate that the basis for differences in susceptibility is for the most part mechanical, involving primarily the cuticle as the deciding factor. The CRUS-GALLI is a difficult group for the rust to invade, except for a very short period in the spring before the foliar cuticle has developed to any extent. However, once the rust has successfully penetrated this cuticle it is just as much at home and can do just as much damage or even more in the CRUS-GALLI than it can in the TENUIFOLIAE, COCCINEAE or any other very susceptible group.

3. The degree and the duration of the period of susceptibility

The rôle of the cuticle also explains the significant phase in the duration of the susceptibility of any host. There is a definite duration to this period of susceptibility for all the groups, the degree of which rises rapidly during the unfurling of the leaves and reaches a maximum during and immediately after the period of leaf expansion, then falls off gradually at a rate depending, in part at least, on the rapidity of deposition of foliar cuticle.

In PLATE 127, FIGS. 1–4 are shown the results obtained from the four respective serial inoculations on *Crataegus Pringlei*. At the time of initial inoculation, April 25, 1934, the leaves, approximately one quarter of an inch long, had just begun to unfurl and a very small amount of infection at the tip of one leaf resulted (Fig. 1). The inoculation on May 9, after the leaves had fairly well expanded, produced severe infection (Fig. 2). Inoculation two weeks later resulted in scattered lesions (Fig. 3), while the inoculation on June 28 gave negative results (Fig. 4).

The same phenomenon but from a different approach is evident in Plate 128, Figs. 1 and 2, which demonstrate the results obtained from inoculations on *Crataegus Jonesae* on May 7 and June 4 respectively.

All the leaves in both inoculations received approximately the same amount of inoculum per unit area of leaf. At the time of the first inoculation the five basal leaves were well expanded, while the two upper leaves were just beginning to expand. As may be noted in Fig. 1, much heavier infection occurred on the older leaves. (The large irregular white areas on the younger leaves are holes caused by insects.) In Fig. 2, showing the results of the later inoculation, the reverse situation is seen; on the younger leaves at the end of the twig abundant infection was obtained, while the older leaves exhibited only scattered lesions.

It is quite evident, therefore, that the cuticle cannot be the sole determining factor for variation in susceptibility throughout the entire life of the foliage; certain physiological factors may also be involved. For example, the leaves apparently are not so susceptible during the period of emergence from the winter scales until they are in a moderately advanced stage of expansion, a period prior to any heavy deposition of cuticle. It is possible that the rust is unable to establish itself in the very young leaf. However, since this rust is not primarily of a systemic nature, probably the dilution effect on the number of lesions resulting from the intussusceptional type of foliar growth and consequent expansion, as well as the relatively small leaf area exposed at the time of inoculation, will account for the major part of this phenomenon. Again, even the most susceptible groups, for example, ANOMALAE or COCCINEAE, are apparently quite resistant to the rust by the latter part of June, at which time the leaves have by no means the amount of cuticle that is formed on the CRUS-GALLI even in the early part of May. It is possible that the rust is unable to establish a nutritional regime in the mature leaf as exhibited in the latter part of June, a point in favor of assuming a physiological antagonism on the part of the host. The relatively high temperature may also be a factor, by inhibiting spore germination.

Nevertheless these two periods play an insignificant part in any determination of the amount of infection that may accumulate on a host, regardless of the group. In the former case the period is relatively short and the leaf area exposed to the basidiospores by the unfurling buds would be small in comparison with that exposed after the leaves have expanded. As for the latter case practically all the teliospores on the red cedar have germinated by May 25, and the degree of susceptibility of any pomaceous host after the last of May would have no significance in determining the amount of infection that might occur. Thus, for practical purposes in the field the significant period within which infection might take place is between the time the leaves are fairly well expanded and the end of basidiospore dispersal. During this time the thickness and rapidity of deposition of the cuticle are the deciding factors. For this reason the inoculations in April and June, respectively, are not considered in determining the relative susceptibility of the various groups.

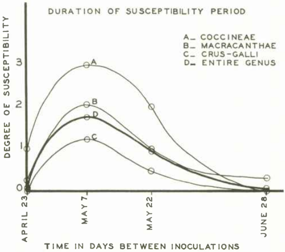

FIG. 3. ILLUSTRATING THE DEGREE AND THE DURATION OF THE PERIOD OF SUSCEPTIBILITY WITHIN THE GENUS CRATAEGUS TO G. GLOBOSUM.

To illustrate further the degree and duration of susceptibility within the different groups, values may be obtained for the relative degrees of susceptibility of the various groups by taking the sum total of the values as expressed by the symbols 0, 1, 2 and 3, and dividing by the number of representatives inoculated.[1] These were obtained from Table I for the COCCINEAE, MACRACANTHAE, and CRUS-GALLI, which are, respectively, typical of the classes very susceptible, moderately susceptible

[1]The objection arises that such a method of correlation utilizes arbitrary qualitative symbols to designate quantitative entities. Nevertheless, its usage here is not to be considered from a statistical standpoint and it does present a clearer picture to illustrate both the degree and the duration of the period of susceptibility within any one group of *Cratægus*. It is interesting to note that if such a method be employed in correlating the data obtained from serial inoculations in this genus (under sub-section D) one will arrive at precisely the same conclusions as in the method finally adopted.

and resistant, and have been plotted in Fig. 3. A similar curve (in heavy line) is given for all the inoculated representatives of the genus. The area enclosed by the respective curves would, to a certain extent, be a measure of both the degree of susceptibility and its duration. The

TABLE II

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF CRATAEGUS TO G. GLOBOSUM, AS INDICATED BY NATURAL INFECTION

Group	No. Sps.	No. Trees	No. trees in the classes				Rel. degree of susceptibility
			No infect.	Mild infect.	Mod. infect.	Sev. infect.	
Anomalae	19	40	0	19	3	18	2.95
Azaroli	1	1	1	0	0	0	.00
Bracteatae	2	2	1	1	0	0	.50
Coccineae	46	82	2	24	20	36	3.22
Crus-galli	71	128	80	46	2	0	.41
Dilatatae	4	11	1	6	0	4	2.36
Douglasianae	8	19	3	16	0	0	.84
Flavae	10	11	11	0	0	0	.00
Intricatae	10	11	8	3	0	0	.27
Macracanthae	68	99	4	78	10	7	1.44
Microcarpae	1	1	1	0	0	0	.00
Molles	37	86	10	40	11	25	2.30
Nigrae	2	2	0	2	0	0	1.00
Oxycanthae	10	17	10	6	0	1	.65
Pinnatifidae	2	4	0	4	0	0	1.00
Pruinosae	58	98	36	57	3	2	.67
Punctatae	34	37	7	26	2	2	1.14
Rotundifoliae	37	66	14	37	8	7	1.45
Sanguinae	4	4	0	4	0	0	1.00
Silvicolae	35	57	3	42	8	4	1.51
Tenuifoliae	81	175	7	104	32	32	2.06
Triflorae	2	2	2	0	0	0	.00
Uniflorae	2	2	2	0	0	0	.00
Virides	18	30	20	9	1	0	.40

Coccineae, characterized by little foliar cuticle, exhibit a much higher degree of susceptibility over a relatively longer period of time than the Crus-galli which have consistently heavy cuticle on the leaves, whereas the Macracanthae, with an intermediate and varying amount of cuticle, assume an intermediate position.

D. Correlation of the Data to Classify the Groups of Crataegus with Respect to their Relative Susceptibility

Bearing in mind that the thickness of the cuticle and its rapidity of deposition on the leaves are the primary factors in determining the relative susceptibility of any host, while geographical distribution and physiological antagonism on the part of the host play a very minor part, if any, it is now possible to evaluate the data obtained by the two previously described methods of approach and determine the relative susceptibility of the various groups within the genus *Crataegus*.

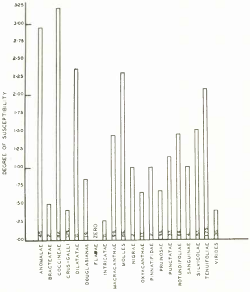

Fig. 4. Relative Susceptibility of the Genus Crataegus to G. globosum as Indicated by Observations on Natural Infection. The number within each column refers to the number of trees considered within the group.

The relative degrees of susceptibility obtained from observations of natural infection, as previously stated, are presented in Table II, and have been plotted in Fig. 4. In regard to data obtained by serial inoculations, it is quite obvious from Table III that inoculations before the leaves unfurl, and again late in June, result in very little infection. However, as the foregoing discussion on the duration of the period of susceptibility demonstrates, such a phenomenon, while interesting, plays an insignificant rôle in determining the amount of infection that might take place on any tree. The two significant inoculations are those made

TABLE III

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF THE GENUS CRATAEGUS TO G. GLOBOSUM AS INDICATED BY SERIAL INOCULATIONS

Percentage of species within the various groups of *Crataegus* falling into the different classes of susceptibility, as indicated by serial artificial inoculations

(a)

Artificial inoculation April 23 and 24

Group	No. species	% species within classes 0	1	2	3
Anomalae	1	100.0	0.0	0.0	0.0
Bracteatae	1	100.0	0.0	0.0	0.0
Coccineae	2	0.0	100.0	0.0	0.0
Crus-galli	43	100.0	0.0	0.0	0.0
Dilatatae	0	-	-	-	-
Douglasianae	2	50.0	50.0	0.0	0.0
Flavae	6	100.0	0.0	0.0	0.0
Intricatae	5	100.0	0.0	0.0	0.0
Macracanthae	13	92.3	7.7	0.0	0.0
Microcarpae	1	100.0	0.0	0.0	0.0
Molles	6	83.3	16.7	0.0	0.0
Oxyacanthae	6	50.0	50.0	0.0	0.0
Pruinosae	30	96.7	3.3	0.0	0.0
Pulcherrimae	1	100.0	0.0	0.0	0.0
Punctatae	14	85.7	14.3	0.0	0.0
Rotundifoliae	8	87.5	12.5	0.0	0.0
Silvicolae	0	-	-	-	-
Tenuifoliae	5	40.0	60.0	0.0	0.0
Triflorae	2	100.0	0.0	0.0	0.0
Uniflorae	3	100.0	0.0	0.0	0.0
Virides	10	70.0	20.0	10.0	0.0

(b)

Artificial inoculation May 7 and 8

Group	No. species	% species within classes 0	1	2	3
Anomalae	7	0.0	0.0	85.7	14.3
Bracteatae	2	0.0	100.0	0.0	0.0
Coccineae	4	0.0	0.0	0.0	100.0
Crus-galli	48	25.0	39.6	22.9	12.5
Dilatatae	2	0.0	0.0	50.0	50.0
Douglasianae	3	0.0	0.0	66.7	33.3
Flavae	10	10.0	50.0	40.0	0.0
Intricatae	11	18.2	36.4	36.4	9.1
Macracanthae	20	15.0	10.0	30.0	45.0
Microcarpae	1	100.0	0.0	0.0	0.0
Molles	16	6.3	12.5	62.5	18.8
Oxyacanthae	6	0.0	66.7	33.3	0.0
Pruinosae	37	21.6	37.8	24.3	16.2
Pulcherrimae	1	100.0	0.0	0.0	0.0
Punctatae	18	5.5	16.7	38.9	38.9
Rotundifoliae	13	7.7	15.4	53.8	23.1
Silvicolae	4	25.0	50.0	0.0	25.0
Tenuifoliae	14	0.0	14.3	21.4	64.3
Triflorae	2	50.0	50.0	0.0	0.0
Uniflorae	2	0.0	100.0	0.0	0.0
Virides	13	0.0	30.7	23.1	46.1

(c)

Artificial inoculation May 22 and 23

Group	No. species	% species within classes 0	1	2	3
Anomalae	1	0.0	0.0	0.0	100.0
Bracteatae	2	0.0	100.0	0.0	0.0
Coccineae	4	0.0	0.0	100.0	0.0
Crus-galli	78	69.2	20.5	10.3	0.0
Dilatatae	0	-	-	-	-
Douglasianae	3	66.7	33.3	0.0	0.0
Flavae	11	18.2	54.6	27.3	0.0
Intricatae	8	12.5	62.5	25.0	0.0
Macracanthae	16	37.5	37.5	25.0	0.0
Microcarpae	1	100.0	0.0	0.0	0.0
Molles	9	77.7	11.1	11.1	0.0
Oxyacanthae	11	27.3	54.5	18.2	0.0
Pruinosae	43	32.6	34.9	23.3	9.3
Pulcherrimae	1	0.0	0.0	100.0	0.0
Punctatae	20	30.0	50.0	10.0	10.0
Rotundifoliae	12	25.0	58.3	16.7	0.0
Silvicolae	1	100.0	0.0	0.0	0.0
Tenuifoliae	14	22.2	44.4	11.1	22.2
Triflorae	2	100.0	0.0	0.0	0.0
Uniflorae	3	100.0	0.0	0.0	0.0
Virides	17	64.7	17.6	17.6	0.0

(d)

Artificial inoculation June 28

Group	No. species	% species within classes 0	1	2	3
Anomalae	1	100.0	0.0	0.0	0.0
Bracteatae	0	-	-	-	-
Coccineae	1	100.0	0.0	0.0	0.0
Crus-galli	22	100.0	0.0	0.0	0.0
Dilatatae	0	-	-	-	-
Douglasianae	1	100.0	0.0	0.0	0.0
Flavae	5	80.0	20.0	0.0	0.0
Intricatae	3	100.0	0.0	0.0	0.0
Macracanthae	6	83.3	0.0	16.7	0.0
Microcarpae	1	100.0	0.0	0.0	0.0
Molles	2	100.0	0.0	0.0	0.0
Oxyacanthae	5	100.0	0.0	0.0	0.0
Pruinosae	23	95.7	0.0	4.3	0.0
Pulcherrimae	1	0.0	0.0	100.0	0.0
Punctatae	18	87.5	0.0	12.5	0.0
Rotundifoliae	6	83.3	16.7	0.0	0.0
Silvicolae	0	-	-	-	-
Tenuifoliae	1	100.0	0.0	0.0	0.0
Triflorae	0	-	-	-	-
Uniflorae	0	-	-	-	-
Virides	5	100.0	0.0	0.0	0.0

in May, (b) and (c), and for fifteen of the major groups the percentage frequency of occurrence of inoculated representatives falling into the respective classes of susceptibility have been plotted in Fig. 5 (p. 118).

In comparing these tables and figures to make a final classification of the groups according to their relative susceptibility, one must remember that these results were obtained from two altogether different methods of approach. For those groups the representatives of which have a heavy cuticle, a much lower degree of susceptibility would be indicated by natural infection than by artificial inoculation where the amount of inoculum and the cultural environment are optimum. The number of representatives examined in each group, and especially for natural infection, must also be given consideration.

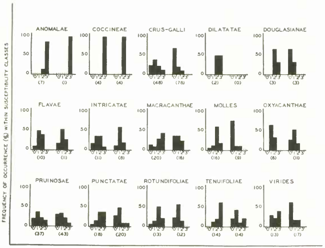

FIG. 5. RELATIVE SUSCEPTIBILITY OF FIFTEEN GROUPS OF THE GENUS CRATAEGUS TO G. GLOBOSUM AS INDICATED BY SERIAL INOCULATIONS. The results of two inoculations, (b) and (c) respectively, are presented in each sub-graph. The numbers on the abscissae of the sub-graphs refer to the classes of susceptibility. The numbers in parentheses refer to the number of species (with the exceptions noted in text) inoculated in each group.

By correlating the degree of susceptibility as indicated by natural infection, and the frequency of occurrence of inoculated representatives falling into the various classes of susceptibility, the groups may be classified and arranged within each class according to susceptibility as follows:[1]

Very susceptible—ANOMALAE, COCCINEAE, TENUIFOLIAE, DILATATAE.

[1]In classifying these groups according to their relative susceptibility, values for minor groups, not included in the figures, were taken directly from the tables.

Moderately susceptible—MOLLES, MACRACANTHAE, ROTUNDIFOLIAE, PUNCTATAE, DOUGLASIANAE, SILVICOLAE, PRUINOSAE, VIRIDES, FLAVAE, OXYACANTHAE, INTRICATAE.

Resistant—CRUS-GALLI, BRACTEATAE, *AZAROLI, *MICROCARPAE, *NIGRAE, *PINNATIFIDAE, *SANGUINEAE, *TRIFLORAE, *UNIFLORAE.[1]

Immune—None.

None of the groups examined proved to be wholly immune. No infection was obtained on the one representative of the MICROCARPAE, namely, *C. Phaenopyrum* (L. f.) Medic. (= *C. cordata* Ait.), but this species has been previously reported as a host to the rust from both Delaware and Tennessee. Of almost five hundred and fifty determined species and varieties studied, less than one percent of the artificial inoculations gave negative results and it is indeed possible that, given optimum conditions for germ-tube penetration, not a single species could be considered totally immune. However, as previously stated, it must be remembered that the conditions favorable for infection set up by artificial inoculation far exceed any that might occur in nature, and many species that are now classed as suscepts would probably never exhibit infection under field conditions.

E. SUGGESTIONS FOR THE SELECTION OF RESISTANT SPECIES AND VARIETIES

The best guide in the selection of Crataegus trees to be planted on estates where *G. globosum* is in the vicinity would be the thickness of the foliar cuticle. A striking example of this was found on an estate at Canton, Massachusetts, where two Crataegus trees, one a COCCINEAE species and the other a CRUS-GALLI species, were planted side by side, surrounded by red cedars bearing heavy infections of *G. globosum.* These have been under observation for the past three years, and each season the foliage on the COCCINEAE species has suffered very severe infection, resulting in more than eighty percent defoliation by the latter part of August. The tree is now in a very weakened condition. The CRUS-GALLI species, on the other hand, has been entirely unaffected by this rust.

In choosing from species of American origin one should definitely avoid the ANOMALAE, COCCINEAE, TENUIFOLIAE and DILATATAE if *G. globosum* be in the vicinity. Certain of the species within the groups

[1]The small number of representatives in the resistant groups indicated by asterisks made it impossible to arrange these groups within the class "Resistant" according to susceptibility and they have been arranged alphabetically.

classed as moderately susceptible have considerable cuticle on the leaves and these may be planted with a relative degree of safety. The CRUS-GALLI, however, are very resistant, and offer a wide variety of species. They are, as Rehder (1927) states, handsome ornamentals with dense, dark green foliage which remains till late in autumn or early winter, and are very attractive in bloom, with decorative bright red fruits that are persistent during the winter. If one desires the Eurasian type, the PINNATIFIDAE offer a group with lustrous leaves and large showy fruit. Some varieties of these are cultivated in northern China for the edible fruit. The OXYACANTHAE will also withstand severe infection unless under abnormal proximity to *Juniperus* rusted by *G. globosum,* with *C. Oxyacantha* Jacq. including some of the most showy garden forms.

This presentation has been confined to foliar lesions, and while infection has been obtained on all parts of the flower as well as the fruit and young twigs, such instances were sufficiently rare that they were not worthy of consideration at this time and have been set aside for a second publication on the life history of *G. globosum* Farl.

No consideration has been given to the possibility of variation in virulence within different strains of this rust. Practically all the inoculum was obtained from two adjacent red cedar trees at Waltham, Massachusetts.

One must also bear in mind that the relative susceptibility of groups within the genus *Crataegus* to *G. globosum* is in no respect correlated with their susceptibility to other *Gymnosporangium* rusts. Crowell (unpublished) has found, for example, that the CRUS-GALLI, so resistant to *G. globosum,* are quite susceptible to *G. clavipes* Cke. & Pk.

Pyrus — RELATIVE SUSCEPTIBILITY AS INDICATED BY SERIAL INOCULATIONS

Studies on relative susceptibility within the genus *Pyrus* were confined to the results obtained from serial inoculations made in 1934. The species represented in the Arboretum were artificially inoculated in a manner similar to that described for *Crataegus*: (a) on April 25, at which time the condition of the foliage varied from buds just bursting through the winter scales to leaves a quarter to a half inch long; (b) on May 9, when the leaves were fairly well expanded on all species; (c) on May 22 when the foliage was fully expanded; and (d) on June 28. Certain of the species which had given negative results in the previous inoculation were omitted in the June inoculation.

In Table IV are given the species inoculated, their distribution, the degree of infection obtained on the respective dates of inoculation, the stages of the rust produced on the foliage, and finally, a classification of their relative susceptibility.

TABLE IV

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF SPECIES OF THE GENUS PYRUS TO G. GLOBOSUM, AS INDICATED BY SERIAL INOCULATIONS

Species	Native distrib.	Deg. suscept. indicated by inoculations (a)	(b)	(c)	(d)	Stages found	Degree suscept.
P. Balansae Decne.	Eurasian	0	2	0	0	0 & 1	2
P. betulaefolia Bge.	Eurasian	3	3	2	0	0 & 1	3
P. Bretschneideri Rehd.	Eurasian	0	1	0	–	0 & 1	1
P. communis L.	Eurasian	0	1	0	–	0	1
P. elaeagrifolia Pall.	Eurasian	0	0	0	–		0
P. Korshinskyi Litv.	Eurasian	1	0	0	–	0	1
P. Michauxii Bosc.[1]	—	0	1	0	–	0	1
P. Lindleyi Rehd.	Eurasian	1	0	0	–	0	1
P. nivalis Jacq.	Eurasian	0	1	0	–	0	1
P. phaeocarpa Rehd.	Eurasian	0	1	1	0	0 & 1	1
P. salicifolia Pall.	Eurasian	0	0	0	–		0
P. serotina Rehd.	Eurasian	0	2	0	–	0 & 1	2
P. serrulata Rehd.	Eurasian	1	1	1	0	0	1
P. syriaca Boiss.	Eurasian	0	1	1	0	0 & 1	1
P. ussuriensis Maxim.	Eurasian	1	1	0	–	0 & 1	1

[1]*P. Michauxii* is a hybrid (*P. amygdaliformis* × *P. nivalis*).

No consistent correlation between the relative susceptibility of the various species and the type of leaf is evident; all species have considerable cuticle on the foliage, and a few are somewhat tomentose. Nor can the differences in susceptibility be correlated with the distribution of the host.

The lesions in general were found to be much smaller than those exhibited on *Crataegus,* and except in the case of *P. betulaefolia* rarely measured more than one to two millimeters in diameter. Certain species, designated in the table, showed spermogonia only; the lesions were extremely small, and died before any hypertrophy or aecial formation was evident. However, it is possible that with a different strain of the rust some of these might produce aecia; *P. communis,* for example, exhibited only spermogonia in my inoculations but has been reported previously from seven different states.

As in *Crataegus,* there is a definite duration to the period of susceptibility, the degree of which reaches its maximum during and immediately after the period of foliar growth and expansion, and then falls off gradually so that by the end of June all species examined are immune.

Classified according to their relative susceptibility, the species examined may be arranged (alphabetically) as follows:

Very susceptible—*P. betulaefolia* Bge.

Moderately susceptible—*P. Balansae* Decne., *P. serotina* Rehd.

Resistant—*P. Bretschneideri* Rehd., *P. communis* L., *P. Korshinskyi* Litv., × *P. Michauxii* Bosc, *P. Lindleyi* Rehd., *P. nivalis* Jacq., *P. phaeocarpa* Rehd., *P. serrulata* Rehd., *P. syriaca* Boiss., *P. ussuriensis* Maxim.

Immune—*P. amygdaliformis* Vill., *P. elaeagrifolia* Pall., *P. salicifolia* Pall.

Previous reports of *Pyrus* suscepts are confirmed, for the most part, to *P. communis*, to the Kieffer Pear (*P. communis* × *P. serotina*) and other varieties used commercially in the orchard. Stevens and Hall (1910) report *G. globosum* as being particularly abundant on the Japanese strain of pear (*P. serotina*), while Stewart (1910) reports the Kieffer pear as suffering infection from this rust at Long Island, New York. In particular he finds that both the fruit and leaves are attacked, and that the diseased fruits are very small and misshapen, usually exhibiting circular black areas devoid of aecia, although a few show aecia. On the other hand, Stewart (1910), and Hesler and Whetzel (1917) classify the Bartlett, Bosc, Duchess, and Worden varieties as being for the most part immune, although the fruit of the Worden variety is subject to infection.

While little can be added to the knowledge of the relative susceptibility of the orchard varieties, one may conclude from the foregoing classification that, with the exception of *P. betulaefolia, P. Balansae, P. serotina*, and as indicated from previous reports, *P. communis*, the remainder of the species can be safely planted in vicinities where the rust is present. This conclusion holds true especially for *P. amygdaliformis, P. elaeagrifolia*, and *P. salicifolia*.

Sorbus — Relative Susceptibility as Indicated by Serial Inoculations

Serial artificial inoculations were made in 1934 on species and varieties of *Sorbus* available in the Arnold Arboretum: (a) on April 25, at which time the foliar buds were just beginning to break open and the tiny leaves in many cases exhibited a heavy tomentose covering which was removed without injury to the leaf by rubbing the latter between the fingers, and the inoculum was placed on the exposed green tissue: (b) on May 9, at which time practically all the foliage was going through a period of rapid growth and expansion; (c) on May 24, at which time the leaves were fully expanded (blossoms where present were also inoculated); (d) on June 28, at which time the leaves for all practical purposes were mature.

The results of these inoculations appear in Table V which presents, where positive results were obtained, the species and varieties inoculated, their native distribution, the degree of infection obtained from the respective inoculations, the stages of the rust exhibited, and finally the resultant classes of susceptibility.

TABLE V

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF SPECIES AND VARIETIES OF THE GENUS SORBUS TO G. GLOBOSUM, AS INDICATED BY SERIAL INOCULATIONS

Species and varieties	Native distrib.	Deg. suscept. indicated by inoculations (a)	(b)	(c)	(d)	Stages found	Degree suscept.
S. americana Marsh.	American	1	3	2	0	0 & 1	3
S. americana var. fructu albo* Hort.	American	1	1	0	–	0 & 1	1
S. americana var. nana Hort.	American	1	0	0	–	0	1
S. arnoldiana Rehd.[1]	Eurasian	1	1	0	–	0	1
S. Aucuparia var. Backhousei Hort.	Eurasian	1	0	0	–	0	1
S. dumosa Greene	American	1	0	0	–	0	1
S. japonica var. calocarpa Rehd.	Eurasian	1	0	0	–	0	1
S. thuringiaca Fritsch[2]	Eurasian	1	1	0	–	0 & 1	1

[1]*S. arnoldiana* is a hybrid (*S. Aucuparia* × *S. discolor*).
[2]*S. thuringiaca* is a hybrid (*S. Aucuparia* × *S. Aria*).

No infection was obtained on the following (alphabetically arranged) species and varieties, which are all of Eurasian origin: *Sorbus alnifolia* K. Koch, *S. amurensis* Koehne, *S. Aria* Crantz, *S. Aria* var. *angustifolia* Hort., *S. Aria* var. *Decaisneana* Rehd., *S. Aria* var. *longifolia* Pers., *S. Aria* var. *lutescens* Hartwig, *S. Aria* var. *magnifica* Hort., *S. Aria* var. *salicifolia* Myrin, *S. Aria* var. *sulphurea* Hort., *S. Aria* var. *theophrasta* Hort., *S. Aucuparia* L., *S. Aucuparia* var. *Dirkenii aurea* Hort., *S. Aucuparia* var. *edulis* Dieck, *S. Aucuparia* var. *nana* Hort., *S. Aucuparia* var. *xanthocarpa* Hartw. & Ruempl., *S. commixta* Hedl., *S. commixta* var. *rufo-ferruginea* Schneid., *S. discolor* Hedl., × *S. hybrida* L., *S. intermedia* Pers., × *S. latifolia* Pers., *S. latifolia* var. *atrovirens* Hort., *S. Matsumurana* Koehne, × *S. Meinichii* Hedl., *S. pohuashanensis* Hedl., *S. Zahlbruckneri* Schneid.

All species of American origin that were inoculated proved to be susceptible, with *S. americana* as the only species on which the foliage was materially injured by the rust. Of the thirty-one inoculated Eurasian types, infection was obtained on only four, and these proved to be quite resistant.

The lesions in all cases were very small, rarely measuring more than one to two millimeters in diameter, with an average of three to five aecial horns per sorus. Those species on which spermogonia only were obtained (see Table V) exhibited bright yellow lesions until the spermogonia were mature, following which time no further development took place and the infections died. An interesting type of natural infection was observed on Mt. Monadnock in New Hampshire; the lesions were as large as any ever obtained on *Crataegus*, some being as much as ten to twelve millimeters long, each bearing abundant aecial horns. Whether this type of infection results from a more susceptible variety of *S. americana*, or another strain of *G. globosum*, is not known.

With the exception of *S. americana*, no infection was obtained on any of the species after the second inoculation, while practically all the suscepts exhibited some infection from the initial inoculation. It would seem, therefore, that the resistant forms at least are most susceptible during, and immediately after, the period when the foliar buds are unfurling; *S. americana*, however, reached its maximum degree of susceptibility immediately after the leaves had expanded.

It is extremely doubtful that, with the exception of *S. americana* and its varieties within the American types, and possibly the hybrid Eurasian type, *S. thuringiaca*, any representative of the genus *Sorbus* would be seriously affected by *G. globosum* regardless of proximity to the rust. This is certainly true for the species of Eurasian origin.

Malus— Relative Susceptibility as Indicated by Serial Inoculations

Serial artificial inoculations were made in 1934, similar to those described for the preceding genera: (a) on April 24, at which time the leaves had already unfurled and were undergoing the period of rapid expansion; (b) on May 9, at which time the foliage was almost mature size, and most of the blossoms were in the pink stage; (c) on May 22, at which time most of the petals had dropped. No inoculation was made in June. Table VI presents the species on which positive results were obtained, the origin of the various species, the results obtained from the respective serial inoculations, the stages of the rust obtained, and finally the relative degree of susceptibility.

TABLE VI

PRESENTING DATA ON THE RELATIVE SUSCEPTIBILITY OF SPECIES AND VARIETIES OF THE GENUS MALUS TO G. GLOBOSUM, AS INDICATED BY SERIAL INOCULATIONS

Species and varieties	Native distrib.	Deg. suscept. indicated by inoculations (a)	(b)	(c)	Stages found	Degree suscept.
M. astracanica Dum.-Cours.[1]	Eurasian	0	1	0	0 & 1	1
M. baccata Borkh.	Eurasian	1	2	0	0 & 1	2
M. coronaria Mill.	American	0	1	0	0	1
M. Dawsoniana Rehd.[2]	Hybrid	0	1	1	0 & 1	1
M. glabrata Rehd.	American	0	1	0	0 & 1	1
M. ioensis var. plena Rehd.	American	1	2	1	0 & 1	2
M. magdeburgensis Schoch[3]	Eurasian	0	1	0	0	1
M. Soulardi Britt.[4]	Hybrid	–	2	0	0 & 1	2
M. sublobata Rehd.[5]	Eurasian	0	1	0	0 & 1	1

[1] *M. astracanica* is a hybrid (*M. prunifolia* × *M. pumila*).

[2] *M. Dawsoniana* is a hybrid (*M. fusca* × *M. pumila*).

[3] *M. magdeburgensis* is a hybrid (*M. pumila* × *M. spectabilis*).

[4] *M. Soulardi* is a hybrid (*M. ioensis* × *M. pumila*).

[5] *M. sublobata* is a hybrid (*M. prunifolia* × *M. Sieboldii*).

The following species, alphabetically arranged according to distribution, gave negative results:

American distribution: *Malus angustifolia* Michx., *M. bracteata* Rehd., *M. fusca* Schneid., *M. glaucescens* Rehd., *M. ioensis* Britt., *M. lancifolia* Rehd., *M. platycarpa* Rehd.

Eurasian distribution: × *Malus arnoldiana* Sarg., *M. asiatica* Nakai, × *M. atrosanguinea* Schneid., *M. brevipes* Rehd., *M. florentina* Schneid., *M. floribunda* Sieb., *M. Halliana* var. *Parkmanii* Rehd., × *M. Hartwigii* Koehne, *M. honanensis* Rehd., *M. kansuensis* Schneid., *M. micromalus* Mak., *M. hupehensis* (Pamp.) Rehd. (= *M. theifera* Rehd.), *M. pumila* Mill., *M. prunifolia* Borkh., × *M. purpurea* var. *Eleyi* Rehd., × *M. robusta* Rehd., *M. Sargenti* Rehd., *M. Sieboldii* Rehd., *M. sikkimensis* Koehne, *M. spectabilis* Borkh., *M. sylvestris* Mill., *M. toringoides* Hughes, *M. Tschonoskii* Schneid., *M. yunnanensis* var. *Veitchii* Rehd., × *M. zumi* Rehd.

A variety of an American species, *M. ioensis* var. *plena*, and the hybrid *M. Soulardi* proved to be moderately susceptible to *G. globosum*, while two species, *M. coronaria*, and *M. glabrata*, and the hybrid *M. Dawsoniana*, may be classed as mildly susceptible. On the remainder of the American species inoculated no infection could be observed; nevertheless, Thaxter (1889) obtained aecia on *M. pumila* Mill. (= *M.*

Malus Britt.). Of all the Eurasian species inoculated only one proved to be moderately susceptible, namely *M. baccata*, and three hybrids between Eurasian species, *M. astracanica, M. magdeburgensis* and *M. sublobata*, proved to be mildly susceptible.

Although a higher percentage of the American species proved to be susceptible, no outstanding correlation could be observed between relative susceptibility and geographic distribution. Nor can susceptibility be correlated with the type of leaf or type of infection produced. In all cases the lesions were small; they were rarely more than one to two millimeters in diameter.

The serial inoculations indicated a definite duration to the period of susceptibility which reaches a maximum about the time the blossoms are in the pink stage, and falls off to almost zero within a period of two weeks.

Excluding the species found to be susceptible it is very doubtful that any of the remaining species considered would suffer from the rust regardless of proximity to red cedars infected by *G. globosum*.

Previous reports would indicate that the commercial varieties of apple are more susceptible than the above ornamental types. Bliss (1931) using telial material from Iowa culturally obtained flecking on the varieties Baldwin, Delicious, Fameuse, Greening, McIntosh, Tolman, Wealthy, Yellow Transparent, and York Imperial. From reports of Clinton (1934), Thomas and Mills (1930), Sherbakoff (1932), Miller, Stevens and Wood (1933), and others, the relative susceptibility of the commercial varieties of apple may be classified as follows:

Varieties on which moderate to severe infection has been observed: Fallawater, Fameuse, Hubbardston, Northwestern Greening, Rhode Island Greening, and Wealthy.

Varieties reported susceptible: Baldwin, Cortland, Esopus, Spitzenburg, Fall Pippin, Gano, Golden Delicious, Jonathan, McIntosh, Newton, Northern Spy, Pewaukee, Rome Beauty, Russett, Stark, Tolman Sweet, Tompkins King, Wagener, Winesap, and York Imperial.

Resistant variety: Ben Davis.

Amelanchier[1]

Farlow (1885) obtained spermogonia on leaves of *Amelanchier canadensis* Med. and Harshberger (1902) lists the same species as a suscept to *G. globosum*, exhibiting both spermogonia and aecia. Stone (1908) lists *A. alnifolia*[2] as a suscept from Alabama. The following species and

[1]Relative susceptibility in this and the following genera was determined by non-serial inoculations.

[2]This probably refers to *A. canadensis* or *A. laevis*, since *A. alnifolia* is not native in Alabama.

varieties of *Amelanchier* were inoculated early in May, 1933: *Amelanchier amabilis* Wieg., *A. asiatica* Endl., *A. Bartramiana* Roem., *A. Bartramiana* × *A. laevis, A. canadensis* Med., *A. florida* Lindl., × *A. grandiflora* Rehd., *A. humilis* Wieg., *A. humilis* × *A. sanguinea, A. intermedia* Spach, *A. laevis* Wieg., *A. oblongifolia* Roem., *A. ovalis* Med., *A. sanguinea* DC., *A. sera* Ashe, *A. spicata* K. Koch, *A. stolonifera* Wieg. All the inoculations gave negative results.

No reports can be found indicating that any of the species and varieties of *Amelanchier* are very susceptible to *G. globosum*.

Cydonia

Thaxter (1888) by culture obtained spermogonia on *Cydonia oblonga* Mill. (= *C. vulgaris* Pers.). Cook (1913) reports *G. globosum* as being of common occurrence on quince in New Jersey. Harshberger (1902), Clinton (1904), and Güssow (1915) report this rust on quince from two other states and from the Niagara Peninsula. *Cydonia oblonga,* inoculated by the writer in early May, 1933, proved to be moderately susceptible to *G. globosum,* producing both spermogonia and aecia. None of the varieties of *Cydonia oblonga* was inoculated, and no information can be given with respect to their relative susceptibility.

The remaining smaller genera were artificially inoculated and the results from these inoculations may be summarized and tabulated as follows:

Comptonia

Comptonia aspleniifolia Ait.—immune.

Crataegomespilus

Crataegomespilus grandiflora Bean (*Crataegus Oxyacantha* × *Mespilus germanica*)—very suceptible; both spermogonia and aecia obtained; severe leaf killing resulted. Natural infection was also observed.

Mespilus

Mespilus germanica L.—moderately susceptible; both spermogonia and aecia obtained.

Myrica

Myrica caroliniensis Mill.—immune. *M. Gale* L.—immune.

Photinia

Photinia villosa DC.—immune.

Sorbaronia

Sorbaronia alpina Schneid. f. *superaria* Zabel (*Aronia arbutifolia* ×

Sorbus Aria)—resistant; exhibited spermogonia only. *Aronia floribunda* × *Sorbus Aucuparia*—no infection obtained.

Sorbopyrus

Sorbopyrus auricularis Schneid. (*Pyrus communis* × *Sorbus Aria*)—resistant; exhibited spermogonia only.

III. RELATIVE SUSCEPTIBILITY OF HOSTS WITHIN THE GENUS JUNIPERUS

To our present knowledge of the relative susceptibility of *Juniperus* little can be added by the writer. From previous reports, including those of Adams (1919), Arthur (1926) (1927), Bliss (1933), Claassen (1897), Connors (1934), Hunt (1926), Kern (1929), Martin (1922) (1925), Stone (1909), and others, and from an examination of the material in the Farlow Herbarium and the herbarium of Professor J. H. Faull, the host list includes at least six species of *Juniperus,* and at least four varieties of *Juniperus virginiana*. These have been presented in the subsequent host list.

It may be added here that Martin (1922) lists *Larix* species as hosts to *G. globosum* from nine states. No infection by this rust has ever been observed on *Larix* in the Arnold Arboretum.

Juniperus virginiana is the most common telial host throughout the eastern and central part of North America, having been reported from twenty-five states and from Ontario. Severe infection may occur, as exemplified at the Morton Arboretum, Lisle, Illinois and from many estates and nurseries surrounding Boston. The writer has observed trees that were killed by the abundance of galls present. Other trees, while not killed, were disfigured to such an extent that they were no longer of ornamental value and had to be removed. *Juniperus scopulorum* has also been reported as suffering from infection by *G. globosum* at the Morton Arboretum.

As far as the eastern and central part of North America are concerned no information to date would indicate that any species other than *Juniperus virginiana* and *Juniperus scopulorum* and their varieties would suffer to any extent from infection by *G. globosum*.

IV. THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM FARL.

The following list includes as far as can be ascertained all the known hosts of *G. globosum*. The hosts have been arranged alphabetically by genera and their included species. Within the genus *Crataegus* the species and varieties have been arranged within their respective groups.

Following each host name in parentheses are symbols which may be defined as follows:

- a—as obtained by inoculations made by the writer; the inclusion of an author's name and reference indicates that this host has been determined previously by inoculation.
- n—as determined by observations of natural infection made by the writer.
- The inclusion of the abbreviated name of a State implies that this species has been reported previously as a host from that State.
- All new hosts submitted would necessarily be records for the State of Massachusetts, as all studies were made in the Arnold Arboretum, Boston.

HOSTS FOR THE 0 & 1 STAGE

An asterisk preceding a host indicates that the 0 stage only was found.

AMELANCHIER:

Amelanchier alnifolia Nutt. (Ala.),[1] *A. canadensis* Med. (Thaxter [1885]; Penn.).

CRATAEGOMESPILUS:

Crataegomespilus grandiflora Bean (a; n).

CRATAEGUS (by groups):

ANOMALAE:

Crataegus affinis Sarg. (a; n), *C. asperifolia* Sarg. (a; n; Vt.), *C. Brockwayae* Sarg. (a; n), *C. Coleae* Sarg. (n), *C. cyclophylla* Sarg. (a; n; Vt.), *C. Dunbari* Sarg. (a; n), *C. Egglestonii* Sarg. (a; n; N. Y., Vt.), *C. errata* Sarg. (a; n), *C. honesta* Sarg. (n), *C. Ideae* Sarg. (n), *C. improvisa* Sarg. (n), *C. misella* Sarg. (n), *C. pinguis* Sarg. (n; Mich.), *C. putata* Sarg. (n), *C. repulsans* Sarg. (n), *C. Saundersiana* Sarg. (n), *C. scabrida* Sarg. (a; n; Vt.), *C. shirleyensis* Sarg. (a; n), *C. urbana* Sarg. (n).

AZAROLI:

Crataegus Heldreichii Boiss. (a), *C. tanacetifolia* Pers. (N. Y.).

BRACTEATAE:

Crataegus Ashei Beadle (a; n), *C. Harbisonii* Beadle (a; Tenn.).

COCCINEAE:

Crataegus acclivis Sarg. (n), *C. arcuata* Ashe (n; Penn.), *C. assurgens* Sarg. (a; n), *C. aulica* Sarg. (n), *C. caesa* Ashe (n), *C. chippewaensis* Sarg. (n), *C. confinis* Sarg. (n), *C. conspecta* Sarg. (n),

[1]See foot-note on page 126.

C. contigua Sarg. (n), *C. cristata* Ashe (n), *C. Dayana* Sarg. (n), *C. delecta* Sarg. (n; Ill.), *C. densiflora* Sarg. (n), *C. Eamesii* Sarg. (n; Conn.), *C. elongata* Sarg. (n), *C. fluviatilis* Sarg. (a; n), *C. fretalis* Sarg. (n; Conn.), *C. Hillii* Sarg. (n), *C. Holmesiana* Ashe (a; n; Conn., N. Y., Vt.), *C. Holmesiana* var. *tardipes* Sarg. (n), *C. Holmesiana* var. *villipes* Ashe (n), *C. irrasa* Sarg. (n), *C. lenta* Ashe (n), *C. lobulata* Sarg. (n), *C. Macounii* Sarg. (n), *C. miranda* Sarg. (n), *C. neolondinensis* Sarg. (n; Conn.), *C. pedicellata* Sarg. (a; n), *C. pedicellata* var. *gloriosa* Sarg. (n), *C. perrara* Sarg. (n), *C. polita* Sarg. (n; previously reported, state not given), *C. polita* var. *Tatnalliana* (Sarg.) Eggl. (Mo., N. Y.), *C. Pringlei* Sarg. (a, Arthur [1907]; n; Conn., Ind., N. Y.), *C. pura* Sarg. (n), *C. sejuncta* Sarg. (n), *C. sertata* Sarg. (n), *C. Thayeri* Sarg. (n), *C. uticaensis* Sarg. (n), *C. vivida* Sarg. (n).

CRUS-GALLI:

Crataegus algens Beadle (a; n), *C. arborea* Beadle (a; n), *C. arduennae* Sarg. (a; n; Ind.), *C. armata* Beadle (a), *C. arta* Beadle (a), *C. attenuata* Ashe (a; n), *C. barbata* Sarg. (a), *C. barrettiana* Sarg. (a), *C. Bartramiana* Sarg. (a), *C. bellica* Sarg. (a), *C. calophylla* Sarg. (a), *C. Canbyi* Sarg. (a; n), *C. cerasina* Sarg. (n), *C. consueta* Sarg. (a; Mo.), *C. crus-galli* L. (a, Thaxter [1891]; n; Ind., Ky., Maine, Mass., Miss., Mo., N. Car., Ohio, Penn., Tenn., Va.), *C. crus-galli* var. *arbutifolia* Hort. (a), *C. crus-galli* var. *exigua* (Sarg.) Eggl. (n), *C. crus-galli* var. *pyracanthifolia* Ait. (a; n), *C. crus-galli* var. *rubens* Sarg. (a), *C. efferta* Sarg. (a), *C. effulgens* Sarg. (a), *C. Engelmannii* Sarg. (a; n; Mo.), *C. erecta* Sarg. (a; n), *C. Farwellii* Sarg. (a; n), *C. fecunda* Sarg. (n), *C. Fontanesiana* (Spach) Steud. (a; n), *C. geneseensis* Sarg. (a), *C. hamata* Sarg. (a), *C. hirtella* Sarg. (a), *C. infesta* Sarg. (a; n), *C. insignis* Sarg. (a), *C. jasperensis* Sarg. (a), × *C. Lavallei* Herincq (a; n), *C. lawrencensis* Sarg. (a), *C. leptophylla* Sarg. (a; n), *C. livoniana* Sarg. (a; n), *C. macra* Beadle (a), *C. Mohrii* Beadle (a; n; Ga.), *C. munita* Sarg. (a), *C. pachyphylla* Sarg. (a), *C. Palmeri* Sarg. (a; n), *C. paradoxa* Sarg. (a), *C. parciflora* Sarg. (a; n), *C. Parkae* Sarg. (a), *C. Pennypackeri* Sarg. (a; n), *C. peoriensis* Sarg. (n), *C. permera* Sarg. (a; n), *C. persimilis* Sarg. (n), *C. persistens* Sarg. (a; n), *C. phlebodia* Sarg. (a; n), *C. pilifera* Sarg. (a), *C. polyclada* Sarg. (a), *C. regalis* Beadle (a; n), *C. Reverchonii* Sarg. (Tex.), *C. rivalis* Sarg. (a; n), *C. robusta* Sarg. (a; n), *C. rotunda* Sarg. (a), *C. rubrifolia* Sarg. (a; n), *C. rudis* Sarg. (a), *C. setosa* Sarg. (a), *C. severa* Sarg. (a), *C. signata*

Beadle (a), *C. sinistra* Beadle (a), *C. sublobulata* Sarg. (a; n), *C. tardiflora* Sarg. (a), *C. tetrica* Beadle (a; Tenn.), *C. triumphalis* Sarg. (a; n), *C. uniqua* Sarg. (a), *C. vallicola* Sarg. (a; n), *C. villiflora* Sarg. (a), *C. Wilkinsoni* Ashe (a).

Dilatatae:

Crataegus coccinioides Ashe (a; n; Mo.), *C. dilatata* Sarg. (= *C. coccinioides* var. *dilatata* [Sarg.] Eggl.) (a; Mass., N. Y., Penn., Vt.), *C. durobrivensis* Sarg. (n), *C. hudsonica* Sarg. (n).

Douglasianae:

Crataegus colorado Ashe (n), *C. columbiana* Howell (a), *C. Douglasii* Lindl. (a, Farlow [1885]; n), *C. Douglasii* f. *badia* Sarg. (n), *C. Douglasii* var. *Suksdorfii* Sarg. (n), *C. erythropoda* Ashe (n), *C. Piperi* Britt. (a), *C. rivularis* Nutt. (n).

Flavae:

Crataegus arrogans Beadle (a), *C. colonica* Beadle (a), *C. dispar* Beadle (a; S. Car.), *C. elliptica* Ait. (a), *C. frugiferens* Beadle (a), *C. ignava* Beadle (a; n), *C. impar* Beadle (a), *C. insidiosa* Beadle (a), *C. limata* Beadle (a), *C. visenda* Beadle (a).

Intricatae:

Crataegus apposita var. *Bissellii* (Sarg.) Eggl. (a; Conn.), *C. biltmoreana* Beadle (Mo.), *C. Boyntonii* Beadle (N. Car.), *C. Buckleyi* Beadle (a; N. Car.), *C. Delosii* Sarg. (a), *C. foetida* Ashe (a), *C. fortunata* Sarg. (a), *C. laetifica* Sarg. (a; n), *C. macilenta* Beadle (Ala.), *C. modesta* Sarg. (a), *C. neobushii* Sarg. (n), *C. Painteriana* Sarg. (a; n), *C. rubella* Beadle (a), *C. Sargentii* Beadle (a), *C. scabra* Sarg. (a; n), *C. Schweinitziana* Sarg. (Penn.), *C. straminea* Beadle (Penn.), *C. tecta* Beadle (Ala.), *C. villicarpa* Sarg.

Macracanthae:

Crataegus ambrosia Sarg. (n), *C. aquilonaris* Sarg. (n), *C. ardua* Sarg. (n), *C. baccata* Sarg. (n), *C. Balkwillii* Sarg. (n), *C. Beckiana* Sarg. (n), *C. bristolensis* Sarg. (n), *C. calpodendron* (Ehrh.) Medic. (Penn.), *C. chadfordiana* Sarg. (n), *C. Chapmanii* (Beadle) Ashe (a; n; N. Car.), *C. conspecta* Sarg. (n), *C. conspicua* Sarg. (n; Vt.), *C. corporea* Sarg. (n), *C. delectabilis* Sarg. (Ont.), *C. Deweyana* Sarg. (a; n), *C. divida* Sarg. (n), *C. dumicola* Sarg. (n), *C. Emersoniana* Sarg. (a; n), *C. ferentaria* Sarg. (a; n), *C. ferta* Sarg. (n), *C. fertilis* Sarg. (a; n), *C. finitima* Sarg. (a; n), *C. flagrans* Sarg. (n), *C. flammea* Sarg. (n), *C. frutescens* Sarg. (n), *C. fulgens* Sarg. (a; n), *C. fulgida* Sarg. (n), *C. Gaultii* Sarg.

(a; n), *C. gemmosa* Sarg. (n), *C. glabrata* Sarg. (n), *C. globosa* Sarg. (a; n), *C. Halliana* Sarg. (n), *C. hystricina* Ashe (n), *C. illinoiensis* Ashe (n), *C. integriloba* Sarg. (n), *C. Laneyi* Sarg. (a; n), *C. laurentiana* Sarg. (n), *C. macracantha* Lodd. (a; n; Conn., N. Y., S. Dak., W. Va., Wis.), *C. macracantha* var. *succulenta* Rehd. (= *C. succulenta* Schrad.) (n; Penn., Wis.), *C. membranacea* Sarg. (n; Vt.), *C. michiganensis* Ashe (n), *C. microsperma* Sarg. (n), *C. missouriensis* Ashe (a; n), *C. neofluvialis* Ashe (n; Penn.), *C. nuda* Sarg. (n), *C. ogdensburgensis* Sarg. (n), *C. Peckietta* Sarg. (N. Y.), *C. pellucidula* Sarg. (n), *C. peramoena* Sarg. (n), *C. pertomentosa* Ashe (Iowa, Kansas), *C. pisifera* Sarg. (n; Vt.), *C. praeclara* Sarg. (a), *C. propixa* Sarg. (a), *C. prunifolia* (Marsh.) Pers. (a; n), *C. pudens* Sarg. (a; n), *C. rhombifolia* Sarg. (n; Conn., N. Y., Mass., Vt.), *C. Robinsonii* Sarg. (n), *C. rupicola* Sarg. (a), *C. saeva* Sarg. (n), *C. Searsii* Sarg. (n), *C. simulata* Sarg. (n), *C. spatiosa* Sarg. (n), *C. spinulosa* Sarg. (a; n), *C. structilis* Ashe (n), *C. tomentosa* L. (a, Thaxter [1880]; n; Ill., Iowa, Ky., Maine, Miss., Mo., Ohio, Ont., Que., Wis.), *C. truculenta* Sarg. (n), *C. vaga* Sarg. (a; n), *C. vegeta* Sarg. (a; n), *C. venulosa* Sarg. (a; n), *C. venustula* Sarg. (n), *C. Wilsonii* Sarg. (n).

MACROSPERMAE:

Crataegus Handyae Sarg. (n).

MICROCARPAE:

Crataegus Phaenopyrum (L. f.) Medic. (= *C. cordata* Ait.) (Del., Tenn.).

MOLLES:

Crataegus anomala Sarg. (n; Conn., N. Y.), *C. arnoldiana* Sarg. (a; n), *C. Berlandieri* Sarg. (n), *C. canadensis* Sarg. (n), *C. champlainensis* Sarg. (a; n; N. Y.), *C. contortifolia* Sarg. (n), *C. corusca* Sarg. (Ill.), *C. digna* Sarg. (n), *C. dispessa* Ashe (a; Mo.), *C. dumetosa* Sarg. (a; Mo.), *C. Ellwangeriana* Sarg. (a; n), *C. exclusa* Sarg. (n), *C. Fulleriana* Sarg. (n), *C. Greggiana* Eggl. (a), *C. induta* Sarg. (a), *C. invisa* Sarg. (n), *C. lanigera* Sarg. (n), *C. lanuginosa* Sarg. (a; n), *C. lasiantha* Sarg. (a; n; Mo.), *C. lauta* Sarg. (n), *C. limaria* Sarg. (a; n), *C. macrophylla* Sarg. (n), *C. meridionalis* Sarg. (n), *C. mollipes* Sarg. (n), *C. mollis* (Torr. & Gr.) Scheele (a, Bliss [1931]; n; Ill., Ind., Iowa, Kan., Ky., Mass., Mo., Nebr., Ohio), *C. noelensis* Sarg. (n), *C. nutans* Sarg. (n), *C. pennsylvanica* Ashe (n), *C. peregrina* Sarg. (a; n), *C. Robesoniana* Sarg. (n), *C. sera* Sarg. (a; n), *C. submollis* Sarg. (a; n; Vt.), *C. Tatnalliana* Sarg. (n), *C. Tracyi* Ashe (a), *C. transmississippiensis* Sarg. (n), *C. Treleasei* Sarg. (Mo.), *C. umbrosa* Sarg. (n), *C. urbica* Sarg. (n).

NIGRAE:

× *Crataegus hiemalis* Lge. (n), *C. nigra* Kit. (n).

OXYACANTHAE:

Crataegus monogyna Jacq. (a; n; Mass.), *C. monogyna* var. *inermis* Rehd. (a), *C. monogyna* var. *laciniata* (Stev.) Regel (a; n), *C. monogyna* var. *pteridifolia* Rehd. (a; n), *C. Oxyacantha* L. a, Farlow [1885]; n; Maine, Mass., Ont.), *C. Oxyacantha* var. *Gireoudii* Bean (a), *C. Oxyacantha* var. *leucocarpa* Loudon (a), *C. Oxyacantha* var. *rubra* Hort. (a), × *C. sorbifolia* Lge. (a; n).

PINNATIFIDAE:

Crataegus pinnatifida Bge. (n), *C. pinnatifida* var. *major* N. E. Br. (n).

PRUINOSAE:

Crataegus alacris Sarg. (a), *C. amoena* Sarg. (a), *C. arcana* Beadle (n), *C. aridula* Sarg. (a), *C. aspera* Sarg. (a; n), *C. ater* Ashe (a), *C. beata* Sarg. (n), *C. bellula* Sarg. (n), *C. bracteata* Sarg. (a), *C. caerulescens* Sarg. (n), *C. cestrica* Sarg. (a), *C. Clintoniana* Sarg. (n), *C. cognata* Sarg. (n), *C. comata* Sarg. (n), *C. comparata* Sarg. (n), *C. confragosa* Sarg. (n), *C. conjuncta* Sarg. (a; n; Conn., Mass.), *C. delawarensis* Sarg. (a), *C. deltoides* Ashe (a; n), *C. disjuncta* Sarg. (a; Mo.), *C. divisifolia* Sarg. (n), *C. exornata* Sarg. (n), *C. Ferrissii* Ashe (n), *C. festiva* Sarg. (Conn., Vt.), *C. formosa* Sarg. (a; n), *C. fusca* Sarg. (a), *C. georgiana* Sarg. (a; n), *C. glareosa* Ashe (n), *C. horridula* Sarg. (a; n), *C. incisa* Sarg. (a; n), *C. inusitula* Sarg. (a; n), *C. iracunda* Beadle (a; n), *C. Jesupii* Sarg. (Penn.), *C. Kellermanii* Sarg. (a), *C. latifrons* Sarg. (n), *C. latisepala* Ashe (a; n), *C. leiophylla* Sarg. (a; N. Y.), *C. levis* Sarg. (a; n), *C. littoralis* Sarg. (a), *C. locuples* Sarg. (a; n), *C. numerosa* Sarg. (a; n), *C. oblita* Sarg. (a; n), *C. Pequotorum* Sarg. (a; n; Conn.), *C. perampla* Sarg. (a; n), *C. perjucunda* Sarg. (a), *C. philadelphica* Sarg. (a; n), *C. pilosa* Sarg. (n), *C. platycarpa* Sarg. (a), *C. Porteri* Britt. (n), *C. procera* Sarg. (a; n), *C. pruinosa* (Wendl.) K. Koch (a; n; Conn., Mo., N. Y., Ohio, S. Car., Penn.), *C. pruinosa* var. *latisepala* (Ashe) Eggl. (Mass., Mich.), *C. pulchra* Sarg. (a; n), *C. quinebaugensis* Sarg. (Conn.), *C. radiata* Sarg. (a; n), *C. relicta* Sarg. (n), *C. remota* Sarg. (n), *C. rubicundula* Sarg. (a; n), *C. scitula* Sarg.

(n), *C. sicca* Sarg. (n), *C. sitiens* Ashe (a; n), *C. tribulosa* Sarg. (n), *C. uplandia* Sarg. (n), *C. virella* Ashe (a).

PRUNIFOLIAE:

Crataegus decorata Sarg. (n; Mo.).

PULCHERRIMAE:

Crataegus ancisa Beadle (Ala.), *C. illustris* Beadle (a).

PUNCTATAE:

Crataegus amnicola Beadle (a; n), *C. angustata* Sarg. (a), *C. barbara* Sarg. (a; n), *C. Brownietta* Sarg. (n), *C. calvescens* Sarg. (n), *C. celsa* Sarg. (n), *C. collina* Chapm. (Ga., Va.), *C. compacta* Sarg. (n), *C. Dewingii* Sarg. (n), *C. Eatoniana* Sarg. (n), *C. Eastmaniana* Sarg. (a; n), *C. florifera* Sarg. (a; n), *C. glabrifolia* Sarg. (a; n), *C. incerta* Sarg. (n), *C. Lettermanii* Sarg. (a), *C. macropoda* Sarg. (a; n), *C. notabilis* Sarg. (n), *C. pausiaca* Ashe (a; n), *C. porrecta* Ashe (n), *C. praestans* Sarg. (a; n), *C. pratensis* Sarg. (a; n), *C. punctata* Jacq. (a; n; Ill., Ind., Iowa, Maine, Mass., Mich., Mo., N. Y., N. Car., Ohio, Ont. Penn., Vt., W. Va.), *C. punctata* var. *aurea* Ait. (a; n), *C. punctata* var. *canescens* Britt. (n), *C. punctata* var. *maliformis* ? (n), *C. punctata mutabilis* Gruber (a; n), *C. secta* Sarg. (a; n), *C. sordida* Sarg. (a), *C. suborbiculata* Sarg. (a; n), *C. succincta* Sarg. (a), *C. sucida* Sarg. (Mo.), *C. swanensis* Sarg. (a; n), *C. tenax* Ashe (a; n), *C. umbratilis* Sarg. (a; n), *C. verruculosa* Sarg. (n), *C. vicina* Sarg. (a).

ROTUNDIFOLIAE:

Crataegus Bicknellii Eggl. (n), *C. Blanchardii* Sarg. (n), *C. Brainerdii* Sarg. (a; n; Vt.), *C. Brunetiana* Sarg. (a), *C. caliciglabra* Schuette (a), *C. chrysocarpa* Ashe (N. Y.), *C. coccinata* Sarg. (n), *C. crassifolia* Sarg. (n), *C. cupulifera* Sarg. (n), *C. divergens* (Peck) Sarg. (a), *C. Dodgei* Ashe (n), *C. Evansiana* Sarg. (a; n), *C. Faxonii* Sarg. (n), *C. illuminata* Sarg. (n), *C. inaudita* Sarg. (a), *C. insolens* Sarg. (n), *C. Jackii* Sarg. (n), *C. Jonesae* Sarg. (a; n), *C. Keepii* Sarg. (n), *C. Kennedyi* Sarg. (n), *C. kingstonensis* Sarg. (n), *C. lemingtonensis* Sarg. (n), *C. maligna* Sarg. (n), *C. mansfieldensis* Sarg. (n), *C. Margaretta* Ashe (n; Iowa, Mo.), *C. Margaretta* f. *xanthocarpa* Sarg. (n), *C. Maribella* Sarg. (n), *C. Oakesiana* Eggl. (a), *C. praecoqua* Sarg. (= *C. praecox* Sarg.) (n; N. Y.), *C. Proctoriana* Sarg. (n), *C. propria* Sarg. (n), *C. rotundata* Sarg. (n), *C. rotundifolia* Moench (= *C. coccinea* L. p. p.) (a, Thaxter [1889]; n; Iowa, Mo., N. Y., Ont., Vt.), *C. rotundifolia* var.

aboriginum Sarg. (n), *C. rotundifolia* var. *pubera* Sarg. (n), *C. rotundifolia* f. *rubescens* Sarg. (n), *C. varians* Sarg. (n), *C. Websteri* Sarg. (n), *C. Williamsii* Eggl. (n).

Sanguineae:

Crataegus altaica Lange (n), *C. dsungarica* Zab. (n), × *C. Lambertiana* Lge. (n), *C. Maximowiczii* Schneid. (n), *C. sanguinea* Pall. (Ont.).

Silvicolae:

Crataegus aemula Beadle (n), *C. allecta* Sarg. (n), *C. Barryana* Sarg. (n), *C. blairensis* Sarg. (n), *C. congestiflora* Sarg. (a; n), *C. cruda* Sarg. (n), *C. delectata* Sarg. (n), *C. diffusa* Sarg. (= *C. silvicola* var. *Beckwithae* [Sarg.] Eggl.) (n; Conn., Vt.), *C. dissona* Sarg. (n; Mass., N. H., N. Y.), *C. effera* Sarg. (n), *C. filipes* Ashe (n), *C. foliata* Sarg. (n), *C. Fretzii* Sarg. (n), *C. gravis* Ashe (n), *C. iterata* Sarg. (n), *C. laetans* Sarg. (n), *C. Livingstoniana* Sarg. (n), *C. luxuriosa* Sarg. (n), *C. macera* Sarg. (n), *C. Maineana* Sarg. (n), *C. medioxima* Sarg. (n), *C. opulens* Sarg. (n), *C. promissa* Sarg. (a; n), *C. prona* Ashe (n), *C. puta* Sarg. (n), *C. radina* Sarg. (n), *C. recordabilis* Sarg. (n), *C. Robbinsiana* Sarg. (Vt.), *C. ruricola* Sarg. (n), *C. stolonifera* Sarg. (n), *C. strigosa* Sarg. (n), *C. tortuosa* Sarg. (n), *C. xanthophylla* Sarg. (a; n).

Tenuifoliae:

Crataegus acuminata Sarg. (a; n), *C. acutiloba* Sarg. (a; n; N. Y., Vt.), *C. alnorum* Sarg. (n), *C. apiomorpha* Sarg. (n), *C. ascendens* Sarg. (n), *C. asperata* Sarg. (n), *C. basilica* Beadle (a), *C. bella* Sarg. (a; n), *C. benigna* Sarg. (a; n), *C. blandita* Sarg. (n), *C. Boothiana* Sarg. (n), *C. colorata* Sarg. (a; n; Ont.), *C. conferta* Sarg. (n), *C. crudelis* Sarg. (n), *C. cyanophylla* Sarg. (a; n), *C. Damei* Sarg. (n), *C. delucida* Sarg. (n; Vt.), *C. demissa* Sarg. (n; Mass., Vt.), *C. dissimilis* Sarg. (a; n; Conn., Mass., Vt.), *C. Edsoni* Sarg. (n; N. H., Vt.), *C. Eganii* Ashe (n), *C. firma* Sarg. (n), *C. flabellata* (Bosc.) K. Koch (a; n), *C. florea* Sarg. (n), *C. Forbesae* Sarg. (a; n; Conn.), *C. fucosa* Sarg. (n), *C. genialis* Sarg. (a; n; Vt.), *C. glaucophylla* Sarg. (a; n; Conn., N. Y.), *C. gracilipes* Sarg. (n), *C. Gruberi* Ashe (n), *C. Habereri* Sarg. (n), *C. Hadleyana* Sarg. (n), *C. heidelbergensis* Sarg. (n), *C. insolita* Sarg. (n), *C. leptopoda* Sarg. (n), *C. lucorum* Sarg. (n), *C. luminosa* Sarg. (n), *C. macrosperma* Ashe (n; N. Y., Penn.), *C. marcida* Ashe (n), *C. matura* Sarg. (n), *C. media* Sarg. (n), *C. merita* Sarg. (n), *C. miniata* Ashe (n), *C. modica* Sarg. (n), *C. monstrata* Sarg. (n), *C. Napaea* Sarg. (n), *C. nescia* Sarg.

(n), *C. otiosa* Ashe (n), *C. Paddockeae* Sarg. (n), *C. Paineana* Sarg. (n), *C. pallidula* Sarg. (n), *C. parviflora* Sarg. (n), *C. pastorum* Sarg. (a; n), *C. paucispina* Sarg. (a), *C. pentandra* Sarg. (a; n; Vt.), *C. perlevis* Ashe (n), *C. populnea* Ashe (n), *C. pumila* Sarg. (n), *C. retrusa* Ashe (n), *C. roanensis* Ashe (Ky., Vt.), *C. rubicunda* Sarg. (n), *C. rubrocarnea* Sarg. (n), *C. rufipes* Ashe (n), *C. sarniensis* Sarg. (n), *C. saturata* Sarg. (n), *C. serena* Sarg. (n), *C. sextilis* Sarg. (n), *C. siderea* Sarg. (n), *C. Slavini* Sarg. (n), *C. Streeterae* Sarg. (n), *C. suavis* Sarg. (n), *C. taetrica* Sarg. (n), *C. tarda* Sarg. (n), *C. tenella* Ashe (n; Conn.), *C. tenera* Ashe (n), *C. tenuiloba* Sarg. (n), *C. trachyphylla* Sarg. (n), *C. uber* Ashe (n), *C. viridimontana* Sarg. (n), *C. vittata* Ashe (a).

TRIFLORAE:

Crataegus austromontana Beadle (a).

UNIFLORAE:

Crataegus armentalis Beadle (a), *C. Brittonii* Eggl. (a).

VIRIDES:

Crataegus abbreviata Sarg. (a; n), *C. atrorubens* Ashe (a; n), *C. blanda* Sarg. (a), *C. enucleata* Sarg. (a; n), *C. lanceolata* Sarg. (a; n), *C. larga* Sarg. (a), *C. lutensis* Sarg. (a), *C. nitens* Sarg. (a), *C. nitida* (Engelm.) Sarg. (a; n), *C. ovata* Sarg. (a; n), *C. penita* Beadle (a), *C. poliophylla* Sarg. (a), *C. uvaldensis* Sarg. (a), *C. velutina* Sarg. (a), *C. viridis* L. (a; n; Okla.), *C. vulsa* Beadle (a; n).

CYDONIA:

Cydonia oblonga Mill. (= *C. vulgaris* Pers.) (a; Thaxter [1889]; Conn., Niagara Peninsula, N. J., Penn.).

MALUS:

Malus angustifolia Michx. (S. Car.), × *M. astranica* Dum.-Cours. (a), *M. baccata* Borkh. (a), *M. coronaria* Mill. (a, Arthur [1907]), × *M. Dawsoniana* Rehd. (a), *M. glabrata* Rehd. (a), *M. glaucescens* Rehd. (Ind.), *M. ioensis* var. *plena* Rehd. (a), × **M. magdeburgensis* Schoch (a), *M. pumila* Mill. (= *M. Malus* [L.] Britt.) (Thaxter [1886]; Conn., Maine, Mass., Mo., N. H., N. J., N. Y., Vt.), × *M. Soulardi* Britt. (a), × *M. sublobata* Rehd. (a).

MESPILUS:

Mespilus germanica L. (a).

PYRUS:

Pyrus Balansae Decne. (a), *P. betulaefolia* Bge. (a; n), *P. Bretschneideri* Rehd. (a), *P. communis* L. (a; Conn., Ind., Iowa, Mass.,

N. Car., N. Y., Penn., R. I.), *P. elaeagrifolia* Pall. (a), **P. Korshinskyi* Litv. (a), **P. Michauxii* Bosc (a), **P. Lindleyi* Rehd. (a), **P. nivalis* Jacq. (a), *P. phaeocarpa* Rehd. (a), *P. salicifolia* Pall. (a), *P. serotina* Rehd. (a), **P. serrulata* Rehd. (a), *P. syriaca* Boiss. (a), *P. ussuriensis* Maxim. (a).

SORBARONIA:

× **Sorbaronia alpina* Schneid. f. *superaria* Zabel (a).

SORBOPYRUS:

× **Sorbopyrus auricularis* Schneid. (a).

SORBUS:

Sorbus americana Marsh. (a; Thaxter [1887 and 1891]; Maine, Mass., N. Y., Penn., Vt.), *S. americana* var. *fructu albo* Hort. (a), **S. americana* var. *nana* Hort. (a), × **S. arnoldiana* Rehd. (a), **S. Aucuparia* L. var. *Backhousei* Hort. (a), **S. dumosa* Greene (a), **S. japonica* var. *calocarpa* Rehd. (a), × *S. thuringiaca* Fritsch (a).

HOSTS FOR THE III STAGE

JUNIPERUS:

Juniperus lucayana Britt. (= *J. barbadensis* Auth., not L.) (Ala.), *J. communis* L. (Penn.), *J. fragrans* Hort. (Ont.), *J. horizontalis* Moench (= *J. prostrata* Pers.) (N. Dak.), *J. scopulorum* Sarg. (Colo., Ill., Iowa, N. Dak.), *J. virginiana* L. (Ala., Conn., Ill., Ind., Iowa, Kansas, Ky., La., Mass., Mich., Minn., Miss., Mo., N. H., N. Y., N. Car., N. Dak., Ohio, Okla., Ont., Penn., S. Car., Tex., Vt., W. Va., Wis.), *J. virginiana* var. *Burkii* Hort. (Ill.), *J. virginiana* var. *Canaertii* Sénécl. (Ill.), *J. virginiana* var. *elegantissima* Hochst. (Ill.), *J. virginiana* var. *glauca* Carr. (Ill.).

LARIX:

Larix sp. (Conn., Kan., Minn., Miss., N. Y., Okla., Tex., Va., W. Va.).

V. SUMMARY

1. At least ten genera, all within the Pomoideae, include hosts on which the aecial phase of *Gymnosporangium globosum* may occur. One genus only, *Juniperus,* is known with certainty to include hosts for the telial phase.

2. Relative susceptibility to *G. globosum* within the respective host genera has been studied by the writer to determine: (1) immune species; (2) resistant species which suffer no material harm from this rust; (3) moderately susceptible species which may be infected but not to the extent of defoliation; and (4) very susceptible species whose foliage can be ruined by *G. globosum.*

3. These investigations were carried out by means of artificial inoculations, substantiated by observations of natural infection where present, in the Arnold Arboretum of Harvard University.

4. The results of these investigations on relative susceptibility, added to those of previous writers, may be summarized as follows:

A. On host genera for the aecial phase of *G. globosum*.

(a) On the genera on which serial inoculations were made.

Crataegus. A marked variation in susceptibility was found within the genus, the degree of which is dependent primarily on the thickness and the rapidity of deposition of the foliar cuticle. Due to the large number of species and the unstable condition of taxonomy within the genus, the classification according to susceptibility to *G. globosum* was made by groups rather than by species. The observations on natural infection substantiated the results obtained by artificial inoculation. Suggestions have been made for the selection of resistant species and varieties within the respective groups.

Pyrus. Of seventeen species inoculated, one proved to be very susceptible, two moderately susceptible, ten resistant, and three immune. Certain of the commercial varieties are classified from previous reports according to their susceptibility to *G. globosum*.

Sorbus. Infection was obtained on all the species and varieties of American origin inoculated. Of thirty-one species and varieties of Eurasian origin inoculated four are resistant, the remainder are immune.

Malus. Of seven American species inoculated three proved to be susceptible, while infection was obtained on only one species and three hybrids of the twenty-seven Eurasian types considered. Infection was obtained also on two hybrids between Eurasian and American species. Certain of the commercial varieties are classified from previous reports according to their susceptibility to *G. globosum*.

(b) On the genera otherwise inoculated.

Amelanchier. Seventeen species and varieties were inoculated; all inoculations gave negative results. Nevertheless, the rust has been reported on two species, *A. canadensis* and *A. alnifolia*.[1] It is not probable that any species in this genus would suffer severely from infection by *G. globosum*.

Cydonia. *Gymnosporangium globosum* has been reported as occurring commonly on quince in New Jersey. *Cydonia oblonga* by culture proved to be moderately susceptible to *G. globosum*.

Crataegomespilus, Mespilus, Sorbaronia and *Sorbopyrus*. The re-

[1]See foot-note on page 53.

sults obtained by inoculations on representatives of these more or less susceptible genera have been tabulated on page 127.

Comptonia, *Myrica* and *Photinia*. These genera were found by inoculation to be immune.

B. Host genera for the telial phase of *G. globosum*.

Juniperus. No information to date would indicate that any species other than *J. virginiana* and *J. scopulorum* and their varieties would suffer to any extent from infection by *G. globosum*.

5. In the genera *Crataegus*, *Malus*, *Pyrus* and *Sorbus* there is a definite duration to the period of susceptibility reaching a maximum during or immediately after foliar expansion.

6. In selecting ornamentals to plant in vicinities where *Gymnosporangium* rusts are present, it must be remembered that the relative susceptibility of any host to *G. globosum* is not necessarily correlated with its susceptibility to other Gymnosporangium rusts.

7. No consideration has been given to the possibility of variation in virulence within different strains of *G. globosum*. Such may very well occur.

8. A complete list of all the known hosts of *G. globosum* is recorded in this paper.

VI. ACKNOWLEDGMENTS

To Professor J. H. Faull for his generous assistance in making this study possible and for his guidance, supervision and other expressions of personal interest the writer acknowledges deep obligation.

To the Arnold Arboretum for permission to use its facilities; to Professor A. Rehder and Mr. E. J. Palmer for their invaluable assistance in the taxonomic treatment of the host genera; to Dr. A. E. Navez for his careful analysis of data and for helpful advice; and to Dr. Ivan H. Crowell for his cooperation and his help in field work the writer also expresses gratitude.

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VIII. EXPLANATION OF PLATES

Plate 125

Illustrations of the tendency of the mycelium to follow along the veins of Crataegus leaves:

Fig. 1. A series of lesions obtained by inoculation on a waxy-type of leaf (*Crataegus fecunda*), giving the appearance of systemic infection along the veins.

Fig. 2. A single lesion at the spermogonial stage on *Crataegus suavis*. The rust mycelium concentrates along the vascular strands causing the latter to show as bright yellow lines within the lesion.

Fig. 3. A single lesion extends along a lateral vein, forking at the junction with a sub-lateral vein.

Fig. 4. A typical vein infection; the long axis of the lesion corresponding with that of the vein.

Plate 126

Types of infections and their resultant effects on Crataegus leaves (explanations in text):

Fig. 1. Illustrates the relative amount of leaf killing caused by vein infections, and by infections not primarily associated with the main veins.

Fig. 2. A single infection on the mid vein resulting in the death of over one-half of the leaf.

Fig. 3. A very small type of lesion, exhibiting no hypertrophy and producing a single aecial horn.

Fig. 4. A single vein infection (indicated by the black spot on the plate), killing the leaf behind the lesion along the vein; suggesting a toxic agent on the part of the rust.

Fig. 5. A large single lesion which died shortly after spermogonia appeared; suggesting hypersensitivity on the part of the host.

PLATE 127

Figs. 1, 2, 3 and 4, illustrate the relative degree of susceptibility of *Crataegus Pringlei,* as indicated by serial inoculations on April 25, May 9, May 23 and June 28, 1934, respectively.

Fig. 5. The type of chamber used in all the inoculations. (Explanations in the text.)

PLATE 128

Serial inoculations on *Crataegus Jonesae* to illustrate the period of susceptibility (explanations in text):

Fig. 1. Inoculated May 7, at which time the two upper leaves were very small, while the five basal leaves were well expanded. As indicated by the number of lesions the latter are the more susceptible.

Fig. 2. Inoculated June 8, at which time all leaves were fully expanded; the two upper (youngest) leaves are now the more susceptible.

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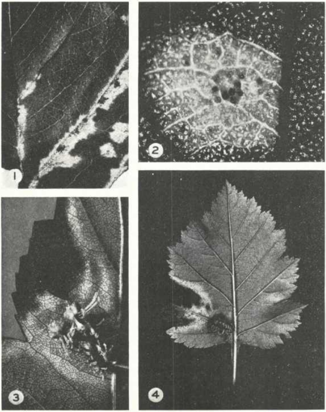
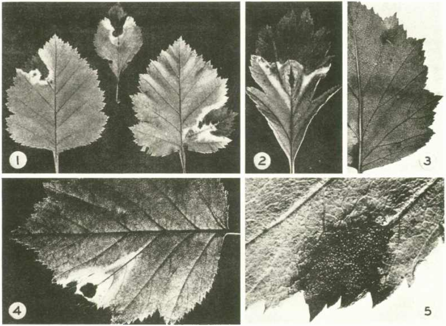
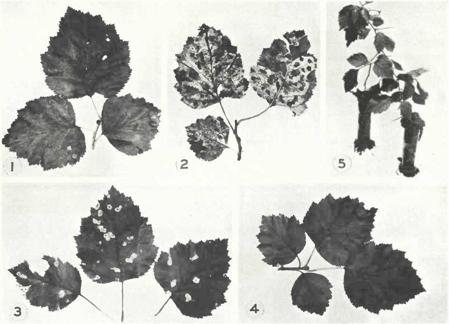


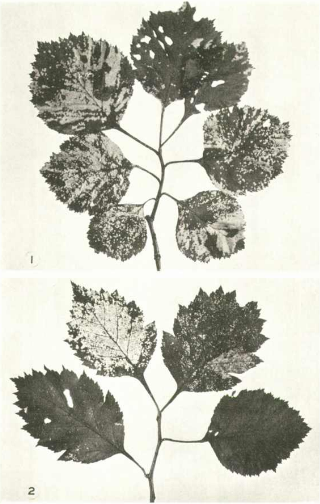
THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM Farl.



THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM Farl.



The Hosts of Gymnosporangium globosum Farl.



THE HOSTS OF GYMNOSPORANGIUM GLOBOSUM Farl.

A PRELIMINARY NOTE ON LIFE HISTORY STUDIES OF EUROPEAN SPECIES OF MILESIA

LILLIAN M. HUNTER

Although eleven species of *Milesia* are known to occur in Europe (FAULL, J. H. Taxonomy and Geographical Distribution of the Genus Milesia. Contr. Arnold Arb. Harvard Univ. II. 1932) up to the present the life histories of two only of them have been worked out, namely, *M. Blechni* (Syd.) Arth. (KLEBAHN, H. Kulturversuche mit Rostpilzen. In Zeitsch. Pflanzenkr. **26**: 257–277. 1916) and *M. Kriegeriana* (Magn.) Arth. from *Dryopteris Filix mas* (L.) Schott (MAYOR, EUG. Notes Mycologiques VIII. In Bull. Soc. Neuchât. Sci. Nat. **58**: 23–26. 1933).

Recently it was my privilege to make certain investigations on life histories of *Milesia* rusts in England. Teliosporic material of several species was assembled and inoculation experiments were made on various firs with the results that spermogonia and aecia of the following species of *Milesia* have been obtained for the first time—

(1) *Milesia Scolopendrii* (Fuckel) Arth. (from *Scolopendrium vulgare* Smith) on *Abies alba* Mill., and *A. concolor* Lindl. and Gord.

(2) *Milesia Polypodii* B. White (from *Polypodium vulgare* L.) on *Abies alba* and *A. concolor*.

(3) *Milesia vogesiaca* (Syd.) Faull (from *Polystichum angulare* Presl) on *Abies alba*.

(4) *Milesia Kriegeriana* (Magn.) Arth. (from *Dryopteris spinulosa* [O. F. Müller] Kuntze) on *Abies alba, A. concolor* and *A. grandis* Lindl.

Spermogonia and aecia were also obtained for *Milesia Kriegeriana* (from *Dryopteris Filix mas*) on *Abies alba* and on two new hosts, namely, *A. concolor* and *A. grandis*.

Aeciospores thus obtained by cultures were used in inoculating various ferns, and uredospores were obtained for the following species—

(1) *Milesia Scolopendrii* on *Scolopendrium vulgare*.

(2) *Milesia Polypodii* on *Polypodium vulgare*.

(3a) *Milesia Kriegeriana* (from *Dryopteris spinulosa*) on *Dryopteris Filix mas, D. spinulosa* and *D. spinulosa* var. *intermedia* (Muhl.) Underw.

(3b) *Milesia Kriegeriana* (from *Dryopteris Filix mas*) on *Dryopteris Filix mas* and *D. spinulosa* var. *dilatata* (Hoffm.) Underw.

LABORATORY OF PLANT PATHOLOGY,
ARNOLD ARBORETUM, HARVARD UNIVERSITY.

JOURNAL

OF THE

ARNOLD ARBORETUM

VOLUME XVI APRIL, 1935 NUMBER 2

STUDIES IN THE BORAGINACEAE, XI

IVAN M. JOHNSTON

CONTENTS

1. THE SPECIES OF TOURNEFORTIA AND MESSERSCHMIDIA IN THE OLD WORLD

THE SPECIES treated here have, in the past, all been referred to the genus *Tournefortia.* I am, however, suggesting that certain of them be segregated to form the redefined genus *Messerschmidia.* During the work on this paper I have been privileged to examine almost all the type-specimens concerned. This has permitted me to place definitely a large number of poorly understood old species that have troubled workers in the past. The work has been undertaken as part of a projected study of the Boraginaceae-Heliotropioideae. It is the first attempt to treat all the Old World species of *Tournefortia* since the presentation by DeCandolle in the ninth volume of the Prodromus in 1845.

Tournefortia Linnaeus, Sp. Pl. 140 (1753) and Gen. Pl. ed. 5, 68 (1754).

The species of *Tournefortia* found in the Old World all belong to the following:

Section EUTOURNEFORTIA Johnston, Contr. Gray Herb. **92:** 66 (1930). — type-species, *T. hirsutissima* L. *Tournefortia — Pittoniae* Humboldt, Bonpland & Kunth, Nov. Gen. et Sp. **3:** 80 (1818). — type-species, *T. hirsutissima* L. *Tournefortia* sect. *Pittonia* Don, Gen. Syst. **4**: 366 (1837). — type-species, *T. hirsutissima* L. *Pittonia* Plumier ex Adanson, Fam. Pl. **2**: 177 (1763). — type-species, *T. hirsutissima* L. *Oskampia* Rafinesque, Sylva Tellur. 123 (1838). — type-species, *O. scandens* Raf. & *O. hirsuta* Raf. *Tournefortia* sect. *Tetrandra* DeCandolle, Prodr. **9**: 527 (1845). — type-species, *T. tetrandra* Blume. *Tetrandra* (DC.) Miquel, Fl. Nederl. Ind. **2**: 928 (1858). — type-species, *Tournefortia tetrandra* Blume.

The species of *Eutournefortia* found in the Old World are remarkable for their parallelism of variation. Most of them have corollas with the tube either long or short, herbage with the pubescence present or absent, as well as leaf-blades that are broad or elongate. The combinations of these variations produce forms very diverse in gross appearance so that it is not at all surprising that botanists have been impressed by them and misled into giving specific names to many of them. A consideration of all the Old World *Eutournefortiae* and observation of the recurrent pattern of variation among them, however, lead one to a proper estimate of the surprisingly diverse phases which they present. Likewise, a consideration of the facts of distribution leads to a similar end. When the variations mentioned are given recognition it is found that the resulting numerous ill defined "species" grow together over most of a common area of dispersal. When the variations mentioned are discounted, species may be defined that have a credible geographic range— a range that is distinct from that of the closely related species and one quite similar and familiar among species of other genera within the region. I am accordingly of the opinion that the variations noted deserve at best no more than mere formal recognition. Since, however, I do not believe that obscure tropical plants should be burdened with numerous subspecific names until some evident use for them arises, I have refrained from any attempt at formally naming the reoccurring combinations of the paralleling intraspecific variations described.

Key to the Species

Ripened fruit breaking up into four equal single-seeded nutlets, these prominently ribbed on their inner surface . . . . 1. *T. sarmentosa*.

Ripened fruit breaking up into two carpels which are each composed of two seminiferous cells and an intervening empty one.

- Flowers 4-merous . . . . 2. *T. tetrandra*.
- Flowers 5-merous.
  - Continental plants from southern Asia (including the Andaman Islands).

Calyx-lobes 3–4 mm. long at anthesis, usually subulate; leaves drying more or less golden-brown beneath; Sikkim. ....3. *T. Hookeri.*
Calyx-lobes 1–2 mm. long at anthesis, linear or lanceolate.
Flowers with evident pedicels 1–2 mm. long; Madras (cf. no. 5) ....4. *T. Heyneana.*
Flowers sessile or subsessile.
Leaves abruptly long acuminate, blade more or less oval; flowers and fruit usually shortly pedicellate; Southern Burma and the Andamans....5. *T. ovata.*
Leaves short-acuminate and usually not abruptly so; blades oblong to lanceolate; flowers and fruit sessile ....6. *T. montana.*
Insular plants.
Western Pacific Ocean.
Leaves opposite, flowers sessile; Philippines.....7. *T. luzonica.*
Leaves alternate; flowers short-pedicellate; Australia and Papua ....8. *T. Muelleri.*
Western Indian Ocean.
Leaves obtuse or rounded at base, 4–11 cm. long...9. *T. puberula.*
Leaves acute at base, 10–20 cm. long.
Stems with minute short closely appressed brownish or golden hairs or quite glabrous; calyx very sparsely strigose, the lobes cuneate, more or less erect; Reunion ....10. *T. acuminata.*
Stems with evident abundant loosely appressed hairs (usually more or less velvety); calyx usually distinctly hairy with the lobes more or less spreading.
Sepals ovate; Reunion ....11. *T. arborescens.*
Sepals lanceolate; Mauritius ....12. *T. Bojeri.*

1. **Tournefortia sarmentosa** Lamarck, Tab. Encyc. **1**: 416 (1791); Poiret, Encyc. **5**: 357 (1804). *Tournefortia orientalis* R. Brown, Prod. 497 (1810); Banks & Solander, Bot. Cook's Voy. **2**: 64, tab. 210 (1901). *Tournefortia tetrandra* var. *hirsuta* Blume, Bijdrag. Fl. Nederl. Ind. 845 (1826). *Tournefortia sarmentosa* var. *hirsuta* Blume ex Miquel, Fl. Ind. Batav. **2**: 927 (1858), lapsus. *Tournefortia hirsuta* Reinwardt ex Boerlage, Hand. Fl. Nederl. Ind. **2**^{2}: 487 (1899). *Tournefortia Urvilleana* Chamisso, Linnaea **4**: 465 (1829). *Tournefortia frangulaefolia* Zippel ex Spanoghe, Linnaea **15**: 334 (1841 ?), in synon. *Tournefortia Horsfieldii* Miquel, Fl. Ind. Batav. **2**: 927 (1858). *Tournefortia acclinis* F. v. Mueller, Frag. **4**: 95 (1864). *Tournefortia macrophylla* K. Schumann & Lauterbach, Fl. Deutsch. Schutzgeb. Südsee 520 (1901). *Tournefortia sarmentosa* var. *magnifolia* Domin, Bibl. Bot. **22**(Heft 89^4): 1097 (1928). *Tournefortia glabrifolia* Domin, Bibl. Bot. **22**(Heft 89^4): 1098 (1928).

Java to New Guinea, southward into northern Queensland and northward through the Celebes, Moluccas and Philippines to Formosa.

A variable plant but readily recognized, even in its most diverse forms, by its characteristic fruit. At maturity this breaks up into four equal single-seeded nutlets. All the other Old World *Tournefortiae* have fruits with two 2-seeded carpels. *Tournefortia sarmentosa* has been repeatedly confused with continental species and has been the victim of numerous unsuccessful attempts at segregation. In *T. sarmentosa* the corollas may be either long or short, the herbage either glabrous or pubescent and the leaf-blades either small or large. These characters in various combinations have produced a host of forms that are superficially very diverse in appearance. These forms, however, agree in fundamental fruiting structures. None of them shows any evident geographical correlation. Grouped together to constitute *T. sarmentosa,* as here accepted, they appear as mere phases in a species which has a range that is natural and is of a type quite familiar to any student of the Malaysian flora.

The type of *T. sarmentosa,* in the Lamarck Herbarium at Paris, is labeled "colitur in horto regio insulae Franciae" and "de M. Sonnerat." It is a good specimen showing leaves and flowers but no fruit. The corolla has a tube ca. 2 mm. long and a limb ca. 2.5 mm. in diameter. The calyx is 1.5 mm. long and has broad hairy lobes. The inflorescence is velvety with a dense short but somewhat shaggy, tan-colored indument. The stems and under surface of the leaves have abundant gray hairs. The upper surface of the leaves are green and only sparsely strigose. The petiole is ca. 1 cm. long. The blade is rounded at the base, acute at the apex, and is 7.5–10 cm. long and 2.8–4 cm. broad. The plant is evidently the small-flowered hairy form of the common *Tournefortia* of the East Indian islands. It is certainly not a native of the Mascarenes! Gagnepain, Not. Syst. **3:** 32–33 (1914), has discussed this species. His notes, except those referring to collections by Spire, Thorel, and Watt, all refer to the species as I have taken it. The excluded collections are from the Asiatic continent. The species is restricted to the islands and is not to be expected from the mainland.

The type of *T. orientalis,* at the British Museum, is labeled as collected in 1770 by Banks and Solander at Endeavor Bay in northern Queensland. It is a glabrous plant with ovate to oblong leaves, 7–9 cm. long and 3.5–6.5 cm. broad. The corollas are large with a tube ca. 8–9 mm. long and a limb 3–4 mm. broad.

The type of *T. Urvilleana* was collected by Chamisso in Luzon. It has corollas 8 mm. long and a limb 3 mm. broad. The leaves are slightly less pubescent but otherwise are as in the type of *T. sarmentosa.*

Blume's *T. tetrandra* var. *hirsuta* is given as from the Moluccas and described as follows: "ramis foliis pedunculisque hirsutissimis." At Leiden there is a specimen labeled: "Variet.; Tournefortia hirsuta; Manado; T. tetrandra Bl. Variet." The first and the last items are in Blume's script. The specimen is a form with elongate corollas and with more or less hairy leaves suggesting those of *T. Horsfieldii*. Menado is near the northern tip of the Celebes. Another specimen at Leiden has the following label: "1531 Tournefortia hirsuta R.; Habitat in insula Celebes ad viam inter Kema et Menado; Oct. 1821." This is associated with a printed label reading "Herbarium Reinwardtianum; in Acad. Lugduno-Batavia." This second specimen is similar to that first mentioned and both are probably collections made by Reinwardt. They are, I believe, the types of *T. tetrandra* var. *hirsuta* and *T. hirsuta*.

The name *T. frangulaefolia* Zippel has appeared only in synonymy. At Leiden this name appears on two sheets having a printed label bearing: "Herb. Lugd. Batav.; Timor" and one in script reading: "1/6 Tournefortia frangulaefolia; Zp."

Miquel based his *T. Horsfieldii* upon material cited: "Java, in Patjitan, Kelak (Horsf.)." I have examined specimens from Horsfield's personal herbarium at the British Museum and those from the set he made for the East India Company (now kept as a unit) at Kew. He made two collections referable to *T. sarmentosa*, **1:** Pajittan (Kalak) Horsfield (borage 6) no. 275; and **2:** Blambangan, Horsfield (borage 7) no. 309. The former is evidently the type collection of *T. Horsfieldii*. It is a plant with very large leaves that are grayish velvety beneath. The blade becomes 10–14 cm. long and 7–9 cm. broad. The corolla-tube is 7–8 mm. long and the limb is 3–4 mm. broad.

Tournefortia acclinis is based upon material from Queensland collected by Bowman at Broad Sound and Amity Creek, and by Dallachy at Edgecombe Bay. A study of the original description and of a duplicate of Dallachy's material at Kew shows this species to have moderately sized leaves (5–10 cm. long and 3.5–6 cm. broad), a coarse appressed pubescence, a corolla with a tube 3–5 mm. long, and a corolla-limb 3–4 mm. broad. It is very similar to *T. Horsfieldii*, except in leaf-size.

The type of *T. macrophylla* was collected by Lauterbach (no. 2003) at Erima in eastern New Guinea. It is in fruit. The leaves are similar in size and shape to those of typical *T. Horsfieldii*. In fact the plant differs from the type of that species only in the practical absence of pubescence. The leaves have only a few weak scattered inconspicuous hairs along the nerves.

Domin's *T. sarmentosa* var. *magnifolia* from northern Queensland

(*Dietrich 724*), to judge from description, seems to be merely a form of *T. sarmentosa* with very large (12–15 cm. long, 6–6.5 cm. broad) hairy leaves, and small corollas (corollae tubo breviore). His *T. glabrifolia* is another large-leaved (10–13 cm. long and 5–5.5 cm. broad) plant. The leaves are glabrous. The corolla-tube is ca. 3–4 mm. long and the limb is ca. 2 mm. broad. The plant comes from Harvey's Creek in northeastern Queensland. It appears to differ from the type of *T. orientalis* only in its larger leaves and smaller corollas.

2. **Tournefortia tetrandra** Blume, Bijdrag. Fl. Nederl. Ind. 845 (1826). *Tournefortia tetragona* Blume ex Steudal, Nomencl. ed. 2, **2**: 694 (1841). (?)*Heliotropium scandens* Norona, Verh. Bat. Genootsch **5**: 78 (1827); Hasskarl, Cat. Hort. Bogor. 137 (1844), nomen. *Tournefortia tetrandra* var. *glabra* Hasskarl, Flora **25**[2]: Beibl., p. 27 (1842); Hasskarl, Cat. Hort. Bogor. 137 (1844); Hasskarl, Pl. Javan. Rariores 492 (1848). *Tournefortia glabra* (Hassk.) Zollinger & Moritzi ex Zollinger, Natuur- en Geneeskundig Archief v. Nederl. Ind. **2**: 5 (1845). *Tetrandra glabra* (Hassk.) Miquel, Fl. Nederl. Ind. **2**: 929 (1858). *Tournefortia tetrandra* var. *longiflora* Hasskarl, Cat. Hort. Bogor. 137 (1844), nomen; Hasskarl, Pl. Javan. Rariores 492 (1848). *Tournefortia Wallichii* DeCandolle, Prodr. **9**: 527 (1845); Ridley, Fl. Malay Penin. **2**: 441, fig. 115 (1923). *Tetrandra Wallichii* (DC.) Miquel, Fl. Nederl. Ind. **2**: 928 (1858). *Tetrandra Zollingeri* Miquel, Fl. Nederl. Ind. **2**: 928 (1858).

Nicobar Islands, Malay Peninsula, Sumatra, Java, Borneo and Celebes.

This is apparently the most common and best known of the Javan species of *Eutournefortia*. The Javan plant has received the following basic names, *Tournefortia tetrandra* Blume, *Tournefortia tetrandra* var. *glabra* Hassk., *Tournefortia tetrandra* var. *longiflora* Hassk., and *Tetrandra Zollingeri* Miquel. The differences between these named forms are minor and variable ones of corolla-size and of distribution of pubescence on the foliage. This variable plant of Java I am quite unable to distinguish from *Tournefortia Wallichii* DC., a species based upon material from Singapore and Penang. I have accordingly accepted *Tournefortia tetrandra* as ranging from the Nicobar Islands eastward to Java and the Celebes. The leaves of this species are ovate-acuminate or lance-ovate and are glabrous or sparsely strigose. The fruit is usually subglobose and 4–6 mm. in diameter. The only notable departure from this is found among material from northern Borneo where the fruit, of several different collections, is narrowly ovoid, 7 mm. long and 4–5 mm.

thick. This form may deserve some nomenclatorial recognition. There are, however, variations of *Tournefortia tetrandra* which I believe do merit recognition at this time. The characters which set these off from typical *T. tetrandra* may be organized as follows:

Leaves 1½–2½ times as long as broad, ovate acuminate or lance-ovate .... *Tournefortia tetrandra*
Leaves 2½–3½ times as long as broad, more or less lanceolate.
Leaves dull, east Java .... var. *angustifolia.*
Leaves somewhat glossy, Ceylon .... var. *Walkerae.*

2A. **Tournefortia tetrandra** Blume var. **angustifolia** Moritzi, Syst. Verzeich. 52 (1845–46).

Known only from the type-collection in eastern Java.

This variety is a peculiar plant with very dull thickish leaves that have only 3–4 pairs of primary veins evident. The secondary nervation is not discernible. I know it only from the type-collection by Zollinger (no. 939), made Dec. 17, 1842, "auf den Kalkfelsen von Kuripan."

2B. **Tournefortia tetrandra** Blume var. **Walkerae** (Clarke), comb. nov. *Tournefortia Walkerae* Clarke in Hooker, Fl. Brit. India **4:** 147 (1883); Trimen, Fl. Ceylon **3:** 198 (1895).

Known only from Ceylon.

This plant is simply a narrow-leaved form of the species that is confined to Ceylon. The blades are lanceolate but are quite similar to those of the species in texture, nervation, etc. The fruit and flowers are similar to the common Malaysian plant.

3. **Tournefortia Hookeri** Clarke in Hooker, Fl. Brit. India **4:** 147 (1883). *Tournefortia Hookeri* var. *subtropica* Clarke in Hooker, Fl. Brit. India **4:** 147 (1883).

Known only from the base and lower valleys of the Sikkim Himalayas.

Specimens Examined: Rangit, May 15, 1876, *Clarke 27953* (K); Great Rangit, April 1850, *Hooker & Thompson* (K, type of var. *subtropica*); Mangpu, 900 m. alt., May 1905, *Meebold 4243* (BD); Rangbi, 1500 m., May 31, 1870, *Clarke 11790* (K, BM); Chunbati, 600 m., June 12, 1870, *Clarke 12024* (K, BM); Chunbati, 600 m., April 1876, *Gamble 579* (K); below Punkabaree, *Hooker* (BD); Pancheni, 1875, *Gamble 3370* (K); Siliguri, Jan. 1873, *Gamble 3369* (K); Dalgaon, mixed forest, April 9, 1893, *Haines 358* (K); Sikkim, 1862, *Andersson 270* (BD); Sikkim, March 1871, *Clarke 16774* (K); Sikkim Terai, *Clarke* (K); Sikkim, *Griffith 5928* (K).

Characterized by its slender well developed calyx-lobes and by the golden or golden-brown under surfaces of the leaves. These latter are nearly glabrous or have only scattered hairs along the dark-colored nerves and veins. The corolla is usually 3–5 mm. long with the tube forming half (or even more) of this total length. In the var. *subtropica,* which is merely the large-flowered form of the species, the corollas become ca. 8 mm. long and the calyx-lobes only about a third as long as the tube. The species is a local one and probably worthy of recognition. It is most closely related to the form of *T. montana* described as *T. khasiana.*

4. **Tournefortia Heyneana** Wallich, Num. List no. 910[1] (1828–29), nomen; Don, Gen. Syst. **4:** 369 (1837); Clarke in Hooker, Fl. Brit. India **4:** 145 (1883); Gamble, Fl. Madras 893 (1923). *Tournefortia reticosa* Wight, Icones **4**[2]**:** 16, tab. 1386 (1848); Wight, Spicileg. Neilgherrense **2:** 83, tab. 189 (1851); Gamble, Fl. Madras 893 (1923).

Hills of southern peninsular India, about lat. 11°–13° N. and long. 76°–77° E.

SPECIMENS EXAMINED: Nilgiri Hills, April 1852, *herb. Wight 2057* (K); Devala, Nilgiris, 900 m. alt., Nov. 1884, *Gamble 15588* (K); S. E. Wynaad, Nilgiris, 900 m. alt., Nov. 1884, *Gamble 15497* (K); Wynaad, *Beddome 5437* (BM); Nadooputtah, June 1846, *herb. Wight* (K); Anamalais, *Beddome 5438* (BM); Carcoor-ghat, Nilgiris, Aug. 1887, flowers varying from ⅛–½ inch according to age, *Lawson* (Oxford); Coorg, *White* (Oxford); Peermade Reav (? spelling), 1350 m. alt., Dec. 1910, *Meebold 12920* (BD); without data, *herb. Wight,* probable basis of Wight's plate and the TYPE of *T. reticosa* (K); without data, *ex herb Heyne, Wallich 910*[1] (herb. Wallich at Kew).

A study of Wallich's herbarium, now at Kew, shows his number 910 to consist of two different species from opposite ends of India. The label reads: "910 Tournef. Heyneana, Wall. — 1. Herb. Heyn. — 2. Pundua F. de S." The Heyne plant represents the species from the Deccan with pedicellate flowers, which is the one treated here. The plant from Pundua, collected by de Sylva, is accompanied by a large special label indicating that is was found in the "Pundouh Hills" in Jan. 1824.

Clarke describes the flowers of *T. Heyneana* as 1/8–1/6 inches (3–4 mm.) long. These measurements are evidently from the duplicate of the Wallich collections now in the general herbarium at Kew. The Heyne material in the Wallich Herbarium at Kew has corollas 9–10 mm. long. The specimens, except for flower-size, are otherwise very similar and I believe they represent minor forms of the species. Significant in this connection is the note made by Lawson on one of his specimens cited above. He states that the corolla varies from 3–12 mm. according to age! Though Don makes no mention of the corolla-size in his description, the first given to the species, we may suppose that it was the large-flowered phase since the Wallich Herbarium, then in charge of the

Linnean Society, was no doubt consulted by him. In any case, since the corolla-size is variable even within the type-collection, the chief character whereby Clarke distinguished *T. reticosa* now disappears. The two species, *T. Heyneana* and *T. reticosa*, are, I believe, trivial forms of one species and quite synonymous.

DeCandolle, Prodr. **9:** 516 (1845), received only the second part of Wallich no. 910, and described this as *T. Heyneana*. His description in the Prodromus, consequently, is based upon de Sylva's specimens from Pundua. Clarke pointed out this mistake, gave a new name (*T. Candollii*) to the de Sylva collection described by DeCandolle, and properly restricted the name, *T. Heyneana*, to the peninsular species collected by Heyne.

5. **Tournefortia ovata** Wallich, Num. List no. 908 (1828); Don, Gen. Syst. **4:** 369 (1837); DeCandolle, Prodr. **9:** 516 (1845); Clarke in Hooker, Fl. Brit. India **4:** 147 (1883).

Southern Burma and the Andaman Islands.

SPECIMENS EXAMINED: Rangoon, Aug. 1826, *Wallich (no. 15) 908* (herb. Wallich, TYPE); Rangoon, *McClelland* (K, three collections); Andamans, April 1891, *Prain* (Cambridge); Middle Andaman, Homfray Straits, climber, 1915, *Parkinson 297* (K); Aberden, South Andaman, *Kurz* (K, parasitized; Delessert, normal); Chauldare, South Andaman,

Characterized by its elliptical abruptly acuminate leaves, its subpedicellate flowers and its southern occurrence. The corolla becomes 8 mm. long. The calyx is only 1.5 mm. long at anthesis. The leaves are mostly rather firm in texture and are usually brown and glabrous beneath. One of McClelland's collections is consequently quite atypical in having the leaves not only thin in texture but golden-brown beneath as well. Another one of his collections is quite hairy on the lower leaf-surface. The pedicels in *T. ovata* are usually at most only 1 mm. long, though in Parkinson's material cited the pedicels become fully 2 mm. long and are quite evident.

6. **Tournefortia montana** Loureiro, Fl. Cochinch. **1:** 122 (1790). *Messerschmidia montana* (Lour.) Roemer & Schultes, Syst. **4:** 544 (1819). *Lithospermum viridiflorum* Roxburgh, Hort. Bengal. 13 (1814), nomen; Lehmann, Asperif. **1:** 30 (1818), in synon.; Roxburgh, Fl. Indica **2:** 4 (1824), description; Roxburgh, Icones ined. Kew. tab. 2120. *Heliotropium viridiflorum* (Roxb.) Lehmann, Asperif. **1:** 30 (1818). *Tournefortia viridiflora* (Roxb.) Wallich, Num. List no. 907 (1828); Clarke in Hooker, Fl. Brit. India **4:** 146 (1883). *Tournefortia Sampsoni* Hance, Jour. Bot. **6:** 330 (1868). *Tournefortia Wightii* Clarke in Hooker, Fl. Brit. India **4:** 146 (1883). *Tournefortia Rox-*

burghii Clarke in Hooker, Fl. Brit. India **4:** 146 (1883). *Tournefortia viridiflora* var. *Griffithii* Clarke in Hooker, Fl. Brit. India **4:** 146 (1883). *Tournefortia Candollii* Clarke in Hooker, Fl. Brit. India **4:** 146 (1883). *Tournefortia khasiana* Clarke in Hooker, Fl. Brit. India **4:** 147 (1883). *Tournefortia Boniana* Gagnepain, Not. Syst. **3:** 33 (1914) and in Lecomte, Fl. Gén Indo-Chine **4:** 217 (1914). *Tournefortia Gaudichaudii* Gagnepain, Not. Syst. **3:** 34 (1914) and in Lecomte, Fl. Gén. Indo-Chine, **4:** 217 (1914). *Tournefortia Heyneana* sensu DeCandolle, Prodr. **9:** 516 (1845).

In the hills, up to 1500 m. alt., in Assam, Upper Burma, northern Siam (Payap and Maharat), middle and northern Indo-China (Anam, Laos and Tonkin) and southern-most China (Yunnan, Kwangsi and Kwangtung).

This species presents a number of diverse phases resulting from combinations of variations in leaf-size, abundance and distribution of pubescence, and size of corolla-tube. These phases have been treated as "species" but their variability, their erratic distribution, and their occurrence together in various localities lead me to believe they are merely further manifestations of the surprising intraspecific variability of these structures among the Old World *Tournefortiae*. After discounting these variations as mere phases, I am struck with the naturalness of the distribution of the resulting aggregate species. The distribution is of the pattern found in numerous species of other genera and families inhabiting this part of Asia.

The type of *T. montana* has not been examined. Its source is not given, but the probabilities are that it came from Anam. Dr. E. D. Merrill, who has devoted much time to the consideration of Loureiro's writings, informs me that he knows no reason for doubting Loureiro's generic attribution in the present case. After a study of the description I am perfectly content to accept Loureiro's name for this species. The leaves are given as ovate-lanceolate and glabrous. Unfortunately, however, no information is given as to the shape or size of the corolla-tube.

The second name applied to our species is *Lithospermum viridiflorum*. It first appears in 1814 as a name in a list of the Calcutta Garden and is given as collected by Roxburgh at Chittagong. It was no doubt this same garden material that was described in 1824 by Wallich in Roxburgh's Flora and is now represented in Wallich's herbarium (no. 907). It is also the plant represented in Roxburgh's unpublished plates (no. 2120) now preserved at Kew. The first description of the plant, as *Heliotropium viridiflorum,* is that by Lehmann in 1818. His material also seems to have come from the Calcutta Garden. Hence, there is every reason for taking the material grown at Calcutta as typical. This is a form characterized by distinctly lanceolate leaves that are velvety all over beneath and by small strigose corollas. The corolla-tube is 2–3 mm. long, usually densely strigose and commonly only twice the length of the calyx or less. This form has not been collected about Chittagong. As Clarke has indicated, l. c. 146, the common form of *T. montana* about Chittagong, particularly in the region in which Roxburgh is known to have collected, is the plant with long corolla-tubes described by Clarke as *T. Roxburghii*. As matters stand, therefore, we may either believe that Roxburgh did not collect his plant at Chittagong, or that having collected the common long-tubed *Tournefortia* there it subsequently became a short-tubed form under garden conditions. I have seen material of the type-form of *T. viridiflora* from Assam, Burma and Siam.

The type of *T. viridiflora* var. *Griffithii* is a collection made in the Khasia Hills by Griffith. It differs from the type-form of *T. viridiflora* in having the leaves much less hairy or nearly glabrous beneath and corollas that are possibly a trifle larger. The type of *T. Boniana* collected by Bon (no. 1932) at O-cach, on the mountain Ma-dong in Indo-China, is quite similar. I have seen this glabrescent small-flowered form from Assam, Burma and Indo-China.

In publishing *T. Wightii*, Clarke gave its source as "Deccan Peninsula, *Wight*." The type is Wight no. 2056 and is accompanied with one of the old printed labels indicating that it was part of the Wight materials handled at Kew in 1866–67. The label proper is headed "Peninsula Indiae Orientalis." We may accept that no. 2056 was part of the Wight Herbarium but as to the collector of the specimen and its original source doubt must remain. Since the plant agrees closely with plants from Burma I suspect that perhaps it came from that general region and may represent material received by Wight from Roxburgh or some other collector of that period. Gamble, Fl. Madras, 894 (1923), reports the species from the Anamalai Hills, Madras. The only *Tournefortia* I have seen from that general region is *T. Heyneana*! Until undoubted material from Southern India is forthcoming I believe that *T. Wightii* should be accepted as clearly applying to the material east of the Ganges here discussed. In the type-form of *T. Wightii* the leaf-surface is velvety beneath much as in typical *T. viridiflora*. The corolla is much larger, however, with the tube 2–4 times as long as the calyx. *Tournefortia Roxburghii* is a form of *T. Wightii* which has lanceolate rather than ovate leaf-blades. It is a rather common form. I have seen plants similar to the type-form of *T. Wightii* and *T. Roxburghii* from throughout the range of *T. montana*.

Tournefortia Candollii is based upon "*T. Heyneana,* DC. Prodr. ix. 516; Wall. Cat. 910, as to the Khasia examples." In the Wallich Catalogue no. 910 consists of two parts, 1. material from Heyne, the type of *T. Heyneana* Wall. and 2. material collected by de Silva at Pundua. DeCandolle's specimen of *Wallich 910* consists only of the second part of the Wallich number, that is to say, the material from Pundua by de Silva. This specimen was described by DeCandolle as *T. Heyneana.* Clarke, l. c. 145, recognizing that the name *T. Heyneana* was obviously to be associated with Heyne's material from southern India, gave a new name, *T. Candollii,* to the plant improperly described as *T. Heyneana* by DeCandolle. The type of *T. Candollii* is accordingly de Silva's material in the DeCandollean Herbarium. The specimen at Geneva is broken and poor but has good corollas. These are somewhat constricted at the throat and very similar to those found in the type of *T. khasiana.* The leaves are lanceolate, dried brown beneath and nearly black above. They are very sparsely strigose above and have only scattered hairs along the principal veins beneath.

I consider *T. Candollii* to be the form of *T. montana* with elongate corolla-tubes and glabrescent leaves. Belonging with it are several further synonymous forms. The type of *T. Sampsoni* is from Sai-chü-shan caverns in the province of Kwangtung and is now deposited at the British Museum. There is some interesting variation within this collection. The corolla-tube is medium to long (5–8 mm.) and the lanceolate leaves are either distinctly appressed hairy or are quite glabrous beneath. The type of *T. khasiana* was collected by Clarke (no. 15227) at Nonpriang in the Khasia Hills. It is a form of *T. Candollii* in which the corolla-tube is contracted upward toward the throat so that the throat is at times almost half the diameter of the base of the tube. The type of *T. Gaudichaudii* is a glabrescent plant with elongate corollas and broadly lanceolate leaves. It was collected in Anam (Tourane) by Gaudichaud.

7. **Tournefortia luzonica** sp. nov., scandens grisea; ramulis obscure tetragonis 2–4 mm. crassis pilis numerosis brevibus divergentibus vestitis; foliis oppositis vel suboppositis; petiolis 5–14 mm. longis; lamina folii ovata vel late lanceolata 5–13 cm. longa 2–7 cm. lata apice breviter acuminata basi rotunda vel (1–4 mm. profunde) cordata, supra pilis rigidulis brevibus ascendentibus plus minusve numerosis vestita, subtus pallidiore pilis gracilibus falcatis saepe numerosis vestita nervis 6–9-jugatis ornata; inflorescentia hispidula; calycibus sessilibus 1–2.5 mm. altis, lobis anguste lanceolatis vel linearibus erectis; corolla virescentibus, tubo 2–4(–8) mm. longo, limbo 2–2.5 mm. lato; fructu globoso

3–4 mm. diametro albo glaberrimo succoso; nuculis 2 biovulatis laevibus.

Endemic to the Philippines where it is confined to the mountainous regions of northern, east-central and southern Luzon.

SPECIMENS EXAMINED: vicinity of Peñablanca, Cagayan Prov., a vine on hillside, fl. green, fruit white, May 3, 1917, *M. Adduru 237* (TYPE, herb. Arnold Arboretum; isotype, Kew); Peñablanca, 1926, *Ramos & Edaño 46663* (BM); Bangui, Prov. Ilocos Norte, *Ramos 27563* (BM); Burgos, Prov. Ilocos Norte, *Ramos 4799* (BD); Bocana del Abra, Prov. Ilocos Sur, *Micholitz* (K); Mt. Pulog, Mountain Prov., Jan. 1909, *Curran, Merrill & Zschokke 16103* (BD); Benguet, *Loher 1541, 1542* (K); dist. of Lepanto, Mountain Prov., *Vidal 3326* (K); Baguio, Benguet, *Elmer 8467* (AA, K); Mt. Maquilong, Prov. Batangas, *Vidal 3327* (K); Prov. Albay, *Cuming 1215* (K, BM, BD).

7A. **Tournefortia luzonica** var. **sublucens**, var. nov., a forma typica speciei differt foliis sparse inconspicueque pubescentibus, supra vix griseis sed sublucentibus.

Confined to the mountains of west-central Luzon.

SPECIMENS EXAMINED: Anuling, Zambales Prov., 1924, *Ramos & Edaño 44553* (TYPE, herb. Arnold Arboretum; isotypes, Kew, Brit. Mus.); Zambales, 1907, *Ramos 4799* (BD); Lamao, Mt. Mariveles, Bataan Prov., *Meyer 2844* (K, BD); Lamao River, Mt. Mariveles, 350 ft. alt., slender vine growing over trees for many yards, *Williams 525* (K).

Among all the Old World species of *Tournefortia* this species is unique in the possession of opposite or subopposite leaves. In the treatments of the Philippine *Boraginaceae* by Robinson, Philip. Journ. Sci., Bot. **4:** 694 (1909), and by Merrill, Enum. Philip. Pl. **3:** 376 (1923), this plant has generally passed as *T. Horsfieldii* Miquel. That species, however, with its alternate leaves and a fruit composed of four uniovulate nutlets is one of the forms of the widely ranging *T. sarmentosa*.

The var. *sublucens* is confined to the mountainous country of west central Luzon, prov. Bataan and Zambales, and seems to have a range quite distinct from the typical form of *T. luzonica* which ranges in the other parts of the island of Luzon. Essentially a glabrate form of *T. luzonica*, with the upper leaf-surfaces more or less glossy, it is significant and worthy of nomenclatorial recognition only if it has a range apart, and is geographically correlated.

8. **Tournefortia Muelleri**, nom. nov. *Tournefortia mollis* F. v. Mueller, Frag. **1:** 59 (1858); Bentham, Fl. Austral. **4:** 390 (1869); Bailey, Queensland Fl. **4:** 1041 (1901); not *T. mollis* Bertol. (1852).

Northern Australia and Papua.

SPECIMENS EXAMINED: Edgecombe Bay, Queensland, *Dallachy* (K); along Burdekin River, *Mueller* (K, isotype); Herbert River, *Dallachy*

(K); Cape York Peninsula Exped., *Hann 146* (K); shores of Montague Sound, W. Australia, 1820, *Cunningham 182* (K, BM) and *324* (BM); erect shrub 1.5–2 m. tall, fringing tidal areas, Kapa Kapa, Papua, *Brass 505* (AA, K); Port Moresby, Papua, 1918, *White 6* (AA).

The carpels seem to be more bony than in other Old World species of this section. The leaves are usually lanate.

9. **Tournefortia puberula** Baker, Jour. Linn. Soc. London, **20:** 211 (1883). *Tournefortia Mocquerysi* A. DeCandolle, Bull. Herb. Boiss. ser. 2, **1:** 581 (1901).

Forests of eastern Madagascar and the Seychelles. Possibly introduced in the latter archipelago.

SPECIMENS EXAMINED: MADAGASCAR: forests east of Ivohibé, 1000 m. alt., fl. white, Nov. 3, 1924, *Humbert 3163* (P); high valley of the Rienana, drainage of the Matitana, 1000–4000 m. alt., fl. white, Nov. 1924, *Humbert 2523* (P); Central Madagascar, *Baron 1957* (Kew, TYPE of *T. puberula;* BM, BD, isotypes), *2798* (K, BM, P), *3106* (K, P) and *6991* (K); forest of Ivohimanitra, Nov. 8, 1894, *Forsyth Major 64* (K, BM, BD, P); forest of Analamazaotra near col d'Amboasary, ca. 950 m. alt., shrub with white flowers, Oct. 23, 1912, *Viguierro & Humbert 978* (P); forest at head of Antongil Bay, a liana with white flowers, *Mocquerys 161* (Deles., TYPE of *T. Mocquerysi*). SEYCHELLES: Mahé, common shrubby climber in hills near streams, Sept. 1871, *Horne 247* (K); Mahé, *Thomasset* (K); Mahé, *Thomasset 10* (BM); Mahé, 1867, *Wright* (BM); Terné, Mahé, 1908, *Gardiner* (K); Silhoutte, common in cultivation, 1908, *Gardiner 113* (K); indefinite, a twining shrub generally on rocks near rivers, May 1902, *Thomassett 22* (K, BM).

The types of *T. puberula* and *T. Mocquerysi* are quite indistinguishable. The species is a readily recognizable one. The leaves are firm, apparently glabrous and the stems are covered with a minute brownish puberulence. There is both a short- and a long-corolla form. The plant of the Seychelles is certainly identical with that of Madagascar. Possibly it represents a horticultural introduction to the islands. In accounts of the Seychelles flora, Baker, Fl. Mauritius and Seychelles 202 (1877), and Summerhayes, Trans. Linn. Soc. London, Zoölogy, **19:** 284 (1931), the species has consistently been misdetermined as *T. sarmentosa*.

9A. **Tournefortia puberula** var. **Kirkii**, var. nov., a varietate genuina differt pilis brevibus pallidis adpressis ornatis.

Islands off the northwest coast of Madagascar.

SPECIMENS EXAMINED: Mohilla Island, Comoro Archipelago, April 1861, *J. Kirk* as "*Tournefortia* (3)" (TYPE, herb. Kew); Nossi-bé, June 1847, *Boivin 2086* (P); Nossi-bé, 1853, *Perrille* (P).

This variety comes from a much more arid region than typical *T.*

puberula and may be only a hairy xerophytic form of that species. In typical *T. puberula* the plant is provided with a minute, frequently somewhat golden puberulence. In the var. *Kirkii* the stems have a sparse pale short strigosity that tends to disappear with age. The petioles are sparsely strigose. The lower surface of the leaf-blades has short white closely appressed hairs scattered along the rib and veins. The upper surface is somewhat strigose but less abundantly so than below. The inflorescence has numerous short ascending pale hairs.

10. **Tournefortia acuminata** DeCandolle, Prodr. **9:** 520 (1845); Cordemoy, Fl. Réunion 479 (1895).

Endemic to the Island of Reunion (Bourbon).

Specimens Examined: les hauts du Boucan Launay, *Boivin 1241* (K, BD, DC, Boiss, P); Bébour au dessus de la plantation de Quinquinas, July 28, 1875, *G. de l'Isle 499 bis* (K, Coss.); Bourbon, arbor, [*?Commerson*] (herb. Smith); chemin que conduit de Sante Rose à Saint Joseph avaunt la descente qui conduit au Volcan, 1812, *Commerson* (P); "l'Ile de France au bourbon," *ex Mus. Paris* (type, herb. DC).

The type of *T. acuminata* at Geneva is given as distributed from Paris in 1821 and as from either Reunion or Mauritius. It represents a form in which the stems, petioles and inflorescence are glabrous or only very scantily strigose. It is obviously a duplicate of the collection at Paris which is labeled as collected by Commerson on the road between Ste. Rose and St. Joseph on Reunion. The material which I have cited from Boivin, which is widely distributed in European herbaria, is a form in which the stems, petioles and inflorescence have a short and evident, though not very abundant nor very conspicuous strigosity that becomes more or less brownish or golden. This I believe is the common form of the species. The leaves in *T. acuminata* are 12–17 cm. long and 3.5–7 cm. broad, are acute at both ends, and have 10–15 pairs of nerves. The calyx is 1.5–2 mm. long at anthesis and has erect, cuneate or more or less lanceolate lobes. The corolla-tube is 3.5–7 mm. long. The limb is ca. 4 mm. broad.

11. **Tournefortia arborescens** Lamarck, Tab. Encyc. **1:** 417 (1791); Poiret, Encyc. **5:** 357 (1804). *Tournefortia velutina* Smith in Rees, Cyclop. **36:** sp. no. 13 (Aug. 1817!), not *T. velutina* HBK. (1818). *Tournefortia Bojeri* sensu Cordemoy, Fl. Réunion 479 (1895).

Endemic to the Island of Reunion (Bourbon).

Specimens Examined: Grand Bassin, Aug. 6, 1875, *G. de l'Isle 454* (K, P); Gauteuron (spelling ?) du Gol, woods, fl. white, *Commerson* (herb. Smith, type of *T. velutina*); Reunion, *Commerson* (herb. Smith, second sheet of *T. velutina*), *Bory* (Deles) *Boivin* (BD) and *Guyot 431* (BD); "in Mauritius," *herb Bojer* as *T. bifida* (BM); "de l'inde" [*? Sonnerat*] (Paris, TYPE of *T. arborescens*).

The type material of *T. arborescens* is accompanied by a small label reading: "Tournefortia d l'inde." The collector is not indicated but both Lamarck and Poiret attribute it to Sonnerat who visited the Mascarenes during his voyage to India and Malaysia. The material consists of two sheets, one bearing a sterile shoot with entire oblanceolate leaves more or less tomentose beneath in the manner common in the spicate *Cordia* species of the section *Varronia*. The second sheet contains a *Tournefortia* in flower. The latter is a form of the species as here defined, having the leaves only very sparsely and obscurely strigose, particularly above. The stems bear numerous but not very abundant short appressed pale hairs. The calyx-lobes are ovate, acute and sparsely pale strigose. The specimen evidently represents the sparsely hairy form of the endemic species of Reunion.

The type of *T. velutina* is the form of the species with very abundant long hairs. It has the leaves pale and silky with a dense indument of slender very pale hairs. The calyx lobes are ovate, densely hairy and more or less golden tawny. Smith mentioned atypical material of his *T. velutina* from Mauritius, but this, in fact, represents a form of *T. Bojeri*. DeCandolle, Prodr. **9:** 514 (1845), incorrectly cited *T. velutina* as a possible synonym of *T. argentea*. I have cited above a specimen given as collected on Mauritius by Bojer. I doubt the accuracy of the geographical data and believe that the specimen is really from Reunion. Its broad calyx-lobes are ovate or orbicular-ovate and hence similar to those found in all material indubitably from that island.

12. **Tournefortia Bojeri** A. DeCandolle, Prodr. **9:** 516 (1845); Baker, Fl. Mauritius, 202 (1877). *Tournefortia bifida* sensu Bojer, Hort. Maurit. 234 (1837).

Endemic to the Island of Mauritius (Ile de France).

SPECIMENS EXAMINED: Mauritius, woods, 1837, *Bojer* as *T. bifida* (TYPE, herb. DC); without locality, 1839, *Bouton* as *T. bifida* (DC, cotype); Mauritius, mountains and forest, *Bouton* (K); Mauritius 1854, *Boivin* (K); Mauritius, 1811, *Hardwick* (BM); Mauritius, [*Commerson*] (herb. Smith); Mauritius, *Sieber 98* (BD); Mauritius, *herb. Labillardière* (Deles); "Bourbon," 1853, *Boivin* (Boiss).

Boivin's collection which it cited above and attributed to Reunion is, I believe, mislabeled. Indubitable collections of *T. Bojeri* come only from Mauritius. The species is very closely related to *T. arborescens* of Reunion, differing chiefly in the narrower calyx-lobes. In the DeCandolle Herbarium there is a branch of *T. Bojeri,* mounted on a sheet with isotypic material of the Philippine *T. Urvilleana*. The only label accompanying this mixed sheet is in the script of Chamisso and belongs to the Philippine species. This mixed sheet makes comprehensible DeCandolle's, Prodr. **9:** 515, adnot. (1845), strange comparison of *T. Bojeri* and *T. Urvilleana*. Since Chamisso never visited the Mascarenes it is evident that the spray of *T. Bojeri* has somehow become divorced from its proper label. The name "*T. cymosa* Heyne" seems to be based upon material from Mauritius. For a discussion of this *nomen* see my list of doubtful and excluded species on p. 166.

In *T. Bojeri* the stems, petioles and inflorescence are more or less velvety with a pale ascending or spreading (or very rarely appressed) usually abundant hairs. The leaf blade is acute at both ends, more or less strigose on both surfaces though usually less so above. It has 10–12 pairs of veins and is 11–17(–24) cm. long and 2–5(–6) cm. broad. The calyx is 2–2.5 mm. long and has the lobes cut at least ¾ way to base. It is more or less silky strigose. The lobes are lanceolate to broadly lanceolate or cuneate-lanceolate. The corolla-tube is 2–8 mm. long, and 2–5 times the length of the calyx. The corolla-limb is 2–3 mm. broad. The fruit is ca. 3 mm. in diameter.

Messerschmidia Linnaeus ex Hebenstreit, Nov. Comment. Acad. Sci. Imp. Petrop. **8:** 315, tab. 11 (1763); Gmelin, Fl. Sibir. **4:** 77 (1769); Murray, Syst. Nat. ed. 13, 161 (1774); Linnaeus fil. Suppl. Pl. 132 (1781). — type-species, *Tournefortia sibirica* Linn. *Messersmidia* Linnaeus, Hort. Upsal. 36 (1748); Linnaeus, Mant. **1:** 5 and 42 (1767); Linnaeus, Syst. ed. 12, 149 (1767); Linnaeus, Mant. **2:** 334 (1771). — a variant spelling of *Messerschmidia,* type-species, *Tournefortia sibirica* Linn. *Tournefortia* sect. *Messerschmidia* (Linn.) DeCandolle, Prodr. **9:** 528 (1845); as to nomenclatorial type only, not as to the species of *Heliotropium* treated. *Argusia* Amman, Stirp. Rar. Ruth. 29 (1739). *Arguzia* [Amman] Rafinesque, Sylva Tellur. 167 (1838); Steven, Bull. Soc. Nat. Moscow **24**[1]**:** 558 (1851). — type-species, *Tournefortia sibirica* Linn. *Tournefortia* sect. *Arguzia* [Amman] DeCandolle, Prodr. **9:** 514 (1845); Ledebour, Fl. Ross. **3:** 97 (1847–49). — type-species, *Tournefortia sibirica* Linn. *Tournefortia* sect. *Mallota* A. DeCandolle, Prodr. **9:** 514 (1845). — type-species, *T. argentea* Linn. *Tournefortia* sect. *Mallotonia* Grisebach, Fl. W. Ind. 483 (1861). — type-species, *Tournefortia gnaphalodes* R. Br. ex R. & S. *Mallotonia* (Griseb.) Britton, Ann. Mo. Bot. Gard. **2:** 47 (1915). — type-species, *Tournefortia gnaphalodes* R. Br.

Segregated here, as the emended genus *Messerschmidia,* are three remarkable species that depart widely in appearance from the numerous and habitually very uniform species formerly associated with them in *Tournefortia*. As I have redefined and amplified *Messerschmidia* it consists of the original Asiatic herb, *Tournefortia sibirica*, the strand-shrub of the Antilles, *T. gnaphalodes*, and the well known strand-tree of the Indian and Pacific oceans, *T. argentea*. All these species differ widely not only in their habit of growth and in their selection of habitat from all the other species that have been traditionally placed with them in *Tournefortia*, but also in their pronounced development of a corky exocarp which sets them off not only from all species of *Tournefortia* but from all other *Boraginaceae* as well. All three of the species show a marked preference for saline conditions. Two of them are tropical strand-plants. The third species grows along the ocean in temperate eastern Asia, in more or less saline soils along streams and about inland seas in Central Asia and eastern Europe. The corky exocarp evidently adapts the three species for water dispersal. The nature of the hairy covering of these three species is of an essentially similar type, consisting of slender silky hairs rather different in texture and appearance from that predominating among the species of true *Tournefortia*.

The generic name *Messerschmidia* (also spelled *Messersmidia* and *Messerschmidtia*) is based upon *Tournefortia sibirica* Linn., and is a synonym of *Argusia* (or *Arguzia*). The type-species was first described by Amman in 1739 who applied to it the mononomial, *Argusia*, and gave a lengthy description of it based upon notes and specimens made by D. G. Messerschmid in 1724 along what is now the northwestern frontier of Manchuria. The source of this material is given as "Locus in glareosis aridisque apricis Argun fluuii et Iike Dalai Noor in Dauria." Although Amman's mononomial was formed from the "loco natali" of the plant, i.e. the Argun River, its author deliberately and repeatedly spelled it "*Argusia*"! Amman states that seeds from Messerschmid's collection germinated and grew in the gardens at St. Petersburg. These same cultures are probably those described and illustrated by Hebenstreit in 1763. The plants growing in the Upsala Garden in 1748 and described by Linnaeus as *Messersmidia* were probably derived from those grown by Amman. In the Correspondence of Linnaeus, ed. Smith **2**: 200 (1821), there is a letter from Amman, dated Nov. 18, 1740, in which questions by Linnaeus concerning *Argusia* are answered and in which it is stated that dried specimens of *Argusia* were being sent him. When he proposed the mononomial "*Argusia*," Amman justified his use of a geographic appellation in forming the name, but added that he had no objection if the genus was named after Messerschmid, its original collector. Linnaeus seems to have preferred the latter. The collector's name was spelled "Messerschmid" by his contemporaries. Linnaeus latinized it, "*Messersmidia*," and was consistent in this usage in all his writings. Other writers of the last half of the 18th century, however, spelled it "*Messerschmidia*" and it is so spelled in the paper by Hebenstreit who was the first to use the generic name subsequent to 1753. Writers of the past century tended to spell the generic name "*Messerschmidtia*." The generic name *Messerschmidia* has variant spellings in "*Messersmidia*" and "*Messerschmidtia*." Although clearly based upon, in fact named after the original collector of *Tournefortia sibirica,* the generic name *Messerschmidia* (variously spelled) eventually became associated with two other very diverse groups of *Boraginaceae*. A study of the facts here presented, however, makes it evident that the name "*Messerschmidia*" is only very improperly applied either to the American species of *Tournefortia* sect. *Cyphocyema,* or to Canary Island and South African species of *Heliotropium* as has been done in some large works. In another paper, Contr. Gray Herb. **92**: 73 (1930), I have given many facts concerning the misuse of the name "*Messerschmidia*." The name was based upon *Tournefortia sibirica* and was originally applied solely to that plant. The type-species of *Messerschmidia* is obviously and logically the original Siberian species.

Key to the Species

Plant a low herb from rhizomes; inflorescence a loose open corymbose cyme; calyx pedicellate, lobes cuneate; anthers several times as long as broad; fruit pubescent, sunken in at apex; carpels embedded in the center of the corky exocarp; temperate Eurasia .... 1. *M. sibirica.*

Plant a tree or shrub; inflorescence of scorpioid cymes; calyx sessile, lobes orbicular or oblong; anthers about two times as long as broad; fruit glabrous, apex conic or rounded; carpels occupying the apical half of the fruit, the lower half composed entirely of corky exocarp; tropical strand plants.

A tree 1–5 m. tall; leaves broadly oblanceolate or obovate, 3.5–9 cm. broad; inflorescence a conspicuous stiff panicle of loosely flowered elongating (up to 8 cm.) scorpioid cymes; corolla-lobes merely imbricate (not plicate) in the bud; anthers partially exserted from the short corolla-tube; fruit dull, breaking in half; apex and dorsal surface of carpels covered with corky exocarpial tissue; tropics of the Old World .... 2. *M. argentea.*

A shrub 3–12 dm. tall; leaves narrowly spathulate-linear, 4–10 mm. broad; inflorescence consisting of single or paired long-peduncled very congested short (1–2 cm.) scorpioid cymes; corolla-lobes distinctly plicate in bud; anthers well included in the cylindrical corolla-tube; fruit brown and lustrous, not breaking in half; apex and dorsal surface of carpels not covered with corky exocarpial tissue; West Indies ....3. *M. gnaphalodes.*

1. **Messerschmidia sibirica** Linnaeus, Mant. **2:** 334 (1771). *Tournefortia sibirica* Linnaeus, Sp. Pl. 141 (1753); Kusnezow & Popow, Fl. Caucas. Crit. **4**[2]**:** 77 (1913). *Messersmidia Argusia* Linnaeus, Mant. **1:** 42 (1767). *Messerschmidia Arguzia* Murray, Syst. Nat. ed. 13, p. 161 (1774); Linnaeus fil. Suppl. Pl. 132 (1781). *Messerschmidia Argunia* Gaertner, Fruct. **2:** 130, tab. 109 (1791). *Tournefortia Arguzia* (L.) Roemer & Schultes, Syst. **4:** 540 (1819); Ledebour, Fl. Ross. **3:** 97 (1847–49); Herter, Act. Hort. Petrop. **1:** 503 (1872). *Messerschmidia rosmarinifolia* Willdenow ex Roemer & Schultes, Syst. **4:** 544 (1819). *Tournefortia rosmarinifolia* Willdenow ex Steudel, Nomen. ed. 2, **2:** 693 (1841). *Tournefortia Arguzia* var. *rosmarinifolia* (Willd.) Turczaninow, Bull. Soc. Nat. Moscow **23**[1]**:** 498 (1850). *Arguzia rosmarinifolia* Steven, Bull. Soc. Nat. Moscow **24**[1]**:** 559 (1851). *Arguzia repens* Rafinesque, Sylva Tellur. 167 (1838). *Tournefortia Arguzia* var. *latifolia* DeCandolle, Prodr. **9:** 514 (1845); Turczaninow, Bull. Soc. Nat. Moscow **23**[1]**:** 498 (1850). *Tournefortia Arguzia* var. *angustior* DeCandolle, Prodr. **9:** 514 (1845); Turczaninow, Bull. Soc. Nat. Moscow **23**[1]**:** 498 (1850). *Tournefortia sibirica* var. *angustior* Turczaninow ex Fedtchenko, Consp. Fl. Turkestan **5:** 39 (1913). *Tournefortia Arguzia* var. *cynanchoides* Turczaninow ex Steven, Bull. Soc. Nat. Moscow **24**[1]**:** 559 (1851), in synon. *Arguzia Messerschmidia* Steven, Bull. Soc. Nat. Moscow **24**[1]**:** 560 (1851). *Arguzia cimmerica* Steven, Bull. Soc. Nat. Moscow **24**[1]**:** 560 (1851). *Heliotropium japonicum* Gray, Mem. Amer. Acad. ser. 2, **6:** 403 (1859).

From Japan, Amur and northern China across Asia, mostly between lat. 40° and 55° N., to Rumania and central Russia; affecting moist gravelly, usually saline soils. For more details on distribution see Ledebour, Fl. Ross. **3**[1]**:** 97 (1847–49); Herter, Act. Hort. Petrop. **1:** 503 (1872) and Kusnezow & Popow, Fl. Caucas. Crit. **4**[2]**:** 78 (1913).

2. **Messerschmidia argentea** (Linnaeus), comb. nov. *Tournefortia argentea* Linnaeus fil., Suppl. Pl. 133 (1781). *Tournefortia arborea* Blanco, Fl. Filip. 129 (1837).

A strand-tree widely distributed within the tropics, on islands in the Indian and Pacific oceans.

The distribution of this species is worthy of a detailed statement. The fruit having a corky exocarp is admirably suited for oceanic dispersal. In this it has been very successful. The species is, in fact, one of the characteristic strand-plants of the Old World Tropics. It is, however, almost exclusively a plant of island-shores. In the Pacific Ocean it ranges from the Paumotas (Ducie Isl.), the Marquesas and Palmyra Island, westward to Bonin Island, the Liu Kiu Islands, Formosa, Tizard Reef (China Sea), "Annam (Turan)," the Philippines, the Moluccas, Timor, tropical Australia, and New Caledonia. In the Indian Ocean it extends from northwestern Australia, Timor and Java, Christmas and Cocos Keeling islands to the Mascarenes, Madagascar (near south end only) and coast of Mozambique (rare), north to Zanzibar, the Seychelles, the Laccadives (Bitrapar in lat. 11°30′ N.), the Maldives, Ceylon, the Andamans (Great Coco Isl. in lat. 14° N.), the Nicobars, the islands (Vogel, lat. 7°46′ N.; Adang calat, lat. 6°30′ N.) off the west coast of peninsular Siam, and the northwestern Federated Malay States ("Kedah"). Miquel, Prodr. Fl. Sumatra, 244 (1855), reports it vaguely from Sumatra. I have seen no material from Sumatra, Borneo or the Celebes. Except for the record from Indo-China and the vague record for the Malay States the species is not known from the Asiatic continent. In Africa it is reported only from the Mozambique Coast. The record for Amboland (*Schinz 757*), found in the Flora of Tropical Africa, **4²:** 30 (1905), is evidently a clerical error for the specimen cited is *Heliotropium tuberculosum!*

The original description of *T. argentea* is based upon material collected on the coast of Ceylon by König. In the Linnean Herbarium there is a characteristic specimen of this plant accompanied by König's label reading "habitat ad Littora maris Zeylanica." Accompanying this is a label in the script of the younger Linnaeus reading "Konig, 1777." The *Buglossum lanuginosum* of Rumphius, cited by the younger Linnaeus, is evidently conspecific with König's material from Ceylon. DeCandolle, Prodr. **9:** 514 (1845), cites *T. velutina* Smith as a possible synonym of *T. argentea*. Smith's plant, however, is a very different species being a synonym of *T. arborescens* Lam. of Reunion.

3. **Messerschmidia gnaphalodes** (Linnaeus), comb. nov. *Heliotropium gnaphalodes* Linnaeus, Syst. ed. 10, p. 913 (1759) and Amoen. Acad. **5:** 394 (1760). *Tournefortia gnaphalodes* (L.) R. Brown ex Roemer & Schultes, Syst. **4:** 538 (1819). *Mallotonia gnaphalodes* (L.) Britton, Ann. Mo. Bot. Gard. **2:** 47 (1915).

A strand-plant widely distributed in the West Indies.

According to Millspaugh, Publ. Field Mus., Bot. **2:** 89 (1900), this species grows "On the beach line facing the open sea, [and is] very seldom, if ever, found in bays or where partially dry reefs guard the shore." Its range may be stated as follows: Bermuda, the Bahamas (north to about lat. 27° N.), southern peninsular Florida (to Miami region) and the Greater Antilles, southward to Granada (in the Lesser Antilles), the islands off Venezuela, the Paraguana Peninsula of northwestern Venezuela (Medanos Isthmus) and westward to Alacran Reef (north of Yucatan), the coasts of Yucatan, Cozumel Island, and Swan Island (off Honduras). The species has been reported from the "Society Islands" in Polynesia by Hooker & Arnott, Bot. Beechey Voy. 67 (1832), but as Drake, Fl. Polynés. Franç. 130 (1893), has stated this is probably the result of some error. This West Indian species is certainly not to be expected in the South Pacific.

This species was founded by Linnaeus entirely upon an illustration and phrase-name given by Plukenet, Phytogr. tab. 193, fig. 5 (1691). This basic phrase-name is as follows: "Heliotropium gnaphaloides litoreum fruticescens Americanum *Sea Lavender*, Barbadensibus dictum." From it we may suppose that Plukenet's material came from the Barbados.

DOUBTFUL AND EXCLUDED NAMES

Tournefortia angustifolia (Lam.) Roemer & Schultes, Syst. **4:** 539 (1819). — *Heliotropium messerschmidioides* Kuntze.

Tournefortia angulosa Desfontaines, Tab. ed. 2, 85 (1815). — A bare name in a garden-list.

Tournefortia bifida Lamarck, Tab. Encyc. **1:** 417 (1791); Poiret, Encyc. **5:** 360 (1804); Poiret, Dict. Sci. Nat. **41:** 177 (1826); Smith in Rees, Cyclop. **36:** sub sp. no. 25 (1819); Baker, Fl. Mauritius, 202 (1877). — The type of this species was collected on l'Ile de France by Commerson and represents *Antirhea frangulacea* DeCandolle, Prodr. **4:** 460 (1830)! The correct name for this Mauritian species of *Rubiaceae* is, accordingly, **Antirhea bifida** (Lam.), comb. nov.

"**Tournefortia cymosa** Heyne in Herb. Rottler, not of Linn." ex Clarke in Hooker, Fl. Brit. India **4:** 145 (1883). — This reference concerns a small specimen at Kew which may possibly represent *T. Bojeri* of Mauritius. It is certainly not *T. Heyneana* as given by Clarke! The specimen bears a printed label reading: "Herbarium Rottlerianum; Penins. Indiae Orientalis; Presented by the Council of Kings College, Feb. 1872." Accompanying this are two labels in script giving the determination as *T. cymosa* Swartz and the collector as Macé. Clarke's citation accordingly is merely a reference to a misdetermined specimen in the Kew herbarium.

Tournefortia Edgeworthii A. DeCandolle, Prodr. **9:** 529 (1845). — *Heliotropium zeylanicum* Burman.

Tournefortia fruticosa (Linn. f.) Ker, Bot. Reg. **6:** tab. 464 (1820). — *Heliotropium messerschmidioides* Kuntze.

Tournefortia linearis E. Meyer in Drege, Flora **26**[2]**:** Beigabe p. 57 and 226 (1843), nomen. — *Heliotropium lineare* (E. Meyer) Wright.

Tournefortia Messerchmidia Sweet, Hort. Suburb. London 31 (1818), nomen subnudum. — *Heliotropium messerschmidioides* Kuntze.

Tournefortia micranthos (Bunge) A. DeCandolle, Prodr. **10:** 67 (1846); Ledebour, Fl. Ross. **3:** 98 (1847–49). — *Heliotropium micranthos* (Bunge) Boissier.

Tournefortia mollis A. Bertoloni, Misc. Bot. **12:** 44, tab. 1 (1852). — Based upon material from Mozambique representing *Vangueria tomentosa* Hochst. This species of Bertoloni's is not mentioned in Robyn's recent monograph of *Vangueria,* Bull. Jard. Bot. Brux., vol. 11 (1928).

Tournefortia mutabilis Ventenat, Choix Pl. tab. 3 (1803). — The basis of this species was given by Ventenat as follows: "Arbrisseau originaire de Java, cultivé chez Cels et au Muséum d'Histoire Naturelle, de semences rapportées par La Haye." I have seen Ventenat's original material in the Delessert Herbarium at Geneva and duplicates of it at Kew, Berlin and Paris. The plant is evidently not a species of the Old World, in fact, it appears to be a form of the Mexican *T. Hartwegiana* Steud. Since Ventenat's name is much older than *T. Hartwegiana* it must be taken up in place of the latter. La Haye (or Lahaia) was a gardener who travelled to the East Indian Islands collecting seeds and plants which were subsequently grown at the garden of J. M. Cels and at the Jardin des Plantes at Paris. Since he is not known to have visited America it is evident that all of Ventenat's original data are incorrect.

Tournefortia Royleana DeCandolle, Prodr. **9:** 527 (1845).—*Heliotropium zeylanicum* Burman.

Tournefortia stenoraca Klotzsch in Peters, Reise Mossamb. 250 (1861). — *Heliotropium zeylanicum* Burman.

Tournefortia subulata Hochstetter ex DeCandolle, Prodr. **9:** 528 (1844). — *Heliotropium zeylanicum* Burman.

Tournefortia tuberculosa Chamisso, Linnaea **4:** 467 (1829). — *Heliotropium tuberculosum* (Cham.) Gürke.

Tournefortia zeylanica (Burman) Wight, Illust. Ind. Bot. **2:** 211, tab. 170 (1850). — *Heliotropium zeylanicum* Burman.

Messerschmidia angustifolia Lamarck, Tab. Encyc. **1:** 415 (1791). — *Heliotropium messerschmidioides* Kuntze.

Messerschmidia cancellata d'Asso, Synop. Aragon. 21, tab. 1 (1779). — *Rochelia* species.

Messerschmidia floribunda Salisbury, Prodr. 112 (1796). — *Heliotropium messerschmidioides* Kuntze.

Messerschmidia fruticosa Linnaeus fil. Suppl. 132 (1781). — *Heliotropium messerschmidioides* Kuntze.

Messerschmidia hispida Bentham in Royle, Ill. Bot. Himal. Mts. 306 (1836). — *Heliotropium zeylanicum* Burman.

Heliotropium pannifolium Burchell ex Hemsley, Voy. Challenger, Bot. **2:** 78 (1884). — This species from St. Helena is known only from Burchell's material. It is now probably exterminated. I have studied Burchell's unpublished drawing of the plant and his specimen at Kew. The plant is evidently a strong shrub much resembling the *Eutournefortiae* of the Andes in foliage and habit of growth. I know of no *Heliotropium* that could be recognized as a close relative of it nor one that could be said to resemble it in gross habit. Burchell's specimen is in the flowering condition only. The corollas, most unfortunately, have been almost completely eaten away by insects. There are consequently no reproductive structures on the type which might help in definitely placing the St. Helena plant generically. Since the plant is no doubt extinct and no further specimens are to be expected, the species will probably remain one of dubious generic affinities, and since a nomenclatorial transfer would add nothing to our regrettably small knowledge of it, I am not giving this obscure plant a new name under *Tournefortia*. However, I do strongly suspect that it belongs in that genus.

2. NOTES ON BRAND'S TREATMENT OF CRYPTANTHA

The treatment of *Cryptantha* by Brand appeared in the second and posthumous volume he contributed on the *Boraginaceae* in "Das Pflanzenreich." It is based almost exclusively upon the material available to him in the German herbaria. Having had no field experience in Western America and having had no opportunity to examine either the very numerous types or the great collections of *Cryptantha* in American herbaria, it is not surprising to find that Brand's treatment of the genus contains numerous errors arising from his restricted opportunities for the study of this large, difficult and characteristic West American genus. I have found some of Brand's statements very puzzling. Hence it is that during a recent visit in Germany I took the opportunity of studying the material available to him and, in the light of these studies, made copious annotations in copies of his published work on the *Boraginaceae*. The data given here concern *Cryptantha* and embody the notes correcting Brand's more serious errors, as well as those clarifying the more puzzling details of his work on that genus. In the following discussion, as a heading for the pertinent notes, I have given the specific name accepted by Brand and have preceded it by the number under which the species may be found in his treatment. Following these is an abbreviated reference to the page of the Pflanzenreich, iv. 252[2] [Heft 97] pp. 28–75 (1931), on which the given species may be found.

5. **Cryptantha macrocalyx** (Phil.) Reiche; Brand, Pflanzenr. 30 (1931). — The specimen cited and described is evidently a duplicate of the material to be found in Philippi's Herbarium at Santiago labelled as collected by San Roman in Quebrada de Serna. The material is so poor that I can add nothing to my previous discussion, Contr. Gray Herb. **78**: 70 (1927), of this peculiar plant. It is most certainly not *C. macrocalyx*.

6. **Cryptantha Buchtienii** Brand, Pflanzenr. 30 (1931). — I have studied the type-specimen. It is a form of *C. glomerata* from a locality in which it has been repeatedly collected.

7. **Cryptantha phacelioides** (Clos) Reiche; Brand, Pflanzenr. 31 (1931). — Brand cites two specimens as seen. The collection by Philippi, from which Brand's description is derived, is an isotype of *Eritrichium Rengifoanum* Phil., which I consider to be a phase of *C. aprica* (Phil.) Reiche. I have not seen the material collected by Buchtien, which is cited by Brand, but suspect that it may be *C. glomerulifera* (Phil.) Johnston, which Buchtien obtained at 2400 m. alt. near Juncal. Neither the name used by Brand nor any of the supposed synonyms he lists belong to either of these species I have mentioned. The synonyms he lists belong to three distinct species.

9. **Cryptantha talquina** (Phil.) Brand, Pflanzenr. 32 (1931). — This species is unquestionably a synonym of *C. alyssoides* (DC.) Reiche. Brand attempted to separate it by stating that basal cleistogenes were present in *C. talquina* and absent in *C. alyssoides*. This is contrary to fact. An isotype of *C. alyssoides* in the DeCandolle Herbarium at Geneva shows a fine display of these cleistogenes. The type at Paris has had them all knocked off.

12. **Cryptantha candelabrum** Brand, Pflanzenr. 33 (1931). — Based upon three collections, all from Philippi. These are: 1. Santiago, *"Philippi* (sub *E. congestum*), 2. Santiago, *"Philippi dedit 1876"* (sub *E. congestum*) and 3. Prov. de Santiago, *"Philippi dedit 1876"* (sub *E. lineare;* "Dimorphocarpum est"). The first specimen has flowers and fruit. The second and third show flowers only. For evident reasons the first specimen is selected as type. It is a form of *C. linearis* (Colla) Greene. The other specimens are quite similar and probably represent immature *C. linearis* or perhaps even *C. aprica*.

13. **Cryptantha fallax** (Phil.) Reiche; Brand, Pflanzenr. 33 (1931). — The specimen from Philippi, cited by Brand, seems to represent *C. Kingii* (Phil.) Reiche. The chasmogamic flowers are in bud only. The label associated with the specimen is in the script of Philippi. There is a question mark following the locality, "La Serena."

15. **Cryptantha campylotricha** Brand, Pflanzenr. 34 (1931). — This species is a synonym of *C. Kingii* (Phil.) Reiche.

16. **Cryptantha diffusa** (Phil.) Johnston; Brand, Pflanzenr. 34 (1931). — The single specimen cited, that collected by Philippi at Paihuano, represents *C. globulifera* (Clos) Reiche.

17. **Cryptantha modesta** Brand, Pflanzenr. 35 (1931). — This species is a synonym of *C. diplotricha* (Phil.) Reiche.

19. **Cryptantha Vidalii** (Phil.) Reiche; Brand, Pflanzenr. 35 (1931). — The only specimen examined by Brand is one grown in the Berlin Garden. It seems to be a form of *C. glomerata* Lehm. It is of course not authentic *C. Vidalii*.

21. **Cryptantha Candolleana** Brand, Pflanzenr. 36 (1931). — This species is based upon specimens from Macrae, Gay, Besser, and two from Philippi. At Berlin there is no specimen of this species collected by Gay in "Colchagua," but there is one given as from "Chile." All the material of this species cited by Brand represents forms of *C. glomerata* Lehm.

25. **Cryptantha globulifera** (Clos) Reiche; Brand, Pflanzenr. 37 (1931). — The only specimen cited by Brand seems to represent *C. linearis* (Colla) Greene. The specimen is immature. The corollas are evident.

28. **Cryptantha capituliflora** (Clos) Reiche, var. **compacta** Brand, Pflanzenr. 38 (1931). — The single specimen cited of this variety rep-

resents a stunted compact form of *C. diplotricha* (Phil.) Reiche. Brand does not appear to have seen any specimens of the true *C. capituliflora*.

33. **Cryptantha barbigera** (Gray) Greene; Brand, Pflanzenr. 39 (1931). — Among the three specimens cited, those of Jones and of Heller represent this species. That collected by Greene represents typical *C. nevadensis* Nels. & Kenn.

34. **Cryptantha nevadensis** Nelson & Kennedy; Brand, Pflanzenr. 39 (1931). — The collection by Rusby, in the Dehra Dun Herbarium, which I examined while still on loan at Berlin, represents *C. barbigera* (Gray) Greene.

38. **Cryptantha affinis** (Gray) Greene; Brand, Pflanzenr. 42 (1931). — The material at Berlin of *Heller 5882* is good *C. Torreyana* (Gray) Greene and that of *Jones 856* is at least in part good *C. affinis*. The data on the latter collection is probably questionable.

39. **Cryptantha microstachys** Greene; Brand, Pflanzenr. 42 (1931). — The single specimen cited by Brand, *Jones 3138* from San Diego, is *C. Clevelandi* Greene.

40. **Cryptantha Lyallii** Brand, Pflanzenr. 42 (1931). — This is a synonym of *C. flaccida* (Dougl.) Greene, all the cited material falling readily into that species.

49. **Cryptantha Hossei** Brand, Pflanzenr. 45 (1931). — This is an evident synonym of *C. diplotricha* (Ph.) Reiche.

63. **Cryptantha Famatinae** Brand, Pflanzenr. 49 (1931). — The type of this species represents *C. diffusa* (Phil.) Johnston.

66. **Cryptantha parvula** (Phil.) Brand, Pflanzenr. 50 (1931). — Of the three specimens cited, *Philippi 694* is *C. diffusa* (Phil.) Johnston, that from Caldera is a form of *C. globulifera* (Clos) Reiche, and that from San Roman is *C. diffusa*.

75. **Cryptantha leiocarpa** (Fisch. & Mey.) Greene, var. **eremocaryoides** Brand, Pflanzenr. 53 (1931). — This is apparently an odd form of *C. leiocarpa*.

81. **Cryptantha confusa** Rydberg; Brand, Pflanzenr. 56 (1931). — Among the specimens cited, *Leiberg 2271*, is *C. Watsoni* (Gray) Greene, the remainder represents *C. affinis* (Gray) Greene.

83. **Cryptantha Fendleri** (Gray) Greene; Brand, Pflanzenr. 57 (1931). — Greene's material from Beaver Creek is *C. ambigua* (Gray) Greene.

84. **Cryptantha Torreyana** (Gray) Greene, Brand, Pflanzenr. 57 (1931). — In the Berlin collections *Rydberg & Bessey 4885* and *Heller 9074* represent *C. ambigua* (Gray) Greene.

85. **Cryptantha Rattanii** Greene; Brand, Pflanzenr. 58 (1931). — The cited material at Berlin is in flower only. The corolla is 3–5 mm. broad. It is probably a form of *C. hispidissima* Greene.

86. **Cryptantha grandiflora** Rydberg, var. **anulata** Brand, Pflanzenr. 59 (1931). — This is a form of *C. Hendersoni* (Nels.) Piper.

91. **Cryptantha hispidula** Greene ex Brand, Pflanzenr. 60 (1931).— The type is *Baker 2966* from Napa County. The collections from Elmer and Eastwood are *C. Clevelandi* var. *florosa* Johnston.

91. **Cryptantha hispidula** var. **Elmeri** Brand, Pflanzenr. 60 (1931). — The cited material represents one of the forms of *C. Hendersoni* (Nels.) Piper having a single polished nutlet.

92. **Cryptantha flaccida** (Dougl.) Greene; Brand, Pflanzenr. 60 (1931). — The specimen collected by Congdon, no. 72, near Soledad represents *C. decipiens* var. *corollata* Johnston.

94. **Cryptantha hispida** (Phil.) Reiche; Brand, Pflanzenr. 61 (1931). — The cited specimen is an isotype of the very different *C. Romanii* Johnston.

96. **Cryptantha albida** (H. B. K.) Johnston; Brand, Pflanzenr. 63 (1931). — Among the cited specimens *Fendler 635* represents *C. Fendleri* (Gray) Greene, and the collection by Echegaray represents *C. diplotricha* (Phil.) Reiche.

106. **Cryptantha granulosa** (Ruiz & Pav.) Johnston; Brand, Pflanzenr. 65 (1931). — Two of the cited collections, *Weberbauer 5693* and *5700*, represent *C. limensis* (A. DC.) Johnston.

107. **Cryptantha Philippiana** Brand, Pflanzenr. 66 (1931). — This is a form of *C. glomerata* Lehm. having a developed chasmogamic inflorescence.

108. **Cryptantha mirabunda** Brand, Pflanzenr. 66 (1931). — I consider this species to be a synonym of *C. utahensis* (Gray) Greene.

113. **Cryptantha ambigua** (Gray) Greene, forma **robustior** Brand, Pflanzenr. 69 (1931). — The material cited from California all represents *C. echinella* Greene. One collection by Howell, no. 48, is *C. simulans* Greene.

115. **Cryptantha Stuebelii** Brand, Pflanzenr. 69 (1931). — The type of this species, from Yosemite Valley, is an equal mixture of *C. muricata* var. *Jonesii* (Gray) Johnston, and *C. simulans* Greene. Hansen's collection seems to be young *C. simulans*.

121. **Cryptantha Hansenii** Brand, Pflanzenr. 71 (1931). — This represents one of the puzzling forms of *C. intermedia* (Gray) Greene found in the foothills of the central Sierra Nevadas. The variety *pulchella* Brand, is merely an immature specimen of this Sierran form.

3. NEW OR OTHERWISE NOTEWORTHY SPECIES

Cordia Weddellii sp. nov., arbuscula 3–4 m. alta laxe ramosa pilis malpighiaceis strigosa; ramulis pallide strigosis; foliis ellipticis 2.5–4 cm. longis 1.5–2.5 cm. latis utrinque strigosis, nervis 7–10-jugis rectis parallelibus inconspicue sparseque ramosis, subtus pallidioribus, margine integris, apice rotundis, petiolis gracilibus 5–9 mm. longis; floribus ad apicem ramulorum in cymulis parvis 3–10-floris breviter pedunculatis affixis; calyce ad anthesim ca. 1 mm. longo, apice irregulariter disrumpente, extus strigoso obscure multisulcato; corolla alba ca. 3 cm. longa extus pilosa intus glabra, tubo ca. 1 cm. longo 3–4 mm. crasso, faucibus late ampliatis, lobis 5 suborbiculatis ca. 1 cm. longis rotundis ascendentibus in alabastro valde plicatis; staminibus 5, supra (4 mm.) basem tubi affixis, filamentis inaequalibus 5 et 6 mm. longis glabris; antheris oblongis 2–2.5 mm. longis; stylo 4 mm. profunde lobato basim versus sparsissime setifero, lobis 1.5 mm. lobulatis, lobulis spathulatis; ovario glabro; fructu ignoto.

BOLIVIA: Prov. of Chiquitos, small shrub 3–4 m. tall at edge of forest, fl. white, Sept.-Oct. 1845, *Weddell 3454* (TYPE, Paris).

A very remarkable species of the section *Eucordia* and related to *C. aberrans* Johnston (*C. mucronata* Fres.) and *C. candida* Vell. These two relatives come from the Brazilian coast near Rio Janeiro. *Cordia Weddellii* was collected in the extreme eastern section of the Dept. of Santa Cruz, Bolivia, and is distinguished at once by its malpighiaceous hairs. This type of pubescence is extremely rare in *Cordia*. In the present species it is particularly interesting since the mid-section of each hair (above where it is attached) is glandular and thickened.

Cordia aberrans, nom nov. *Cordia mucronata* Fresenius in Martius, Fl. Bras. 8^1: 9 (1857); Johnston, Contr. Gray Herb. **92**: 42 (1930); not Poiret (1818).

The existence of an earlier homonym makes it necessary to rename this remarkable species. The type has been examined at Munich. It is labeled: "Inter Vittoria et Bahia; S. Princ. Maxim. Vidensis; Martius comunic. 1856."

Cordia taguahyensis Vellozo, Fl. Flum. 98 (1825) and Icones, **2**: tab. 154 (1827). *Cordia amplifolia* Mez, Bot. Jahrb. **12**: 538 (1890); Johnston, Contr. Gray Herb. **92**: 62 (1930); not A. DeCandolle (1845). *Lithocardium Mezianum* Kuntze, Rev. Gen. **2**: 976 (1891). *Cordia Meziana* (Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. 3a, p. 84 (1893).

An examination of the type of *C. amplifolia,* at Munich, proves it to be simply a very large-leaved northern form of *C. taguahyensis.* Blanchet has collected similar luxuriant forms in Bahia.

Cordia revoluta Hooker fil. Trans. Linn. Soc. London **20**: 199 (1847); Riley, Kew Bull. **1925**: 225 (1925). *Varronia revoluta* Hooker fil. ex Andersson, Kung. Svensk. Vet. Akad. Handl. **1853**: 204 (1855); Andersson, Freg. Eugenies Resa, Bot. 84 (1861). *Lithocardium revoluta* (Hook. f.) Kuntze, Rev. Gen. **2**: 977 (1891). *Sebestena revoluta* (Hook. f.) von Friesen, Bull. Soc. Bot. Genève, sér. 2, **24**: 183 (1933). *Cordia linearis* Hooker fil., Trans. Linn. Soc. London **20**: 199 (1847), not DeCandolle (1845). *Varronia linearis* Hooker fil. ex Andersson, Kung. Svensk. Vet. Akad. Handl. **1853**: 204 (1855) and Freg. Eugenies Resa, Bot. 84, tab. 11, fig. 4 (1861). *Sebestena linearis* (Hook. f.) von Friesen, Bull. Soc. Bot. Genève sér. 2, **24**: 182 (1933). *Lithocardium Hookerianum* Kuntze, Rev. Gen. **2**: 976 (1891). *Cordia Hookerianum* (Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV, Abt. 3a, p. 83 (1893).

GALAPAGOS ISLANDS: Narborough: *Stewart 3177; Snodgrass & Heller 327.* Albemarle: *Snodgrass & Heller 28, 155, 196, 272, 897; Stewart 3169, 3170, 3172, 3173; Baur 213; Macrae* (cotype of *C. revoluta*). James: *Stewart 3175, 3176; Cheesman 388; Darwin* (TYPE of *C. linearis*). Charles: *Baur 214; Schimpff 215; Darwin* (TYPE of *C. revoluta*).

I have had the opportunity of examining the types of *Cordia,* from the Galapagos Islands, described by Hooker and by Andersson. The study of this critical material, supplementing a careful examination of the large general collections from the islands preserved at the Gray Herbarium, has established specific identities which necessitate changes in the names currently applied to the island species. The above cited species and the three following are the only endemic species of *Cordia* on the islands. All belong to the section *Varronia.* While it may be generally stated that they are most closely related to the species of western Peru and Ecuador, their immediate relationships on the continent are quite obscure. The three following species are closely related to one another but probably not immediately related to the well marked *C. revoluta*. The following key will aid in distinguishing the four insular endemics:

Corolla elongate, tubular, length of tube 3–4 times the breadth of the weakly developed limb; leaves linear; stems and upper surfaces of the leaves covered with stout short appressed falcate hairs; inflorescence capitate ....*Cordia revoluta* Hook f.
Corolla coarsely funnelform, length of tube less than 2 times width of the conspicuous spreading limb; leaves lanceolate; stems and upper surfaces of leaves with erect or ascending (at times minute) hairs; inflorescence tending to elongate; flowers short-stipitate at maturity.
  Upper surface of leaves with abundant minute stout forked hairs ....*Cordia Anderssoni* Gürke
  Upper surface of leaves with stiff slender spreading simple hairs.
    Stems and lower surface of leaves bearing a mixture of minute appressed forked or stellate hairs and coarser stiff erect simple hairs ....*Cordia Scouleri* Hook. f.
    Stems and lower surface of leaves with only stiff erect simple hairs ....*Cordia leucophlyctis* Hook, f.

Cordia Scouleri Hooker fil., Trans. Linn. Soc. London **20:** 200 (1847). *Varronia Scouleri* Hooker fil. ex Andersson, Kungl. Svensk. Vet. Akad. Handl. **1853:** 204 (1855) and Freg. Eugenies Resa, Bot. 83 (1861). *Lithocardium Scouleri* (Hook. f.) Kuntze, Rev. Gen. **2:** 977 (1891).

GALAPAGOS ISLANDS: Albemarle: *Stewart 3162.* James: *Baur 209; Scouler* (TYPE). Indefatigable: *Svenson 7.*

This plant is particularly close to the two following. It appears to be rare. The few collections seen, other than the type, are all misdetermined as *C. galapagensis* or *C. leucophlyctis.* The mixed pubescence on the leaves and stems decisively separates it from those species.

Cordia Anderssoni (Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. 3a, p. 83 (1893). *Lithocardium Anderssonii* Kuntze, Rev. Gen. **2:** 976 (1891). *Varronia canescens* Andersson, Kungl. Svensk. Vet. Akad. Handl. **1853:** 203 (1855) and Freg. Eugenies Resa, Bot. 83, tab. 11, fig. 2 (1861), not *Cordia canescens* HBK. (1818).

GALAPAGOS ISLANDS: Albemarle: *Stewart 3195.* Abingdon: *Stewart 3158.* James: *Stewart 3157.* Duncan: *Baur 215.* Charles: *Lee; Andersson* (TYPE). Chatham: *Stewart 3165, 3166; Baur 216; Andersson* (det. *V. leucophlyctis*).

Cordia leucophlyctis Hooker fil. Trans. Linn. Soc. London **20:** 199 (1847). *Varronia leucophlyctis* Hooker fil. ex Andersson, Kungl. Svensk. Vet. Akad. Handl. **1853:** 203 (1855) and Freg. Eugenies Resa, Bot. 83 (1861). *Lithocardium leucophlyctis* (Hook. f.) Kuntze, Rev. Gen. **2:** 977 (1891). *Varronia scaberrima* Andersson, Kungl. Svensk. Vet. Akad. Handl. **1853:** 202 (1855) and Freg. Eugenies Resa, Bot. 82, tab. 11, fig. 3 (1861), not *Cordia scaberrima* HBK. (1818). *Lithocardium galapagosenum* Kuntze, Rev. Gen. **2:** 976 (1891). *Cordia galapagensis* (? Kuntze) Gürke in Engler & Prantl, Nat. Pflanzenf. IV. Abt. 3a, p. 83 (1893).

GALAPAGOS ISLANDS: Narborough; *Snodgrass & Heller 331, 342.* Albemarle: *Snodgrass & Heller 75, 136, 195, 291, 857, 881, 893; Stewart 3159; Baur 210, 212; Macrae; Darwin* (TYPE of *C. leucophlyctis*). Indefatigable: *Baur 211; Andersson* (TYPE of *Varronia scaberrima*). Barrington: *Stewart 3164.* Hood: *Stewart 3168.*

The type of *C. leucophlyctis* and *Varronia scaberrima* are remarkably similar. The plant illustrated as *V. leucophlyctis* by Andersson, Freg. Eugenies Resa, Bot. tab. 11, fig. 1 (1861), appears to be *Cordia Anderssoni* from Chatham Island.

Cordia setigera, sp. nov., dumosa; ramulis gracilibus strigulosis; foliis lanceolatis 3–6.5 cm. longis 12–24 mm. latis tenuibus, apice acutis, basi cuneatis, margine evidenter irregulariterque arguto-dentatis, dentibus apiculatis, faciebus pilis numerosis 0.5–1 mm. longis ascendentibus asperatis (basibus pilorum saepe pustulatis) subtus pallidioribus, nerviis 4–6-jugatis perinconspicue pauceque ramosis, petiolis 1–5 mm. longis; pedunculis terminalibus gracillimis 1–7 cm. longis; inflorescentia congesto-capitatis 7–10 mm. diametro; corolla alba infundibuliformi 15–18 mm. longa, limbo ascendenti ca. 1 cm. diametro, lobis rotundis ca. 3 mm. longis; calycibus ad anthesim ca. 6 mm. longis sparse strigosis, tubo 2–2.5 mm. longo et crasso, lobis triangularibus ca. 1–1.5 mm. longis, apice lineraribus 2–3 mm. longis attenuatis; fructu ca. 5 mm. longo apice exserto.

BRAZIL: near Fazenda de Bom Jardin, Rio Jequitinhonha, in northeastern Minas Geraes, 1817, *St. Hilaire B[1] 1478* (TYPE, Paris).

A very well marked species which keys out with *Cordia grandiflora* and *C. paucidentata* in my revision of the Brazilian species of *Cordia*, cf. Contr. Gray Herb. **92:** 20 (1930). From both of these species it is distinguished by its smaller corollas, its thin leaves, its sparsely setulose herbage, and its very sparsely strigose calyces. It is evidently a very slender loosely branched bush and hence quite different in habit from the much more southerly ranging *C. paucidentata*. *Cordia grandiflora* has different pubescence, very much larger differently shaped corollas, and comes from the Amazon Valley. The closest relative of the proposed species is probably *C. Neowediana* DC., of the forests back of Ilhéos, Bahia. That species has more finely serrate, more hairy leaves, larger corollas, much larger brown-hairy calyces, and only short tips on the calyx-lobes. It is a plant of the wet coastal forests, *C. setigera* is a plant of the dry catingas inland.

Cordia Neowediana DeCandolle, Prodr. **9:** 498 (1845); Fresenius in Martius, Fl. Bras. 8^1: 23 (1857), as *C. Neowidiana;* Johnston, Contr. Gray Herb. **92:** 64 (1930). *Varronia macrocephala* sensu Nees & Martius, Nov. Acta Acad. Caes. Leop.-Carol. Nat. Cur. **11:** 78 (1823). *Lithocardium Neowiedianum* (DC.) Kuntze, Rev. Gen. **2:** 977 (1891).

The type of this species is preserved at Brussels. Through the kindness of Prof. W. Robyns I have had the privilege of borrowing it for study. The species is a well marked one and is certainly worthy of recognition. The single collection upon which it is based was obtained in southern Bahia, in the country back of Ilhéos. It is one of the species of the section *Varronia* having the flowers capitately congested. The large white corollas, in size and shape, are very suggestive of those found in the distantly related *C. paucidentata*. The stems, calyces and both leaf-surfaces are conspicuously bristly. There is no other kind of pubescence. The hairs are stiffish, spreading and mostly ca. 2 mm. long. Most of them spring from a small pustulate base. The hairs on the calyx are brown. The leaves are lanceolate, serrate and about 7 cm. long and 2 cm. broad. The calyx is ca. 1 cm. long, bristly, and sparsely glandular above the middle. The lobes are nearly 3 mm. long and triangular with a short subulate tip 1–1.5 mm. long. In my revision of the Brazilian species, l. c. p. 20, *C. Neowediana* keys out with *C. longifolia, C. poliophylla* and *C. leucocephala,* which are rather closely related to it. From these three species it can be quickly distinguished by its very bristly leaves and much larger bristly calyx.

Cordia Braceliniae, sp. nov., fruticosa diffusa; caulibus ca. 3 dm. longis laxe ramosis strigosis; foliis elliptico-obovatis vel oblanceolatis 2–3 cm. longis 10–17 mm. latis basim versus attenuatis, apice obtusis, margine crenatis, nervis 3–5-jugatis rectis ascendentibus vix ramosis supra impressis subtus prominentibus, facie laminae superiore sparse rigideque strigosis pilis pustulae insidentibus, facie inferiore pallidioribus strigosis vix pustulatis; pedunculis terminalibus gracilibus 2–3 cm. longis strigosis; inflorescentia capitata ca. 8 mm. diametro 20–25-flora; calycibus inflatis sparse strigosis ca. 3 mm. longis tubo pallido, lobis triangularibus viridibus ca. 1.5 mm. longis breviter ca. 0.5 mm. longeque attenuatis; corolla alba 10–15 mm. longa; fructu irregulariter turbinato lacunoso vix exserto.

BRAZIL: Corinto beyond Retiro, Fazenda do Diamante, Minas Geraes, 590 m. alt., in thickety grassland, low spreading bush, fl. white and early deciduous, April 14, 1931, *Ynez Mexia 5617* (TYPE, Gray Herb.; isotype, Arn. Arb.).

A very distinct species perhaps most closely related to *C. paucidentata* of southern Brazil and adjacent regions. It is quickly separated from that species by its low branching habit, sparse strigose indument, and short-appendaged calyx-lobes. In my treatment of the Brazilian species of *Cordia*, Contr. Gray Herb. **92:** 20 (1930), it keys out with *C. latifolia*, *C. poliophylla* and *C. leucocephala*, though it does not seem closely related to any of them. From these species, however, it is readily distinguished by its low spreading habit, small leaves lacking in secondary nervation, and different pubescence. The proposed species is strigose on the leaves, younger stems, peduncles and calyx. The hairs are abundant but do not cover the leaf-surfaces. They are stiff, straight and closely appressed. Those on the upper leaf-surface spring from small disks of dark mineralized cells. The type material has shrivelled corollas only. It has been distributed incorrectly determined as "*C. truncata*."

I find it a pleasure to associate with this well marked species the name of Mrs. H. P. Bracelin, of California. Her effective handling and distribution of the extensive collections of Mrs. Mexia make it fitting that her name should be associated with them and that it should be remembered by the students of the Brazilian flora.

Cordia campestris Warming, Kjoeb. Vidensk. Meddel. **1867:** 12, fig. 2 (1868).

BRAZIL: Minas Geraes: Lagoa Santa, Pinhões, in campis, Jan. 28, 1866, *Warming* (Copenh., TYPE); Lagoa Santa, in campis ad Cabejeiras da lagoa, March 8, 1864, *Warming* (Copenh.); Formigas, *St. Hilaire sine no.* (Paris); indefinite, *Claussen 221* (G, K, Copenh., Stockh., Paris). Goyaz: Formosa, shrub, corolla white, Dec. 24, 1894, *Glaziou 21781* (K, BD, Paris).

Warming's species has been treated by me, Contr. Gray Herb. **92:** 29 (1930), as a synonym of *C. multispicata* Cham. and several of the above collections cited under that species. *Cordia campestris* is very distinct from *C. multispicata*, however, and probably most closely related to *C. verbenacea* DC. and *C. chacoensis* Chodat, particularly to the latter. Among the Brazilian spicate species of the *Varronia* section, *C. multispicata* is readily recognized by having the pedunculate spikes prevailingly lateral (and axillary) and the petiole of the subtending leaf evidently decurrent upon the peduncle, quite in the manner observable in *C. buddleyoides* Rusby, *C. axillaris* Johnston, and *C. guazumaefolia* (Desv.) R. & S. The specimens I have cited above, including the type of *C. campestris,* have terminal spikes and the petioles not decurrent on the peduncles. They are quickly separable from *C. verbenacea* by having the upper leaf-surface abundantly and evidently hairy. *Cordia campestris* is separated from *C. chacoensis* by its low habit of growth, and general coarseness of its parts. It appears to be a small (under 1 m. tall), sparsely branched shrub of the open country. The leaves are usually 3–5 cm. broad, and the spikes 5–10 cm. long. The flower buds are usually apiculate. It ranges in the campo of Minas Geraes and Goyaz. Its relative, *C. chacoensis,* ranges from southern-most Brazil into Paraguay and across northern Argentina.

Cordia guazumaefolia (Desv.) Roemer & Schultes, Syst. **4:** 463 (1819). *Varronia guasumaefolia* Desvaux, Jour. de Bot. **1:** 276 (1809). *Lithocardium guazumifolia* (Desv.) Kuntze, Rev. Gen. **3**[2]: 206 (1898). *Cordia axillaris* var. *gymnocarpa* Johnston Contr. Gray Herb. **92:** 35 (1930).

In my treatment of the Brazilian species of *Cordia,* l. c. p. 30, I cited *C. guazumaefolia* as a synonym of *C. corymbosa* (L.) Don. A recent study of Desvaux's type at Paris, however, has proved this to be quite incorrect. Among material from Jussieu's herbarium at Paris I have found specimens of this species determined by Desvaux. One of these is labeled, "Brasil, envoyé de Lisbonne pour M. Vandelli 1790." The plant described by Desvaux is evidently that which I treated as *C. axillaris* var. *gymnocarpa.* This plant should bear the name *C. guazumaefolia.* It may be added that while there is an evident relation between *C. axillaris* and true *C. guazumaefolia,* I am now of the opinion that their differences warrant specific rather than mere varietal separation.

Cordia insignis Chamisso, Linnaea **8:** 122 (1833). *Cordia Haenkeana* Mez, Bot. Jahrb. **12:** 560 (1890).

An examination of the type of *C. Haenkeana,* at Munich, makes it evident that it is only a form of *C. insignis.* The collection is given as having been collected by Haenke in Peru. The accuracy of this data, however, I greatly doubt. *Cordia insignis* is known only east and south of the Amazon Basin, from eastern Brazil to eastern Bolivia, and is certainly not to be expected in Peru.

Cordia laevior, sp. nov., arborescens, 6 m. alta; ramulis fusculis, juventate pilis brevibus adpressis vel ascendentibus vestitis mox glabrescentibus; foliis homomorphis oblongo-lanceolatis 15–26 cm. longis 4–10 cm. latis medium versus latioribus, basi acutis, apice longissime acuminatis, supra in costa et nervis primariis hirsutulis ceteris glabris, subtus pallidioribus, costa et nervis numerosis puberulentibus, nervis 7–8-jugatis, nervis tertiaribus obscuris, petiolis 5–10 mm. longis; cymis in furcis ramulorum ortis laxe ramosis; calyce in alabastro obovato 4–5 mm. longo 2.5–3 mm. crasso pilis minutis abundantibus vestito obscure costato, apice rotundo, lobis 5 plus minusve irregularibus triangularibus; corolla alba, tubo ca. 4 mm. longo, lobis ca. 2 mm. longis et latis, filamentis ca. 3 mm. longis basim versus pilosis; stylo sparse piloso; supra medium ovarii evidenter pilosis; fructu ignoto.

PERU: Pongo de Cainarachi, Rio Cainarachi, tributary of the Huallaga, dept. of San Martin, ca. alt. 230 m., tree 6 m. tall, fl. white, Sept.-Oct., 1932, *Klug 2756* (TYPE, Arn. Arb.; isotype, Gray Herb.).

This species is related to *C. Sprucei* Mez, of the Rio Negro and the Guianas, from which it differs in having smoother, more elongate, less hairy leaves and a more loosely branched inflorescence. The leaves are not roughened above by slightly prominent repeatedly branched veinlets. The lower surface is much less hairy. The specimen was distributed as *C. Ulei* Johnston, from which, like *C. Sprucei,* it differs in having a very hairy ovary, finer pubescence on the lower leaf-surfaces, and more papery, more hairy, less regularly and sharply lobed calyces.

Cordia ripicola, sp. nov., arborescens 8–10 m. alta dichotome ramosa; ramulis sordidis pilis brevibus rigidulis scabridis; foliis subhomomorphis oblongis vel obovato-oblongis vel lanceolatis 8–14 cm. longis 3–7 cm. latis medio vel supra medium latioribus, apice acuminatis, basi acutis, supra sublucidis sparsissime breviterque strigosis, subtus minute rigideque hispidulis, nervis 6–8-jugis, nervis tertiaribus obscuris, petiolis 2–6 mm. longis; cymis gracilibus 3–10 cm. crassis laxe ramosis; calyce strigoso in alabastro obovato ca. 4 mm. longo 2–3 mm. crasso, intus supra medium strigoso, apice rotundo, ad anthesim in lobos 2–5 irregulares disrumpente; corolla alba 4–5 mm. longa, lobis ca. 2.5 mm. longis, filamentis ca. 3.5 mm. longis basim versus pilosis; ovario glabro vel summum ad apicem sparse pubescente; fructu ignoto.

PERU: Florida, Rio Putumayo, at mouth of Rio Zubineta, dept. Loreto, ca. 180 m. alt., "Chore-ey," forest along river, fl. white, tree 8–10 m. tall, May-June 1931, *Klug 2262* (TYPE, Arn. Arb.; isotype, Gray Herb.) and *2277* (AA, GH).

A species related to *C. Sprucei* Mez and *C. laevior* Johnston, from which it differs in having scattered appressed hairs on the upper face and abundant minute appressed ones on the lower face of the smaller, more oblong leaves. The calyx is more papery in texture and opens more irregularly. The style and ovary are sparsely hairy. The character of the calyx, the appressed hairs on the leaves and the hairiness of the pistil readily separate it from *C. Ulei* Johnston, the species under which the type has been distributed. *Cordia Ulei* comes from southwestern Brazil, at ca. lat. 11°S. The proposed species was collected nearly under the Equator. **Cordia ucayaliensis**, comb. nov. (*C. Ulei* var. *ucayaliensis* Johnston), readily distinguished by having the upper surface of the leaves strigose, comes from northeastern Peru.

Saccellium brasiliense, spec. nov., gracile; foliis lanceolatis 4–7.5 cm. longis 18–28 mm. latis medium versus latioribus, margine obscure sinuatis vel supra medium sparse denticulatis, supra viridibus pilos graciles rectos valde adpressos gerentibus, subtus pallidis distincte sericeis pilos abundantissimos minutos valde adpressos gerentibus, apice basique acutis, nervis 8–10-jugatis, petiolis 3–6 mm. longis strigosis; ramulis gracilibus laxe ramosis brunescentibus juventate sordide pubescentibus mox glabrescentibus, lenticellis numerosis orbiculatis pallidis punctatis; ramulis fertilibus 3–5 cm. longis ca. 5-foliatis; inflorescentia terminali paniculata 2–6 cm. longa folia vix superante; calycibus strigosis, dentibus laxe recurvatis.

BRAZIL: Corumba, Matto Grosso, Dec. 23, 1902, *Malme 2759* (TYPE, Herb. Berol.); Corumba, Dec. 22, 1902, *Robert 804* (BM, BD).

The two collections cited are devoid of corollas and are in early fruiting condition only. A study of the immature calyx and ovary, however, leave no doubt as to the generic relations of this interesting plant. The species is evidently a relative of the Bolivian *S. Oliveri*, but is readily separable by its small silky-strigose leaves and generally more compact habit of growth. *Saccellium brasiliense* has been reported from Corumba, doubtfully as *S. lanceolatum*, by Moore, Jour. Bot. **45**: 405 (1907). Following I give the names of the known species of *Saccellium* and cite all the collections I have examined of these relatively rare species. The three known species may be separated as follows:

Plant glabrous or practically so; leaves 3–5 cm. broad, broadest at or slightly above the middle .... *S. Oliverii* Britt.
Plant evidently pubescent; leaves less than 3 cm. broad, broadest at or below the middle.
  Leaves broadest near the middle, beneath silky strigose, lustrous, blade 4–7.5 cm. long; fertile branches 3–5 cm. long, bearing about 5 leaves; old branches brown, with evident pale lenticels .... *S. brasiliense* n. sp.

Leaves broadest near base, beneath velvety or somewhat tomentose, dull, blade 5–12 cm. long; fertile branches 10–20 cm. long, bearing about 10 leaves; old branches gray or only rarely brown, without evident lenticels.... .... *S. lanceolatum* H. & B.

Saccellium Oliverii Britton ex Rusby, Bull. Torr. Bot. Cl. **26:** 147 (1899).

This species is known only from the type-collection made by Rusby, no. 2535, in May 1886 at 600 m. alt at Guanai (or Huanay), Bolivia. The locality is in the department of La Paz at the confluence of the Rio Mapiri and Rio Tipuani at about lat. 15°30′ S. and long. 68° W. in Amazonian Bolivia. Only fruiting specimens of the species are known. In its slender brownish branches, rather evident pale lenticels, and general leaf-outline, the species resembles *S. brasiliense* more than it does *S. lanceolatum*. The leaves are glabrous except for a few short inconspicuous ascending hairs along the midrib and principal veins. A similar scanty inconspicuous indument is also found in the inflorescence.

Saccellium lanceolatum Humboldt & Bonpland, Pl. Aequin. **1:** 47, tab. 13 (1806); Humboldt, Bonpland & Kunth, Nov. Gen. **7:** 209 (1825); Miers, Trans. Linn. Soc. London, Bot. **1:** 25, tab. 6 (1875).

In two widely separated areas, 1. Northern Peru in northern parts (prov. Jaen) of the Dept. Cajamarca, lat. 5°–6° S., in the Amazonian drainage; 2. mountains of southern Bolivia (prov. Chuquisaca and Tarija) southward along the mountains of northern Argentina to Tucuman, ca. lat. 27° S.

PERU: between Jaen and Bellavista, prov. Jaen, 600–700 m. alt., shrub or small tree, common, April 29, 1912, *Weberbauer 6209a* (BD); Valley of the Marañon between Bellavista and the mouth of the Rio Chinchipe, prov. Jaen, 500 m. alt., small tree 4 m. tall, flowers white; accrescent calyces yellow-green, May 1, 1912, *Weberbauer 6226* (G, BD); Valley of the Marañon at the mouth of the Rio Chinchipe, prov. Jaen, 400–500 m. alt., tree 6 m. tall, flowers white, accrescent calyces yellowish green, April 30, 1912, *Weberbauer 6217* (G, BD); near Rio Huancabamba, *Bonpland* (TYPE, Paris; fragments, DC, Lindl., Gray). BOLIVIA: between Atajado and Parapiti, 700 m. alt., small tree, Dec. 1910, *Herzog 1192* (BD); south of Rio Pilcomayo, prov. Tarija, Feb. 18, 1916, *Steinbach 1776* (BD); Bolivia, Pampas, evergreen tree 4.5–6 m. tall, woods, May 1864, *Pearce* (BM). ARGENTINA: Islota, Sierra Sta. Barbara, Jujuy, dry open place, tree 15–20 m. tall, July 5, 1901, *Fries 260* (Munich); Sierra Sta. Barbara, Salta, *Schuel 38* (G); Rio Blanco, dept. Oran, Salta, 650 m. alt., flowers yellowish, tree 10 m. tall, trunk 5 dm. thick, in high forest, Nov. 19, 1927, *Venturi 5546* (AA, G, K, BM); Abra Grande, dept. Oran, March 1927, 750 m. alt., tree 5 m. high, flowers yellowish, *Venturi 6780* (AA); Rio Piedras, dept. Oran, Nov. 15, 1911, *Rodriguez 85* (G); Campo Duran, dept. Oran, a tree common on higher slopes, "Guayabil," Jan. 28, 1930, *Parodi 9269* (G); Tartagal, Salta, a tree, Feb. 1923, *Hauman* (G); hills near the crossing of the Rio Juramente, Salta, tree or shrub up to 6 m. tall, Feb. 21, 1873, *Hieronymus & Lorentz 295* (BD, Deles); Alemania, dept. Guachipas, Salta, 1100 m. alt., flowers white, tree 6 m. tall, in high forest, trunk 2 dm. thick, Dec. 22, 1929, *Venturi 10005* (G, K, BM); El Cadillal, dept. Burruyacu, Tucuman, Dec. 20, 1909, *Lillo 9823* (Deles); Tucuman, dept. Capital, alt. 450 m., tree 10 m. tall, flowers white, Dec. 12, 1907, *Lillo 7234* (G); Estate of Professor Lillo, dept. Capital, Tucuman, 460 m. alt., March 1925, *Venturi 3816* (AA); Tucuman, Dec. 12, 1907, *Stuckert 18375* (Deles); Tucuman, Feb. 10, 1910, *Lillo* (G).

The distinctly lanceolate leaves and the leafy, elongate stiffish branches readily characterize this species. The range of the tree is peculiar for it occurs in two far-separated regions in Peru and Argentina. Though this behavior suggests that two species or that a species and a variety is involved, a careful comparison of copious material has failed to produce any differences that would justify the proposal of even a new variety. The Peruvian plant differs from that of Argentina only in its perhaps somewhat sparser and slightly more slender pubescence on the herbage and in its somewhat darker stems.

In the Plantae Aequinoctiales **1:** 47 (1806), the source of the original Humboldt & Bonpland collection of *Saccellium* is given as "ad rivos fluvii Guancabamba." Similar data are on the type-specimen at Paris. In the Nova Genera, **7:** 208 (1825), the locality is given in more detail as follows: "inter Loxam et Tomependam Bracamorensium, ad ripas fluminis Guancabambae." The locality, Loja, of course, is in southern Ecuador. Tomependa is a ruined village near the junction of the Rio Chinchipe and the Rio Marañon. The Rio Huancabamba joins the Marañon about 50 km. above Tomependa. In all probability the type was collected in or near the province Jaen, in the region of northern Peru in which it has been collected by Weberbauer, Bot. Jahrb. **50:** suppl. p. 92 (1914).

Coldenia conspicua, sp. nov., prostrata ut videtur annua; caulibus articulatis laxe ramosis 2–15 cm. longis, juventate dense graciliterque hispidulis et plus minusve glanduliferis; foliis aggregatis numerosis, lamina late lanceolata vel elliptica 5–13 mm. longa 2–5 mm. lata, subtus prominenter costata et nervosa (nervis 2–3-jugatis vix conspicuis) pilis gracilibus brevibus numerosis erectis asperata, supra pustulosa pilis robustioribus longioribus rigidioribus numerosis ascendentibus asperata, margine laxe revoluta integra vel obscurissime sparsissimeque crenata; petiolis gracilibus 2–9 mm. longis glanduliferis pilis abundantibus longis gracilibus erectis setosis; calyce 5-partito, lobis gracilibus basim versus subinduratis et subnavicularibus praeterea linearibus hispidis glanduliferis ad anthesin ca. 9 mm. longis fructiferis ad 15 mm. longis; corolla conspicua coerulea, tubo ca. 9 mm. longo 2.5–3 mm. crasso lobis calycis subaequilongo intus glaberrimo, limbo 10–12 mm. lato patenti, lobis 4–5 mm. diametro, faucibus haud appendiculatis, filamentis 4–5 mm. longis glabris apicem versus tubi affixis ca. 2 mm. longe extrusis, antheris oblongis medio-affixis 1–1.4 mm. longis; stylo filiformi glabro 15 mm. longo 2 mm. profunde bilobato, stigmatibus 2 minutis obscure bilobulatis; nuculis 4 globosis 1.5–2 mm. diametro dense minuteque tessellato-tuberculatis per carunculas 1 mm. longas et crassas in apice receptaculi basaliter affixis; receptaculo ad anthesin cylindrico, fructifero turbinato.

PERU: sand flat near Mejia, Dept. Arequipa, 40 m. alt., flowers blue, Oct. 26, 1923, *Guenther & Buchtien 155* (TYPE, Inst. Bot. Hamburg); Mejia, July 21, 1923, *Guenther & Buchtien 156* (Hamburg); Mollendo, Dept. Arequipa, *Miss D. Stafford K60* (Kew).

A very distinct and remarkable species belonging to the Chilean and southern Peruvian section *Sphaerocarya*, Johnston, Contr. Gray Herb. **70**: 57 (1924). The nutlets of the new species are quite similar to those of this section in size, shape and markings. From the previously described species of the section, however, *C. conspicua* differs in its extremely large corollas, its protruding stamens and its remarkable nutlet-attachment. The corollas are at least twice the size of those of any other species of *Coldenia*. The nutlet-attachment is also unique in the genus. In the known species of the section *Sphaerocarya* the immature nutlets are attached laterally at the middle of the sides of an erect subcylindrical gynobase. This is distorted somewhat by the crowding of the growing nutlets and tends to become constricted medially. After the nutlets have fallen away it is consequently more or less spool-shaped. In the proposed species the immature nutlets are borne laterally, not about the middle, but about the summit of the subcylindrical gynobase. By growth and the consequent pressure of crowding, the nutlets at maturity come to be attached basally in the expanded summit of the now turbinate gynobase. What is most peculiar is that each nutlet has a well developed strophiolate basal plug which is immersed in the gynobasal tissue. At maturity the strophioles loosen from the gynobase and with their attached nutlets fall away leaving 4 deep more or less united sockets in the much broadened apex of the gynobase. The mature gynobase, hence, becomes more or less cupulate.

The species is known only from along the coast in southern Peru in the general region of the port of Mollendo. The type has been reported, Bruns, Mitt. Inst. Allgem. Bot. Hamburg **8**: 67 (1929), as *C. dicho-*

toma, but that species, of course, has small corollas and utterly different fruit-structures. The other species of the section *Sphaerocarya* are poorly understood. Since publishing, l. c., on the South American species of *Coldenia* I have seen the types of Philippi's species. I have been unable to separate his *C. litoralis*, *C. atacamensis* and *C. parviflora,* though from geographic considerations one would expect that the plant from the coastal region (*C. litoralis*) would be distinct from that of the high Puno de Atacama (*C. atacamensis* and *C. parviflora*). The type of *C. parviflora* is quite distinct from the Peruvian plants of the Arequipa region, which I cited under that name in my synopsis of the South American species of *Coldenia*. The correct name for this species is *C. elongata* Rusby! Its elongate leaf-blades, woolly petioles and calyces, and usually evidently crenate leaf-margins serve to distinguish it from Philippi's species. *Coldenia elongata* is known only from middle altitudes east of the coastal deserts of southern Peru and northern-most Chile. In Peru only two species of the section *Sphaerocarya* are known. These are *C. conspicua* which grows along the coast and *C. elongata* which grows along the cordilleras in the interior.

Coldenia Nuttallii Hooker, Kew Jour. Bot. **3:** 296 (1851); Johnston, Contr. Gray Herb. **75:** 43 (1925). *Coldenia decumbens* Hauman, Apuntes Hist. Nat. Buenos Aires **1:** 55 (1909) and Anal. Soc. Cient. Argentina **86:** 301 (1918).

This species so wide-spread in the intermontane area of the western United States has been known only from two small areas in the high cordilleras of Argentina, in northwestern San Juan, Johnston, Physis **9:** 316 (1929), and in the Uspallata Pass region in Mendoza, Hauman, l. c. The plant was collected around 3000 m. alt. in San Juan and about 2300 m. alt. in Mendoza. A third locality for the species in South America, one much further south and so, not surprisingly, at lower altitudes, may now be put on record. I have seen a collection of *C. Nuttallii* in the herbarium at Munich which was obtained by Erik Ammann (no. 5) in Oct.-Nov. 1927, at 700 m. alt. near Cobunco, Neuquen, Argentina.

Tournefortia brasiliensis Poiret, Encyc. **5:** 357 (1804); Johnston, Contr. Gray Herb. **92:** 89 (1930).

I have studied the type of this doubtful species in the Lamarck Herbarium at Paris. It represents a specimen of *Vernonia scorpioides* (Lam.) Pers., with the flowers just beginning to develop. It is remarkably like, and probably a part of the collections by Commerson made at Rio Janeiro ("de l'île aux chats") in July, 1767. Consequently it may be a part of the same material as the type of *Conyza scorpioides* Lamarck, Encyc. **2:** 88 (1790).

Heliotropium transalpinum Vellozo, Fl. Flum. 68 (1825) and Icones, **2:** tab. 40 (1827). *Heliotropium tiaridioides* var. *schizocarpum* Johnston, Contr. Gray Herb. **81:** 7 (1928), where other synonyms are cited.

Vellozo in describing and illustrating his species gave no indication as to whether the carpels were dorsally sulcate or not. Suspecting that the carpels were sulcate, however, since only plants with such developments were known about Rio Janeiro, I provisionally cited the name *H. transalpinum* among the synonyms of my *H. tiaridioides* var. *schizocarpum*. Vellozo's name, unhappily, is several years older than *H. tiaridioides* Cham., the species I then accepted. Subsequent study and consideration of much South American material of *Heliotropium*, not available when my monograph was written, has left no reasonable doubt as to the identity of the plant described and illustrated by Vellozo. The scores of specimens examined from São Paulo, Rio Janeiro, Minas Geraes and northward in Brazil, uniformly have sulcate nutlets, and there seems every reason for believing that Velloza's plant had them also. I am accordingly taking up *H. transalpinum* as the correct appellation for the plant formerly treated by me as *H. tiaridioides* var. *schizocarpum*. The southern plant with non-sulcate nutlets, which I treated as *H. tiaridioides* var. *genuina* must have the new name I am publishing below. The type of *H. transalpinum* was collected in the state of Rio Janeiro near Boa Vista, ca. 9 km. up the Rio Parahyba from the town of Parahyba do Sul and beyond the coastal mountains (whence the specific name) from the city of Rio Janeiro.

Heliotropium transandinum var. **tiaridioides** (Cham.) comb. nov. *Heliotropium tiaridioides* Chamisso, Linnaea **4:** 453 (1829). *Heliotropium tiaridioides* var. *genuina* Johnston, Contr. Gray Herb. **81:** 6 (1928), where other synonyms are cited.

Heliotropium angiospermum Murray, Prodr. Stirp. Göttingen 217 (1770); Johnston, Contr. Gray Herb. **81:** 10 (1928). *Heliotropium humile* Lamarck, Tab. Encyc. **1:** 393 (1791).

In my treatment of the South American species of *Heliotropium,* Contr. Gray Herb. **81:** 66 (1928), I cited *H. humile* Lam. as a doubtful synonym of *H. fruticosum* L. This I now find is incorrect. In the Lamarck Herbarium at Paris there is only one specimen determined by Lamarck as *H. humile,* this bears a label in his script reading: "heliotr. humile lam. illustr." The specimen is small but represents good *H. angiospermum*. The original description of Lamarck's species reads: "1757 HELIOTROPIUM **humile**. H. foliis ovato-lanceolatis villosis;

spicis solitariis lateralibus. Ex ins. Carib. Annuum. *H. Dict. no. 6 Quoad descr.*" The reference is apparently to Lamarck's earlier account of *Heliotropium* in vol. 3 of the Encyclopédie, pp. 92–95 (1789), but no mention of *H. humile* is to be found there. Species no. 6 in the work is *H. fruticosum,* described as having linear-lanceolate leaves. Poiret, Encyc. Suppl. **3:** 25 (1813), was evidently puzzled by Lamarck's description of *H. humile*. He mentions that species under *H. ternatum* but suggests that it might be *H. fruticosum*. I am content, however, to place *H. humile* among the synonyms of *H. angiospermum,* for the named specimen in Lamarck's herbarium seems authentic and agrees with the few words in the original description.

Lasiarrhenum pinetorum, sp. nov., herba; caulibus erectis simplicibus 10–15 cm. altis gracilibus strigosis foliosis; foliis lineari-subulatis 1–3 cm. longis 1–1.5 mm. latis sessilibus medio-costatis sed vix nervatis apicem versus caulis gradatim reductis margine valde revolutis supra sparse strigosis; floribus cymas terminalis 3–7-floris lineari-bracteatas aggregatis; pedicellis 2–3 mm. longis strictis strigosis; calycibus 5-lobatis ca. 4 mm. longis, lobis lineari-lanceolatis strigosis; corolla flava ca. 10 mm. longa extus strigosa, tubo ca. 4 mm. longo ca. 1.5 mm. crasso in fauces 3.5–4 mm. longas ca. 3 mm. crassas abrupte transmutato intus glaberrimo, lobis erectis oblongis 2.5 mm. longis 2 mm. latis apice rotundis; antheris glaberrimis 2 mm. longis oblongis basi sagittatis erectis (vix versatilibus) sub medium affixis; filamentis 4 mm. supra basim corollae affixis inclusis 1–1.3 mm. longis late alatis (in ambitu obovatis) apicem versus ca. 0.7 mm. latis; stylo 12 mm. longo filiformi longe (ca. 5 mm.) exsertis; fructu ignoto.

MEXICO: growing in the mountains in pine-forest, very rare, September, *Ghiesbreght 311* (TYPE, Paris).

This is a remarkable species which is placed in *Lasiarrhenum* chiefly because of its broadly winged filaments. From *L. strigosum,* formerly the only known member of its genus, it differs in its very small size, its uninerved leaves, its glabrous anthers and its precociously long-exserted style. The rounded corolla-lobes and the expanded filaments separate *L. pinetorum* from the genus *Onosmodium,* while the long-exserted style, the erect corolla-lobes, the obovate filament and the sagittate anthers distinguish it from *Lithospermum*. No locality is given for this interesting plant. Ghiesbreght, however, collected chiefly in southern Mexico and mostly in the state of Oaxaca.

Lithospermum Muelleri, sp. nov., perenne; caulibus erectis gracilibus foliosis simplicibus vel rariter stricte et simpliciter longeque ramosis

2–5 dm. altis e radice crasso dense multicepite rumpentibus strigosis vel basim versus breviter hispidis; foliis strictis firmis costatis sed vix nervatis vel rarissime perinconspicue sparseque nervatis, inferioribus oblongo-ellipticis, aliter lanceolatis, sessilibus, apicem versus caulis gradatim reductis 1–4 cm. longis 3–8 mm. latis, apice acutis, supra minute strigosis et pustulatis, subtus in margine et costa strigosis sed ceterum glabris; inflorescentia bracteata scorpioidea terminali solitari vel geminata vel ternata 3–10 cm. longa; calyce ad anthesin ca. 6 mm. longo, lobis inaequalibus cuneatis, pedicellis 1–3 mm. longis strigosis; corolla subcylindrica 15–19 mm. longa ca. 3 mm. crasso ut videtur flavescente intus glaberrima extus adpresse pubescente, lobis minutis ascendentibus suborbicularibus ca. 1 mm. diametro, faucibus inconspicue plicato-appendiculatis saepe plus minusve constrictis; staminibus 2 mm. sub apice tubi corollae affixis, filamentis ca. 1 mm. longis, antheris oblongis ca. 2 mm. longis inclusis; stylo filiformi ad anthesin 1–3 mm. longe extrusis; fructu ignoto.

MEXICO: common in pine belt above Mesa de la Camisa on the north slope of Sierra Tronconal between Cañon de los Charcos and Cañon de San Miguel, Sierra Madre Oriental, ca. 25 km. s. w. of Galeana, Nuevo Leon, 1800–2700 m. alt., June 4, 1934, *C. H. & M. T. Mueller 739* (TYPE, Gray Herb.).

A very distinct species of uncertain affinities. Its subtubular corolla, frequently with a narrowly constricted ring about the throat, and its extremely small round ascending lobes, separate it from *L. strictum*, the only species I am inclined to believe which possibly may be a close relative of it.

Macromeria leontis, sp. nov., perennis erecta ca. 5 dm. alta e radice crasso profunde oriens; caulibus subsimplicibus pilis brevibus gracilibus erectis vel subretrorsis dense vestitis; foliis lanceolatis medium versus caulis grandioribus 4–10 cm. longis 1–2 cm. latis utroque acutis sessilibus evidenter nervatis, subtus pilis gracilibus brevibus erectis abundantibus vestitis vix pustulatis, supra viridis pustulatis et breviter hispidis; inflorescentia terminali evidenter bracteata; calyce 1.5–2 cm. longo, lobis linearibus, pedicello 1–5 mm. longo; corolla 5–7 cm. longo intus glaberrimo extus breviter pubescenti, tubo 2–3 cm. longo 1.5–2 mm. crasso supra in fauces 2 cm. longos 7–8 mm. latos gradatim ampliato, lobis triangularibus ca. 9 mm. longis et 6 mm. latis non rariter plus minusve recurvatis; antheris elongatis ca. 3.5 mm. longis; filamentis ca. 4 mm. infra apicem faucium corollae affixis 10–15 mm. longe exsertis; stylo filiformi tarde exsertis; fructu ignoto.

MEXICO: scattered in dense oak-woods on the ascent into Taray, Sierra

Madre Oriental, ca. 25 km. s. w. of Galeana, Nuevo Leon, ca. 2400 m. alt., June 5, 1934, *C. H. & M. T. Mueller 754* (TYPE, Gray Herb.); scattered in dense pine and oak woods along the descent into Alamar, Sierra Madre Oriental, May 29, 1934, *C. H. & M. T. Mueller 594* (G).

Probably a relative of *M. Pringlei*, but differing in having a fine slender spreading indument throughout. In *M. Pringlei* the more rigid, somewhat longer sparser hairs are closely appressed and the upper leaf-surfaces are a much clearer green than in *M. leontis*. The latter species has leaves noticeably grayer and duller in color.

Macromeria barbigera, sp. nov., perennis, setosa, robusta; caulibus erectis 5–8 dm. altis saepe simplicibus; foliis lanceolatis vel ovatis evidenter nervatis, inferioribus parvis vix persistentibus, ceteris latioribus 3–5 cm. latis 5–11 cm. longis subsessilibus basi plus minusve rotundis, superioribus elongatioribus et minoribus; floribus terminalibus in cymas racemosas bracteatas aggregatis; bracteis foliaceis 2–7 cm. longis 1–4 cm. latis; pedicellis ca. 5 mm. longis; calyce ad anthesin ca. 18 mm. longo, lobis inaequalibus subulato-linearibus erectis; corolla ut videtur flavescenti intus glaberrima 5–6 cm. longa recta vel plus minusve curvata, tubo 1.5–2 cm. longo 1.5–2 mm. crasso lobis calycis paullo longiore, faucibus e tubo abrupte ampliatis ca. 2 cm. longis 5–6 mm. crassis cylindraceis in alabastro paullo asymmetricis, limbo abrupte dilatato 12–15 mm. diametro, lobis 5–6 mm. longis acutis ascendentibus apicem versus recurvatis; filamentis in faucibus ca. 8 mm. infra sinibus loborum affixis inaequalibus 12–15 mm. longis glabris filiformibus exsertis; antheris oblongis medio-affixis; stylo filiformi breviter tardeque extruso; stigmato minimo bilobulato; fructu ignoto.

MEXICO: common in dense oak wood beyond the pine and fir belt, north slope of Sierra Tronconal between Cañon de San Miguel and Cañon de los Charcos, 1800–2700 m. alt., Sierra Madre Oriental about 25 km. s. w. of Galeana, Nuevo Leon, June 4, 1934, *C. H. & M. T. Mueller 741* (TYPE, Gray Herb.).

Related to *M. Thurberi* but quickly separable by its more robust habit, larger broader leaves and very different pubescence. The foliage of *M. Thurberi* is copiously and finely strigose with an admixture of coarse more or less spreading hairs. In the proposed species the strigosity is lacking and the spreading hairs much longer and very conspicuous. The corollas of *M. Thurberi* have a much more abundant and paler indument than do those of *M. barbigera*. The range of the new species is to the southeast of the most easterly station of its relative.

Evidently to be identified with *M. barbigera* are collections made by Mueller in 1933. These specimens have been kindly sent to me from the Field Museum by Mr. P. C. Standley. One of these collections, no. 174 from the "Trail to Puerto," Nuevo Leon, has leaves becoming 17 cm. long and 7 cm. broad. Its flowers are immature. The second collection, no. 173 from Diente Canyon, 21 km. south of Monterey, is evidently from a very mature plant and consists of the elongated inflorescence showing mature bracts and the old pedicels and calyces.

Among his collections of 1934 Mueller obtained one which may also represent a form of *M. barbigera*. This specimen, no. 830, was collected on Sierra Infernillo, about 25 km. s. e. of Galeana, Nuevo Leon, where it was common over small areas just below the crest, 2700–3000 m. alt. In leaf-outline and in general habit the plant suggests *M. Thurberi,* but differs in its lack of strigosity and in its very much less hairy flowers. The corollas differ from those of *M. barbigera*. They are somewhat smaller. The tube is gradually expanded towards the lobes and not abruptly expanded into a well developed cylindrical throat as I have indicated in my formal description above. In addition the corolla is slightly less hairy and the lobes not so acute. The plant is evidently related to *M. barbigera* and chiefly because of geographical considerations I am tentatively, at least, referring it to that species as a possible ecological form.

Havilandia opaca, sp. nov., procumbens; caulibus foliosis abundanter ascendenterque ramosis 1–1.5 mm. crassis in nodis radiculas graciles gerentibus pilis brevibus rigidis appressis dense vestitis, internodiis 3–10 mm. longis; foliis firmis subcoriaceis costatis sed enervatis numerosis, apice rotundis vel obtusis, supra glaberrimis sparsissime pustulatis in costa sulcatis, subtus supra medium pustulatis in costa prominente strigosis ceteris glabris vel sparsissime strigosis, margine strigoso-ciliatis vel basim versus sparse ciliatis; foliis ramorum fertilium ellipticis 4–10 mm. longis 3–5 mm. latis, basi rotundis et oblique 1–2 mm. lateque sessilibus; foliis ramorum sterilium plus minusve oblanceolatis 8–12 mm. longis paullo sub apicem basim versus in petiolum 1 mm. latum ca. 2 mm. longum gradatim attenuatis; floribus solitariis numerosis axillaribus; corolla alba 4 mm. diametro, tubo ca. 1.2 mm. longo 1 mm. crasso intus glaberrimo, limbo patenti, lobis suborbicularibus ca. 1.5 mm. diametro, appendiculis faucium 5 intrusis trapeziformibus; antheris oblongis inclusis ca. 0.4 mm. longis, filamentis perbrevibus paullo supra medium tubi affixis; calyci ad anthesin 2 mm. longo, lobis 5 ciliatis latis, pedicello 0.5–1 mm. longo; nuculis 4 erectis angulate ovoideis 1 mm. longis opacis dense minutissimeque papillatis, dorso convexis, ventre angulatis, imam ad basim anguli ventralis ad gynobasim planum affixis.

British New Guinea: common in open grassland, Murray Pass, Wharton Range, 2840 m. alt., prostrate herb forming masses 3 dm. broad or more, flowers white, June 12, 1933, *Brass 4178* (type, Gray Herb.; isotype, NY).

A species evidently related to *H. papuana* Hemsl., from which it differs in its stout somewhat ovate, gray, dull, minutely papillate, rather than elongate, somewhat lance-lunate, black, lustrous, smooth nutlets. The margins of the leaves in *H. papuana* are evidently ciliate. In *H. opaca* the marginal hairs of the leaves, similar in size, number and position, are not spreading, but antrorsely appressed along the leaf-margin. The habit of growth in *H. papuana* is quite similar to that of *H. opaca*.

Havilandia robusta, sp. nov., procumbens; caulibus elongatis sparse ramosis; foliis coriaceis oblanceolatis 2–4.5 cm. longis 5–9 mm. latis paullo sub apicem basim versus in petiolum vaginatum gradatim attenuatis, apice rotundis vel subemarginatis, margine sparsissime strigosis, supra sparse strigosis, subtus glaberrimis vix nervosis, costa prominente sparsissime strigosa; floribus axillaribus; calycibus ad anthesin ca. 4 mm. longis, lobis lanceolatis margine sparsissime strigosis, pedicellis 5–7 mm. longis; calycibus maturitate ca. 6 mm. longis pedicellis 8–12 mm. longis; corolla 8–10 mm. diametro; nuculis 4 angulato-ovoideis opacis ca. 2 mm. longis dense minutissimeque papillatis, dorse convexis, ventre angulatis.

British New Guinea: common about forest borders, Mt. Albert Edward, 3680 m. alt., June 1933, *Brass 5681* (type, N. Y. Bot. Gard.).

Evidently related to *H. opaca*, also of southeastern New Guinea, from which it differs only in being much larger in all its parts, and in having well developed pedicels and more elongate leaves. The upper surface of the leaves is lustrous and distinctly strigose.

Havilandia papuana Hemsley, Kew Bull. **1899**: 107 (1899).

British New Guinea: thickly massed on shallow soil over rock in grasslands, Mt. Albert Edward, 3680 m. alt., flowers white with yellow throat, June 18, 1933, *Brass 4245* (G, NY).

This species was briefly, though adequately described by Hemsley from material obtained on Mt. Scratchley, 3660 m. alt., and in the Wharton Range, 3330 m. alt. It is known only from the high mountains of eastern British New Guinea.

The genus *Havilandia* is confined to high altitudes and consists of the three above enumerated species from British New Guinea, and *H. borneensis* Stapf from Mt. Kinabalu in British North Borneo. It is possible, in addition, that *Lithospermum minutum* Wernh., described from the Mt. Carstensz region in Dutch New Guinea, may also belong to *Havilandia*. Unfortunately the type and only known collection of this puzzling species is so scanty and inadequate that it must remain an obscure, troublesome element in the flora of New Guinea until someone recollects it. The type consists of two minuscule snips in flower only, a ridiculously inadequate basis for the proposal of any species of Boraginaceae and certainly for one whose acquaintance with the genera of that family may be judged by his selection of the genus under which he essayed to publish the imperfect specimen from Dutch New Guinea.

Plagiobothrys Scouleri (H. & A.) Johnston, Contr. Gray Herb. **68**: 75 (1923) and Contr. Arnold Arb. **3**: 51 (1932). *Myosotis Scouleri* Hooker & Arnott, Bot. Beechey Voy. 370 (1840). *Allocarya media* Piper, Contr. U. S. Nat. Herb. **22**: 107 (1920). *Plagiobothrys medius* (Piper) Johnston, Contr. Arnold Arb. **3**: 58 (1932). *Allocarya divaricata* Piper, Contr. U. S. Nat. Herb. **22**: 107 (1920).

The original and only mention of *Myosotis Scouleri* in the writings of Hooker & Arnott appears in the Botany of Capt. Beechey's Voyage in a note on a collection of *Plagiobothrys Chorisianus* from California. The note is as follows: "The flowers here are on pretty long pedicels, while the Columbia plant has them shortly pedicellate; the latter presents, besides, a different aspect, and may be called *M. Scouleri;* it appears very closely allied to *M. californica,* Fisch. et Meyer, but the corolla is longer than the calyx." Gray, who apparently never studied the type of *M. Scouleri,* applied the name to an erect-growing plant with geminate spikes of conspicuous corollas, which is widely distributed in western Oregon and Washington, and all subsequent writers have followed him in that identification. A study of the type, however, shows this usage to be quite incorrect.

The specimens evidently the type of *M. Scouleri* are to be found on a mixed sheet, formerly in the Hooker Herbarium, now at Kew. This sheet bears three different collections: (1) the specimen of *P. Chorisianus* mentioned in the Botany of Beechey's Voyage, (2) specimens of *P. scopulorum* (?) or *P. cognatus* (?) collected by Nuttall, and (3) three plants labeled: "N. W. Coast, Dr. Scouler." The latter evidently constitute the type of *Myosotis Scouleri* H. & A. Duplicates of this Scouler collection are to be found on a sheet from Bentham's herbarium, at Kew, labeled: "Am. bor. occ. Scouleri, 1828," and in the herbarium at Edinburgh labeled: "Columbia, Scouler, 1827, (932)." These collections appear to represent a form of the plant I have treated in my monograph as *Plagiobothrys medius* (Piper) Johnston. They have the rufous calyx-lobes, evident corollas, and the general habit of that species.

Scouler is known to have collected about the mouth of the Columbia and at many small ports along the coast of Washington and Vancouver Island. *Plagiobothrys medius* is the common species near the coast in northwestern Washington and on Vancouver Island, and there is every reason that Scouler should have encountered it. Though the nutlets of Scouler's collection show certain peculiarities not matched in the available material of *P. medius,* I believe that they can be accommodated in that concept. The nutlets of the type of *M. Scouleri* have the rather bony pericarp common in *P. medius,* but the ridge attending the lateral scar is very closely appressed to the latter and encloses an areole (entirely filled by the scar) scarcely, if at all, broader than long. The nutlets of *P. medius* are, however, very variable and I believe the nutlet-variations of *M. Scouleri* can be admitted without destroying the naturalness of the concept.

Plagiobothrys hirtus (Greene), comb. nov. *Allocarya hirta* Greene, Pittonia **1**: 161 (1888). *Allocarya Scouleri* var. *hirta* (Greene) Nelson & Macbride, Bot. Gaz. **61**: 36 (1916). *Plagiobothrys Scouleri* var. *hirtus* (Greene) Johnston, Contr. Arnold Arb. **3**: 52 (1932). *Allocarya calycosa* Piper, Contr. U. S. Nat. Herb. **22**: 101 (1920).

I have indicated above that the type of *Myosotis Scouleri* H. & A. has been misinterpreted. The earliest correct name for the plant that has been called *Krynitzkia, Allocarya* and *Plagiobothrys Scouleri* is *Allocarya hirta* Greene. It is, however, strictly applied only to a local plant of the Umpqua Valley, Oregon, which has evidently spreading rather than appressed pubescence. The common form of this species must bear the following name:

Plagiobothrys hirtus var. **figuratus** (Piper), comb. nov. *Allocarya figurata* Piper, Contr. U. S. Nat. Herb. **22**: 101 (1920).

This strigose form ranging from Oregon to Vancouver Islands is common.

Plagiobothrys hirtus var. **corallicarpus** (Piper), comb. nov. *Allocarya corallicarpa* Piper, Proc. Biol. Soc. Wash. **37**: 93 (1924). *Plagiobothrys Scouleri* var. *corallicarpus* (Piper) Johnston, Contr. Arnold Arb. **3**: 52 (1932).

A local form of southern Oregon characterized by its deeply alveolate nutlets.

Plagiobothrys calandrinioides (Phil.) Johnston, Contr. Gray Herb. **78**: 91 (1927). *Allocarya alternifolia* Brand in Fedde, Repert. **26**: 169 (1929).

The type of Brand's species has been examined. The lowermost leaves are weathered and crowded and so account for the very misleading specific name. The plant is the common Patagonian *P. calandrinioides*.

Thaumatocaryon dasyanthum var. **Sellowianum** (Cham.), comb. nov. *Anchusa Sellowiana* Chamisso, Linnaea **8:** 115 (1833). *Moritzia Sellowiana* (Cham.) Fresenius in Martius, Fl. Bras. 8^1: 63 (1857). *Thaumatocaryon Sellowianum* (Cham.) Johnston, Contr. Gray Herb. **70:** 13 (1924) and **78:** 16 (1927). *Moritzia dasyantha* var. *Sellowiana* (Cham.) Brand in Fedde, Repert. **27:** 148 (1929).

This plant differs from typical *T. dasyantha* only in its smaller corollas and appressed pubescence. Difficulty with connecting forms has convinced me that Brand might best be followed in treating *Sellowianum* as a mere variety. A collection of this variety from the state of Rio Janeiro, by Glaziou (no. 8731), supplies the basis for Glaziou's astonishing report of *Cyphomattia lanata* in Brazil, Bull. Soc. Bot. France **57:** Mém. **3:** 480 (1910). I have examined the specimen at Paris so determined by Glaziou.

Hackelia patens (Nutt.), comb. nov. *Rochelia patens* Nuttall, Jour. Acad. Phila. **7:** 44 (1834). *Lappula coerulescens* Rydberg, Mem. N. Y. Bot. Gard. **1:** 328 (1900). *Lappula subdecumbens coerulescens* (Rydb.) Garrett, Fl. Wasatch Reg. 78 (1911). *Hackelia diffusa* var. *caerulescens* (Rydb.) Johnston, Contr. Gray Herb. **68:** 48 (1923). *Hackelia caerulescens* (Rydb.) Brand, Pflanzenr. [Heft 97] IV. **252^2:** 130 (1931). *Hackelia Nelsonii* Brand in Fedde, Repert. **26:** 170 (1929). *Lappula decumbens* Nels. ex Brand, Pflanzenr. [Heft 97] IV. **252^2:** 126 (1931), lapsus calami.

I have examined Nuttall's type of *Rochelia patens* at the British Museum. The specimen was collected "near the Flat-Head River" on June 8, 1833, by N. B. Wyeth. The specimen is a good one and is evidently conspecific with *Lappula coerulescens,* a species also based upon material from western Montana. The species is known from western Montana and Wyoming and westward into Idaho, northern Utah and northern Nevada.

Hackelia grisea (Woot. & Standl.), comb. nov. *Lappula grisea* Wooton & Standley, Contr. U. S. Nat. Herb. **16:** 164 (1913).

A readily recognizable species of New Mexico and adjacent Texas. Its relatively small corollas, with ascending lobes, quickly distinguish it among the west American annual and biennial species of this genus.

Lappula echinata Gilibert, Fl. Lituanica, **1:** 25 (1781). *Cryp-*

tantha Lappula Brand in Fedde, Repert. **24:** 56 (1928) and Pflanzenr. [Heft 97] IV. **252**[2]**:** 147 (1931).

In the Pflanzenreich Brand placed his *Cryptantha Lappula* among the synonyms of *Lappula Redowskii* (Hornem.) Greene. I believe, however, that the species belongs under *L. echinata* Gilib. The evident corollas and the gross aspect of the type are of that species. A microscopic study of the (immature) nutlets of *C. Lappula* seems to show a double row of lateral prickles. Finally the type is given as from Concepcion, Chile, a locality at which *L. Redowskii* is certainly not to be expected to grow naturally, though a busy port at which an aggressive weed, such as *L. echinata,* might be introduced without any cause for surprise.

Lappula echinata is generally accepted as introduced into North America. This seems probable, though it is to be noted that the plant was collected in the New World at a very early date. A specimen in the DuBois collection at Oxford is labeled "brot from Maryland by Mr. Wm. Vernon, 1698." Among Michaux's collections at Paris there is one of this species labeled as "Dans ville de Montreal, 1792." The Smith collections in London contain a specimen labeled: "North America, 1817, F. Booth." In the British Museum there is a collection made by Douglas, during 1826, "In the valleys of the Rocky Mts.," most likely in northeastern Washington. It seems to have been again collected in the latter region only within the past ten years, though it has been well known in the southern parts of western Canada for at least a generation. There are reasons to believe that the railroads may have much aided in the distribution north of the International Boundary. The plant has exhibited an evident, progressive increase and migration westward across the more northern of the western United States. It is now rapidly increasing in eastern Washington where it gives every evidence of being a recent immigrant.

Cryptantha circumscissa (H. & A.) Johnston, Contr. Gray Herb. **68:** 55 (1923).

A few years ago, l. c. **81:** 75 (1928), I reported this characteristic plant of western United States from near Zapala, Neuquen, Argentina. A second station in Neuquen may now be recorded. At Munich I have seen specimens labeled as collected by Erik Ammann (no. 7) at Cerro Mesa between Sept. and Nov. 1927. The new station is nearly 90 km. southeast of Zapala.

Cryptantha clandestina (Trev.), comb. nov. *Lithospermum clandestinum* Treviranus, Del. sem. a 1832 in hort. Bonnensi collect. p. 2 (1832–3). *Cryptantha glomerata* Lehmann, Del. Sem. Hamb. **1832:** 4 (1832), nomen nudum; Fischer & Meyer, Ind. Sem. Hort. Petrop. **2:** 8

and 35 (1836); Johnston, Contr. Gray Herb. **78:** 58 (1927). *Cryptantha microcarpa* Fischer & Meyer, Ind. Sem. Hort. Petrop. **2:** 8 and 35 (1836).

A study of the original description of *Lithospermum clandestinum*, and of old garden material representing it, has made it clear that it is that well known cleistogamic species of Chile, the two forms of which have passed as *Cryptantha glomerata* and *C. microcarpa*. Fischer & Meyer, when describing *C. microcarpa,* in fact, actually cited *L. clandestinum* as a synonym. In the Bonn seed-list for 1832, published in Dec. 1832 or Jan. 1833, the name *Lithospermum clandestinum* appears in the alphabetic list on the second of the pages of that quarto catalogue. A reference leads to a footnote which reads as follows: "Diffusum hispidum; fol. lanceolatis amplexicaulibus; calycibus subsessilibus ventricosis corollam excedentibus; seminn. granulatis. Annuum. Corolla alba, tubo ventricoso, limbo conniventi. Semina duo plerumque abortiunt. T[reviranus]." The name, *L. clandestinum,* appears again in the Bonn list for 1833, but not in those for 1834 or 1835.

Cryptantha glomerata Lehm. is the type-species of *Cryptantha*. Recently I had the privilege of consulting the extensive collections of old seed-catalogues at Berlin and Geneva. I now find it possible to record several important references in the history of that genus and species which were either unknown or unavailable to me at the time of my work on the group. The first mention of *Cryptantha glomerata* Lehm. and of the generic name appears in Lehmann's seed-list of the Hamburg Garden for the year 1832. The binomial appears as a mere name on page 4, thus: "*Cryptantha glomerata* Lehm." No description or explanation of the name is given! The list is dated 1832 and was probably published, as was customary with such lists, around the close of the year. No mention of the binomial is found in the Hamburg lists for 1830, 1831 or for 1833 or 1834. In 1835, p. 4, again without description, appears: "*Cryptantha glomerata* Lehm. (Del. Sem. 1832)." In 1836, p. 4, the following two names appear bare of description: "*Cryptantha glomerata* Lehm." and "*Cryptantha microcarpa* F. & M." These are repeated in the list for 1837, p. 4. In the list for 1838, p. 4, there is merely the name, "*Cryptantha microcarpa* F. & M." Fischer & Meyer, in their St. Petersburg seed-list for 1835, supplied the first descriptions of *Cryptantha glomerata* Lehm. and *C. microcarpa* F. & M. This Russian list bears a censor's date, Dec. 25, 1835, the equivalent of Jan. 5, 1836 of our present calendar. There is no mention of *Cryptantha* in the St. Petersburg list for 1834! Fischer & Meyer, when publishing and describing "*C. glomerata* Lehm." in their list for 1835, attribute the name to "Bernhardi in litt." A study of Bernhardi's seed-lists, Sel. sem. hort. Erfurt., shows that the name "*C. glomerata* Lehm." appears as a mere binomial in those for 1833 (Jan. 18, 1834), 1834 (Feb. 24, 1835) and 1835. There is no mention of *Cryptantha* in the Erfurt list for 1832!

From the facts I have given it becomes evident that *Cryptantha glomerata* was in cultivation at Bonn and Hamburg in 1832. Treviranus immediately described the Bonn cultures as *Lithospermum clandestinum*. Lehmann applied to his Hamburg cultures the name *Cryptantha glomerata,* but did not describe it, that being done for him three years later by Fischer & Meyer who based their description on plants grown at St. Petersburg. There is no information as to the channels by which the species was introduced into cultivation. I suspect, however, that the original seed may have been obtained by Bertero, who collected the plant near the Rio Quillota, Chile, as early as 1828, and that seeds from this source may have been distributed from Turin.

Amsinckia intermedia Fischer & Meyer, Ind. Sem. Hort. Petrop. **2:** 2 and 26 (1836).

This name appears bare in the alphabetic list on page 2 of the seed-list cited above. On page 26 (p. 1 of reprint) the following description is found, "A. INTERMEDIA. A. corolla fauce glabra nuda, limbo tubo subbreviore; staminibus ad faucem insertis. — Corollae tubus 1½ lin. longus, limbus fere 3 lin. in diametro, saturate aurantiacus maculisque 5 saturatioribus pictus. — Species intermedia *A. lycopsioidem* inter et *A. spectabilem;* a priore dignoscitur insertione staminum, a posteriore corollis longe minoribus et praesertim corollae tubo non (ut in illa) ad faucem plicis intrusis semiclausa. — Hab. cum sequente specie [*A. spectabilis*] circa coloniam ruthenorum Ross in portu Bodega Novae Californiae. Annua." The seed-list in which this description occurs bears the printed censor's date, Dec. 25, 1835. This equals Jan. 5, 1836 of the present calendar.

Through the kindness of Prof. B. A. Keller, Director of the Institute and Botanic Garden at Leningrad, I have received authentic material of *Amsinckia intermedia.* This consists of an authentic fragment of the species, from the herbarium of Meyer, one of the co-authors of the species, and a fine specimen from the plantings in the St. Petersburg Garden in 1836. The specimens agree with the interpretation of *A. intermedia* given by Suksdorf, Werdenda **1:** 88 (1931). The plant is a member of that variable and bewildering island species that Macbride, Contr. Gray Herb. **49:** 12 (1917), and Jepson, Man. Fl. Pl. Calif. 844 (1925), have incorrectly called "*A. Douglasiana.*" Greene, Bot. S.

Francisco Bay, 262 (1894), and Jepson, Fl. W. Mid. Calif. ed. 2, 350 (1911), earlier treated it, partly as *A. intermedia* and partly as *A. spectabilis*. The name, *A. intermedia* F. & M., is properly applied to the polymorphous species which is common in California in the interior valleys and on hillsides back from the immediate vicinity of the ocean.

Amsinckia spectabilis Fischer & Meyer, Ind. Sem. Hort. Petrop. **2:** 2 and 26 (1836).

This species appears on page 2 of the above publication as a bare name in an alphabetic list of seeds. On page 26 (p. 1 of reprint) the following description is found: "A. SPECTABILIS. A. corolla fauce glabra plicis intrusis semiclausa, limbo longitudine tubi; staminibus ad faucem insertis. Species pulchritudine florum insignis atque distinctissima. Corolla aurea, limbo 6 lin. in diametro, ad faucem plicis 5, squamulas simulantibus, aucta. Annua."

In 1925 through the kindness of Prof. Boris Fedtchenko, with the assistance of Miss Olga Enden, I received two generous fragments of authentic specimens of this species. The specimens were grown in the St. Petersburg botanic garden in 1835–36. They are given as grown from seeds collected at Fort Ross, California, by Wiedemann. These fragments were examined by Suksdorf, Werdenda **1:** 96 (1931). He correctly identified them with the coastal plant that Brand, in Fedde's Repert. **20:** 319 (1924), has described as *A. nigricans*. Brand's plant, *Heller 5614,* is from the type-locality of *A. spectabilis*. I have seen many specimens of this plant in various herbaria from numerous garden-cultures. While evidently conspecific, these specimens rarely have the corollas as well developed as that found in the original culture at St. Petersburg in 1835. This is not surprising. I have grown *Amsinckia* in a botanic garden and under glass and have in most cases discovered remarkable differences in habit of growth and corolla-size between my cultures and the wild specimen from which the seed was obtained.

Macbride, Contr. Gray Herb. **49:** 7 (1917), in his monograph of the genus, has treated the coastal plant (the true *A. spectabilis* F. & M.) under the name "*A. intermedia*." Jepson, Man. Fl. Pl. Calif. 844 (1925), attempted to follow him and has described the coastal plant as "*A. intermedia*." His illustration, however, is the inland species, which just happens to be the true *A. intermedia* F. & M. Previous to Macbride's paper in the writings of Gray, of Greene, and of Jepson, the coastal plant appears as "*A. lycopsoides*." Macbride, l. c. 5, of course, was quite incorrect in applying the name "*A. spectabilis*" to the smooth-fruited *A. grandiflora* Kleeb ex Gray. The name *A. spectabilis* F. & M. properly belongs to the strictly coastal plant of California that has small dark nutlets, acute more or less denticulate leaves, and a pair of the calyx-lobes frequently more or less united. Abrams, Fl. Los Angeles, 335 (1904), seems to have been the only author who has properly applied the names *A. spectabilis* and *A. intermedia*.

Amsinckia lycopsoides Lehmann, Del. Sem. Hort. Hamburg **1831:** 1 and 7 (1831).

On the first page of the Hamburg seed-list for 1831 appears the name "*Amsinckia lycopsoides* Lehm.[1]" The exponent refers to a note on page 7 where the following is found, "[1]Genus novum e familia Borraginearum, praeter alias notas cotyledonibus 4 distinctissimum. Benthamia Lindl. in litteris (non Richard Monog. des Orchidees iles de France et de Bourbon pg. 43, t. 7, fig. 2)." In the seed-list for 1833, p. 3, and 1834, p. 3, the binomial appears perfectly bare. In 1835, p. 3, it is listed in company with *A. angustifolia* Lehm. In 1836, p. 3, and 1837, p. 3, it is listed as one of four species, *A. angustifolia, A. intermedia, A. lycopsoides* and *A. spectabilis*.

In the writings of Fischer & Meyer the binomial, *A. lycopsioides* Lehm., appears as a bare name in company of *A. angustifolia* Lehm., in the first St. Petersburg list, Ind. Sem. Hort. Petrop. **1:** 2 (1835). In the next list, **2:** 2 (Jan. 1836), it appears with *A. angustifolia, A. intermedia* and *A. spectabilis* and on page 26 (p. 1 of reprint) has the following note concerning it: "AMSINCKIA LYCOPSIOIDES. A. corolla fauce barbata, limbo tubo triplo breviore; staminibus corollae tubo paulo supra basin insertis. — *A. lycopsioides Lehm. delect. sem. h. Hamburg.* 1831. — Tubus corollae 3½ lin. longus; limbus 2 lin. in diametro, vix latior."

The species, *Amsinckia lycopsoides* Lehmann, is the type of the genus *Amsinckia*. The Hamburg seed-list in which it was first published is dated 1831. That it was actually published that year is proved by the review of this publication in the Litteratur-Bericht zur Linnaea (vol. 6) which bears the title-page date of 1831. The description of the species, *Amsinckia lycopsoides* Lehm., by Fischer & Meyer, appears in a seed-list for the year 1835 but this pamphlet bears a printed censor's date, Dec. 25, 1835 which is the equivalent of Jan. 5, 1836 in our present calendar.

It is to be noted that when, in 1831, Lehmann published his generic name, *Amsinckia*, that he definitely associates it with *Benthamia* of Lindley. This latter generic name was published by Lindley, in the same year, but only as a nomen nudum, Lindley, Nat. Syst. 241 (1831).

It was undoubtedly based upon material collected by Douglas along the Columbia River. This is clearly indicated by specimens in herbaria at Cambridge, Kew, London and Geneva. In the Lindley Herbarium at Cambridge there is only one sheet that has been determined as *Benthamia* by Lindley. This contains Cuming's no. 512 from Valparaiso and a specimen labeled "North West Amer. H. H. G. 1827, Douglas." Lindley has written in the corner of the sheet "*Benthamia lycopsoides* Mihi." There are various strong reasons for believing that this sheet in Lindley's herbarium formerly bore only the material from Douglas and that the Cuming material was later added to it, probably after Lindley's annotation. At Kew there are two significant specimens. One from the Bentham Herbarium is labeled "*Benthamia lycopsoides* Lindl. M. S. sem. ex Amer. occid. ex Douglas, Hort. Soc. Hort. London, 6–6–28." A similar sheet from the Hooker Herbarium is labeled "*Anchusa*, fl. yellow, *Benthamia* Lindl. mss. N. W. Am. Douglas, cult." Lindley published only the genus name, *Benthamia*. The binomial "*Benthamia lycopsoides*" seems to have been published first by DeCandolle, Prodr. **10:** 118 (1846). This reference is clearly based upon a specimen at Geneva bearing the following data: "*Benthamia lycopsoides* Lindl. ined., Hort. Sociét. horticult. in Chiswick 6 jun. 1828." The name on the label is in the script of Lindley. The source is written by DeCandolle. The date given is the same as that found on the sheet in Bentham's herbarium and falls within the period when A. DeCandolle visited London for work on his *Campanulaceae*. The herbarium of the Horticultural Society was sold to the British Museum. There is a specimen from this source at South Kensington labeled: "sandy plains of the Columbia, 1825 (according to Lindley a new genus)." Lindley was in charge of identifying the plants grown in the gardens of the Horticultural Society at Chiswick. All the specimens mentioned are probably from seeds grown at Chiswick. They all represent the plant recently described as *A. simplex* Suksdorf, Werdenda **1:** 33 and 53 (1927 and 1931).

There are a number of good reasons for believing that Lehmann's genus *Amsinckia* and his species *A. lycopsoides* are based upon Lindley's genus *Benthamia* and *B. lycopsoides*. In the first place shortly before 1830 Lehmann travelled in England and met various botanists there. He was a well known student of the *Boraginaceae*. Lehmann, in any case, was later in correspondence with Lindley, for he cites his authority for *Benthamia* as "Lindl. in litteris," and we may well believe that he received seed or specimens of Douglas's curious borage from Lindley and grew it in the Hamburg garden. Lehmann devotes about half of his short description of *Amsinckia* to citing Lindley's unpublished *Benthamia* and its earlier published homonym. The specific name used by Lehmann is that selected by Lindley. What is most important, however, is that an *Amsinckia* conspecific with Douglas's plant was in cultivation in various European botanic gardens under the name "*Amsinckia lycopsoides*." There is a specimen at Kew collected by J. Gay in the Jardin des Plantes at Paris in June 1833, only a year and a half after Lehmann published *Amsinckia*. This plant was grown under Lehmann's binomial and represents the species collected on the Columbia by Douglas. In conclusion it may be noted that the short descriptive notes concerning *A. lycopsoides,* given in 1835 by Fischer & Meyer, apply to the plant collected by Douglas.

A study of Douglas's Journal, p. 116 (1914), fortunately reveals some information as to the original source of *Amsinckia lycopsoides*. The plant is evidently that mentioned under the date of May 2, 1825, in an enumeration of collections made on "Menzies Island, in the Columbia river, opposite the Hudson Bay Company's establishment at Point Vancouver." According to Piper, Contr. U. S. Nat. Herb. **11:** 620 (1906), Menzies Island is that now known as "Haydens Island." The notes by Douglas are as follows: "(151) *Myosotis* sp., annual; hirsute, branching; leaves long, entire; linear-lanceolate; flowers bright yellow; tube long; mouth of the corolla spreading, with a dark spot opposite teeth; seeds not yet known; this very interesting species was found on Menzies Island in company with Mr. Scouler, who agreed with me to call it *Myosotis Hookeri* [not *Myosotis Hookeri* Clarke (1883)] after Dr. Hooker of Glasgow; scarce, only three specimens of it were found, two of which are in my possession. — I have since found it in abundance near all the Indian lodges above the Rapids of the Columbia. S[eeds]." From these notes it is evident that seeds were not obtained on Menzies Island and that, later, they were obtained somewhere above the Columbia Rapids. *Amsinckia simplex* Suksd. is known only from the general vicinity of Portland, Oregon (just south of Menzies Island). It is scarcely separable from *A. arenaria* Suksd. which is reported from the Columbia Gorge and in eastern Washington. The name *Amsinckia lycopsoides* (Lindley) Lehmann is properly applicable to these concepts.

It has been shown that *Amsinckia lycopsoides* Lehm. is based eventually upon material collected by Douglas along the Columbia River. In subsequent paragraphs I have shown that *Lithospermum lycopsoides* Lehm. (1830) is based upon collections made by Scouler on the northwestern coast of Washington. In the writings of A. DeCandolle, Prodr. **10:** 118, adnot. (1846), Gray, Synop. Fl. **2:** 198 (1878), Macbride, Contr. Gray Herb. **49**: 7 (1917), Suksdorf, Werdenda **1**: 101 (1931), etc., the binomial *Amsinckia lycopsoides* has been considered as merely a nomenclatorial transfer and as based upon *Lithospermum lycopsoides*. The similarity of the specific epithet is a mere coincidence. There are no reasons at all for supposing that these two species are identical. I have shown that *Amsinckia lycopsoides* is a plant from along the Columbia. *Lithospermum lycopsoides* is an earlier binomial, but since the specific name is preoccupied under *Amsinckia* it can not be legitimately transferred to that genus. A new name for the coastal plant of northwestern Washington is accordingly needed.

Lithospermum lycopsoides Lehmann, Pugil. **2**: 28 (1830); Lehmann in Hooker, Fl. Bor. Am. **2**: 89 (1838).

As was his custom in the Pugillus, Lehmann cited no specimens when he originally described *L. lycopsoides*. In the Flora Boreali-Americana, in which he contributed the *Boraginaceae*, however, he repeated his original description verbatim and cited the basic specimen. This latter is given as "Straits of de Fuca, N. W. America, *Dr. Scouler*." At Kew, from the herbarium of Hooker, there is a specimen that agrees perfectly with Lehmann's description and is labelled "*Lith. lycopsioides* Lehm. De Fuca, N. W. Am. Scouler." I agree with E. L. Greene, who has written on this sheet that "This, along with fragments in Herb. Benth. constitutes the type of *Lithospermum lycopsoides* Lehm. It has never been in cultivation." The plant is undoubtedly conspecific with that of northwestern Washington and adjacent Vancouver Island which has passed as "*Amsinckia lycopsoides*" in Piper's Flora of Washington, Contr. U. S. Nat. Herb. **11**: 480 (1906), and in the monographs by Macbride, Contr. Gray Herb. **49**: 7 (1917) and Suksdorf, Werdenda **1**: 101 (1931). It is not the same species as *Amsinckia lycopsoides* Lehm., which is based upon specimens collected by Douglas near the Columbia. The present plant, a coastal species related to true *A. spectabilis* F. & M. of California, strangely has no synonyms. Since the specific name is preoccupied under *Amsinckia* a new name is needed. The plant may be called:

Amsinckia Scouleri, nom. nov. *Lithospermum lycopsoides* Lehmann, Pugil. **2**: 28 (1830) not *A. lycopsoides* Lehmann (1831).

Amsinckia Douglasiana A. DeCandolle, Prodr. **10**: 118 (1846).

I have examined the type of this species in the DeCandollean Herbarium at Geneva. It is clearly a species with tessellate nutlets and large showy corollas. I consider it conspecific with *A. Lemmonii* Macbride, Contr. Gray Herb. **48:** 50 (1916). Suksdorf, Werdenda, **1:** 102 (1931), who has examined authentic material of *A. Douglasiana,* preserved at the Gray Herbarium, has considered it closely related to *A. Lemmonii* but separable from it. He places these two species together in his monograph. Gray erroneously cited the name *A. Douglasiana* in the synonymy of the common inland species of California. Not having seen the type of *A. Douglasiana,* Macbride, Contr. Gray Herb. **49:** 12 (1917), was misled by Gray's erroneous citation and applied it to the common inland species of California. The plant treated as *A. Douglasiana* by Macbride, and by Jepson, Man. Fl. Pl. Calif. 844 (1925), who followed him, is properly identified as true *A. intermedia* F. & M. *Amsinckia Douglasiana* A. DC. is a relatively rare plant of the South Coast Ranges of California and was probably originally collected by Douglas in San Luis Obispo or southern Monterey counties during his journey from Monterey to Santa Barbara and return.

Amsinckia parviflora Bernhardi, Selec. Sem. Hort. Erfurt. **1833:** 1 and 4 (Jan. 1834).

On the first page of the Erfurt seed-list for 1833 two Amsinckias appear in the alphabetic list of names, *Amsinckia lycopsoides* Lehm. and *A. parviflora* Bernh. A reference to the last, fourth but unnumbered page of the seed-list gives the following note concerning *A. parviflora* Bernh.: "(1) *Lithospermum calycinum* Moris, cui cotyledones 4, s. potius 2 bipartitae, speciem Amsinckiae sistit, quam A. parvifloram vocarem. An A. angustifolia Lehm. eodem planta ?" The list bears a printed date, Jan. 18, 1834. No species of *Amsinckia* are mentioned in the Erfurt seed-lists for the year 1832. *Amsinckia parviflora* Bernh. appears to be no more than a mere renaming of *Lithospermum calycinum* Moris. The two names are, accordingly, exact synonyms and apply to Bertero's plant from Rancagua, Chile, described and figured by Moris, Mem. Accad. Torino **37:** 98 tab. *22* (1834). In 1834 Lehmann cited Bernhardi's binomial as a synonym of *A. angustifolia* Lehm. I am inclined to believe this is correct, for as I shall discuss, I suspect that Lehmann's species is also based upon Chilean material.

Amsinckia angustifolia Lehmann, Del. Sem. Hort. Hamburg **1832:** 3 (1832), nomen; Fischer & Meyer, Ind. Sem. Hort. Petrop. **2:** 26 (1836), description.

The above binomial appeared as a bare name in the seed-list of the Hamburg garden for 1832. It appeared again as a bare name in the list for 1833, p. 3, was omitted in that for 1834, and in the list for 1835, p. 3, was cited as follows: "*Amsinckia angustifolia* Lehm. (*A. parvifolia*

Bernh. Sel. sem. h. Erf. 1833)." This reference was repeated in 1836, p. 3. In the list for 1837, p. 3, it again appears as a bare name.

In the first list from the garden at St. Petersburg, **1:** 2 (1835) the name *Amsinckia angustifolia* also appears bare. In the next list from St. Petersburg, **2:** 2 and 26 (1836), the name appears in the list of seeds and on page 26 (p. 1 of reprint) the following description and references are published: "A. ANGUSTIFOLIA. A. corolla fauce glabra nuda, limbo tubo duplo breviore; staminibus ad faucem insertis. *A. angustifolia Lehm. delect. sem. h. Hamburg. 1832. A. parviflora Bernhardi select. sem. h. Erfurt. 1833. Lithospermum calycinum Moris. Enum. sem. h. r. bot. Taurinens. 1831 et in Mem. della Acad. d. Scienze di Torino Tom. XXXVII. p. 108. tab. XXII.* — Corollae tubus vix 2 lin. longus, limbus vix 2 lin. in diametro. — A praecedente [*A. lycopsioides* Lehm.] floribus parvulis et praesertim staminum insertione diversissima." All the references cited by Fischer & Meyer trace back to material, collected by Bertero in central Chile. What is more all the garden material, under the name *A. angustifolia,* seems best referred to the Chilean forms of the genus. All authors have applied *A. angustifolia* to the austral plant. There seems every reason for continuing to do so. I suspect that the cultures in European gardens were originally from seeds obtained by Bertero at Quillota or Rancagua, Chile, and subsequently distributed from Turin by Morris or Colla.

Omphalodes erecta, sp. nov., herba perennis erecta e caudice laxe ramoso oriens pilis mollibus gracillimis subcinerea; caulibus foliosis simplicibus vel supra medium sparsissime fertiliterque stricto-ramosis 3–6 dm. altis partibus maturis plus minusve glabrescentibus brunnescentibus 2–4 mm. crassis; foliis lanceolatis vel late lanceolatis 5–11 cm. longis 15–30 mm. latis (superioribus non-conspicue reductis) sub medium apicem versus in acuminem 1–3 mm. longam gracilem gradatim attenuatis, margine integerrimis basi angulatis vel subrotundis 3–6 mm. longe petiolatis, supra viridis sparse inconspicueque pubescentibus non rariter minute pustulatis, subtus pallidis saepe pilis abundantibus longioribus subcinereis; inflorescentia gracili laxe racemosa simplice vel basaliter furcata ebracteata 5–15 cm. longa 0–1 cm. longe pedunculata; pedicellis ad anthesin 3–6 mm. longis ascendentibus, fructiferis ad 2 cm. longis saepe decurvatis vel subcontortis; calyx ad anthesin pallide denseque strigoso, lobis 5 inaequalibus lanceolatis ca. 4 mm. longis; corolla coerulea vel medium versus violacea, tubo ca. 3 mm. longo, appendiculis faucium 5 trapeziformibus ca. 1.3 mm. longis et latis apice subemarginatis, margine pubescentibus, limbo ca. 13 mm. diametro patente ultra medium lobato, lobis 4–5 mm. longis rotundis, sinibus loborum inconspicue plicatulis; antheris oblongis inclusis medium versus bubo corollae affixis; filamentis perbrevis; stylo ad anthesin 2 mm. longo, fructifero conspicuis 9 mm. longo; stigmato disciformi; fructu 4-ovulato; nuculo solitario (3 abortis) minute appresseque strigoso depresse lateque ovoideo, (cum alis) ca. 8 mm. diametro, margine evidenter 1–1.3 mm. late alato, ala plana patenti leviter denticulata, dorso nuculae convexo.

MEXICO: common in dense oak-wood along an arroyo near Santa Ana, between Alamar and Taray, Sierra Madre Oriental, ca. 25 km. s. w. of Galeana, Nuevo Leon, corolla blue with a light violet center, July 3, 1934, *C. H. & M. T. Mueller 992* (TYPE, Gray Herb.); scattered in fields and waste places in cañyon above Alamar, Sierra Madre Oriental, 1500–1800 m. alt., June 2, 1934, *C. H. & M. T. Mueller 680* (G).

A remarkable species differing from all its congeners in its coarse erect habit of growth. The general habit and appearance of the plant, indeed, is more suggestive of *Cynoglossum* than of *Omphalodes*. From the American species of its genus it is further distinguished by its large solitary nutlets which possess a weakly denticulate and spreading wing, rather than a strongly toothed upcurved one. The foliage of *O. erecta* is very distinctive. All the American species of the genus have long-petioled more or less cordate leaves. The new species has them very short-petioled and lanceolate. Only one Mexican species, *O. aliena,* has a similar bractless inflorescence. The plant is a remarkable addition to the list of Mexican Boraginaceae.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

LORANTHACEAE COLLECTED IN THE SOLOMON ISLANDS BY L. J. BRASS AND S. F. KAJEWSKI, ON THE ARNOLD ARBORETUM EXPEDITION, 1930–1932

B. H. DANSER

With plate 129

Amylotheca sp.

San Cristóval Island: Waimamura, *Brass* 2849, Sept. 9, 1932, "common, parasitic on rain forest trees, stout shrub, branches smooth and glaucous, leaves very thick and fleshy, perianth of unopened flowers lower half pale red, upper greenish-yellow."

Indeterminable for lack of open flowers, but closely allied to *Amylotheca Versteegii* (Lauterb.) Danser from New Guinea and New Ireland, differing, however, by longer-pedicelled lateral flowers of the triads, more thickish inflorescences and flowers, obtuse bracts and more distinct calyx lobes.

Dactyliophora salomonia, n. sp. Plate 129 a-b

Glabra, inflorescentiis floribusque iuventute forte parce tomentellis exceptis. Rami robusti; internodia foliifera teretia, iuventute apicem versus applanata nonnunquam ancipita, nodis dilatatis, postea teretia, 3–5 mm. crassa, nodis ad sesquiplo crassioribus. Folia opposita vel subopposita; petioli 14–24 mm. longi, basi teretes, laminam versus facie superiore profundius canaliculati; laminae triangulari-ovatae, plerumque 10–15 cm. longae, 5.5–7.5 cm. latae, basi rotundatae vel leviter cordatae, in petiolum contractae, apicem obtusum versus gradatim attenuatae, crassiusculae, fragiles, penninerves, costa facie inferiore basin versus magis prominente, costa cetera et nervis lateralibus primariis valde incurvatis utrinque distinctis paulum prominentibus. Inflorescentiae singulae in axillis foliorum et plures circum nodos defoliatos; pedunculi teretes, apice basique paulum incrassati, 15–20 mm. longi, 1–1.25 mm. crassi; axes ex internodiis 2 vel 1 compositi, quorum inferius 1–5 mm. longum, superius brevissimum; nodi deinceps circiter 8, 6, paucas triades ferentes; pedicelli triadum inferiores 8–10 mm. longi, c. 0.3 mm. crassi, superiores paucis mm. breviores; pedicelli florum lateralium 2–3 mm. longi; bracteae bracteolaeque ovatae obtusae 1.25–1.5 mm. longae. Calycis tubus obovato-campanulatus, 3.5–4 mm. longus, 1.5–2 mm. latus, limbus brevissimus erectus vel nonnihil inflexus. Corolla statu alabastri adulti 25 mm. longa, tertia parte inferiore inflata ad 3 mm. lata, tertia parte media gradatim ad 1 mm. attenuata, tertia parte superiore in clavam 6-angulam obtusam 1.5–2 mm. crassam incrassata, postea divisa in petala 6 sublinearia, a basi c. 1 mm. lata in duabus tertiis inferioribus gradatim ad 0.5 mm. angustata, in tertia parte superiore angustissime spathulata, apice acutiuscula crassiuscula, latere interiore c. 2 mm. supra basin squamula minima. Filamentorum pars libera c. 2 mm. longa; antherae c. 4 mm. longae, obtusae. Stylus a basi c. 0.6 mm. crassa gradatim angustatus, sub stigmate c. 0.25 mm. crassus; stigma obovatum, styli apice vix crassius. Fructus obovato-ellipsoides, ad 9 mm. longi, 6 mm. crassi, superea collo solido 2 mm. longo et lato coronati, calycis rudimento vix ullo.

G u a d a l c a n a l I s l a n d : Vulolo, Tutuve Mt., 1200 m. alt., *Kajewski* 2497, April 14, 1931; "common, a loranthus growing on trees; there are two different coloured flowers, yellow and yellow pink, but there is no specific difference; fruit green when ripe, length 1.1 cm., diameter 6 mm., with a white flesh inside; fruit with a blunt point at end; the leaves are heated and rubbed on sore legs." — Vernacular name "Bitorchi."

The genus *Dactyliophora* was known, before now, only from New Guinea and New Ireland. *Dactyliophora salomonia* is closely allied to the New Guinea *D. verticillata* (Scheffer) Van Tieghem, and perhaps only a variety of it, but it differs by less cordate, longer-petioled leaves, axillary inflorescences, longer and less thick peduncles and pedicels, more slender calyces and shorter corollas. The peculiar beak on the fruit is not described for any other species, but as in most *Dactyliophorae* the fruit are unknown, and those of *D. Novae-Guineae* (Bailey) Danser are figured with a similar prolongation (cfr. Bull. Jard. Bot. Buitenz., sér. 3, **11**: 359, fig. 14, h), it probably is not a characteristic of *D. salomonia* only.

Sogerianthe versicolor, n. sp. Plate 129c-e

Omnis glabra (vel pedicellis, bracteis, calycibusque minute puberulis). Rami graciles, parce dichotome ramosi, internodiis foliiferis 1–2.5 (–3) mm. crassis, plerumque 3–9 cm. longis, nodis valde incrassatis, duplo vel fere triplo crassioribus. Folia opposita; petioli 5–10 mm. longi, supra applanati praesertim laminam versus, subtus rotundati; laminae oblongo-ovatae, plerumque 6–10 cm. longae, 2.5–4.5 cm. latae, sub basi rotundata in petiolum contractae vel magis attenuatae, apicem obtusum versus magis minusve acuminatae, crassiusculae, fragiles, utrinque opacae (vel facie superiore lucidulae), penninerves, costa facie inferiore prope basin valde prominente, ceterum costa nervisque lateralibus primariis incurvatis utraque facie visibilibus vix prominentibus. Flores singuli vel in umbellis paucifloris omnino sessilibus in scrobiculis corticis inserti, pauci in axillis foliorum vel plures circum nodos foliatos et defoliatos; pedicelli teretes, basi saepe paulum clavati, 2–4 mm. longi, 0.3(–0.5) mm. crassi; bracteae bracteolaeque triangulares vel ovatae, 0.5–1 mm. plerumque 0.75 mm. longae, obtusae vel acutae, basi nonnihil connatae. Calycis tubus campanulatus, subcylindricus, (1.5–)2–2.5 mm. longus, 1.25 mm. latus, limbus erectus paulum cupuliformis, 1(–1.25) mm. longus, ore (1.75–)2 mm. lato, integerrimus (vel irregulariter incisus). Corolla sympetala, statu alabastri adulti (24–)30–31 mm. longa, in duabus tertiis inferioribus fusiformiter inflata ad 3 mm. lata, in tertia parte superiore subcylindrica, c. 1.5 mm. lata, apice obtusa, postea divisa usque ad dimidiam longitudinem in lacinias 6 lineares reflexas et volutas apice crassiusculas acutiusculas, facie interiore prope basin squamulis nullis. Filamentorum pars libera 3.5–4 mm. longa; anthera basifixa, 3.5 mm. longa, obtusa. Stylus corollae aequilongus (vel paulo longior), a basi ad apicem aequicrassus; stigma globosum, styli apice circiter sesquiplo crassius. Fructus ellipsoides, ad 8 mm. longus, 4 mm. diametro, calyce integro erecto paulum aucto coronatus.

San Cristóval Island: Waimamura, lowlands, on rain forest trees, *Brass* 2676 (type), Aug. 18, 1932, "plentiful, leaves very pale, corolla-tube white, segments pink, filaments pink, style green." Malaita Island: Quoimonapu, 200 m. alt., rain forest, *Kajewski* 2355, Dec. 12, 1930, "common, a large loranthus growing on the rain forest trees, base of corolla pink, ends of petals white cream." Ysabel Island: Tiratona, 600 m. alt., *Brass* 3227, Nov. 26, 1932, "common, leaves stiff, margins incurved; perianth reddish, with brown lobes." — Vernacular names "Oong" (under no. 2355), and "Buraronu" (under no. 3227).

Description after the type Brass 2676, the dimensions between brackets after Kajewski 2355, which mainly differs by shorter corollas 24–26 mm. long, and puberulous pedicels, bracts and calyces. The number Brass 3227 is much like the type, but the leaves are much smaller, including the petioles 2–5.5 cm. long and 1–1.6 cm. broad.

The new species does not show the articulation in the pedicel nor the scales at the inside of the corolla tube considered characteristic for the genus *Sogerianthe* till now. As, however, it has a 6-merous long-tubed sympetalous corolla and 3 bracts at the base of the flower, and moreover agrees with the species already known in general appearance, I do not hesitate to place it in the same genus with *S. sogerensis* (S. Moore) Danser and *S. sessiliflora* Danser.

DACTYLIOPHORA SALOMONIA Danser (a-b)
SOGERIANTHE VERSICOLOR Danser (c-e)

Dendrophthoë falcata (Linn. fil.) Ettingshausen in Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Cl. **32:** 53 (1872). — Danser in Bull. Jard. Bot. Buitenz. sér. 3, **11:** 403 (1931).

Loranthus falcatus Linn. fil., Suppl. 211 (1781).

Guadalcanal Island: Berande River, sea level, *Kajewski* 2415, Jan. 6, 1931, "common, a loranthus growing on rain forest trees, petals green-cream with orange edges, very showy, the largest fruit on specimens, the natives say are pretty full growth, length 1 cm., diameter 4 mm.; the natives use this plant superstitiously to stop rain by placing twigs upright in the ground." — Vernacular name "Ti-nu-issi."

Distribution: from tropical southeastern Asia all over the Malay Archipelago to tropical Australia, but before now not collected farther eastward than the Bismarck Archipelago.

For the very numerous synonyms cfr. Verh. Kon. Akad. Wetensch. Amsterdam, Afd. Natuurk., sect. 2, **29**, **6:** 44 (1933).

Notothixos leiophyllus K. Schumann in Schumann & Lauterbach, Nachtr. Fl. Deutsch. Schutzgeb. Südsee, 260 (1905). — Danser in Bull. Jard. Bot. Buitenzorg, sér. 3, **11:** 456 (1931).

Ysabel Island: Tataba, 50 m. alt., parasitic on branches of tall rain forest trees, *Brass* 3432, Jan. 4, 1933; "plentiful, small much branched shrub, leaves brittle, underside glaucous in old leaves, indumentum golden yellow."

Distribution: Philippine Islands, eastern part of the Malay Archipelago, Queensland, but before now not farther eastward than New Britain.

EXPLANATION OF PLATE 129

Fig. a and b: *Dactyliophora salomonia* (type, Kajewski 2497); a, twig with leaves and inflorescences in bud, × ½; b, fruit, × 1. Fig. c-e: *Sogerianthe versicolor* (type, Brass 2676); c, twig with flowers in bud, × ½; d, flower, × 1; e, fruit, × 1.

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CHROMOSOME NUMBERS IN THE HAMAMELIDACEAE AND THEIR PHYLOGENETIC SIGNIFICANCE

EDGAR ANDERSON AND KARL SAX

With three text figures

REINSCH[1] introduced his morphological survey of the Hamamelidaceae by the observation that they form one of those natural families as to whose precise delimitation and relationships there has been much difference of opinion. The forty years which have elapsed since the appearance of his paper have merely provided further illustrations of the justice of his remarks. Though universally conceded to be a natural group, the only general agreement as to its phylogenetic position seems to be the opinion that it occupies an important one. Because of this uniformly recognized phylogenetic significance an effort has been made to make as complete a survey of chromosome numbers as possible. The living collections of the Arnold Arboretum fortunately include several genera such as *Sinowilsonia* and *Parrotiopsis* which are very rare in cultivation but the work has been hindered by the very great technical difficulties involved. The chromosomes are small, there is much secondary pairing, the cytoplasm is murky and the chromosomes do not stain sharply. In most of these details the family shows cytologically a strong resemblance to the Rosaceae, paralleling the morphological resemblances which have been commented on by most students of the group.

The following chromosome counts have been made. The genera are arranged according to the classification of Harms in Engler and Prantl. In each case the counts were obtained from aceto-carmine smears. Typical meiotic plates are illustrated in Figure 1.

SUB-FAMILY HAMAMELIDOIDEAE		CHROMOSOME NUMBER
Tribe 1	Hamamelis vernalis	12
Tribe 3	Corylopsis pauciflora	12
	Corylopsis spicata	36
	Corylopsis Veitchiana	36
Tribe 4	Parrotiopsis Jacquemontiana	12
	Fothergilla major	36
	Fothergilla monticola	24
Tribe 5	Sinowilsonia Henryi	12
SUB-FAMILY LIQUIDAMBAROIDEAE		
	Liquidambar Styraciflua	15

[1]Engler in Bot. Jahrb. **11**: 347 (1890).

Meiotic irregularities, accompanied by a high percentage of pollen sterility were encountered in ***Liquidambar Styraciflua***. This is somewhat puzzling since this species exhibits none of the morphological peculiarities which are usually associated with irregular meioses. It is a "good" species with no closely related forms occurring within the same area. Its behavior is more probably to be explained as due to climatic influences. It is a southern species and at the Arboretum is being culti-

FIGURE 1. Camera lucida drawings (× 3000) of pollen mother cells: 1. Liquidambar Styraciflua. — 2. Parrotiopsis Jacquemontiana. — 3. Fothergilla major. — 4. Corylopsis pauciflora. — 5. Sinowilsonia Henryi. — 6. Hamamelis vernalis.

vated somewhat north of its natural range. Whitaker[1] has demonstrated the effect of abnormal temperatures upon meiosis in ***Cyphomandra***. It is possible that the irregular chromosome behavior and consequent pollen sterility of ***Liquidambar Styraciflua*** at the Arnold Arboretum may have a similar explanation. It would be interesting to know if ***L. Styraciflua*** is characterized by low percentages of fertile pollen in its native home.

The cytological studies present a number of facts of taxonomic significance. 1. The Hamamelidoideae are a coherent group with a com-

[1]Jour. Arnold Arb. **15**: 113–117 (1933).

mon base number. 2. The count on *Liquidambar* suggests that the Liquidambaroideae may possibly be derived from a different stock than the Hamamelidoideae since they apparently have a different base chromosome number. If this difference in base number should be found to persist in the other genus of that sub-family it would indicate that the divergence between the two sub-families occurred before the differentiation of the family as a whole. This is in accordance with the views expressed by Harms.[1] Summarizing the anatomical evidence he states[2] that the Hamamelidoideae are a unified group anatomically while the other subfamilies, particularly the Liquidambaroideae, have many distinctive peculiarities. Reviewing the entire evidence of relationship[3] he suggests that the Liquidambaroideae are so distinctive that they might well be considered a separate family.

3. Polyploid series have been found in *Fothergilla* and *Corylopsis* and are not to be unexpected in other genera of the family when these are investigated more extensively. This discovery is of some taxonomic consequence since it indicates that in such genera we may expect phylogenetic relationships between species which will be, in part at least, reticulate. That is to say that a complete phylogenetic tree of the genus *Fothergilla* or *Corylopsis* would show anastamosing branches. It will be noted that *Fothergilla monticola* has 24 pairs of chromosomes and is therefore a tetraploid and that *F. major* with 36 pairs is a hexaploid. The phylogenetic relationships within and between these two species, as indicated by these chromosome counts, must be intricate. These two species are so similar that it is very doubtful if *F. monticola* deserves more than varietal rank.[4] The cytological evidence would suggest that *F. monticola* is merely a tetraploid variety which arose spontaneously from the hexaploid species *F. major*. Such relationships are not unknown in other genera of the flowering plants. Erlanson for instance has shown[5] that *Rosa acicularis* var. *Sayi* (Schw.) Rehder is an octoploid race ($2n = 56$) of the hexaploid species *Rosa acicularis* ($2n = 42$).

To the larger problem of the phylogenetic position of the family itself this cytological survey contributes important evidence, though unfortunately not as decisive as the obscurity of the case requires. Before going into details it may be said that on the whole the cytological evidence favors Hutchinson's interpretation of the phylogenetic position of

[1] Engler Prantl Nat. Pflanzenf. 2. Aufl. **18a**: 303–345 (1930).
[2] loc. cit. p. 307.
[3] loc. cit. p. 316.
[4] Anderson in Arnold Arb. Bull. Pop. Inform. ser. IV, **1**: 61–64 (1933).
[5] Bot. Gaz. **96**: p. 231 (1935).

the Hamamelidaceae.[1] Comparisons of two treatments of the family are presented in Figure 2. The numbers in the diagram are the base chromosome numbers so far as they have been determined.[2, 3]

By inference and by actual experimental test two kinds of change of chromosome number have been established as occurring in the higher plants; (1) the addition of whole sets of chromosomes, that is of two

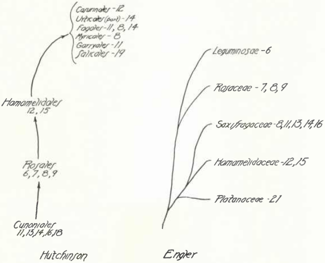

FIGURE 2. The phylogenetic position of the Hamamelidaceae, according to Hutchinson and Engler. The numbers are the basic chromosome numbers, so far as is known.

sets of six to make a 12 or the addition of an eight and a nine to make a 17; (2) the gradual stepping up or stepping down of the chromosome number by fusion and fraction of one or two pairs of the chromosomes in the previous set, that is, the derivation of an 11 chromosomed species from one with 12, etc. The whole subject is still in the experimental stage but it is at least far enough advanced to indicate that these two processes are among the main forces involved in the separation of genera in the higher plants. It will be seen that higher numbers may be derived

[1] The Families of Flowering Plants. I. Dicotyledons. Macmillan and Co., London 1926.

[2] Gaiser, L. O. in Genetic, 12: 161–320 (1930).

[3] Sax, K. Published and unpublished work on chromosome numbers.

from lower by either process or by both, but that lower numbers can be derived from higher ones only by the second. Everything else being equal, therefore, those genera with high base numbers will be farther out towards the tips of the phylogenetic net-tree than those with much lower numbers. In the present case the cytological evidence favors the view that the Hamamelidaceae with their base numbers of 12 and 15 are derived *from* the Rosales stock where base numbers of 6, 7, and 8 are characteristic. Another cytological fact points in the same direction.

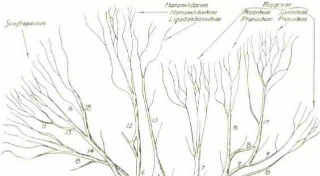

FIGURE 3. Phylogenetic relationships of the Hamamelidaceae as suggested by the cytological evidence. Numbers represent basic chromosome numbers. Further explanation in the text.

There is very strong secondary pairing throughout the family. As shown in figure 1, the chromosomes are not scattered equally over the plate but tend to be more or less grouped. This phenomenon which was first described by Darlington and Moffett[1] and which has been extensively studied by Lawrence[2] indicates that the chromosome complement under observation arose ultimately from the duplication of separate complements.

These facts, together with such other information as bears upon the subject, have been utilized in constructing the diagram in Figure 3. It

[1]Jour. Gen. **22**: 129–151 (1930).
[2]Cytologia, **2**: 352–384 (1931).

should be emphasized that the diagram is purely speculative. It has been worked out for those morphologists who would be interested in knowing how a cytologist with such information as is available would speculate as to the relationships of the groups involved. It might well be used as one of a set of possible working hypotheses by students of phylogeny. While the anastamoses of the main trunks of the Rosales stock represent supposed true-breeding allo-polyploid hybridizations, they do not necessarily indicate a cross between families as such. On any evolutionary hypothesis, related families derive, ultimately, from forms no more differentiated than present day genera or species. All that need be hypothecated for these hybrids is that they are between forms as diverse morphologically as certain hybrids which have been experimentally obtained, those between Zea and Tripsacum, for instance.[1] The diagram is based upon the evidence from chromosome number, secondary association and, in the case of the Pomoideae, from breeding experiments. It is much more speculative for the Saxifragaceae than for the Rosaceae. The Saxifragaceae, with base numbers of 8, 11, 13, 14, and 16 show a cytological complexity[2] paralleling their morphological diversity. Only a few of the fossil "dead branches" have been indicated. There must certainly have been many more. In this respect as in several others the actual details of the diagram are probably incorrect. The general conception, however, of a more or less webbed net-tree for the Rosales is strongly supported by the cytological evidence. In some other groups of the flowering plants (the Tubiflorae, for instance) the webbing would be so much more complex that one would scarcely use the word tree in describing it. In the Cyperaceae, on the other hand, there would be few if any anastamosing branches. The cyto-genetic evidence shows with increasing force that the actual pattern of evolutionary progress has been different in different groups of plants. The main point of the diagram in figure 3 is to suggest the general nature of the evolutionary pattern of the Rosales.

SUMMARY

1. Chromosome counts are given for nine species and six genera of the Hamamelidaceae.

2. The phylogenetic position of the family is discussed in the light of these results.

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[1]Mangelsdorf & Reeves in Jour. Hered. 22: 329–343 (1931).
[2]Sax, K. in Jour. Arnold Arb. 12: 198–206 (1931).

CHROMOSOME STRUCTURE IN THE MEIOTIC CHROMOSOMES OF RHOEO DISCOLOR HANCE

KARL SAX

With plates 130 and 131

COILED CHROMONEMATA have been observed in both mitotic and meiotic chromosomes in various species of plants. The degree of coiling in mitotic chromosomes may vary from an irregular corrugation or loose spiral to a rather compact regular coil. At meiosis in certain plants the coils are much larger and can be analyzed in more detail.

The behavior of the meiotic chromosomes of *Rhoeo discolor* provides additional information regarding the nature of the coiled chromonemata. The observations are based on both aceto-carmine preparations and permanent smears fixed in Flemming's solution. In both cases the microsporocytes, after smearing, were usually pretreated with alcohol and ammonia before fixing. Immersion in tap water for a few seconds and a brief exposure to ammonia fumes also gave good results. This is essentially the method used by Kuwada. The ammonia vapor seems to dissolve the chromosome matrix and permit the spiral chromonemata to expand.

The chromosomes of *Rhoeo* are arranged in a ring or one or more chains at the first meiotic division. At early metaphase each chromosome contains a coiled chromonema consisting of two closely associated chromatids. The general appearance of these rings is shown in the photographs from aceto-carmine preparations (Figs. 1 and 2), but the finer details are best observed in permanent smears (Figs. 3 and 4). The number of coils is four or five per chromosome. At this stage the two chromatids are so closely associated that the coils appear to be single, but their double nature can be observed at certain loci. The diameter of the coil decreases gradually before the separation of the chromatids.

At late metaphase the coiled chromatids separate. The number of coils in each chromatid remains the same, but they are much smaller, even though there is little or no elongation of the chromosome as a whole (Figs. 5 and 6). At this stage both the terminal chiasmata and the fiber constrictions are very conspicuous, so that the order of the individual chromosomes in the ring can be determined. As observed earlier (Sax 1931), the order of the twelve chromosomes is always the same, thus supporting Belling's suggestion that such rings are the result of segmental interchange. Six of the twelve chromosomes are distinctly heterobrachial, and the short arms are paired.

The meiotic chromosomes are always paired by terminal "chiasmata" and, in the chromatids at late metaphase, most of the chiasmata appear to be symmetrical. The chromatids are often parallel in several successive chromosomes or even in most of the chromosomes in the ring.

As the chromosomes pass to the poles at the first meiotic division, the chromatids separate except at the fiber constriction and become shorter (Fig. 7). During interphase the chromatids elongate considerably. At the second meiotic division they are about twice as long as they were at the first division. At this time the minor or somatic type of coiling can be observed. The coils are only about half as wide as the major coils found in the first division, and the number of coils is about 12 per chromatid (Fig. 8). These coils appear to be single at metaphase. There is some evidence of a split at late anaphase, as indicated by narrow regions at certain loci. If the chromatids are split at second metaphase, the two halves must be coiled together. At late anaphase they may tend to separate, but the slipping apart of the coils is difficult to detect except where there is a twist which appears to constrict the chromosome at such loci. More definite evidence of split chromatids has been obtained from microsporocytes which were subjected to low temperatures during development.

Under normal conditions the microspores receive six chromosomes, but occasionally there are seven, owing to irregularities in the first meiotic division. About 80 per cent of the microspores fail to develop, owing to segmental non-disjunction. The normal fertile microspores undergo a single nuclear division, followed by the differentiation of the daughter nuclei into the large and more or less degenerate tube nucleus and the compact elongated generative nucleus.

When the plants are kept at a temperature of about 6° C., two kinds of abnormalities appear. The chromosomes of the one nucleate microspore may divide but do not form daughter nuclei. The 12 chromosomes pass back into the resting stage and divide regularly at the next division to form diploid gametes. The other type of abnormal development begins when the low temperature inhibits chromosome pairing at meiosis. The twelve univalent chromosomes pass into the resting stage without nuclear division. They come out of the resting stage, divide without nuclear division and form a giant nucleus with 24 chromosomes, each of which consists of two coiled chromatids held together only at the fiber constriction (Fig. 9). Throughout this process the chromosomes never pass through the contraction characteristic of normal telophase stages.

The chromatid spirals are much looser than those found in the chromatids of the normal chromosomes at the second meiotic division, and it is perfectly clear that many of these chromatids are split. The splits are especially clear near the ends of the chromatids. At a somewhat later stage the two chromatids become completely separated, the chromatids elongate, and their structure is very clear. In the same chromatid one can observe the transition from a single coil to two parallel finer coils (Fig. 10). The mechanism of separation of daughter chromatids in these chromosomes, which are essentially of the somatic type, is similar to that found in the coiled chromatids in the first meiotic division.

The structure of the meiotic chromosomes in the permanent preparations was clear enough to permit an analysis of direction of coiling in the spiral chromonemata. We were able to determine the direction of coiling at all loci in each of the twelve chromosomes in 14 cells with complete chromosome rings. The classification of right- or left-handed spirals is purely arbitrary, since the direction depends on the sequence of determination in the ring. There is a strong tendency for the direction of coiling to be in the same direction in both arms of a chromosome. Of the 168 chromosomes examined, 50 had a right-handed spiral in both arms, 52 a left-handed spiral, and 66 showed a reversal of coiling, presumably at the fiber attachment. In only two chromosomes was there a second change of direction of coiling. Individual chromosomes could not be identified consistently, so that the direction of coiling could not be established for any one chromosome in all the different cells, but there is good evidence that direction of coiling is not a stable character. The number of chromosomes with left-handed coils ranged from 1 to 5, with reversed coils from 2 to 8, and with right-handed coils from 1 to 7, in different cells. The direction of coiling of chromonemata of paired adjacent chromosome arms is at random, with 85 coiling in the same direction and 83 coiling in reverse directions.

Both rings and chains of chromosomes are found at meiosis. If one or more chains are formed, the breaks may occur between either the long segments or the short segments. Three of the terminal chiasmata are formed between short segments, and eight of the terminal chiasmata are formed between long segments. The extra chiasma is between a long and a relatively short segment. The position of the breaks, or failure of chiasma formation, was obtained for 20 cells containing one or more chains. There were 9 breaks between the short segments and 16 between the long segments. These results suggest that chiasma formation is somewhat less likely to occur, or less likely to persist until late metaphase, between the short segments. The latter possibility is more probable because we have found chromosome rings in practically all cells in some preparations.

The lengths of the chromosomes at different stages in meiosis were obtained to aid in the analysis of factors involved in chromosome contraction. It was not possible to get an accurate measurement of the length of the pachytene spireme in *Rhoeo,* but the total length is approximately 700 microns or an average of somewhat more than 100 microns per chromosome. The approximate average chromosome length at meiotic metaphase is 5–6 microns, and is about 9 microns at the second meiotic division.

The Mechanism of Chromosome Contraction

The great contraction in chromosome length between pachytene and meiotic metaphase stages in *Rhoeo* is associated with the coiling of the chromonema. This coiling may not be the only factor involved. Belling (1928) believed that the approximation of chromosomes caused about one-third of the contraction in the chromosomes of *Lilium,* and that the coiling of chromonema effected the final shortening to give approximately a 10 to 1 reduction in length of the meiotic chromosome. Bridges (Alexander, 1928), on the other hand, assumed that coiling is the primary factor in chromosome contraction, and that the gene string maintains approximately the same length at all stages in the chromosome cycle. Another factor in chromosome contraction is the secondary or minor coils within the primary or major coils as described in *Tradescantia* by Fujii, Kuwada and Nakamura (1933) and found in *Sagittaria* by Shinke (1934).

We believe that three factors are involved in the great decrease in length of the meiotic chromosomes of *Rhoeo;* first, a linear contraction of the gene string; second, the major coiling of the chromonema; and third, the formation of minor spirals within the major spiral. The minor coils are not clearly differentiated at the first meiotic division in *Rhoeo,* but there is some evidence of loose coiling. The contraction of the chromonema and reduction in the width of the major coils between early and late metaphase are attributed to the further coiling of the minor spirals in each chromatid. A similar reduction in the major coils with no increase in chromosome length is found in *Secale* (Sax, 1930).

The coiled chromonema at early metaphase consists of two chromatids coiled together so that the chromonema often appears as a single coil, as is the case in *Tradescantia, Secale, Lilium,* and *Vicia.* The free separation of coiled chromatids has been explained by Kuwada (1927).

The reverse twists postulated by Kuwada can be observed in *Tradescantia* (Sax and Humphrey, 1934) and in *Trillium* (Huskins and Smith, 1935).

The direction of coiling in the chromonema spirals is more or less at random in *Rhoeo* and in *Tradescantia* (Nebel, 1932, Sax and Humphrey, 1934). According to Huskins and Smith, the paired meiotic chromosomes of *Trillium* usually coil in opposite directions, although no statistical evidence is presented, nor is there any adequate explanation for such behavior. Within a single meiotic chromosome the direction of coiling may change at the spindle fiber point, but is seldom reversed at other loci in *Rhoeo, Secale, Gasteria* (Taylor, 1931), *Tradescantia,* and *Sagittaria* (Shinke, 1934). Huskins and Smith find frequent changes in direction of coiling of anaphase chromosomes in *Trillium*. These changes in direction of coiling are usually associated with chiasmata. We have found changes in direction of coiling at chiasmata in the meiotic chromosomes of *Vicia*. If the chromonema coiling is caused by a contraction of the matrix, as suggested by Kuwada, the fiber attachment points and the chiasmata would tend to break any continuity of stress on the chromonema and changes in direction of coiling would be expected to be more or less at random at these points. There is a strong tendency, in both *Rhoeo* and *Tradescantia,* for the direction of coiling to be the same on both sides of the spindle fiber attachment, and only about one-third of the chromosomes show reversal of coiling at this locus. Huskins and Smith find that the reversals in direction of coiling between the fiber attachment and the distal ends of the chromatids at first anaphase is about twice the chiasma frequency at metaphase. This relation would be expected if the direction of coiling in homologous chromosomes is at random, and if reversals in coiling occur at random at the chiasmata.

In *Rhoeo* all chiasmata are terminal, and most of them appear to be symmetrical. The short chromosome arms are paired almost as frequently as the long arms. Changes in direction of coiling are rarely observed between the fiber and the distal end of the chromosome. These observations seem to indicate that chromosome pairing in *Rhoeo* is not dependent on the formation of interstitial chiasmata, but is dependent on a terminal association of homologous chromosome segments. This terminal association in certain rod bivalents in *Tradescantia* seems to involve the chromosome pellicle or matrix, but in *Rhoeo* there is evidence of fine chromatic connecting fibers.

During interphase the meiotic chromosomes of *Rhoeo* elongate but maintain some evidence of loose coils during the resting stage. At the second meiotic division, a new spiral appears which has finer and more numerous spirals than the major coils at the first meiotic division. These minor spirals have been described in *Lilium, Rhoeo, Allium, Tricyrtis, Najas,* and *Hosta* by Shinke (1930), and in *Tradescantia* by Nebel (1932), Kuwada and Nakamura (1933) and Sax and Humphrey (1934). These coils in *Rhoeo* are wider than the minor spiral within the major spiral at the first meiotic division and presumably are formed independently during the prophase of the second meiotic division. These spirals are much like those found in certain somatic chromosomes. The transition from about five major spirals to 20–25 minor spirals in the successive meiotic divisions in *Tradescantia* and a similar behavior in *Rhoeo* is difficult to reconcile with the "heterogonic growth" hypothesis of spiralization suggested by Huskins and Smith.

The anaphase chromosomes at the second meiotic division have been described as two-parted in a number of plants (*Gasteria,* Taylor, 1931; *Galtonia,* Smith, 1932; *Tradescantia,* Nebel, 1932; *Trillium,* Huskins and Smith, 1935; et al.; Cf. Sharp, 1934). Both Kuwada and Nakamura, and Sax and Humphrey found only single coils in the second anaphase chromosomes of *Tradescantia*. In *Rhoeo* there is evidence that the anaphase coil is double, but that the two half-chromatids are coiled together so intimately that they appear as a single coil at early anaphase. As the coils begin to separate the gyres are matched so closely that the dual structure is not clear, but where a twist occurs there is a narrow region in the chromosome. The abnormal "microspores" of *Rhoeo* show the chromatid splits clearly in various stages of separation. The minor coils, characteristic of somatic chromosomes, are similar in structure to the major coils; the two chromatids (or half-chromatids) are coiled together in parallel in such a manner that they can separate freely without entangling. If the split occurs while the chromosome is coiled, there must be some lateral polarity so that the division occurs in only one plane parallel to the axis of the chromosome, as Nebel (1933) has suggested.

If there is a chromatid split in the anaphase chromosomes of the second meiotic division in *Tradescantia,* the chromatid must behave as a single unit until midprophase of the microspore division. Tradescantia microspores subjected to x-rays show chromatid breaks for about two days after raying, but after three or four days only chromosome breaks are observed at metaphase (Riley—unpublished).

We find that either abnormally low or high temperatures will cause nuclear irregularities. These include failure of chromosome pairing at meiosis, chromosome division without nuclear division, and failure of normal differentiation of nuclei. Since these temperatures are within the range occasionally experienced in nature, it is probable that temperature fluctuations have played an important part in chromosome changes in nature (Cf. Randolph, 1932). This work with temperature effects has been aided by a grant from the American Academy of Arts and Sciences.

SUMMARY

The twelve chromosomes of *Rhoeo discolor* are arranged in a segmental interchange ring at the first meiotic division. Each chromosome contains a spiral chromonema consisting of two chromatids coiled together. There is some evidence, both direct and indirect, that there is a minor spiral within the chromatids of the major spiral. During metaphase the major spirals become smaller, and the two chromatids separate. The chromosomes elongate greatly during interphase, but there is evidence of a spiral structure during the resting stage. At the second meiotic division, new minor spirals are formed which are smaller and more numerous than the major spirals of the first division. The chromatids at anaphase of the second meiotic division are split, but the two half-chromatids are so closely coiled together that they are not easily observed. They can be differentiated easily in cells where the normal chromosome cycle is disturbed by subjection to low temperatures.

The reduction in the length of the meiotic chromosomes of *Rhoeo,* between prophase and first metaphase is attributed to three factors:—a linear contraction of the gene string, the coiling of the chromonema into major coils, and the development of minor coils in the chromatids of the major spirals. The direction of coiling in the major spirals seems to be at random. In a single chromosome the direction of coiling may change at the fiber attachment point, but it is seldom reversed at other loci.

The meiotic chromosomes are paired at the ends, apparently without the formation of interstitial chiasmata.

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EXPLANATION OF PLATES

PLATE 130

Meiotic chromosomes of *Rhoeo discolor*. Figs. 3 and 4 from permanent smears. All others from aceto-carmine preparations. × 2000.

Figs. 1 and 2. The coiled chromonemata in the chromosome ring at early metaphase.

Figs. 3 and 4. Coiled chromonemata showing reversal of coiling and reduction in width of coiling at metaphase.

Figs. 5 and 6. Separation of coiled chromatids at late metaphase. The same number of coils are found in the coiled chromatids as in the coiled chromonemata, but the spirals are smaller.

Fig. 7. Telophase of first meiotic division.

Fig. 8. Chromosomes at the second meiotic division showing minor spirals which appear to be single.

PLATE 131

Chromosomes from abnormal "microspores" produced by chromosome multiplication induced by cold treatment. Magnification × 2000.

Fig. 9. A giant cell derived from a microsporocyte by chromosome division without nuclear division. Each of the 24 chromosomes consists of two chromatids held together at the fiber attachment. Many of the chromatids are split.

Fig. 10. Chromatids at a somewhat later stage showing the transition from a single coiled chromatid to two coiled daughter chromatids.

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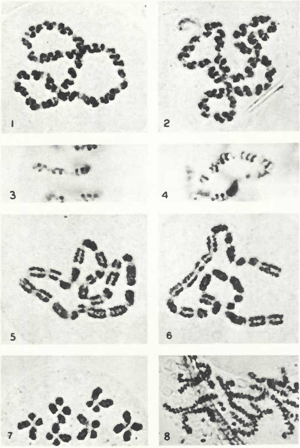

CHROMOSOME STRUCTURE IN MEIOTIC CHROMOSOMES
OF RHOEO DISCOLOR

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10

Chromosome Structure in Meiotic Chromosomes of Rhoeo discolor

ELAIOPLASTS IN IRIS: A MORPHOLOGICAL STUDY

ANNA F. FAULL

With plates 132 to 137

INTRODUCTION

ELAIOPLASTS are a heterogeneous group of intracellular bodies presenting the characteristics of fatty substances to a marked degree but not recognizable as ordinary types of plastids, chondriosomes or vacuoles. There is no general agreement in the literature regarding their structure, origin, development, classification or chemical composition. They have been variously described as aggregations of lipoid globules, as modified or unusual types of plastids or vacuoles, as nuclear derivatives, as aggregations of mitochondria-like bodies or as independent structures. They have been linked with various physiological processes such as assimilation, excretion or degeneration.

Much of the confusion regarding elaioplasts is due to the use of inadequate techniques and to a consequent lack of accurate information about the early developmental stages of these bodies. Many of the discrepancies are also due to failure to visualize and interpret correctly the full range of morphological variability of chondriosomes and plastids.

The investigations described in this paper were undertaken to clarify our conception of the elaioplasts in *Iris* and to compare these bodies with those in other monocotyledons and in liverworts. By using an improved technique critical evidence has been obtained to show the early stages in the development of the elaioplasts in *Iris* and the changes which these bodies undergo in different tissues and at different seasons.

In addition to the morphological study an extraction and preliminary analysis of the so-called oil in the elaioplasts of *Iris* and some physiological experiments on the metabolism of two types of Iris rhizome, one of which contains abundant elaioplasts, have been made. The results of these investigations are being published elsewhere.

HISTORICAL RÉSUMÉ

Since the middle of the last century papers have appeared from time to time describing cytoplasmic bodies associated with oil. The writers have used various names for these structures which through usage have become more or less interchangeable. Thus they are termed elaioplasts, oléoplasts, oléosomes, ölkörper, oil bodies, Zellenbläschen, Zellenkörper, fatty bodies, elaiosferer, oelplastids, oléoleucites, éléments oléifères and système oléifère. Sometimes the terms are restricted in their application. For example ölkörper is used only for oily bodies in the liverworts, and elaioplast is kept for those in the monocotyledons. But recently with an increasing tendency to consider all of these oily bodies essentially similar, one name is often used to designate all of them.

The earliest references to elaioplasts are found in the writings of Mirbel (35) in 1835, of Gottsche (13) in 1843, of Holle (24) in 1857, of Hofmeister (23) in 1867 and of Ward (49) in 1883. But the first adequate descriptions of oil bodies were published in papers by Pfeffer (38) in 1874 and by Wakker (47) in 1888. These, together with a paper by Lidforss (32) in 1893, provide a description of the three main types of mature oil bodies; from this later authors have diverged little. Although often resembling one another, the three main types present certain distinct features which are further emphasized by their restriction to a given group of plants.

Pfeffer (38) described oil bodies characteristic of the liverworts. In common with such bodies in general, they are highly refractive structures which stain brilliantly in "fat" dyes, such as alkannin, and which are more or less soluble in 95% alcohol and in fat solvents such as ether. They are distinguished from other oil bodies by their almost complete solubility in alcohol, by a characteristic residual ring left after treatment with alcohol, by their location commonly in the peripheral cytoplasm but within the chloroplast-bearing layer, by their presence in practically every species of the group, by their appearance commonly in every cell of a plant and by their permanency as cell structures. The Marchantiales present a contrast to other elaioplast-bearing hepatics in the restriction of the oil bodies to special cells scattered throughout the thallus and in the location of a single large oil body in the center of each of these cells. Oil bodies in the liverworts vary in shape from round to spindle-shaped as a rule, though some are irregular in form. They vary in color from colorless to dark brown and in appearance from granular to segmented or homogeneous.

The oil bodies described by Wakker (47) differ from those in the liverworts in their location near the nucleus, in their invariably granular appearance, in their often irregularly lobed shape, and in their character of being more or less temporary cell structures. Elaioplasts of this type are often yellowish in color and are marked by their reaction with some reagents which cause an extrusion of the oil and leave a characteristic net-like structure. Although reported from most tissues, they are often restricted to certain ones. Raciborski (41) and Beer (4) found them only in flower or fruit tissues, while Politis (39) described them in these tissues and in those of bulbs. Oil bodies of this type are further restricted to a few groups of flowering plants. Lists published by Zimmermann (51) and by Politis (39) record them in groups of species in the Orchidaceae, Liliaceae, Amaryllidaceae, Iridaceae and Malvaceae, while Beer (4) found them in one of the Compositae.

The third type of oil body described by Lidforss (32) is characterized by its homogeneous appearance, by its spherical shape and by its unrestricted location in the cell. It is reported from leaf tissues of flowering plants and is of common occurrence in this group.

Besides these three classes of oil bodies there are isolated descriptions of elaioplasts that are not included in any of the types described. Such are the reticulate, highly refractive structures saturated with an amber-colored oil described by Keene (26, 27) in two molds. Such also are the yellow, green or black oil bodies near the nucleus found by Hieronymus (22) in some algae.

In 1888 Wakker (47) demonstrated by abnormal plasmolysis that the oil bodies in the monocotyledons and in the liverworts are located in the cytoplasm. He showed that, although these structures often protrude into the vacuole, they are never located in it as Pfeffer (38) and Rattray (42) had thought. Later investigations have substantiated Wakker's observations and extended them to include all types of elaioplasts.

There is no general consensus of opinion on the structure of the non-homogeneous oil bodies. Pfeffer (38) described them as aggregations of homogeneous oil globules, a view expressed in modern times by Guilliermond (20), by Meyer (34) and by Kozlowsky (28). Other students have described a stroma with embedded oil globules. This view was first expressed by Wakker (47). It was elaborated upon by Zimmermann (51), who pointed out less refractive inclusions which he termed vacuoles or portions not producing oil. Later Beer (4) and Politis (39) described the elaioplasts in *Gaillardia* and in the monocotyledons as aggregations of smaller bodies, each composed of a stroma with included oil globules. A more elaborate structure was postulated by Woycicki (50) and by Keene (26, 27). Woycicki described elaioplasts in *Vanilla* with central oily drops surrounded by a mucilaginous layer which in turn was covered by a granular layer. Keene described a somewhat similar structure in the oil bodies of *Sporodinia* which showed a denser reticulate center and a coarser reticulate outer portion. The presence of an unfixable stroma in the oil bodies of the liverworts in contrast to the fixable one in those of the monocotyledons was pointed out by Küster (29). Later Gargeanne (9) and Dombray (7) attempted to show that this unfixable stroma was a fluid or a semi-fluid.

The question of an enveloping membrane has been raised with reference to the oil bodies in the liverworts. Pfeffer (38) inferred the presence of a membrane from the characteristic ring left after treatment with alcohol. Küster (29) demonstrated in 1894 that this ring is an artefact. Gargeanne (9) repeated the demonstration but maintained that, although the ring is an artefact, the bodies possess a true membrane homologous with the tonoplast of the vacuole. Later writers have not agreed with Gargeanne in recognizing a membrane. The presence of a membrane about elaioplasts in the monocotyledons has been described only by Raciborski (41) who considered the stroma at times to be reduced to a surrounding layer.

The development of the oil bodies is also a disputed point in the literature. Pfeffer (38), Rivett (43), Lidforss (32), Chalaud (5), Meyer (34) and Guilliermond et al. (20) have considered the formation of elaioplasts to be a process of aggregation of small drops in the cytoplasm with more or less fusion. Kozlowsky (28) has further stated that the drops are first extruded from the chloroplasts. A second theory has been postulated by Wakker (47), by Küster (29) and by Harper (21). They consider that a stroma appears first as a shadowy, wrinkled structure in which refractive oil drops appear later. Gargeanne (9) stated that the oil drops are secreted by a surrounding membrane, while Dombray (7) described the deposition of substances from the cytoplasm and their transformation by the cell sap as a catalyser. Another theory is expressed by Hieronymus (22) and by Beer (4) who described elaioplasts formed by the aggregation of degenerating plastids with the production of oil. Somewhat similar is Woycicki's (50) theory of the aggregation, partial degeneration and fusion of mitochondria-like bodies forming oil. Keene (26, 27) postulates the formation of a reticulate structure in homogeneous bodies with the later fusion of several of these bodies. Still another theory by Politis (39) and by Raciborski (41) describes the development of elaioplasts by the growth of refractive drops and the subsequent fusion of the bodies so formed.

The division of elaioplasts has been noted in a few instances. Raciborski (41) in 1893 described a fragmenting of the bodies after they had passed maturity and a breaking off of bud-like protrusions. Again in 1914 Politis (39) described division of the elaioplasts. Politis considered division not merely an incidental or degeneration phenomenon, but a method of increasing the number of these bodies. Besides the budding already described by Raciborski, Politis described passive division of the body by the cell wall during cell division.

The history of oil bodies after they have reached maturity has been studied. In the liverworts they are generally thought to remain unchanged even after the death of the cell, although Dombray (7) noted a decrease in size, fusion of the oily globules and aggregation of the oil bodies before death. Elaioplasts in the monocotyledons are generally thought to degenerate some time after reaching maturity. Wakker (47) described their disappearance in older tissues of *Vanilla*. Beer (4) and Woycicki (50) described a resolution of the oil bodies into scattered oily spheres. Politis (39), on the other hand, described the disappearance of the oil first, leaving a vacuolated protein mass which might later disappear also.

Movement has been noted in connection with elaioplasts. In 1893 Zimmermann (51) first recorded the rotation at times of oil bodies in the monocotyledons, a phenomenon observed also by later investigators. A second type of motion consisting of Brownian movement of the globules within the oil bodies appears in oily structures in the hepatics. Gargeanne (9) described this as an injury phenomenon, but recently it has been noted by Dombray (7) as a normal condition in the elaioplasts of some species.

The chemical composition of the elaioplasts and particularly of the oily portion has received much attention. The theories advanced are based chiefly upon microchemical reactions. Dombray (7) has interpreted microscopical observations in the light of analyses of extraction products. Two opposing theories regarding the composition of the oil have been formulated. In one the oil is said to be chiefly a mixture of essential oils. This is the view recently expressed by Popovici (40) and by Rivett (4) in her description of the oil as a mixture of essential oils with small amounts of protein and fatty oils. Dombray (7) stated that the oily substance was a mixture of essential oil and "tannoides." The opposing theory considers the oil to be composed chiefly of fatty oils. This is the opinion of most investigators. Pfeffer (38) described the oil as a mixture of fatty oil with some water and protein and with traces of wax and resins. Later Küster (29) designated the oil in the elaioplasts of liverworts as a fatty oil resembling castor oil. Lidforss (32) identified the oil in the homogeneous oil bodies of flowering plants as a non-drying oil containing fatty acids of the type $C^n H_{2n-2} O_2$. The stroma, if present, is generally considered to be a protein, a view first expressed by Zimmermann (51).

There is little agreement among investigators concerning the origin and identity of oil bodies. Raciborski (41), Küster (29) and Gavaudan (10, 11, 12) have considered them to be cell systems independent of the vacuome, chondriome or plastidome and originating more or less *de novo* in the cytoplasm. Wakker (47) considered them to be special plastids, while Beer (43) and Hieronymus (22) described them as degenerating plastids. Kozlowsky (28) has stated that they are products of the chloroplasts. That they are special or transformed vacuoles has been postulated by Keene (26, 27), by Dombray (7), by Gargeanne (9) and by Rivett (43). Woycicki (50) and Lundström (33) have described oil bodies originating from mitochondria-like bodies. Politis (39) has ascribed a nuclear origin to them.

A relationship between elaioplasts in the monocotyledons and crystal formation has been suggested. Wakker (47), Politis (39) and Monteverde (36) stated that there is no connection between the oil bodies and the calcium oxalate crystals found in the same plants. But Warlich (48) considered them to be interdependent structures, while Woycicki (50) in 1929 described crystals forming in some of the elaioplasts in *Ornithogalum*.

Many writers have ventured theories on the physiological and biological significance of the oil bodies. In general they have considered those in the liverworts and also the homogeneous ones in the flowering plants to be excretions. But those in the monocotyledons they term assimilation products, although Raciborski (41) stated them to be excretions. Various other theories have been offered. Beer (4) in 1909 demonstrated that the bodies in *Gaillardia* are degeneration products of the plastids with the secondary function of producing color. Hieronymus (22) and Lundström (33) suggested that the bodies are protective in function, a theory opposed by Dombray (7).

In concluding the summary of the literature on oil bodies it should be noted that these structures do not include the ölplasma described by Leiner (31) and by others of Tschirch's school, nor do they include the oil cells described by Lehmann (30) and others. The former (ölplasma) deals with oil in the cytoplasm — chiefly of fatty seeds. The subject is well summarized in the account by Tunman and Rosenthaler (46). The phenomenon of the appearance of oil in special oil cells involves the transformation of large portions of the cytoplasm or secretion from the modified cell wall rather than the appearance of oily bodies in the cytoplasm.

In addition to the literature on oil bodies, some reference should be made to the literature on the structure of Iris cells. The most recent and complete studies are those by Guilliermond (15–20) and by Dangeard (6). They have developed a method of vital observation especially adapted to this type of study. They have pointed out the presence in Iris cells of vacuoles and their inclusions, of cytoplasm, of oil globules, of chondriosomes of various types and of plastids. In particular Guilliermond has described the chondriosomes and plastids and their developmental stages. He has noted the presence of oil globules in most plastids and chondrioconts in *Iris*. These globules which he has found associated more often with young or degenerating types of plastids he considers to be lipoids separating out from the plastid substance. He has described the development of plastids from mitochondrial types differentiated from other mitochondria by their potentiality for plastid formation. He has described the formation of chloroplasts from an intermediate chondriocont stage by budding and fragmenting. Other phases of studies carried out on *Iris* include the action of hypo- and hypertonic solutions on chondriosomes, observations of the amoeboid movements of chondrioconts, and the identification of an oily body in the vacuoles of certain cells as a phenol compound.

MATERIAL

The plants used in my studies of elaioplasts included numerous irises, some liverworts and a few representative flowering plants. They were obtained from several sources. The major part of the study was made on colonies of *Iris versicolor* and of an *Iris pallida* of hybrid origin which grew in abundance near the laboratory. For work on living tissues it was desirable to have the plants as close at hand as possible. It was also desirable to locate single colonies in a natural habitat for the basic study of variations. In this way differences due to season, development, etc., were less likely to be confused with those due to location, to abnormal habitat or to individual variations.

As a rule the material was used as soon as it was collected. But in some instances it was kept in water or in wet sand in the greenhouse for later observations, or it was transplanted to garden beds. In the early part of the study a few plants of *I. pallida* and of *I. versicolor* were transplanted to pots in the greenhouse to supplement the outdoor material. Although some interesting observations were made on these plants, they grew so poorly that this method of providing material was abandoned. Fortunately, it was not necessary to rely on greenhouse or garden material at any period.

The *Iris versicolor* was taken from a swampy field at the corner of Weston St. on the Cambridge-Concord turnpike about an hour's drive from the laboratory. The *Iris pallida* hybrid, a garden plant, grew in beds within a few rods of the laboratory. Both of these species were sufficiently near at hand to be obtained as they were needed for examination.

The other irises used as supplementary material and for a general survey of the genus were obtained from several places. A group of native West Coast species was studied in California. Three of these, *I. macrosiphon, I. Douglasiana* and *I. longipetala,* grew naturally within a few hours' drive of the laboratory. But *I. Hartwegii* and *I. missouriensis* had to be brought to Palo Alto from the eastern part of the state. A large number of other species were obtained from the Missouri Botanical Garden, from the Brooklyn Botanical Garden and from the New York Botanical Garden. Those at the Missouri Garden were examined *in situ,* but the ones from New York were brought to Boston for examination.

For a list of the species of *Iris* studied see the table on page 246.

In addition to the Iris plants, a group of rhizomatous plants and a number of liverworts were obtained. The former were studied at the Missouri Botanical Garden for the most part, although a few were collected around Boston. Two species of *Vanilla,* the plant used by Wakker (47) in his classical studies on elaioplasts, were obtained from Panama. The liverworts were collected in the New England woods for study in Boston or they were sent from Oregon to the California laboratory for use there. The hepatics were kept in the laboratory in moist glass containers over a period of weeks.

A list of the flowering plants studied is given on page 248 and one of the hepatics on page 254.

TECHNIQUE

In choosing a method for the morphological examination of the elaioplasts one fundamental requirement was kept in mind. It was desirable to observe the bodies in as unaltered a condition as possible in order to discover their normal development and variations due to seasonal, environmental or specific differences in the plants examined.

At the present time there are two methods used in the study of cytoplasmic bodies. The first of these is the fixation technique introduced in the later decades of the nineteenth century and developed to the highest degree in the complicated "mitochondrial techniques" and "silver or osmic impregnation methods." Essentially it consists of killing and fixing blocks of tissue in reagents that solidify proteins and fats, rendering them insoluble in specific fluids, and then staining sections differentially. Incidentally the technique involves a rather complicated process of embedding and one or more dehydrations.

The other method is that of examining untreated tissue either with or without the aid of vital dyes. Although untreated tissue was used before the introduction of fixatives, it was superseded by them. Recently the so-called vital technique has been revived and developed, notably by the Dangeards and by Guilliermond in France and by Bailey in America. Guilliermond has described a technique for vital staining in his studies of the vacuome and has contributed data on various aspects of injury and death in his studies of the chondriome. Bailey (1) in his investigations of the cambium has tabulated criteria that can be used in distinguishing living from dying or dead cells. Bailey and Zirkle (2, 3) have clarified the vital staining technique by their investigation of the toxicity of a large number of dyes, of the most suitable media in which to use the stains, of the staining properties of different dyes and of the varying reaction of vacuoles to given stains.

Both of these methods were tried in the study of ***Iris,*** but that of fixation was eventually discarded because of the difficulties involved. The vacuoles in the rhizome were found to contain large quantities of a substance that precipitated with fixatives and stained deeply, obscuring the sections, while the elaioplasts in the rhizomes of ***Iris versicolor*** contained quantities of "oil" that either was dissolved or was extruded in large masses obscuring the cell structure. In the one or two instances where this did not occur, a good fixation was obtained in mature but not in meristematic cells. The fixation images in sections of rhizome meristem were not comparable with those obtained in root-tip meristems, nor could they, as in the case of the root-tips, be identified with structures clearly seen in similar "living" cells. A third difficulty, that might in time have been overcome, lay in the persistent plasmolysis of cells in the rhizome meristem and in leaf tissue. For these reasons it was felt that the fixed material did not give an image of unaltered cells, nor could it be relied upon for comparative work. Better results were obtained with the "vital" technique where dead and dying cells could be observed and where those that survived for some hours without undergoing lethal changes seemed to present a more reliable picture of an unaltered condition. Consequently after some months of unsuccessful experimenting with fixatives and dehydrating reagents and with different hydrogen ion concentrations of single fixatives, the method was entirely abandoned and the "vital" technique alone retained.

Although fixation methods were finally discarded, it should be noted that in certain instances satisfactory results were obtained in this way. Thus the mitochondrial fixatives and stains proved successful for root-tips where they apparently produced little or no alteration in the cell structure. Likewise, since chromic and osmic acids fixed the elaioplast "oil," occasional slides were obtained of mature rhizome tissue quite comparable with that examined "vitally." Other fixations, although they did not give exact images of the cytoplasmic contents of the cell, proved useful in determining the structure of the oil bodies. The fixatives that proved most successful for the occasional rhizome slides were 0.5% osmic acid solution and Flemming's weak solution followed by Flemming's triple stain. The most satisfactory of the mitochondrial fixatives was ammonium Erliki solution (25 cc. each of 1% solutions of ammonium and potassium bichromates plus 25 cc. of an 8% solution of formaldehyde) followed by Milovidov's modification[1] of Volkonsky's stain. With these fixatives the usual dehydrating and paraffin embedding schedules were satisfactory. A third instance of useful fixation was found for the mitochondrial fixatives. These, although not entirely successful except for root-tips, did fix mitochondria throughout the plant sufficiently well for a rough survey of the distribution of these elements.

The "vital" method was preferred and finally used exclusively because it presented a more reliable picture of unaltered cell structures. Although this was the main consideration, there were other factors that made the "vital" technique especially favorable for the study of developmental and other changes within the cell. Of primary importance was the possibility of observing fluctuating changes of a moment's duration, as well as those more permanent ones associated with age or season. This was possible only with a technique which left the more or less fluid contents of the cell unchanged. The "vital" method provided such a technique. Another factor favoring the "vital" method was its practical simplicity. Although some skill was required in sectioning, after this was obtained the actual preparation required but a few seconds. Not only was this a saving of time but it was possible to examine material as it was brought in, a method that enabled one to proceed quickly with the study. A third factor of importance was the applicability of the method without modification to all kinds of material. In a comparative study of tissues and plants this was an essential requirement for the technique.

As used in this study the "vital" technique was essentially that developed by Bailey (1) for the study of cambium. The material was

[1]Stain in acid fuchsin over flame for 5 min.; stain in 0.5% aurantia in alcoholic solution for 20 min.; stain in gentian violet; differentiate in alcohol. [Milovidov, P.F. Sur les méthodes de double coloration du chondriome et des grains d'amidon. — Archiv. Anat. Micro. (24), 1:9. 1928.]

sectioned, placed in appropriate solutions and examined immediately and at intervals. For distinguishing the living from injured or dead cells criteria were established based upon comparisons between obviously injured cells and those that survived for some hours before showing signs of injury. The only differences in the technique for *Iris* lay in the details of sectioning and of preparing solutions and in the possibility of more firmly establishing criteria for living cells by comparisons with mounts of thin, unsectioned tissue.

The sectioning was done with a "Gem" razor blade freehand, or, for some rhizomes, with a Thomson-Spence sliding microtome. Although the microtome sections were more uniform in thickness and more convenient for mature rhizomes, they were less satisfactory with the other tissues. Apparently a thinner blade produced less injury in rhizome meristems, while it was the simplest means for sectioning leaf, flower or root tissue. The razor blade was used for mature rhizomes also when a microtome was not available. In either case, sections were obtained varying from one to several cells in thickness. Measured by the microtome, sections of mature rhizome varied from 30 μ to 50 μ or more, while those of the smaller-celled meristem were 15 μ to 20 μ or less.

The solutions in which these sections were immersed consisted of a basic solution plus one or more of the "vital" dyes, or merely of the basic solution alone. Of the three fluids tried, water, nujol and sucrose solution, the sucrose solution in a five to ten per cent concentration, proved most satisfactory.

The dyes most commonly used were Neutral Red, Janus Green BB, Chrysoidin Y and Benzene-azo-alpha-naphthylamine. Although Chrysoidin Y is the only one of these dyes which stains the elaioplasts, the light staining of the vacuole with Neutral Red throws the cytoplasm into relief and makes its structures more clearly visible. The other dyes in combination with Neutral Red and Chrysoidin Y have a clarifying effect. None of these dyes stain the immature oil bodies, while the staining of the mature oil bodies by Chrysoidin Y is but temporary. Almost all dyes will stain dead, mature oil bodies. In practice, only traces of the dyes were used (one drop of a concentrated aqueous solution to 25 cc. of sugar solution). Staining is better and more rapid when the sucrose solution is made alkaline with Clark's buffers (pH 8.2 to 8.6) which shorten the staining period from an hour or more to fifteen minutes or less. Since most stains, even in small amounts, are toxic after a time, sections that it was desired to keep were removed to pure sucrose solutions. In this way cells were kept "living" for twelve hours or more.

An essential part of the technique was the establishment of criteria for distinguishing living from dead or dying cells. By comparing obviously injured cells with those which survive sectioning for some hours without sign of injury, such criteria have been established for cambial tissue. By the same method criteria were found for Iris cells. In addition unsectioned roots, bracts and flower parts of *Iris* and the thin leaves of a *Potamogeton* were examined. Living cells in *Iris*, like those in cambium, are marked by the following characters: regular cyclosis, absence of Brownian movement in the cytoplasm and a staining of the vacuole in the presence of Neutral Red. Two additional criteria were found for living cells of *Iris*, namely, a pulsation of the cytoplasm in isodiametric cells and the amoeboid movement of the chondriosomes. Both of these phenomena are essentially a swelling or contraction of parts of the structure involved. The pulsation, for example, is the swelling of one part of a protoplasmic thread at the expense of another, a phenomenon involved in changes in the concentration of the substance at a given point. The pulsation of the cytoplasm occurs principally in isodiametric cells where there is no streaming. The amoeboid movement of the chondriosomes may occur in any cell. Both criteria proved valuable as indications of the condition of the cells. Dead cells of *Iris*, as of the cambium, show one or more of the following characteristics: coagulation of the protoplasm, a general formation of granules in the cytoplasm, staining of the nucleus and cytoplasm in the presence of dyes, increasing opacity of the whole cell and Brownian movement in the cytoplasm. Dying cells in *Iris* were found to show the following characters: jerky or irregular streaming and Brownian movement within the plastids. Parallel phenomena were found in the irregular streaming and degenerating plastids of some epidermal, bract and flower tissues.

The validity of these criteria for distinguishing living from dying or dead cells should be considered. The possibility of injury lies in the sectioning, in the action of the solutions in which the sections are placed, in the pressure of the cover glass used in mounting sections and in the strong light used for microscopic observations. In establishing criteria, the use of unsectioned material eliminated the possibility of injury due to sectioning, while the examination of water plants in the water of their natural habitat provided a check upon the effects of the solutions used in the study of *Iris*. A similar check upon the effects of pressure from the cover glass was provided by removing it. The possibility of injury due to strong light alone remains. That strong light will produce injury and death is clear, but the effects are slow in appearing and, if the light is removed in time, they are temporary. They can be taken into account in establishing criteria for distinguishing living from dying or dead cells. That there are undetected, instantaneous changes is improbable, for the reactions in plants are in general slow. The effect of the light appears chiefly in the slowing down of streaming, and, if exposure is continued, unmistakable signs of death such as coagulation of the cytoplasm finally are observed.

It should be noted that the observation of minute details of cytoplasmic structures can be carried on only with the aid of the best high-powered microscopic equipment. For the observation of sections mounted in aqueous media a water immersion objective is essential. Without such equipment, many of the details of structure described in the following section cannot be seen.

OBSERVATIONS

Description of Elaioplasts in Rhizomes of Iris versicolor

Elaioplasts occur typically in the parenchyma of the rhizomes of *Iris versicolor*. They appear in every cell as granular, highly refractive masses with a decidedly yellowish cast (Fig. 1). The individual elaioplasts are almost spherical in shape and seem to be composed of closely compacted globules approximately one micron in diameter (Fig. 2). They are relatively constant in size within a given rhizome, generally averaging 10 to 13 microns in diameter. Although in some material they may be twice this size, they are never as large as the nucleus which has a diameter of the order of 40 to 50 microns. Often a hundred or more of these elaioplasts will be found in a single cell, aggregated for the most part into one large mass. Sometimes there are as few as twenty to a cell, but often they more than half fill the cell lumen, obscuring the nucleus and protruding into the huge vacuole.

All evidence shows that the elaioplasts are located in the cytoplasm. Although they protrude into the vacuole, protoplasmic threads are often observed to spread at their surface as if to include them (Fig. 1). Occasionally one is seen moving in the streaming protoplasm. The study of similar bodies in the root, where they obviously are included in the cytoplasm, substantiates these observations.

Microchemical tests indicate that the bodies are mainly lipoid in character. They stain brilliantly in "fat" dyes such as Sudan III, alkannin and nascent indophenol blue.[1] They are almost completely

[1]For this technique see Zweibaum, J. Sur la coloration des graisses dans la cellule vivante. Comp. Rend. Soc. Biol. 1923. — Zweibaum, J. and G. Mangenot. Application à l'étude histochimique des végétaux d'une méthode permettant la coloration vitale et post vitale des graisses de la cellule végétale. Comp. Rend. Soc. Biol. 1923.

soluble in lipoid solvents such as ether, chloroform and carbon tetrachloride. They also dissolve largely in 95% alcohol, a solvent for some oils. They are insoluble in hydrochloric acid, sulphuric acid and potassium hydroxide, although they are more or less structurally disorganized by these reagents. They are not volatile at 100°C., which indicates the presence of lipoids rather than essential oils.

The reaction of the elaioplasts to heat and to many reagents in which they are insoluble is marked by the extrusion of the lipoid in drops (Fig. 5). The reaction occurs relatively slowly so that it can be watched. A net-like residue remains which is not distinctly lipoid in character. The drops characteristically remain in contact with the net and are flattened on their attached side. The reaction occurs with heat, picric acid, dilute sulphuric acid, Gram's solution, etc.

Injury to the cell typically produces active Brownian movement of the globules within the limits of the elaioplast which eventually bursts, freeing the globules within the cell lumen. A similar phenomenon occurs in elaioplasts which escape from cut cells. It can be induced by mechanical pressure.

Structure of Elaioplasts in Rhizomes of Iris versicolor

The structure of the elaioplasts in the mature rhizome is that of a matrix with embedded globules. This is best shown in sections of fixed material, for the globules in fresh material are so refractive and so closely packed that it is difficult to distinguish any structure clearly. With osmic acid and some of the chrom-osmic fixatives the globules are preserved *in situ* (Fig. 3b). They clearly show a network of a different substance between them. With other fixatives the globules are never preserved, but a net-like structure with lacunae of the approximate size of the globules remains (Fig. 3a). This can be seen best by the use of mitochondrial or plastid fixatives such as ammonium Erliki and an appropriate stain. It is well shown, too, by Wakker's method for double staining elaioplasts with anilin blue and alkannin after fixation of sections in picric acid. In this case, the extruded globules are stained red and the matrix appears as a purple network with blue interstices.

The behavior of the bodies in fresh material supports the observations on their structure as seen after fixation. The globules show no tendency to fuse, a fact which indicates a separation by the presence of at least a surface film. In injured material, they move apparently unchanged in a liquid portion of the intact body. Further proof of a matrix is found in developmental forms and in homologous oil-bearing bodies in other species. Here the matrix is often so abundant as to be clearly visible in untreated material. Such is the case in very young cells of the rhizome, in some cells of the root-tip, in rhizomes of *Iris pallida* and of *Iris Hartwegii*, etc. The matrix is also clearly shown in the root during the degeneration of elaioplasts. Here before death the refractive globules disappear leaving only a net with lacunae. This net is very similar in structural appearance, although not in shape, to the net-like image of rhizome elaioplasts in fixed material.

The globules were identified as the material which gives the elaioplast as a whole its lipoid characters. They show the reactions previously described for the elaioplasts and additional ones equally characteristic of lipoids. They stain in the "fat" dyes. This is apparent in intact bodies, but it is more clearly seen with the moving globules in disintegrating ones. They are highly refractive, a property seen in both intact and disintegrated elaioplasts. They disappear from sections treated with "fat" solvents such as carbon tetrachloride, ether, etc., but they may be preserved in sections treated with "fat" fixatives such as osmic acid and chrom-osmic mixtures. They are completely soluble in alcohol. This was demonstrated with globules in suspension in alkaline water. Upon the addition of 95% alcohol a homogeneous fluid resulted indicating the complete solution of the globules.

The matrix was shown to be of a different substance from the globules. It appears to be more like the cytoplasm in composition. Unlike the globules it requires no special fixative for its preservation. At least a portion of it is insoluble in alcohol and lipoid solvents such as carbon tetrachloride, for it sometimes remains intact after the use of these reagents. It is not refractive, for this character can be seen in young tissue and in injured cells to be a property of the globules only. Nor is it stained to any extent by the "fat" dyes such as Sudan III, etc. This is evident in elaioplasts with globules in Brownian movement where the stain is largely confined to the globules. That the matrix is of a plasma substance was suggested by the difficulty of staining it differentially from the protoplasm. This view was substantiated later by the identification of the elaioplasts with the plastidome and chondriome.

No evidence of a differentiated membrane about the elaioplasts could be found. None could be seen in fresh material, nor has any been brought out by reagents or fixation techniques. The only observation that might be interpreted as indicative of a membrane was the "bursting" of injured elaioplasts already described. But no fragments of membrane remained. It is more probable that the sudden freeing of the globules depended upon changes in the matrix which made it miscible with the surrounding medium.

Seasonal Variations in Elaioplasts in Iris versicolor

Certain variations in the form and structure of the elaioplasts are due to the seasonal appearance of starch. In New England the elaioplasts are without starch from early November through June. By July or August the starch begins to appear, while by September or early October a maximum development has been reached. The disappearance of the starch then begins and proceeds rapidly. By early November no traces of it can be found.

The starch can be identified with Gram's solution and polarized light. In the former the grains stain a blue to a bluish-black, a reaction typical of starch in the presence of iodine. In polarized light they appear as bright grains with a black maltese cross on each.

The type of starch formation in rhizomes of *Iris versicolor* is characteristic and constant. Each elaioplast develops several included grains (Figs. 4b and c). Counts made in early October showed commonly from 8 to 12 grains, with a recorded range of 1 to 16 per elaioplast. Although the grains are always grouped more or less centrally within the globule-filled portion, they form bulges in the otherwise rounded contour of each elaioplast (Fig. 4). The individual starch grains are approximately isodiametric. They show the central hilum characteristic of this shape of grain when it is included within the plastid. In size they are small, generally 6 to 7 microns in diameter as measured in material collected in early October.

Climatic differences in the disappearance of the starch from the growing point of the rhizome are indicated. In material from the vicinity of Boston and of New York the starch disappears completely in the winter. But in plants grown in the Missouri Botanical Garden it may be found about the growing point in March, although completely absent from the rest of the rhizome.

The disappearance of the refractive globules of the elaioplasts has not been observed. Numerous observations have been made from September to May, during which time they remain in abundance. They are likewise present in the rhizome during June, July and August, although a less thorough study has been made of their behavior during those months.

Development of Elaioplasts in Rhizomes of Iris versicolor

By tracing back to the meristem, the elaioplasts in the rhizome were found to develop from mitochondria-like primordia by increase in size, in visibility and in the number of contained globules (Fig. 19). In the youngest cells there are small, irregular, shadowy proplastids with two or three included non-refractive globules. In increasingly older cells these bodies become more distinct and larger with a greater number of included globules. At the same time the globules become refractive and the whole body even more irregular in contour. Later with further increase in size and in the number of included globules, the irregular contour is lost. The cells then contain the granular, smoothly rounded, mature elaioplasts characteristic of the rhizome.

The young elaioplasts are distinguished by the following characters. They have more matrix in proportion to the number of globules than the mature forms. They do not stain after death to any degree in Sudan III nor in any other anilin dyes in contrast to the brilliant staining of the mature elaioplasts. They are restricted to a small region about the growing point, while the youngest stages are found only in the cells of the growing point. They are all irregular in contour, but this irregularity is emphasized in the intermediate forms which are almost nodulose.

The youngest stages show characters ordinarily associated with mitochondria. They are about the size of Iris mitochondria, ranging from this up to several times their size. They are indistinctly visible like much of the chondriome with a peculiar fading and reappearing quality. Thus a period of clear definition of these shadowy forms will be followed by a fading and disappearing. This, in turn, after a few minutes or after several hours may be succeeded by another period of clear definition, and so on. In general, although not always, these forms show included non-refractive globules. This is a character shared by the rod-shaped mitochondria of the species. In the young elaioplasts there is no definite arrangement of the globules which in the rod-like mitochondria always form a single row.

The formation of starch occurs in any of the young or mature forms of plastids. It was found during the season of its formation in all of them. In the young forms the starch grains ordinarily protrude from the globule-filled mass of the elaioplast, in contrast to the completely included grains of the mature elaioplast.

No evidence of increase by division was found in mature or developmental stages. No division was seen at any time, although material was collected from September to June and kept under observation for hours at a time. In the rhizome tissue even the "dumb-bell" figures so often cited as evidence of division were absent.

Degeneration of Elaioplasts in Rhizomes of Iris

No evidence of degeneration was found in the rhizomes of *Iris versicolor*. Elaioplasts are found unchanged and in abundance even in the oldest living cells.

Two isolated cases of degeneration of elaioplasts similar to those in *Iris versicolor* have been noted in the rhizomes of other species. One of these is an abnormal condition produced in a slowly dying plant. The second is a normal phenomenon in otherwise morphologically unchanged cells. It is apparently unassociated with the death of the cells, for no other signs of degeneration appear. This phenomenon occurs consistently in the cortex of the rhizomes and in the epidermis and sub-epidermis of the roots of *Iris macrosiphon* var. *californica*.

In *Iris macrosiphon,* elaioplasts in the mature cells of the cortex of the rhizome appear as large lipoid spheres (Fig. 14c). These spheres are marked by their large size, by their distinct yellow color and by their brilliant staining in "fat" dyes, Sudan III, etc. They may be demonstrated to be in the cytoplasm by coagulating the surrounding protoplasm with fixatives (Fig. 15). The study of developmental forms which can be seen to be carried in the streaming protoplasm offers further proof of their inclusion in the cytoplasm.

Stages in the formation of the lipoid spheres from mature elaioplasts can be seen in cells not far from the growing point. The process consists of the formation of homogeneous spheres by the fusion of the globules and the disintegration of the matrix (Fig. 14). A single elaioplast resolves itself into one or more of these spheres. In older cells still further fusion occurs for the spheres in them are larger and fewer. In these cells each sphere probably includes the substance of more than one elaioplast.

A similar formation of lipoid spheres can be observed in epidermis and sub-epidermis of the root-tip (Fig. 18). The phenomenon is identical with that in the rhizome, although starch is present in the root elaioplasts. It shows more clearly than in the rhizome the steps in the resolution of the elaioplasts. The fusion of the globules proceeds for some time before the apparent structure of the elaioplast is lost. The final degeneration products include starch grains as well as lipoid spheres. The grains and spheres remain distinct in the cytoplasm, although the starch is indiscriminately scattered among the lipoid spheres.

Proof that the formation of lipoid spheres in *Iris macrosiphon* is a degeneration phenomenon is based on two points. First, the structure of the elaioplast characteristic of the functioning body is lost. There is no evidence that the lipoid spheres can produce starch as the elaioplasts do, or function actively in any way. Secondly, the phenomenon occurs in tissue which tends to die and slough away. In the root, the epidermal cells in which the spheres form are short-lived. This is less evident in the cortex of the rhizome where the cells may live for a season or more after the formation of the spheres. But even in this tissue the outer cells die and the formation of lipoid spheres is more marked in the outer cells. It is not found in the inner cells of the cortex or elsewhere in the rhizome.

A second case of degeneration was found in rhizome cells of *Iris tectorum* (Fig. 7). In a slowly dying plant the elaioplasts appeared closely compacted in each cell into one or two masses. The rounded contour of each elaioplast was lost, while the matrix seemed to have become more plastic. The identity of each elaioplast was lost in the mass which appeared as a single granular body with indistinct partitions within it (Fig. 7b). Where starch was present the grains were included in the composite mass. This condition has never been found in healthy plants.

Oil-bearing Plastids in Rhizomes of other Species of Iris

Oil-bearing plastids are found in the rhizomes of practically all species of *Iris*. They show the same fundamental structure and development as those in *Iris versicolor* just described. But they differ from one another in their formation of starch. Two clearly marked types based on the mode and time of starch production occur.

The first type is that found typically in *Iris versicolor* (Figs. 1, 2 and 4). It has already been described. In contrast to the second type, it is marked by the disappearance of starch during the winter dormant season, by the formation of several starch grains in each plastid and by the inclusion of the starch within the plastid. Plastids of this type vary considerably, but they usually show at least two of the general characters. In some species of *Iris* the starch persists more or less throughout the winter; in others it may persist one season and not the next, and in still others, such as *I. versicolor,* it always disappears. The inclusion of the starch in mature plastids, although not in the younger forms, is complete in most instances. But in some cases the starch grains tend to protrude slightly. This is more often the case in the cortex, although it may characterize the whole rhizome. An extreme case accompanied by an unusually reduced number of lipoid globules in the plastids (Fig. 12d) was found in one of two collections of *Iris Hartwegii.*

The second type is characterized by the persistence of the starch through the dormant season, by the formation of one, large, asymmetric starch grain or sometimes two in each plastid and by a conspicuous protrusion of the grain from the globule-filled portion of the plastid (Fig. 9). Caplike elaioplasts attached to one end or side of the large starch grains are typical of these plastids. Often the lipoid globules are larger than in the plastids of *I. versicolor*, while the matrix is abundant enough to be clearly seen between them. A typical example of this type of plastid is found in rhizomes of *Iris pallida* (Fig. 8).

Although the disappearance of starch is not general in this second type, it has been noted in one or two instances. The starch disappears from the main part of the rhizome of *Iris pumila* during flowering (Fig. 11), although it persists around the growing point. The solution of the starch leaves peculiarly cup-shaped elaioplasts (Fig. 11c). A second case of the disappearance of starch may occur under abnormal conditions. It was induced in the rhizomes of *Iris pallida* placed in the greenhouse during the winter. It is accompanied by a lack of vigor and the disappearance from the rhizome cell vacuoles of substances ordinarily present at that season. The change in the vacuoles is apparent in fixed material in a lack of the precipitate characteristically produced in them by reagents during the winter. The plastids in the rhizomes of the greenhouse plants resembled the spherical ones of winter material of *Iris versicolor* except for their smaller size and fewer numbers.

The distribution within the genus of the two types of rhizome plastids has been found to follow closely the recognized taxonomic grouping. The homogeneous and closely related groups show the same type of plastid, while a heterogeneous group such as the Apogon shows both types. In the latter case aberrancies from the prevailing type in the group are often correlated with anomalous taxonomic characters. Sufficient material has been examined to show definitely the condition in the two largest groups, Pogoniris and Apogon, and in several of the smaller groups, Evansia, Regelia and the Pardanthopsis and Gynandiris species. An indication of the prevailing type in each of the other groups may be found in the notes made on a few representative species.

Rhizomes have been examined largely during the late winter. In late winter the pallida type of plastid shows its characters clearly, while the versicolor type is generally without starch at that season. An indication of the mode of starch formation in the latter type of species can often be obtained from the persistent starch in the plastids about the growing point. In this study, such observations have been supplemented by notes made during the starch-forming season.

The pallida type of rhizome plastid occurs characteristically in Pogoniris, Regelia and Oncocyclus. These are homogeneous groups which together with Pseudoregelia form a unit of closely related species. The same type has been found in a Juno Iris and in a Xyphium Iris. In the latter case it occurs only in tissue about the vascular bundles but not in the large parenchyma cells which are filled with starch. It is also found in Pardanthopsis, in the closely related hexagona sub-group of the Apogons, in the anomalous Apogon, *I. verna,* and in one of the variable Apogon spuria group, *I. spuria ochroleuca.*

The versicolor type of plastid appears in the Evansia group and in the majority of the Apogons. In the latter it characterizes the following sub-groups: Sibirica, Laevigata, Longipetala, Californian, Tripetalous, Spuria and Ensata. Its distribution is more limited than that of the pallida type, for the Evansia and Apogon sub-groups include but one-third of the species. The pallida type appears to characterize the other two-thirds of the genus. Since the Evansia and Apogon sections include all of the American irises, the versicolor type is predominantly the type found in North American species. The only exceptions are the anomalous Apogons cited in the preceding paragraph and one to be described later. A similar predominance of the versicolor type is to be found in the Asiatic species. The American and Asiatic species contrast in this respect with the more strictly European and Mediterranean species, which belong chiefly to groups showing a pallida type of plastid, notably Pogoniris and related groups and the bulbous forms.

The absence of oil-bearing plastids has been noted in five irises. In these cases the rhizome cells are filled with starch. The starch is of two types paralleling in distinguishing characters and in distribution the two kinds formed by the oil-bearing plastids. One is present as large, single, asymmetrical grains similar to those in the pallida type of oil-bearing plastid. They characterize the anomalous Apogon, *Iris unguicularis,* the Reticulata Iris and Gynandiris. The last of these is not always included in the genus; in the formation of starch and no lipoid in its corms it resembles the closely related genus, *Moraea.* The Reticulata is a group closely related to the Xyphium, which shows similar starch grains and a few oil-bearing plastids of the pallida type. The second starch grain type resembles the starch grains of the versicolor plastids in their small size, in their isodiametric shape and in their formation in groups within a single leucoplast. Like the versicolor type of plastid they are found in Apogon Irises, the Japanese Iris and *Iris Sintenisii.* The former is a hybrid of *I. laevigata,* one of a group characterized by the versicolor type of plastid, and another member of the same group. The other *Iris* belongs to the Spuria sub-section, a group of intergrading and variable forms, for which no single characteristic type of plastid was found.

For the type of plastid found in individual species, the reader is referred to the table on page 246 and also Figs. 12 and 13. The table also includes data on the material, its source, the season of examination, etc.

TABLE OF IRISES EXAMINED SHOWING THE TYPE OF RHIZOME PLASTID AND THE SOURCE OF THE MATERIAL FOR EACH SPECIES[1]

Species	Section	Group	Type	Source of Material	Parts	Season Collected	See Pl. 133, Fig. 13
I. pallida Lam. ×?	Pogoniris	Pallida	2	Bussey Garden	All	All	Qa
I. pallida variety	Pogoniris	Pallida	2	Mo. Bot. Gard.	r, l	March	—
I. Cengialti Amb.	Pogoniris	Pallida	2	Mo. Bot. Gard.	r, l	March	Qf
I. pumila L.	Pogoniris	Pumila	2	Mo. Bot. Gard.	r, l	March	Qe
I. pumila variety	Pogoniris	Pumila	2	Mo. Bot. Gard.	r, l	March	—
I. Korolkowi Regel	Regelia		2	Brooklyn Gard.	r	April	Pb
I. Hoogiana Dykes	Regelia		2	Brooklyn Gard.	r	April	Pa
I. susiana L.	Oncocyclus		2	Brooklyn Gard.	r	April	O
×*I.* "*Zwannenburg*" Hort.	Oncocyclus		2	Mo. Bot. Gard.	r, l	March	—
I. alata Poir.	Juno		2	Brooklyn Gard.	bulb	April	N
I. Xyphium L.	Xyphium		2	Florist	f, l	Feb.	—
				Florist	bulb	March	M
I. dichotoma Pall.	Pardanthopsis		2	Mo. Bot. Gard.	r, l	March	R
I. foliosa Mack. & Bush	Apogon	Hexagona	2	Mo. Bot. Gard.	r, l	March	Ic
I. fulva Ker	Apogon	Hexagona	2	Mo. Bot. Gard.	r, l	March	Ia
				Brooklyn Gard.	r	April	—
×*I. hexagona* Walt. ×?	Apogon	Hexagona	2	Mo. Bot. Gard.	r, l	March	—
I. vinicolor Small	Apogon	Hexagona	2	Brooklyn Gard.	r	April	Ib
I. verna L.	Apogon	Verna	2	Virginia	r	May	H
I. spuria Pall. var. *ochroleuca*	Apogon	Spuria	2	Mo. Bot. Gard.	r, l	March	Ee
I. halophila Pall.	Apogon	Spuria	1	Brooklyn Gard.	r	April	Ea
I. ensata Thunb.	Apogon	Ensata	1	Brooklyn Gard.	r	April	C
I. setosa Pall.	Apogon	Tripetalous	1	Brooklyn Gard.	r	April	Fb
I. setosa var. *canadensis* Foster	Apogon	Tripetalous	1	Brooklyn Gard.	r	April	Fa
I. Douglasiana Herb.	Apogon	Californian	1	Brooklyn Gard.	r	April	Da
				California	r, l, o	Aug.	—
I. Hartwegii Baker	Apogon	Californian	1	California	r, l, o	Aug.	—
				Brooklyn Gard.	r	April	Dc
I. macrosiphon Torr. var.	Apogon	Californian	1	California	r, l, o	Aug.	—
I. tenax Dougl.	Apogon	Californian	1	Brooklyn Gard.	r	April	Db
I. longipetala Herb.	Apogon	Longipetala	1	California	r	Sept.	—
I. missouriensis Nutt.	Apogon	Longipetala	1	California	r	July	—

TABLE (*Continued*)

Species	Section	Group	Type	Source of Material	Parts	Season Collected	See Pl. 133, Fig. 13
I. virginica L.	Apogon	Laevigata	1	Mo. Bot. Gard.	r, l	March	Bb
I. versicolor L.	Apogon	Laevigata	1	Mo. Bot. Gard. Boston	r, l All	March All	Ba —
×*I. robusta* E. Anders.	Apogon	Laevigata	1	Mo. Bot. Gard.	r, l	March	—
I. pseudacorus L.	Apogon	Laevigata	1	Bussey garden Arnold Arbor. Mo. Bot. Gard.	r r r, l	 March	Bc — —
I. Kaempferi Sieb.	Apogon	Laevigata	1	Brooklyn Gard.	r	April	Bd
×*I. Wilsoni* Wright ×?	Apogon	Sibirica	1	Brooklyn Gard.	r	April	Ad
I. sibirica L.	Apogon	Sibirica	1	Mo. Bot. Gard.	r, l	March	Aa
I. prismatica Pursh	Apogon	Sibirica	1	Duxbury, Mass. N. Y. Bot. Gard.	r, l r	 April	Ae —
I. orientalis Mill.	Apogon	Sibirica	1	Brooklyn Gard.	r	April	Ac
×*I. "Quest"* Hort.	Apogon	Sibirica	1	Mo. Bot. Gard.	r, l	March	—
I. Clarkei Baker	Apogon	Sibirica	1	Mo. Bot. Gard.	r, l	March	—
I. chrysographes Dykes	Apogon	Sibirica	1	Brooklyn Gard.	r	April	Ab
I. cristata Ait.	Evansia		1	N. Carolina Mo. Bot. Gard.	r r, l	May March	— Ja
I. gracilipes A. Gray	Evansia		1	N. Y. Bot. Gard.	r	April	Jb
I. tectorum Maxim.	Evansia		1	N. Y. Bot. Gard. Mo. Bot. Gard.	r r, l	April March	Jc Jc
I. lacustris Nutt.	Evansia		1	Brooklyn Gard.	r	April	Je
I. japonica Thunb.	Evansia		1	Brooklyn Gard.	r	April	Jd
I. unguicularis Poir.	Apogon		3	Brooklyn Gard.	r	April	G
I. reticulata Bieb.	Reticulata		3	N. Y. Bot. Gard.	bulb	April	L
I. sisyrinchium L.	Gynandiris		3	Brooklyn Gard.	corm	April	K
I. Sintenisii Janka	Apogon	Spuria	4	Brooklyn Gard.	r	April	Eb
I. laevigata Fisch. ×?	Apogon	Laevigata	4	Mo. Bot. Gard.	r	March	Be

1—versicolor type of rhizome plastid
2—pallida type of rhizome plastid
3—rhizome plastid with single large starch grain and no oil
4—rhizome plastid with several small starch grains and no oil
r—rhizome, l—leaf, f—flower, o—root

[1] Nomenclature according to Dykes, The Genus Iris.

Oil-bearing Plastids in Rhizomes, Bulbs etc. of other Plants

No oil-bearing plastids have been found in any other rhizomes or bulbs examined. None are present in either of the species of *Moraea* examined, a closely related genus replacing *Iris* in the southern hemisphere. Nor are there any in the many Araceae, Bromeliaceae, Commelinaceae, Liliaceae and Scitamineae examined. Rather, all of these plants contain large asymmetric starch grains in their storage organs.

The chloroplasts in all of these plants characteristically contain more or less refractive granules. In general, such appears to be the condition in all of the monocotyledons and in many of the dicotyledons. Indeed it seems to be true even of some of the lower forms such as the liverworts and mosses, although in these the granules are often not refractive.

The following is a list of the species of monocotyledons examined. The species are grouped according to families.

Araceae: *Acorus Calamus* L., *Aglaonema* sp., *Arisaema triphyllum* (L.) Schott, *Dieffenbachia* sp., *Nephthytis* sp., *Philodendron Selloum* C. Koch, *Philodendron cordatum* Kunth, *Schismatoglottis crispata* Hook. f., *Schismatoglottis rupestris* Zoll. and Mor., *Spathiphyllum* sp.

Bromeliaceae: *Ananas macrodontes* E. Morr., *Billbergia* sp., *Cryptanthus* sp.

Commelinaceae: *Palisota* sp.

Iridaceae: *Moraea iridioides* L., *Moraea* sp.

Liliaceae: *Allium* sp., *Hemerocallis* sp., *Ornithogalum umbellatum* L., *Yucca filamentosa* L.

Orchidaceae: *Vanilla planifolia* Andr., *Vanilla pompona* Schiede.

Musaceae: *Strelitzia* sp.

Zingiberaceae: *Alpinia nutans* Rosc., *Amonum* sp., *Hedychium* sp.

Marantaceae: *Calathea* sp.

Oil-bearing Plastids in other Parts of the Plant of Iris Species

The observations in this section apply to any species of *Iris* unless otherwise stated. A careful study has been made of the conditions in *Iris pallida* and in *Iris versicolor*. Additional notes have been made on other species.

The formation of oil globules is characteristic of plastids throughout the tissues of plants of the genus *Iris*. The globules are not always so numerous as those in the rhizome plastids of *Iris versicolor* where they are developed to an unusual degree. An extreme example of a limited formation of globules is found in the chloroplasts of the guard cells where the matrix of the plastids is relatively abundant and clearly visible. Nor are the lipoid globules usually the only observable product of the plastids. Ordinarily starch is also present, while in some plastids chlorophyll or a yellow pigment is formed.

The elaioplast condition described for rhizome plastids of the versicolor type may occur in any of the uncolored tissues. It is dependent upon the absence of starch and pigment and upon a large production of oil. Such conditions are found at times in the rhizome, in the root and in uncolored leaf and flower tissues.

In the rhizome and root elaioplasts occur generally throughout the tissues of these organs. They are restricted to certain species and, at least for the rhizome, to certain seasons. There is no connection between their presence in the rhizome of a species and their appearance in the root of the same species. For example elaioplasts were found in the rhizome of *Iris versicolor* but not in the root (Figs. 2 and 35). On the other hand, they were found in the root of *Iris pallida* but not normally in the rhizome (Figs. 9 and 30). An example of their formation as a seasonal phase of the leucoplasts in the rhizome has already been described for *Iris versicolor*. Whether or not they also form a seasonal phase for leucoplasts in the root has not been investigated.

In the leaf and flower the elaioplasts are restricted to a few cells. Often they are but transitional forms appearing for a very brief time. Such is the case in the flower where they may occur in the course of the development of the chromatophores. Because of their limited occurrence in a few cells it is usually easy to identify them with the leucoplasts or chromatophores in neighboring cells. In these tissues they do not develop the brownish color so characteristic of the rhizome elaioplasts in *Iris versicolor*. Instead they remain entirely colorless.

The development of elaioplasts can be induced under unfavorable conditions. An example of this has already been cited in their formation in rhizomes of *Iris pallida* grown in the greenhouse (p. 244). In this case they were formed by the dissolution of the starch leaving only the oil-bearing plastid. By growing plants in semi-darkness chloroplasts can be prevented from forming pigment or starch. They then appear as elaioplasts. In neither of these cases is an increase in the number of oil globules involved. Nor has the formation of unusual numbers of elaioplasts been observed as a result of abnormal conditions.

The oil-bearing plastids in other parts of the plant show essentially the same features as those described for the rhizome. They differ from those in the rhizome in minor characters, also in the absence of a general elaioplast phase except in the root and in the formation of pigments. In addition they show in some cases chondriome types as an intermediate stage in their development from the proplastids. In some tissues, notably in the flower and in epidermal tissues, the mature plastids often show further changes involving chondriome types not found in the rhizome. These points will be taken up separately in the succeeding paragraphs.

Minor differences between the plastids in other parts of the plant and the type found in the rhizome and root appear in the lesser production of lipoid globules and in their complete lack of color in colorless tissue. Correlated with the smaller number of globules is a greater stability. This is shown in their greater resistance to injury by mechanical pressure and to distortion or destruction by reagents. Their lack of color when not pigmented can be seen in colorless leaf tissue in marked contrast to the strongly yellowish cast in the equally unpigmented rhizome plastids. This is particularly well shown in *Iris versicolor*.

The formation of pigment, chlorophyll or yellow pigment, occurs ordinarily in the young plastids. But there is no specific stage at which it is developed. In the leaf chloroplasts it often forms shortly after the appearance of starch in the young plastids, although it may not develop for some time. In the chromatophores of the root it sometimes appears before the formation of starch, for example in the rootcap of *Iris versicolor*. At other times yellow pigment appears in plastids which do not form starch, for example in the chromatophores of roots of *Iris pallida*. In many cases yellow pigment is found in chondriocont types of plastids, but its formation is quite unconnected with the phenomena producing these forms. Proof of this is found in its formation in the approximately spherical plastids of the root-tip before they pass into a chondriocont state and in those of the rootcap of *Iris versicolor* where the mature plastids retain a more or less spherical state.

The location of pigment in the refractive globules and also in the matrix and its greater solubility in the former was demonstrated. In the guard cells of *Iris pallida*, where there is little chlorophyll, the green color can be seen to be confined to the globules, while the matrix remains colorless. That it may also be dissolved in the matrix is shown in degenerating chromatophores of the root where color remains in the matrix after the disappearance of the refractive globules.

Intermediate developmental forms of the plastids are found in the root-tip (Figs. 20–24). They differ from the small plastids in other differentiating tissue by the retention for a longer period of the shadowy visibility of the proplastids and by a plasticity amounting in the younger stages to an almost fluid character. They resemble other young plastids in their origin in the proplastids, in their development by increase in size, in visibility, in the number of included globules and in their final development in many cells into the same type of plastid. In their often elongated shape they resemble the chondrioconts of many authors.

The shadowy character of the younger intermediate forms is evident in the peculiar fading and reappearing already described for the proplastids (p. 241). With the differentiation of the tissue this shadowy quality is lost (Figs. 20–24), but the bodies do not become refractive until a late stage (Figs. 24 and 25). Often the more or less indistinct forms persist for long periods.

The plastic quality of the intermediate forms is shown in their more or less elongated shape and in their movement in the streaming protoplasm. The movement consists of a continuous changing of form (Figs. 20–23). Both movement and elongation are more marked in the younger stages, some of which are almost fluid. In older cells the plastids become less and less elongated with increasing viscosity until they are more or less spindle- or tadpole-shaped. At the same time the motion of the plastid becomes reduced to a moving about of the ends. In the fully differentiated plastid the shape is roughly spherical and there is no movement. Often the plastids remain in the spindle- or tadpole-stage for some time.

The continuous motion of the intermediate types is essentially an amoeboid movement of the plastid (Figs. 20–23). This appears to some degree in all of the intermediate types. In its most exaggerated expression in the youngest stages, it consists of a change in form from a filament, through intermediate stages, to a sphere. Another example characteristic of the plastids before the globules have become refractive is the formation of two swollen ends connected by a thread. In some cases the thread becomes invisible, but it always reappears and shortens to reunite the two ends. In its least pronounced form in the older spindle- and tadpole-shaped forms, the movement is confined to a turning from one side to another of the tapered ends.

That the movement is not wholly connected with cyclosis, although probably aggravated by it, appears likely. In cells where there is no cyclosis, the intermediate forms customarily show a pulsating movement associated with changes in thickness. An example of this is seen in young plastids in the isodiametric cells of the rootcap.

It is worthy of note that in none of these forms has division of the plastids been seen. Many observations have been made at different times and over periods of an hour or more. But even plastids which appear to be divided are seen shortly to be connected by a thread which after a time thickens to reunite the two parts.

The liquid character of the youngest forms is shown in the movement of the globules within the plastid. This consists of a sloshing about of the globules. In older forms this movement does not appear. Any rearrangement of the globules in them is due to the amoeboid movements of the plastid.

The intermediate plastid types develop into leucoplasts in the cortex of the root or into chromatophores in the rootcap. But in other regions of the root and in the elongated cells of the fibrovascular bundles throughout the plant they persist as chondriocont types. The shadowy, very plastic forms are found in the central cells of the root. In other parts of the central cylinder more differentiated forms are found. Similar ones appear in the fibrovascular bundles throughout the plant. In the inner cortex the tadpole- and spindle-shaped forms with refractive globules often remain. The chromatophores of the rootcap often retain their chondriocont-like shape and plasticity after the formation of pigment and oil (Fig. 29b).

Associated with the persistent developmental forms are shadowy leucoplasts and mitochondrial types not ordinarily linked with plastids. In *Iris*, the latter are marked by their gradation into the plastid forms. In the same cells with the persistent chondriome-like plastids, they appear as long filaments with a single row of globules and a twisting or wavy motion in the streaming protoplasm (Figs. 26–27). Some of the filaments are shadowy, while the granules in others are refractive. The filaments with refractive granules sometimes show thickened ends which contain more than one row of granules.

It may be noted here that in addition to the proplastids and filamentous chondriosomes, the more usual types of mitochondria, that is globular or rod-shaped forms, are found in *Iris*. They appear in all cells but are concentrated about the apical meristems and in tissues of the leaf and root. They are less evident in the cells of the rhizome. Two observations are worth recording. The so-called spherical mitochondria were observed to be more or less fluctuating in form and only approximately spherical. The rod-shaped ones were seen to contain globules.

Changes in plastids after "maturity" are found in epidermal cells and in the flower. The changes in both cases are marked by an increasing fluidity of the matrix and by the disappearance of the refractive globules. In the epidermis of the root and in the flower the changes culminate in the death of the cell. But in the leaf epidermis the plastids remain as more or less shadowy chondrioconts (Fig. 37). These are quite similar in appearance and in motion to the developmental types in the root.

The changes in the plastids in the epidermal cells of the root have been carefully studied. The more or less spherical leucoplasts or chromatophores first become somewhat elongated (Fig. 31). This is followed in older cells by increasing fluidity of the matrix and the gradual disappearance of refractive globules (Figs. 31–33). Where the plastids are pigmented some of the pigment remains after the globules are gone, but this also tends to disappear. Where these changes progress far, the plastids become shadowy nets much elongated in shape (Fig. 33). In the streaming protoplasm, they are often partially drawn out into long filaments (Fig. 32). In some cases the attenuated portions are bent back upon the rest of the plastid so as to include a small amount of protoplasm (Figs. 30, 33, 34). When an oil globule is included with protoplasm it is often in Brownian movement. The attenuated forms persist until the death of the cell.

During flowering the leucoplasts of the floral tissue were seen to undergo a series of changes similar to those described as occurring in the root. These have not been studied in detail, but the following general changes have been noted. The leucoplasts become pigmented and chondriocont-like in shape. As the flower opens and fades the chromatophores become more and more fluid. At the same time the refractive globules disappear. An advanced stage shows them partially drawn out into long filaments (Fig. 34). Unlike the chromatophores of the root the pigment is retained. These forms remain until the death of the cell. Similar changes occur in the leucoplasts of the bracts.

In *Iris Xyphium* the formation of refractive bosses on the pollen grains from oil-bearing chromatophores has been demonstrated (Fig. 17). In unripened anthers the pollen shows no markings except the small refractive dots forming a part of the wall structure. The grains are surrounded by the tapetal fluid in which are numerous oil-bearing chromatophores. In the shed pollen the grains show not only the refractive dots but the closely appressed chromatophores which appear as granular, yellowish, refractive bosses. No similar observations have been made on pollen grains of other species. Although the latter show refractive spines or a network of refractive structures, these are in every case associated with wall formation. They are in no way connected with the plastidome or chondriome.

All of the plastids described are found to show the following general characters. They tend to aggregate about the nucleus, a character also shown by mitochondria. Unless degeneration is involved they retain the ability of the proplastids to form the pigments and other products differentiating the different types of plastids. They also retain the ability to change from the plastid shape into a chondriocont form and *vice versa.*

Elaioplasts in Plants Described in the Literature

Of the plants recorded in the literature as forming elaioplasts the following have been examined: *Vanilla planifolia* Andr., *V. Pompona* Schiede., *Marchantia polymorpha* L., *Lunularia cruciata* (L.) Dum., *Pellia epiphylla* (L.) Corda, *Porella* sp., *Bazzania trilobata* (L.) S. F. Gray, *Scapania nemorosa* (L.) Dum., *Cephalozia* sp., *Trichocolea tomentella* (Ehrh.) Dum., *Plagiochila asplenioides* (L.) Dum., *Lophocolea heterophylla* (Schrad.) Dum., two thallose species of the Jungermanniales from Oregon and two leafy species of the Jungermanniales from Oregon.

The two classes of elaioplasts described by Pfeffer, Wakker and later writers were examined. These are the oil bodies characterizing the liverworts and those in *Vanilla*, a classical example of elaioplast-bearing monocotyledons. In both cases certain of the observations of previous writers have been verified and some additional notes made.

The following observations made by earlier writers for *Vanilla* have been verified. The elaioplasts are present as highly refractive granular bodies near the nucleus in cells which contain also leucoplasts and chloroplasts. Structurally they consist of globules of refractive oil in a protein or plasma matrix. They are marked by their brilliant staining in "fat" dyes and by the extrusion of large globules of oil after treatment with various reagents.

In addition it has been noted that the elaioplasts are generally distributed in all the cells of leaf, stem and root tissues rather than restricted to particular tissues in certain parts of the plants.

It has also been observed that the single large elaioplasts are aggregates of smaller granular bodies (Fig. 45). The aggregation is more or less compact. In some cells it is difficult to distinguish the individual bodies, while in other cells they are but loosely grouped or freely circulating in the streaming cytoplasm (Fig. 46). In some cells the smaller bodies could be observed to aggregate into one or more groups from which individuals were carried away from time to time by the streaming protoplasm.

The development of the smaller bodies from non-refractive granular ones can be observed in younger cells of leaf and root. In successively older cells the included globules gradually become more and more refractive until the bodies assume the highly refractive condition typical of mature cells. In the less refractive stages the bodies seldom form compact aggregations. No specific stage has been noted in which aggregation becomes the rule. The formation of compact groups appears possible at any time, although more characteristic of mature tissue.

The rotary movement of elaioplasts described by Zimmermann and others as characteristic of these bodies has been shown to be an injury phenomenon. It is observed in cells which soon show unmistakable signs of injury followed by death. It is not seen in any cells which remain normal in appearance and actively streaming for a period of hours. The movement consists of rotation within a liquid vacuole. It is followed by Brownian movement of cytoplasmic inclusions and a general coagulation or disintegration of the cellular structure, that is by unmistakable signs of death.

In the liverworts the following observations of earlier writers have been verified. Bodies included within the cytoplasm and marked by their refractivity, by their staining in "fat" dyes and by their solubility in alcohol appear generally throughout the group. They are located within the ring of chloroplasts, but, unlike those in *Vanilla,* show no particular affinity for the nucleus. They all characteristically leave a residual ring in solution with alcohol, etc. They vary in color from colorless to dark brown. Two or three classes are distinguishable. The first appears as a single large granular mass almost filling the cell lumen (Fig. 38). It is located in scattered cells throughout the plant body and is characteristic of the Marchantiales. The second and third types are found in the Jungermanniales which they characterize. They are smaller than those in the Marchantiales and are round, spindle- or disc-shaped in form (Figs. 40-44). They grade from a homogeneous type to a very granular one. Commonly there are from one to twenty in a single cell, located more or less characteristically in the peripheral cytoplasm. In this group they are not restricted to particular cells but are found in every cell. Unlike the bodies in *Vanilla* there is little or no tendency for them to aggregate.

The development of the bodies has been observed in the Jungermanniales (Fig. 42). In the younger cells the oil-bodies appear as shadowy, wrinkled, granular bodies. They develop into the mature bodies of older cells by an increase in substance and in the refractivity of the granules. By the time the cells are fully mature, the bodies have become plump and refractive. There is no indication of a vacuolar origin postulated by some writers.

In addition the following new observations were made. The homogeneous type found in the Jungermanniales are sometimes seen with attached granular bodies (Fig. 44). These appear in the younger cells.

The single bodies in the Marchantiales can be shown to be aggregations of smaller ones. This is apparent in younger cells where they are less refractive and less highly colored (Fig. 39). In older cells the structure is obscured by the dark color. Likewise in older cells the bodies appear to be more closely compacted.

The Brownian movement described by some as characteristic of the bodies in certain species has been shown to be associated with older bodies or with injury. It is never seen in younger tissue, even in cells with mature oil bodies. It appears in some of the older cells of the Marchantiaceae and can be induced in any cell by injury.

DISCUSSION

It has been shown in the preceding observations that the oil bodies in *Iris* are a phase of ordinary plastids. In studying the development and variations of these plastids, many interesting observations have been made which have a bearing upon the status of elaioplasts and upon various problems concerning plastids. In particular the observations provide further evidence of the plastid character of elaioplasts and of a relationship between the various types of oil bodies described in the literature. They also clarify our conception of the interrelationships of plastids and chondriosomes.

1. Significance of Present Study in the Interpretation of Elaioplasts

To identify the anomalous bodies in *Iris* as a seasonal elaioplast phase of plastids adds another instance to the accumulating evidence of the plastid character of oil bodies. This substantiates the theories of Wakker (47), of Beer (4), of Hieronymus (22) and of Kozlowsky (28) who postulate a relationship with plastids rather than with vacuoles or with the nucleus. There is no evidence in any of the observations described in this paper of a vacuolar origin or identity. On the contrary, the structural, developmental and chemical similarities between vacuoles and oil bodies recorded by some authors were not observed in any of the material examined. Nor was there any evidence of a nuclear derivation of the elaioplasts, a theory based upon the similarity in the staining properties of the nucleolus and elaioplasts and in the aggregation of the elaioplasts about the nucleus. Both of these phenomena have been found to be characteristic of plastids in general. The possibility remains that some elaioplasts may be more or less fused aggregations of oil globules which bear no relationship to plastids. The phenomenon was not observed, but the possibility of its occurrence was not disproved.

It is probable that the granular elaioplasts of the monocotyledons and liverworts are types of plastids. They show the same structure as that of the plastids, that is a matrix with embedded globules. That the stroma in the liverworts is non-fixable is not significant morphologically, although it indicates a chemical difference between the oil bodies in the liverworts and plastids in general. Further evidence of the plastid character of the granular oil bodies in the monocotyledons is found in their similarity in appearance and in general characters to those found in *Iris*. A comparison between the elaioplasts in *Vanilla*, as a classic example of the type found in monocotyledons, and those in *Iris* shows the following characters common to both: presence of refractive granules, brilliant staining in "fat" dyes, extrusion of oil with picric acid, etc., aggregation about the nucleus, yellowish color, plastid structure and the absence of the more usual plastid products such as starch and pigment.

That the homogeneous oil bodies in the liverworts may be classed like the granular types as plastids is suggested. Heretofore no distinction has been made between the two types because of the intergradation occurring between the two extremes. The appearance of attached granular portions in the younger stages of the homogeneous forms substantiates the view that they should be classed with the granular types which, as has been suggested, are plastids.

That elaioplasts are sometimes a phase of functional plastids as well as degenerate forms has been brought out in these studies. Heretofore they have been considered to be degenerate forms or secretions of plastids. In *Iris* they are found as functional plastids, as evidenced in the formation of starch and their apparently continuous presence in individual cells from season to season. That elaioplasts sometimes form by degeneration of plastids involving the production of oil has been shown by Beer (4). There is no evidence that they are ever secretions from plastids.

It is probable that the granular elaioplasts described in the literature are sometimes functional plastids and sometimes degenerate forms. Those found in such organs as leaves, roots and bulbs or those found widely distributed throughout the plant as is the case in *Vanilla* are doubtless active plastids, while those restricted to the more or less evanescent floral tissues are probably degenerate plastids.

The interpretation of the homogeneous oil bodies in the liverworts is not clear. They might be degeneration products, but they might also be an accumulation of normal plastid products within a plastid.

It has also been shown in the studies of *Iris macrosiphon* that elaioplasts of the type described by Lidforss (32) as homogeneous oily spheres may form by the degeneration of oil-bearing plastids. A similar phenomenon has been described by Beer (4) as a final step in the degeneration of plastids in floral tissue of *Gaillardia*. That the spheres described by Lidforss (32) are likewise degeneration products of plastids can only be surmised. It is possible that they are more or less fused aggregations of oil globules unconnected with plastids.

Evidence of a relationship between the various types of elaioplasts described in the literature has been found in these studies. A structural similarity is seen between the oil bodies in the Marchantiaceae and those in *Vanilla* in that they are both aggregations of plastid-like bodies. I have found no record in the literature of the aggregation of these bodies in the Marchantiaceae, although the phenomenon was noted for elaioplasts in the monocotyledons as early as 1914. In addition to this direct evidence of structural similarity the observations upon the development and variations of elaioplasts in *Iris* have demonstrated that these oily plastids show, at one time or another, the widely varying phenomena which have heretofore been considered distinctive of different types of oil bodies. It has already been pointed out that elaioplasts of the homogeneous type described by Lidforss (32) sometimes result as a degeneration product of a granular type of elaioplast. It has also been found in *Iris* that the oily plastids show at one time or another the following phenomena described in the literature for oil bodies: aggregation and fusion of homogeneous oil globules, aggregation and compacting of plastid-like bodies, aggregation about the nucleus, unrestricted position in the cell, degeneration involving the disappearance of the oil and degeneration involving the formation of oily spheres. In brief the morphological distinctions between the various classes of oil bodies appear to be breaking down, while it is evident that plastids can show widely varying phenomena which, considered separately, might be interpreted as bases for the distinction of fundamentally different types. Further study on this subject is highly desirable. In particular further observations on oil bodies and plastids in *Vanilla, Ornithogalum* and the hepatics are needed, for much of the literature deals with elaioplasts found in them.

An additional point which tends to reduce the number of recorded distinctions between the oil bodies in the liverworts and those in the monocotyledons appears in the permanent character of the elaioplasts in the rhizomes of *Iris*. Heretofore elaioplasts in monocotyledons have been described as temporary structures, while those in the hepatics have been thought to be more permanent. It may be noted here that my own limited studies made on *Vanilla* indicate that elaioplasts are not the temporary structures even in this classical plant that one would infer from the literature.

That conditions producing oil bodies are more or less restricted in their occurrence in the monocotyledons has again been brought out in these studies. Elaioplasts do not appear generally throughout the group, although the appearance of oil-bearing chloroplasts is not uncommon. This study adds another genus and many species to the published lists of monocotyledons in which elaioplasts occur. Although oil-bearing plastids occur in the rhizomes of practically all species, it is noteworthy that the elaioplast condition is restricted for the most part to the Apogon irises of Asia and America. This is the first record that I find of the occurrence of oil bodies in rhizomes, although Politis (39) has described them in bulbs.

Evidence of the function and significance of the oil bodies has been found. In ***Iris*** the bodies are clearly assimilative organs as shown by their formation of starch. That the oil itself is a reserve food supply is indicated. In certain species it replaces at least morphologically the starch stored in the rhizomes of other species. There is no evidence that the elaioplasts are ever excretions, although they may be at times degeneration products.

There is no evidence of the division of elaioplasts recorded by a few writers. The fragmentation described by Raciborski (41) and Politis (39) is but the separating of the aggregated plastid-like bodies. This can be seen in *Vanilla*. That there is ever a passive division of an aggregated mass of oil bodies by the cell wall is improbable. Neither such aggregations nor a great development of oil was found in the meristems of ***Iris***, *Vanilla* and the hepatics.

2. Significance of Present Study in Interpretation of Plastids and Chondriosomes

With the recognition of elaioplasts as plastids, a study of their variations became a study of the variations in plastids and chondriosomes. No new phenomena have been noted, but significant interpretations of those already recorded in the literature[1] have been made.

Most striking of the phenomena observed was the development of large quantities of oil globules in plastids. The formation of oil globules in plastids has been known for a long time and has recently been emphasized by Guilliermond's (15–20) studies of ***Iris***. But even Guilliermond's extensive investigations have not shown an accumulation of oil in plastids comparable to that found in ***Iris versicolor*** where the quantity is

[1]A summary of the present status of plastids and chondriosomes may be found in books and papers by Schürhoff (44), Sharp (45), Guilliermond et al. (20) and Mottier (37).

so great as to obscure the structure of the plastids and render them unrecognizable for months at a time.

The association of oil globules with young or degenerating forms more frequently than with mature plastids has been suggested by Guilliermond et al. (20). But such is not the case in *Iris* where the largest formation of oil is in the functioning plastids of the rhizomes.

A second phenomenon noted was the plastic quality of chondriosomes and of transitional types of plastids. As evidenced in amoeboid movements this has often been recorded in the literature, while it has been emphasized in the recent studies by Guilliermond and his associates. But I have found in the literature no reference to the extreme plasticity amounting to fluidity such as occurs in some young leucoplasts where the included globules are moved about at random within the plastid.

The significance of the chondrioconts has been brought out clearly in the survey of the variations of plastids and chondriosomes made in this study. The chondrioconts are essentially plastids producing at times all of the visible products of plastids such as starch, chlorophyll or a yellow pigment. They share, too, the plastic qualities of plastids which they display to a much greater degree. They occur in restricted tissues as transitional stages in the formation of plastids from mitochondria-like primordia or as more or less degenerating forms of plastids. Often in the rootcap and in floral tissue they are pigmented, although the formation of pigment is not confined to them. It should be noted that in some tissues chondrioconts persist without assuming the more usual plastid form.

Chondrioconts should not be interpreted as invariably forming a stage in the development of chloroplasts [Guilliermond et al. (20)]. On the contrary my studies show that the majority of chloroplasts and other plastids develop from mitochondria-like primordia without the intervention of a chondriocont stage. Where chondrioconts do form a stage in the development of plastids, the whole chondriocont develops into a plastid. There is no budding or fragmenting of the chondriocont involved. The appearances that have been interpreted as budding in chondrioconts or as evidence of fragmentation are but temporary shapes of the plastic chondrioconts.

It may be noted here that the studies of chondrioconts emphasize Kassmann's (25) observations that plastids do not divide under normal conditions. This is a much debated point in the literature upon plastids.

There was no evidence of vacuole formation in degenerating plastids or chromatophores such as have been described in flowers [Guilliermond et al. (20)]. The appearance which has been interpreted as a vacuole is rather the inclusion of a small amount of protoplasm as a result of the amoeboid movements of the plastid at this time.

It is worth emphasizing here that the complete degeneration of the plastids may occur without involving the death of the cell. It has already been noted by Beer (4) that such a phenomenon occurs in some floral organs where the life of the mature cells is comparatively brief. I have found no record, however, of the degeneration of the plastids in cells which remain alive for months thereafter, a phenomenon found in the rhizomes of *Iris macrosiphon*.

In general, it may be stated that there is no sharp line of demarcation between elaioplasts, plastids, chondrioconts and mitochondria. In *Iris* they have all been observed to form starch and, with the exception of mitochondria, chlorophyll, oil and a yellow pigment. In some instances several of these products may appear at once, or they may develop in succession, or none of them may form. Nor should any of the chondrioconts and plastids be considered end products of a developmental series originating from mitochondria-like bodies, for until irreversible changes occur such as a resolution into structureless spheres of oil, the shapes assumed are reversible. In other words there is no clear distinction between amyloplasts, leucoplasts, chloroplasts, chromoplasts and elaioplasts; nor is it possible to consider plastids, chondrioconts, proplastids and mitochondria as unrelated cell structures. Rather it appears that these are all forms of the same fundamental cell organ differing only in size and in the chemical products being formed at the time.

3. Significance of the Study of Oil-bearing Plastids in Iris from a Taxonomic Viewpoint

The occurrence of two types of plastids in rhizomes of *Iris* each more or less restricted to certain groups of species appears to be of taxonomic significance. The consistent appearance of the same type in well defined species indicates a character that may be useful in separating species. In addition it should be noted that the substitution of compound starch grains for the elaioplasts in rhizomes of a known hybrid and in one or two questionable species, although not an invariable phenomenon, suggests a possible means of identifying some plants as of hybrid origin.

CONCLUSIONS

1. The anomalous bodies in the rhizomes of *Iris versicolor* are an elaioplast phase of leucoplasts persisting throughout the resting season, but forming starch throughout the actively growing period.

2. Some, if not all, of the so-called "elaioplasts" are plastids in some form or other.

3. Elaioplasts of the plastid type are not necessarily degeneration types: in *Iris* they are functional plastids.

4. The rotary movement of elaioplasts described in the literature is an artefact due to slow death or injury; the Brownian movement described as characteristic of globules in certain liverworts is a degeneration or injury phenomenon.

5. The elaioplasts in *Lunularia* and *Vanilla* are morphologically similar in that they are aggregations of small plastid-like bodies that form oil. This establishes another link between elaioplasts in the liverworts and those in the monocotyledons.

6. There is no sharp line of demarcation between the different kinds of plastids and chondriosomes each of which is a more or less temporary form capable of changing to the other types.

7. At all times the plastids are more or less plastic but particularly so in young tissues, fibrovascular tissue or slowly dying cells.

8. Leucoplasts, chloroplasts and chromatophores do not go through a set series of changes in developing from plastid types characteristic of meristematic tissues. They may pass through various series depending upon the type of mature tissue involved, or they may merely increase in size with probable changes in their physico-chemical structure. They never form by budding of chondrioconts succeeded by separation of the buds so-formed.

9. Chondrioconts may form an intermediate developmental stage in the formation of "mature" plastids, although not necessarily; they may persist in some tissue; or they may be an intermediate stage in the degeneration of plastids.

10. Plastids and chondriosomes in *Iris* all show the structure of a matrix with embedded globules. Pigments are more soluble in the globules than in the matrix, although they are found in both.

11. Two types of degeneration of plastids occur involving (a) an increasing fluidity and a decreasing refractivity or (b) a complete breaking down into large homogeneous spheres of oil. Degeneration of the plastids does not necessarily involve the death of the cell.

12. The formation of a vacuole with at times an included oil drop in degenerating chondrioconts is in reality an inclusion of protoplasm.

13. Different species of *Iris* are characterized by distinct types of elaio-leucoplasts in their rhizomes. The distribution of types follows closely the taxonomic groupings and may be of significance in separating species.

14. The occurrence of such elaioplasts as those in rhizomes of *Iris versicolor* is confined, so far as could be ascertained, to rhizomes of this genus. For the most part they are restricted to rhizomes of certain species, chiefly Apogons of Asia and America.

15. Refractive bosses on pollen grains of *Iris Xyphium* are oil-bearing chromatophores adhering from the tapetal fluid. Other markings found on pollen grains were part of the wall structure.

ACKNOWLEDGMENTS

I am under deep obligations to Professor I. W. Bailey of Harvard University for his continuously helpful suggestions and interest throughout the course of the investigations recorded in this paper. I also wish to thank Dr. George M. Reed of the Brooklyn Botanical Garden and Dr. Edgar Anderson, recently of Washington University and the Missouri Botanical Garden for the material which they kindly placed at my disposal. Dr. Anderson also aided materially in connection with pertinent taxonomic matters. I wish to express my appreciation too of the advice and material offered by Dr. Conway Zirkle and others.

Most of the work was done in Professor Bailey's laboratory in Harvard University. I spent one summer in Professor Bailey's laboratory at the Stanford Laboratory of the Carnegie Institution of Washington, Division of Plant Biology, Palo Alto, California, and several weeks at the Missouri Botanical Garden in St. Louis. I am grateful to these institutions for the facilities that they afforded.

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DESCRIPTION OF PLATES

Figs. 1–4, 6, 8–10, 38, 39, 45, 46 were made with a camera lucida; the magnifications given for these figures are exact. The other figures were drawn free-hand; the magnifications given for them are approximate.

Plate 132

Fig. 1. *Iris versicolor* L. Living cells of the rhizome from material collected in December. × 475.

Fig. 2. Individual elaioplasts from cells shown in Fig. 1. × 1600.

Fig. 3. Individual elaioplasts from cells shown in Fig. 1 after treatment with (a) ammonium Erliki fixative, and erythrosin and cyanin; and (b) 0.5% osmic acid. × 1600.

Fig. 4. *Iris versicolor* L. Individual elaioplasts from rhizomes collected in October: (a) surface view; (b) included starch grains; (c) diagram to illustrate position, size, number and shape of starch grains. × 1600.

Fig. 5. *Iris versicolor* L. Individual elaioplasts treated with Gram's solution: (a) material from Duxbury, Mass.; (b) material from Lincoln, Mass. These were drawn at the same magnification.

Fig. 6. Isolated starch grain from elaioplast shown in Fig. 4. × 1600.

Fig. 7. *Iris tectorum* Maxim. Elaioplasts from young cells of rhizomes collected in March: (a) normal plant; (b) dying plant. × 845.

PLATE 133

Fig. 8. *Iris pallida* Lam. × ? Living cell of the rhizome from material collected in December. × 475.

Fig. 9. Individual oil-bearing plastids from cell shown in Fig. 8 showing plastids: (a) without starch; (b) with starch; (c) is a diagram showing the relative positions of plastid and starch. × 1600.

Fig. 10. Individual starch grains from plastids similar to those shown in Fig. 9. × 1600.

Fig. 11. *Iris pumila* L. Oil-bearing plastids from living cells of a rhizome collected at St. Louis in March: (a), (b) and (c) are plastids from successively older cells. × 1270.

Fig. 12. Oil-bearing plastids from living cells of rhizomes of the following California species of *Iris*: (a) *I. missouriensis* Nutt.; (b) *I. Douglasiana* Herb.; (c) *I. longipetala* Herb.; (d) *I. Hartwegii* Baker. Material collected in California in August. × 1270.

Fig. 13. Diagram showing the types of oil-bearing plastids found in *Iris* species in March. See table p. 246 for names.

PLATE 134

Fig. 14. *Iris macrosiphon* Torr. Elaioplasts in living cells from the cortex of a rhizome collected in July: (a), (b) and (c) are taken from successively older cells. × 1245.

Fig. 15. Elaioplasts shown in (a) Fig. 14b and (b) Fig. 14c treated with Gram's solution to show the surrounding cytoplasm. × 1245.

Fig. 16. *Iris Xyphium* L. Optical section of living pollen grain. × 500.

Fig. 17. *Iris Xyphium* L. Untreated pollen grains in surface view: (a) in tapetal fluid of immature anther; (b) from a ripened anther. × 475.

PLATE 135

Fig. 18. *Iris macrosiphon* Torr. Oil-bearing plastids in living epidermal cells of root-tip: (a), (b), (c) and (d) are from successively older cells. × 1280.

Fig. 19. *Iris versicolor* L. Elaioplasts from living cells of the meristem of a rhizome: (a) from one of the youngest cells; (b) and (c) from successively older cells. × 1620.

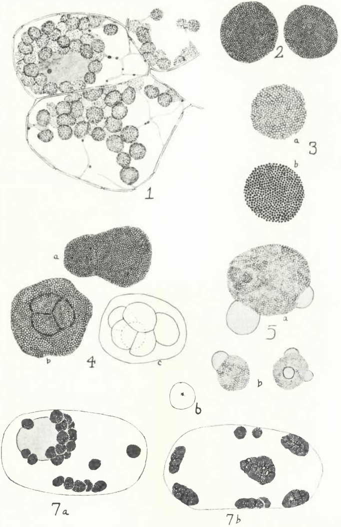
Fig. 20. *Iris pallida* Lam. × ? Plastids from living, elongated, differentiating cells of root-tip: (a) successive observations on a single plastid to show fluctuating variations in form; (b), (c), (d) and (e) similar observations on four additional plastids. × 1620.

Fig. 21. Plastid similar to those in Fig. 20 but from an older cell. × 1620.

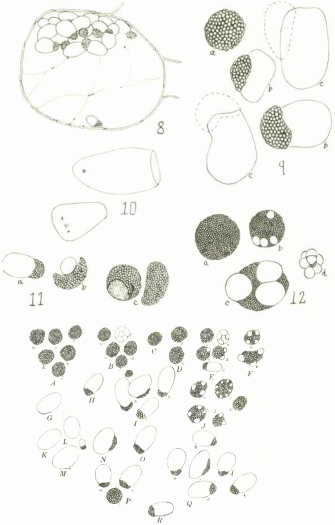
Fig. 22. Plastid similar to that shown in Fig. 21. × 1620.

Fig. 23. Plastid similar to that shown in Fig. 21. × 1620.

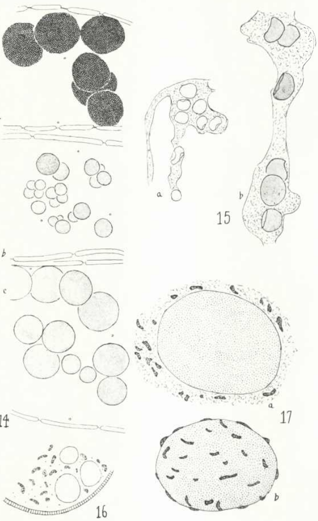
Fig. 23a. Plastid similar to that shown in Fig. 21. × 1620.



Elaioplasts in Iris



ELAIOPLASTS IN IRIS



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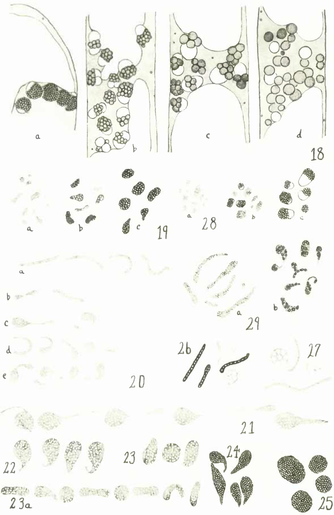
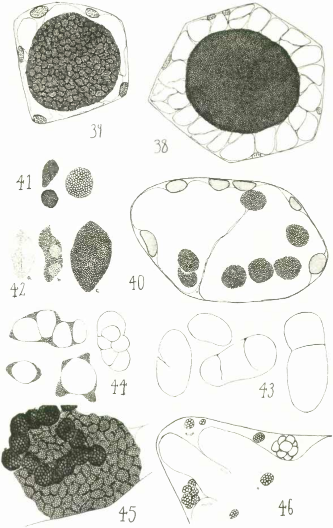


ELAIOPLASTS IN IRIS

ELAIOPLASTS IN IRIS



ELAIOPLASTS IN IRIS

Fig. 24. *Iris pallida* Lam. × ? Elaioplasts from living cells of cortex of root-tip. × 1620.
Fig. 25. *Iris pallida* Lam. × ? Elaioplasts from living cells of cortex of older root. × 1620.
Fig. 26. *Iris pallida* Lam. × ? Plastids and chondriosomes from a single living cell of the central cylinder of a root-tip. × 1620.
Fig. 27. Plastids and chondriosomes from another cell of the central cylinder. × 1620.
Fig. 28. *Iris pallida* Lam. × ? Oil-bearing plastids from living cells of the meristem of a rhizome: (a), (b) and (c) are from successively older cells and show the appearance of starch. × 1620.
Fig. 29. *Iris pallida* Lam. × ? Chromoplasts from living cells of the root-cap: (a) and (b) are from successively older cells. × 1620.

PLATE 136

Fig. 30. *Iris pallida* Lam. × ? Elaioplasts from living cells of cortex of root-tip. × 1650.
Fig. 31. *Iris pallida* Lam. × ? Chromatophores from living cells of the epidermis of the root-tip: (a), (b), (c) and (d) from successively older cells. × 1650.
Fig. 32. *Iris versicolor* L. Plastids from living cells of the epidermis of a root-tip. × 1650.
Fig. 33. *Iris pallida* Lam. × ? Chromatophores from living cells of the epidermis of a root-tip. × 1650.
Fig. 34. Chromatophores from living cells of the epidermis of a flower of a Pogoniris, probably of *I. variegata* L. × 1650.
Fig. 35. *Iris versicolor* L. Oil-bearing plastids from living cell of cortex of root. × 1650.
Fig. 36. *Iris versicolor* L. Chloroplasts from living parenchyma cells of a leaf: (a) without starch; (b) with starch. × 1650.
Fig. 37. *Iris versicolor* L. Plastids from living cells of the epidermis of a leaf. × 1650.

PLATE 137

Fig. 38. *Lunularia cruciata* (L.) Dum. Living elaioplast-bearing cell from a mature thallus. × 1080.
Fig. 39. *Lunularia cruciata* (L.) Dum. Living elaioplast-bearing cell from the younger tissue of a mature thallus. × 1080.
Fig. 40. One of the Jungermanniales. Living cell from a mature leaf. × 1250.
Fig. 41. Oil bodies from living cells of leaves of three different species of the Jungermanniales. × 1250.
Fig. 42. One of the Jungermanniales. Oil bodies from living differentiating cells of stem: (a), (b) and (c) from successively older cells. × 1250.
Fig. 43. One of the Jungermanniales. Oil bodies from living cells of mature plant. × 1250.
Fig. 44. One of the Jungermanniales. Oil bodies from living cells of younger tissue. × 1250.
Fig. 45. *Vanilla Pompona* Schiede. Elaioplast and chloroplasts from living cell of a leaf. × 915.
Fig. 46. *Vanilla Pompona* Schiede. Elaioplasts, chloroplast and chondriosomes in living cell of cortex of root-tip. × 1720.

ARNOLD ARBORETUM,
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NOTES ON YUCCA

Susan Delano McKelvey

With plates 138 and 139

Yucca Thornberi, spec. nov. Plate 138

Trunci 0.75–1.75 m. alti, congesti, infra foliis siccis reflexo-patentibus arcte obtecti, supra comam magnam satis elongatam foliorum viridium gerentes. Folia lineari-lanceolata, 0.30–1 m. vel ad 1.20 m. longa, 1.5–3.5 cm. lata, a basi vel a medio paullo latiore apicem versus attenuata, acuminata, pungentia, concava, utrinque laevia, luteo-viridia, stricta vel leviter recurva, flexibilia, initio margine saepe evanescenter denticulata, mox filifera filis crassiusculis curvatis tarde deciduis, parte basali 2.5–7.5 cm. longa et 7–12.5 cm. lata. Inflorescentia scapo 22–45 cm. longo incluso 1–1.30 cm. alta, angusta, basi et apice attenuata, folia quarta parte vel dimidio superantes; ramuli circiter 25, initio erecto-ascendentes, demum patentes; bracteae magnae, late triangulares; flores campanulati, 7.5–12.5 cm. longa; pistillum 5.5–7.5 cm. longum, ovario plerumque oblongo rarius attenuato, 4½ ad 6½ longiore quam lato, stylo 5–6 mm. longo, stigmatibus sub anthesi erectis vel fere erectis; filamenta 4–6.5 cm. longa, apice clavato brevi pro parte inferiore longo gracili. Fructus 13–17.5 cm. longus, 3–4.5 cm. diam., baccatus, incrassatus, apicem versus attenuatus et 2.5–5 cm. sub apice subito constrictus parte constricta plus minusve recurvata.

Arizona. Pima Co.: foothills of the Rincon Mts., slightly north of Rincon Creek, a tributary of Pantano Wash, elevation 3600 ft., *S. D. McKelvey*, no. 1627, March 23, 1930 (type; herb. Arnold Arboretum). Also from the same region are the author's collections nos. 1585, 2123, 2556, 2557, 2558, 2559, 2561, 2562, 2682, 2684.

Yucca Thornberi forms large and crowded clumps and produces many rather long stems 2–5 ft. in height which are covered below with a thick thatch of reflexed-spreading dead leaves and are crowned by large, somewhat elongated heads of green foliage which are constricted near the base and spreading above; the slightly broadened, concave, not conspicuously angled leaves are commonly smooth on both surfaces, yellow-green in color, with acuminate apex and, when young, often evanescently denticulate margins which, when the foliage is more mature become abundantly filiferous; the fibres are late-deciduous, moderately coarse and loosely curled. The inflorescence is for some time rather fleshy and brittle, 3–4 ft. in length overall, with a scape 9–18 in. in length; the inflorescence proper is long, narrow, tapered at both ends, and extends for $\frac{1}{4}$–$\frac{1}{2}$ its length above the leaves; its branchlets are about 25 in number, at first erect-ascending, eventually spreading; its bracts are large, fleshy to leathery, broad-triangular in form. The flowers are campanulate, large, 3–5 in. in length; the pistil is $2\frac{1}{8}$–3 in. long with a commonly oblong, only rarely tapered, ovary which is $4\frac{1}{2}$–$6\frac{1}{2}$ times as long as broad, the short style is $\frac{3}{16}$–$\frac{1}{4}$ in. long and, at anthesis, with erect, or nearly erect stigmas; the filaments vary from approximately $1\frac{1}{2}$–$2\frac{1}{2}$ in. in length and reach anywhere from slightly below to slightly above the shoulders of the ovary; their clavate tip is short in proportion to the long, slender, lower portion. The baccate fruit is 5–7 in. in length, slightly enlarged and tapered upward for its major lower portion, for 1–2 in. below the tip much contracted and commonly somewhat recurved.

Yucca Thornberi appears to be most closely related to *Y. arizonica* and to *Y. baccata* Torr., differing conspicuously from the latter in habit of growth, from both species it is distinct in form of inflorescence, in character of foliage and, though less so, in fruit.

It is a pleasure to give to this new species the name *Yucca Thornberi* in recognition of the fact that Dr. J. J. Thornber of the University of Arizona called the author's attention to the plant and with her spent considerable time in its study.

Yucca brevifolia Engelm. var. **Jaegeriana,** var. nov. Plate 139

A typo recedit habitu humiliore vix 3–4 m. excedente, trunco brevi circiter 75–90 cm. longo, ramis brevibus fere erectis arcte congestis, foliis circiter 10 cm. longis vel 20 cm. vix excedentibus comam congestam et symmetricam formantibus, inflorescentiis vix 30 cm. longis, scapo 2.5–5 cm. longo et 2.5–3 cm. crasso incluso, ramulis tantum 2.5–6.5 cm. longis.

CALIFORNIA. San Bernardino Co.: vicinity of the Shadow Mts., elevation approximately 4000 ft., *S. D. McKelvey*, no. 2732, April 30, 1932 (type; herb. Arnold Arboretum).

In several of the broad basins and foothill areas of the eastern part of the Mohave Desert of California and also in southern Nevada, occurs a form of the Joshua-tree which deserves varietal recognition. The plant—in appearance a miniature Joshua-tree—was brought to the attention of the writer by Mr. Edmund C. Jaeger of Riverside Junior College, Riverside, California, and is named in appreciation of this fact.

This variety is primarily distinguished from the better known plant by its dwarfer habit,—the plants not exceeding, except rarely and only in extremely old specimens, 10–12 ft. in height; the trunk is short, about 2½–3 ft. in length, stout (although, proportionately to that of the type of the species, slender); the branches are short, nearly erect and form an extremely dense, compact crown; the clusters of green leaves are crowded and symmetrical, about 1–2 ft. in length; the leaves are short, including the base about 4 in. long, not exceeding 8 in.,—or about the length of the shorter leaves of the type of the species; the inflorescence scarcely reaches 1 ft. in length; the scape is 1–2 in. long, 1–1¼ in. in diameter at base, and the flowering portion 9–10 in. in length with stout branchlets only 1–2½ in. long. In flower and in fruit characters it is very similar to the plant of taller habit.

Mr. Jaeger states (in litt., Oct. 2, 1934) that the distribution of the variety "reaches its greatest density in the vicinity of the New York Mts. in California." It has been collected by the writer in southern Nevada between the Colorado River and Searchlight (no. 4094), in the Spring Mts. (no. 4142) and on the eastern slopes of the Charleston Mts. (nos. 4097, 4098, 4099, 4100, 4132), in the first and last of which regions it occurs in abundance.

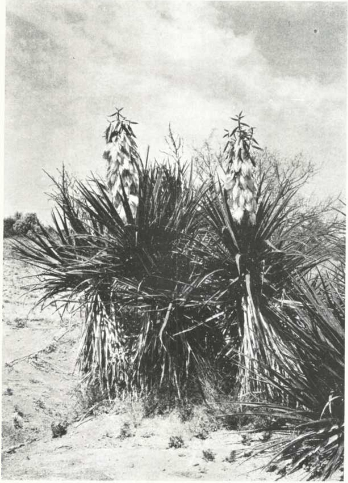
Yucca arizonica, nom. nov.

Yucca puberula sensu Torrey in Botany, Emory Report, 221 (1859), in part, not Haworth.

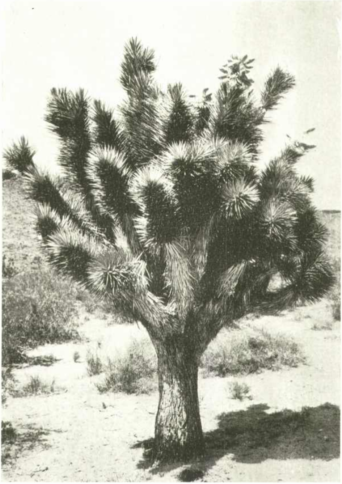
Yucca brevifolia Schott ex Torrey, Botany, Emory Report, 221 (1859), in part, as synonym of *Y. puberula* Torrey, not Haworth. — Engelmann in Trans. Acad. St. Louis, **3**: 46 (1873), in part, as synonym of *Y. Schottii* Engelm. — Trelease in Rep. Mo. Bot. Gard. **13**: 100, tt. 57–59, 96 (fig. 2, range map) (1902), first appearance as a valid species. — Not *Y. brevifolia* Engelm. (1871).

Yucca Treleasei MacBride in Contrib. Gray Herb. ser. 3, no. **56**: 15 (1918); not *Y. Treleasii* Sprenger (1906).

The name *Y. puberula* Haw. was first erroneously applied by Torrey to specimens collected by Arthur Schott in regions adjacent to Nogales, Arizona. Because of its connotation it is in the main referable to *Y. Schottii* Engelm., the inflorescences of which species are commonly puberulous. Schott's material represented a complex. For a certain portion of this material the name *Y. brevifolia* used by Schott in his notes was adopted by Trelease in 1902. This name, as pointed out by MacBride in 1918 was antedated by the name *Y. brevifolia* used by Engelmann in 1871 for the Joshua-tree; MacBride in consequence gave to Schott's plant the new name *Y. Treleasei.*



YUCCA THORNBERI McKelvey
A plant growing at the type locality.



YUCCA BREVIFOLIA var. JAEGERIANA McKelvey
A plant, 12 ft. in height, growing at the type locality.

Unfortunately the name *Y. Treleasii* was used by Carl Sprenger in 1906 for a hybrid *Yucca* (See Bull. Soc. Tosc. Ort. **31**: 134. 1906.—Molon, Yucche, 192, t. 6. 1914); the plant is without a name and the new name *Yucca arizonica* is here adopted for this species.

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JOURNAL

OF THE

ARNOLD ARBORETUM

VOLUME XVI JULY, 1935 NUMBER 3

THE VISIBLE STRUCTURE OF THE SECONDARY WALL AND ITS SIGNIFICANCE IN PHYSICAL AND CHEMICAL INVESTIGATIONS OF TRACHEARY CELLS AND FIBERS

I. W. BAILEY AND THOMAS KERR[1]

With plates 140–149

INTRODUCTION

THE SECONDARY WALL of plant cells has long been known to be a heterogeneous structure. That it is more or less conspicuously striated and laminated was shown by Mirbel, Von Mohl, Valentin, Meyen, Th. Hartig, and other pioneer anatomists who demonstrated, in addition, that it may be resolved by specific chemical and mechanical treatments into lamellae, fibrils, granules, and other visible units of fairly constant form and size. This led, during the second half of the last century, to prolonged discussions concerning the fundamental structure of cell walls in general, and to much speculation regarding the physiological processes involved in their formation.

Although a voluminous literature developed between 1850 and 1900, no consensus of opinion was reached concerning the exact physical and chemical significance of the visible heterogeneity of the secondary wall. Nor is there a general agreement among different groups of investigators at the present time. It is true that the study of anisotropy, of rod double refraction, of various types of dichroism, and of X-ray diagrams has in recent years contributed much toward a clearer understanding of sub-microscopic structures, and regarding the orientation of such structures in the grosser layers of the secondary wall, but it has not afforded as yet an adequate explanation of the finer types of visible heterogeneity.

[1]Parts of these investigations were made by the junior author as a National Research Fellow in Botany.

In view of such facts as these, it seemed desirable to the writers to undertake a detailed investigation of the secondary wall in an endeavor (1) to verify and, if possible, to amplify the observations of previous workers; (2) to correlate results obtained by different techniques and by the study of divergent cell types; and (3) to interpret the visible heterogeneity of the secondary wall in terms of its sub-microscopic structure and of its chemical composition.

In an investigation of this character one is faced, at the outset, by a serious difficulty, upon the solution of which success or failure clearly depends. The range of recorded cases in which the details of wall structure are even vaguely visible — without resorting to the use of softening or hardening processes, of macerating or swelling agents, and of other more or less drastic chemical and mechanical treatments — is very limited. Severe treatments are capable of yielding extremely useful and significant data, but are likely to produce distortions and other artifacts, and therefore must be checked by observations on untreated material. In other words, an adequate system of controls — or means of accurately visualizing the normal structure of the secondary wall — is indispensable.

As indicated in the preceding paper of this series (18), it is possible to section dense woods and other hard tissues without resorting to the use of softening processes which might modify their structure and chemical composition. It seemed advisable, accordingly, to make an extensive survey of a wide range of gymnosperms and angiosperms in search of species that afford clearly defined images of cell wall structure in untreated sections. More than 3000 species, representing 160 families and 40 orders, were examined. It was found that the large-celled woods of various tropical dicotyledons provide unusually favorable material for microscopic investigations. These plants are not bizarre or unusual forms; nor are they confined to any restricted group or genus. They are widely distributed and of not uncommon occurrence in such families as the Theaceae, Monimiaceae, Icacinaceae, Rhizophoraceae, Euphorbiaceae, Flacourtiaceae, etc. When thin (5–10 μ), smoothly-cut sections of the wood are examined in liquids of the right index of refraction, using the best modern optical equipment, the relatively broad expanse of wall in the fiber-tracheids and libriform fibers of certain of these plants reveals finely laminated, striated, and reticulated structures in exquisite detail. By using untreated sections of such plants as controls, it is possible to determine the exact effects upon normal structures of varied chemical and mechanical treatments, and thus to extend the scope of investigation to cover a wide range of less favorable species and tissues.

The following discussion of tracheary cells and fibers is divided into two parts. The grosser and more conspicuous types of layering of the secondary wall are dealt with in Part I; structures which more nearly approach the limits of microscopic visibility, in Part II. As previously stated, considerable is known[1] concerning the physical factors involved in the differentiation of the former structures, which must be clearly visualized and accurately correlated before proceeding to a detailed consideration of the finer types of visible heterogeneity.

TERMINOLOGY

The terms *middle lamella, primary wall, secondary wall,* and *tertiary wall* have been employed in several fundamentally different senses and to designate entirely different structures. This has led to much confusion in the literature and to serious discrepancies, not only in descriptive morphological work, but also in physiological, biophysical, and biochemical investigations. As a result of our detailed study of the cambium and its derivatives and of our preliminary investigations of other meristems and their derivatives, we attempted, in a former paper (18), to clarify the situation by suggesting that (1) the term *middle lamella* be used synonymously with intercellular substance in referring to the truly isotropic material which separates the walls of adjoining cells; (2) the term *primary wall* should no longer be applied to the first-formed layer of secondary thickening, but should be reserved for the original wall of the cell which is formed in the meristematic region and is carried over in more or less modified form into the fully differentiated tissues; and (3) the term *secondary wall* be used in referring to the strongly anisotropic layers of secondary thickening which are formed after a cell has attained its final size and shape. The term *tertiary wall* is so variously used and interpreted and so confusing that its use should be discontinued. We propose to employ our revised terminology in this and succeeding papers.

I. THE PRINCIPAL LAYERS OF THE SECONDARY WALL

A. Layering Due to Physical Factors

The secondary wall of normal tracheids, fiber-tracheids, and libriform fibers commonly consists of three layers of different refractive character; (1) a relatively narrow outer layer, (2) a narrow inner layer, and (3) an intervening layer of variable thickness. When thin, per-

[1]For comprehensive reviews of the literature relating to this subject, the reader is referred to Van Iterson (30, 31) and Frey-Wyssling (13).

fectly transverse sections of such cells are examined in polarized light between crossed nicols, *Fig. 3,* the inner and outer layers exhibit strong double refraction and are brilliant — except in positions of extinction — whereas the central layer is dark or noticeably less birefringent. The conditions tend to be reversed in longitudinal sections, *Fig. 2,* in which the central layer shows intense double refraction, and the inner and outer layers are dark or less conspicuously birefringent. In other words, as shown long ago by Dippel (7) and others, the secondary wall consists of anisotropic layers which are dark or brilliant in polarized light depending upon the plane of sectioning of the cell or upon the angle from which the wall is viewed.

Our extensive survey of gymnosperms and angiosperms has demonstrated that most tracheids, fiber-tracheids, and libriform fibers are provided with a secondary wall of this 3-layered type. The narrow inner and outer layers are of relatively constant thickness, not only in different parts of a given plant but also in plants of different systematic affinities. Variations in thickness of the secondary wall are due, therefore, primarily to fluctuations in the width of the central layer. When the secondary wall is thin, as in the tracheids of the early wood of many conifers, the inner and outer layers are so closely approximated that the tenuous intervening central layer is invisible in polarized light, except in very thin (3–7 μ), perfectly transverse sections of straight-grained tissue. In thicker or obliquely cut sections, the width of the inner and outer layers is much exaggerated by the scattering of light from these intensely birefringent structures. This fogs and conceals the central layer, just as the closely approximated brilliant outer layers of adjacent cells commonly obscure the tenuous primary walls and middle lamella (compare *Figs. 1* and *3*).

Deviations from the normal 3-layered type of secondary wall are of not infrequent occurrence. Thus, many thick-walled libriform fibers and fiber-tracheids have no clearly differentiated inner layer, whereas others have more than three layers of varying width and birefringence, *Fig. 4.* Walls of a multiple-layered, anisotropic type, which are of relatively sporadic occurrence in the fiber-tracheids and libriform fibers of dicotyledons, are characteristic features of the fibers of many monocotyledonous stems. In transverse sections of such fibers, *Fig. 6,* there are narrow brilliant zones in polarized light which alternate regularly with broader and conspicuously less birefringent ones. Variations in the thickness of the secondary wall of these cells are due largely to variations in the number of successively formed layers.

The optical behavior of the anisotropic layers of the secondary wall of tracheary cells and fibers is closely correlated with the orientation of striations and so-called fibrillar structures, which are visible in cells that have been subjected to various chemical and mechanical treatments. When the striations and fibrils are arranged parallel, or nearly parallel, to the long axis of a tracheary cell or fiber, a layer is dark in sections cut at right angles to this axis, but is brilliant in longitudinal sections and in surface view — except, of course, in the four positions of extinction. The intensity of the birefringence varies in obliquely cut intervening sections, decreasing as the plane of section approaches that of a truly transverse section. On the contrary, where the striations and fibrils are arranged approximately at right angles to the long axis of a cell, a layer is brilliant in cross sections and in surface view, but is dark in thin longitudinal sections, *Fig. 2,* which transect the fibrillar structure. When the striations and fibrils have a helical arrangement and, therefore, are obliquely oriented in relation to the major axis of the cell, a layer is brilliant in surface view and more or less birefringent in both transverse and longitudinal sections. If the helix has a pitch of approximately 45°, an oblique section, which is cut parallel to the striations and fibrils on one side of the cell, will transect these structures on the opposite side of the cell. Thus, in such sections, the layer will exhibit both isotropy and strong double refraction; i.e., it will be dark on one side of the section and brilliant on the opposite side. Changing the fibrillar orientation from a left-handed to a right-handed helix or *vice versa* will not alter the birefringence in transverse or in longitudinal sections so long as the angle of obliquity remains constant.

In the typical 3-layered secondary walls of tracheids, fiber-tracheids, and libriform fibers, the striations and fibrils of the central layer are oriented parallel to the long axis of the cell, or at angles which do not deviate excessively from that axis; whereas those of the inner and outer layers are arranged more nearly at right angles to the major axis of the cell. Thus, the central layer exhibits strong double refraction in longitudinal sections, *Fig. 2,* and isotropy or relatively feeble double refraction in transverse sections, *Figs. 1* and *3;* whereas the conditions are reversed in the case of the inner and outer layers of the secondary wall. In multiple-layered walls of the type illustrated in *Fig. 6,* the orientation alternates regularly from parallelism to the major axis of the cell in the broader layers to marked obliquity in the narrower ones. The former layers exhibit intense double refraction in longitudinal sections; the latter layers, in transverse sections.

In the case of optical anisotropy, the so-called index-ellipsoid has, according to Frey-Wyssling (13), a major axis (N_γ) which is oriented parallel to the striations and fibrils, and two minor axes (N_α and N_β) which are placed at right angles to these structures. On the contrary, in the case of swelling-anisotropy, the ellipsoid of expansion has two major axes which are oriented at right angles to the striations and fibrils, and a minor axis which is parallel to these structures. Therefore, the dark layers of *Figs. 1, 3,* and *6,* which have longitudinal striations, expand laterally, increasing in both width and circumference; whereas the strongly birefringent layers, the striations of which are oriented more nearly at right angles to the long axis of the cell, are unable to do so and expand longitudinally. Where the dark layers are of considerable width, they tend, by their excessive lateral expansion, to disrupt the thin birefringent layers, as indicated in *Fig. 7.*

The strongly anisotropic behavior of the secondary wall suggests that its layers are composed of sub-microscopic units which have definite planes of orientation, and that there is a close correlation between the orientation of these units and of such visible structures as striations and fibrils. It was in fact a consideration of these phenomena which led Nägeli to formulate the Micellar Hypothesis.

More recently, X-ray analyses and other physico-chemical investigations have indicated that native cellulose consists of chains of anhydrous glucose residues which are bound together by secondary valences into a space lattice of definite dimensions. These chains are arranged parallel to each other, and, in the case of the secondary wall of fibers and of *Valonia*, are oriented parallel to the striations and fibrils — as shown by Katz (17) and by Astbury and his co-workers (1). Furthermore, there is much cumulative evidence[1] from detailed investigations of anisotropy, of rod double refraction, of various forms of dichroism, and of X-ray analyses which suggests that the cellulose chains are not uniformly distributed throughout the secondary wall, but are aggregated into more or less vaguely defined anisotropic units the major axis of which is oriented parallel to that of the visible striations and fibrils.

In view of such facts as these, it is evident that layering of the type discussed on preceding pages is not due fundamentally to differences in chemical composition, but rather to changes in the orientation of anisotropic units of cellulose in the successively formed layers of the secondary wall.

B. Layering Due to Chemical Factors

The broad central layers of normal fiber-tracheids and libriform fibers frequently have subsidiary layers of varying width which are much

[1]This evidence has recently been summarized and discussed by Frey-Wyssling (13).

intensified by differential staining, *Fig. 8*. These subsidiary layers, unlike those illustrated in *Fig. 4,* are not closely correlated with variations in the orientation of the anisotropic cellulose, but are due to differences in lignification or to variations in the distribution of non-cellulosic constituents. They may be eliminated by delignification and other standard treatments for the purification of cellulose. It should be emphasized in this connection that the anisotropic layers of normal tracheids, fiber-tracheids, and libriform fibers are coherent even in walls that have been treated to remove their non-cellulosic constituents. There are evident planes of weakness but no actual discontinuities in the cellulosic matrix.

Conspicuous discontinuities are, however, of not infrequent occurrence in the peculiar tracheids of "compression wood," in so-called gelatinous fibers, in certain types of bast fibers, and in sclereids. They are due to narrow layers of *truly isotropic* material which contain little, if any, cellulose. Thus, when sections of unlignified or delignified cells are treated with standard solvents of pectic compounds and hemicelluloses, the layers dissolve and liberate the anisotropic layers of cellulose which may be slipped apart as shown in *Fig. 26*. These truly isotropic layers may be accentuated by differential staining and are clearly visible in ordinary light, *Fig. 21*. They present some difficulties, however, when sections are examined in polarized light between crossed nicols. For example, the entire laminated structure in *Fig. 21,* with the exception of the narrow outer layer, is dark in polarized light, owing to the fact that the orientation of cellulose in the anisotropic layers is parallel to the long axis of the cell. Therefore, the truly isotropic layers are concealed in transverse sections, but they are clearly visible in radial longitudinal sections and appear as dark lines between the birefringent layers of cellulose. There are similar tenuous isotropic films in the fibers of ***Pandanus*** on the outside of each narrow anisotropic layer, *Fig. 6*. They are masked in both transverse and longitudinal sections, since the broader anisotropic layers of cellulose are dark in cross sections, and the narrower ones are dark in longitudinal sections.

C. Layering in Sclereids and Non-fibrous Sclerenchyma

It should be noted, before passing to a detailed consideration of the finer types of visible structures, that sclereids and other types of non-fibrous sclerenchyma have a fundamentally different type of secondary wall. The anisotropic layers of such cells—at least in tissues of the higher plants that we have examined thus far—show no conspicuous striations or fibrillar structures, either in the untreated or in the swollen condition of the cell wall. Furthermore, the anisotropic layers are brilliant in polarized light in all planes of section of the secondary wall, but are dark in surface view. The birefringent layers alternate more or less regularly with others which are dark in all planes of view, *Fig. 5*. A detailed discussion of these cells and of other non-fibrous types is reserved for subsequent papers of this series.

II. THE FINER VISIBLE STRUCTURES OF THE SECONDARY WALL

A. Normal 3-Layered Tracheids, Fiber-Tracheids, and Libriform Fibers

As stated in Part I, variations in thickness of the secondary wall of normal tracheids, fiber-tracheids, and libriform fibers are due primarily to fluctuations in the width of the central layer, which may attain a radial breadth of more than 15 μ in the large-celled woods of various tropical dicotyledons. Therefore, the central layer provides more favorable material for sectioning and for study at high magnifications than either the inner or the outer layers which are so tenuous as to present serious optical difficulties.

Figure 10 is a transverse section of the wood of *Siparuna bifida* (P. & E.) A. DC. cut without preliminary softening or other modifying treatments. The broad central layer of the secondary wall is strikingly heterogeneous and exhibits a complex pattern of anastomosing radial striations. The striations are clearly visible in unstained sections mounted in water and in other liquids of varying indexes of refraction; and, in white light, are optically of two types, i.e., light and dark. There are corresponding light and dark striations in tangential longitudinal sections, *Fig. 13*. It is evident, accordingly, that the central layer of the secondary wall in these cells is composed of thin plates or lamellae which have a radio-longitudinal or radio-helical orientation. The lighter lamellae are strongly birefringent in polarized light, *Fig. 13*, except in positions of extinction and in sections cut at right angles to the longitudinal axis of the lamellae; whereas the alternating lamellae are dark, or at least comparatively isotropic, in all planes of view.[1]

The birefringence of the lighter lamellae is not due entirely to rod double refraction, as may be determined by examining sections in a graded series of liquids of varying indexes of refraction. Nor is the

[1]Extremely thin, smoothly cut sections are essential for critical examination in polarized light. If the sections are too thick or are scratched or roughened in cutting, the tenuous dark lamellae will be completely masked by the glare of light from the strongly birefringent lamellae.

apparent isotropy of the intervening lamellae due solely to the masking effects of lignification or to the presence of other non-cellulosic constituents. The walls of immature unlignified cells show identical patterns and a similar differentiation into lamellae of two distinct categories of birefringence, as do delignified cells that are treated for the removal of hemicelluloses and other non-cellulosic constituents.

By subjecting untreated sections to the action of such swelling agents as acids, alkalies, chloro-iodide of zinc or cuprammonium hydroxide, and by carefully controlling the reactions, it is possible to expand the central layer and its constituent lamellae without distorting or seriously modifying the original structural pattern (compare *Figs. 10* and *11*). As the central layer expands and enlarges under the microscope, successively finer details of structure become visible. The lamellae are not discrete homogeneous entities, and are resolved during the expansion of the central layer into aggregations of elongated heterogeneous complexes of varying degrees of fineness which grade down to the limits of microscopic visibility. The darker lamellae are compact sheets of relatively isotropic material which contain a low ratio of birefringent complexes. On the contrary, the lighter lamellae are aggregations containing a high ratio of birefringent complexes and a low ratio of apparently isotropic ones. There are no discontinuities in the structural pattern which is firmly knit together by lateral anastomoses and interlocking complexes.

After treatment for the removal of non-cellulosic constituents, the purified cellulose exhibits a similar structural pattern, which upon swelling, *Fig. 14,* is resolved into a complex and firmly coherent matrix, having elongated, intercommunicating interstices of varying degrees of fineness. The darker and more compact parts of the matrix, which correspond to the lighter lamellae of *Fig. 10,* are strongly birefringent in longitudinal sections and show conspicuous dichroism when carefully stained with congo red or chloro-iodide of zinc; whereas the lighter and more porous parts of the matrix, which correspond to the darker lamellae of *Fig. 10,* are so feebly birefringent that they appear to be comparatively isotropic.

Conversely, when the central layer is freed of cellulose by treatments with 72% sulphuric acid, the details of the swollen pattern are preserved in the so-called "lignin" residue, *Fig. 11,* which also is a complex and firmly coherent structure, having elongated, intercommunicating interstices of varying degrees of fineness. The lighter, finer residues of the originally birefringent lamellae exhibit well defined rod double refraction in longitudinal sections; whereas the darker, denser residues of the originally isotropic lamellae do not.

It is evident from a detailed comparison of *Figs. 11* and *14*, that the denser parts of the "lignin" residue correspond to the more porous parts of the matrix of purified cellulose, and that the "lignin" residue may be interpolated within the interstices of the swollen cellulose. Furthermore, the rod double refraction of the lighter lamellae of the "lignin" residue suggests that the two interpenetrating complexes grade downward in size far below the limits of microscopic visibility. In other words, each of the visible parts of the original structural pattern is heterogeneous and composed of optically different complexes. Removal of either the "lignin" or the cellulose leaves a coherent matrix of varying texture and porosity.

It is possible to reconstruct the structural pattern of the swollen cellulose from the "lignin" residue or *vice versa,* since they are positive and negative images of the same pattern. Although swollen sections of purified cellulose afford excellent preparations for visual examination, they are difficult objects for photographic reproduction. Therefore, a majority of our photomicrographs were made from "lignin" residues.

The structural pattern of the central layer is not a constant; it varies greatly not only in different groups of plants, but also at times in homologous cells of the same plant, and even within the wall of a single cell. For example, in *Siparuna bifida,* the two optically different complexes may be segregated into coarsely radial patterns which are clearly visible in untreated sections, *Fig. 10,* or they may be diffused in finer radio-reticulate patterns, *Fig. 16*, the finest of which are invisible in unswollen sections of the secondary wall. In such cells, conspicuous concentricities usually are due either to abrupt changes in the texture of the structural pattern, *Fig. 11,* or to zones of varying intensities of lignification, *Fig. 9*. The former persist in purified cellulose; the latter are eliminated during delignification.

Structural patterns of a basically concentric type are, however, of common occurrence in the normal tracheids of conifers, *Fig. 18,* and in the fiber-tracheids or libriform fibers of such dicotyledons as *Poraqueiba sericea* Tul., *Fig. 15*. In the central layer of these cells, the optically different complexes are segregated into concentric lamellae of varying widths and spatial groupings. The lamellae are of two types, i.e., strongly birefringent and comparatively isotropic. They are not discrete homogeneous entities, but may be resolved by treatment with swelling agents into complexes of varying degrees of fineness. As in the case of *Siparuna bifida,* the darker lamellae are compact aggregates of relatively isotropic material, *Figs. 15* and *18,* and contain a low ratio of birefringent cellulose; whereas the alternating lighter lamellae are composed largely of birefringent cellulose and contain a low ratio of isotropic material. The structural pattern persists in delignified sections which are treated with standard solvents of hemicelluloses and of other non-cellulosic constituents. When the purified cellulose is swollen, it appears as a complex and firmly coherent matrix, which exhibits a structural differentiation into compact, strongly birefringent and looser, comparatively isotropic lamellae.

It should be emphasized, in this connection, that the concentric structure of swollen cotton hairs — to which the work of Balls (2) has directed so much attention — appears to be due fundamentally to a similar structural pattern. When extremely thin, very smoothly cut sections of raw or purified cotton are treated with diluted Schweizer's reagent and are examined in polarized light between crossed nicols, the lamellae are, during the early stages of swelling, clearly of two optically different types, i.e., strongly birefringent and comparatively isotropic. During subsequent swelling, *Fig. 17,* the central layer is resolved into a complex and firmly coherent, spongy structure, the conspicuously birefringent parts of which are denser and obviously contain a higher ratio of cellulose than the more porous, intervening parts. In other words, the structural patterns of the central layers of cotton hairs, *Fig. 17,* of coniferous tracheids, *Fig. 18,* and of the fiber-tracheids of *Poraqueiba sericea, Fig. 15,* appear to be of a fundamentally similar type. In cotton hairs, as in tracheary cells, the width of the concentric lamellae is not a constant, but varies within relatively wide limits.

The structural pattern of cotton can not be due to a segregation of cellulosic and non-cellulosic constituents, since the central layer of cotton is composed of practically pure cellulose — the low ratio of non-cellulosic constituents in cotton is confined chiefly to the so-called cuticle or primary wall and to the lumen of the cell. Nor can the concentricities be due merely to inequalities in the penetration or modifying effects of the swelling agent, as may be demonstrated by cross-correlating the structural patterns of different hairs from the same boll. For example, in *Fig. 17,* in passing outward from the lumen, there is the following sequence of lamellae: six narrow alternating light and dark zones, an unusually wide light zone, two broad dark zones separated by a narrower light zone, two narrow dark zones and three narrow light zones, and six broad dark zones separated by narrower light zones. The fact that this identical complex of varying concentricities occurs in other hairs from the same boll can not be due to purely fortuitous circumstances, but might be due, either directly or indirectly, to the modifying effects of environmental factors upon the developing hairs.

Nor can the structural patterns of tracheids, fiber-tracheids, and libriform fibers be due to inequalities in the penetration and modifying effects of the swelling agents, since the patterns are visible under favorable conditions in untreated sections. Thus, the striking similarities in the finer visible structures of the central layer of unlignified and delignified cells and of "lignin" residues indicate that there are fundamental structural differences in the underlying cellulose to which the pattern of lignification must more or less closely conform.

Combinations of radial and concentric patterns of varying texture and complexity are of common occurrence in the fiber-tracheids and libriform fibers of dicotyledons.[1] In such cells there may be abrupt transitions within the central layer from coarse to fine texture and from radio-reticulate to concentric arrangements and *vice versa*. *Fig. 19* is a transverse section of the wood of *Tetramerista glabra* Miq., cut without preliminary softening or other drastic treatments. It illustrates a type of complex radio-concentric structure which is clearly visible in unstained sections mounted in water and other liquids of varying indexes of refraction. The pattern is complicated, however, as is so often the case in cells of this type, by the presence of zones of varying intensities of lignification. A radio-concentric pattern of much finer texture is illustrated in *Fig. 20*.

In the case of the more heavily lignified zones of such central layers, *Figs. 9* and *20*, both the birefringent and the comparatively isotropic parts of the structural pattern persist in "lignin" residues; whereas, in the less intensely lignified zones, the birefringent parts leave no structural residue. It is of interest, in view of the significance that has been attached to the work of Freudenberg and his co-workers (12), that in longitudinal sections the residues of heavily lignified parts exhibit conspicuous rod double refraction; whereas the residues of the less intensely lignified parts do not.[2] In other words, there appear to be submicroscopic structural differences in the two optically different complexes of the structural pattern which are reflected in their "lignin" residues. Furthermore, as previously noted, when delignified sections are stained with chloro-iodide of zinc or congo red, the strongly birefringent parts of the structural pattern may become markedly dichroic; whereas the more nearly isotropic parts do not.

The observational and experimental data that we have assembled in

[1]Concentric patterns with tenuous radial groupings are of not infrequent occurrence in the tracheids of conifers.

[2]Rod double refraction is visible only in the parts of the lignin residue which are strongly birefringent in the original material. Therefore, it can not be seen in sections which transect the so-called fibrillar structure, since all the cellulose is dark in polarized light in such planes of section.

our extensive survey of a wide range of gymnosperms and angiosperms indicate that the central layer of normal tracheids, fiber-tracheids, and libriform fibers is composed, in all cases, of a complex and firmly coherent matrix of cellulose with elongated, intercommunicating interstices. Within these interstices more or less "lignin" and other non-cellulosic constituents may be deposited. The denser and more porous parts of the cellulosic matrix exhibit striking contrasts in birefringence, which are accentuated by lignification. Where these optically different parts are diffused in various patterns of fine texture — as is usually the case in the tracheids of conifers and in the fiber-tracheids and libriform fibers of many dicotyledons — the structural complexes are invisible in untreated sections of the secondary wall, but may be swollen to microscopically visible dimensions, *Figs. 9, 12, 15, 16, 18,* and *20.* On the contrary, where the two optically different parts are segregated into coarser structural complexities, *Figs. 10, 13,* and *19,* the patterns are clearly visible in unswollen sections.

The cellulosic matrix of the central layer is composed, in all cases, of anastomosing elongated complexes which are oriented parallel to the long axis of the cell or in a helical arrangement. In fact, it is these elongated complexes of two optically different types, *Fig. 13,* which give a longitudinally or helically striated appearance to the central layer and determine its helical or longitudinal planes of cleavage into so-called fibrils. In other words, fibrils are heterogeneous shredded parts of an originally continuous and coherent matrix.

Although there are serious optical difficulties in studying the tenuous inner and outer layers of the secondary wall in sectional view, the striated appearance of these layers in surface view strongly suggests that they have similar structural patterns, the elongated, strongly birefringent complexes of which are oriented more nearly at right angles to the longitudinal axis of the cell.

B. Multiple-layered Fibers

The orientation of the elongated complexes of the structural pattern may be relatively uniform throughout the central layer of tracheids, fiber-tracheids, and libriform fibers, or it may deviate more or less in successively formed parts of this layer. Not infrequently, the changes in orientation are correlated with fluctuations in the texture of the structural pattern. Where the deviations are of considerable magnitude, they may be detected in polarized light, as illustrated in *Fig. 4.* The brilliant internal zones resemble the inner and outer layers of the secondary wall in having their birefringent complexes oriented more nearly at right angles to the longer axis of the cell, and therefore are bright in transverse sections.

Although there is a superficial similarity between *Fig. 4* and *Fig. 6,* the two cell walls are of a fundamentally different type. In the fibers of *Pandanus, Fig. 6,* as in the libriform fibers of various representatives of the Flacourtiaceae, *Figs. 21* and *26,* and in the bast fibers of ramie and of other dicotyledons, there are, as previously stated, actual discontinuities in the cellulosic matrix produced by narrow isotropic films of a non-cellulosic character. It should be emphasized, in this connection, however, that the individual anisotropic zones of these multiple-layered fibers have complex structural patterns of the general types discussed on preceding pages. For example, *Fig. 21* is a transverse section of the unswollen wall of *Homalium luzoniense* F. Villar. The layers of cellulose have a radio-reticulate pattern, the finer structural details of which are more clearly visible in swollen sections or in "lignin" residues, *Fig. 22*. The elongated birefringent complexes of the structural pattern are oriented parallel to the long axis of the cell. Therefore the entire complex of layers is dark in polarized light in transverse sections. Coarsely radial patterns of the type illustrated in *Fig. 10* are of not uncommon occurrence in the individual anisotropic layers of certain bast fibers; whereas in *Pandanus, Fig. 7,* the two optically different aggregates of cellulose are diffused in a pattern of unusually fine texture. Where the strongly birefringent complexes are oriented closely parallel to the longitudinal axis of the cell, the layer is dark in cross sections, *Fig. 6,* and merges with the truly isotropic film of non-cellulosic material; where they are oriented more nearly at right angles to the major axis of the cell, the layer is brilliant in transverse sections.

Variations in the orientation of cellulose in successively formed parts of the secondary wall have a marked effect upon the swelling of tracheary cells and fibers. Owing to its specific anisotropy, the cellulose expands at right angles to the so-called fibrillar axis, and, during extensive lateral swelling produced by strong chemical reagents, actually contracts in a direction parallel to this axis. In the case of isolated, delignified tracheary cells and fibers having normal 3-layered secondary walls, the laterally expanding central layer frequently splits the tenuous, longitudinally expanding outer layer into a series of constricting rings and helical bands, *Fig. 23,* and bulges outward between these structures. This ring-bead type of swelling occurs in cotton and has received considerable attention in literature dealing with commercial fibers. Although the so-called cuticle or primary wall may aid at times in bead formation, the controlling factor in cotton hairs, as in tracheary cells and fibers, appears to be differences in orientation of cellulose in the outer and central layers of the secondary wall. There are no transverse plates of non-cellulosic material in the secondary wall which are concerned in ring-bead formation as hypothesized by Lüdtke (21).

In the case of multiple-layered tracheary cells and fibers, it is possible to verify conclusions based upon the study of cells of the 3-layered type. We have shown that the concentric anisotropic layers of various representatives of the Flacourtiaceae, *Figs. 21, 22,* and *26,* are separated by films of non-cellulosic material, and that the orientation of the cellulose is constant except in the outermost layer of the secondary wall, where it is more nearly at right angles to the longitudinal axis of the cell. When such cells are partly or completely delignified and are swollen in cuprammonium hydroxide, the internal complex of anisotropic layers expands laterally and disrupts the tenuous outer layer into constricting rings, *Fig. 27,* or helical bands, *Fig. 24.* The internal layers of cellulose — which may be slipped apart as shown in *Fig. 26* — expand more or less in unison, *Figs. 24* and *27,* and no subsidiary internal constrictions are formed.

On the contrary, in the multiple-layered fibers of *Pandanus* and of other monocotyledons — which have similar isotropic films of non-cellulosic material, but where the orientation of the cellulose changes in the successively formed anisotropic lamellae — each of the narrow anisotropic layers, *Fig. 6,* may be disrupted by the lateral expansion of the broader layers, *Fig. 7,* and in the case of entire, delignified fibers, may give rise to constricting rings and helical bands, *Fig. 25.* In other words, the fiber behaves as if it were composed of several two-layered secondary walls, each of which swells in turn, forming similar ringed and beaded structures, *Fig. 25.* The two outermost layers swell first, the expansion working from the ends towards the center of the cell. The first formed ringlike constrictions commonly determine the position of subsequently formed internal constrictions.

Multiple-layered fibers of the Pandanus type are of common occurrence in the primary tissues of the stems of many monocotyledons. It is evident from Lüdtke's (20, 22) figures and descriptions that the fibers of bamboo are of this structural type, and that they exhibit similar phenomena during their expansion in such swelling agents as cuprammonium hydroxide. It is obvious, in addition, that purely physical phenomena of swelling have been misinterpreted by Lüdtke as evidence for the existence of transverse plates (Querelemente) of non-cellulosic material.

DISCUSSION

A. Concentricities

The secondary walls of tracheary cells and fibers are extremely complex and variable structures. Therefore, it is misleading and fruitless to attempt to homologize all types of fibers in a single structural model. For example, there are five different types of visible concentricities, due to:

1. The segregation of two optically different aggregates of cellulose into concentric patterns.
2. Abrupt changes in the form or texture of the structural pattern.
3. Changes in the orientation of the elongated birefringent complexes of the structural pattern.
4. Varying intensities of lignification or differences in the distribution of non-cellulosic constituents within the structural pattern.
5. Alternation of cellulosic and non-cellulosic layers.

In so far as we are able to judge from a study of a wide range of gymnosperms and angiosperms, most, if not all, tracheary cells and fibers exhibit more or less conspicuous concentricities of the third type, i.e., those due to changes in the orientation of the elongated birefringent complexes of the structural pattern, but the number and magnitude of the deviations in orientation are variable. Inability to detect such concentricities appears to be due to inadequate techniques or to errors of interpretation. In most cases, the third type of layering occurs in association with one or more of the other four types of concentricities. Thus, in the secondary wall of cotton hairs, it occurs with the first type; in the fiber-tracheids of *Siparuna bifida,* with the second and fourth types; in the fiber-tracheids of *Tetramerista glabra,* with the first, second, and fourth types; in the fibers of *Pandanus,* with the first and fifth types, etc.

Variations in the intensity of lignification or in the distribution of other non-cellulosic constituents may at times be closely correlated with changes in the orientation or the texture of the structural pattern. For example, the narrow inner and outer layers of the secondary wall may be more heavily lignified than the central layer or *vice versa.* Similarly, the coarser parts of the structural pattern of the central layer may be more heavily lignified or contain a higher ratio of hemicelluloses than the finer parts or *vice versa.* It is such fortuitous correlations as these which have led, in certain cases, to the unwarrantable conclusion that all types of visible heterogeneities in the secondary wall are due primarily to differences in chemical composition.

There are investigators who believe that all fibers are composed of concentric lamellae of cellulose which are held together by non-cellulosic material. Thus, Lüdtke (21, 22), who has attempted to homologize all types of fibrous cells in a single structural model, is of the opinion that the lamellae are separated by a "Fremdsubstanz" which differs from both cellulose and lignin in its chemical composition. Ritter (26) argues that it is possible to dissect the secondary wall by chemical means into concentric lamellae which may be slipped apart as shown in *Fig. 26*. Lüdtke's conclusions appear to have been derived largely from a study of bamboo fibers; and Ritter's, from investigations of the libriform fibers of elm. We have shown that the anisotropic lamellae of monocotyledonous fibers frequently are separated by films of non-cellulosic material. The libriform fibers of elm are commonly of the so-called gelatinous type, which also are characterized in many cases by having both cellulosic and non-cellulosic lamellae. In such fibers, where there are actual discontinuities in the structural pattern of cellulose, the anisotropic lamellae may readily be separated by chemical treatments and slipped apart. On the contrary, in cotton hairs and in normal tracheids, fiber-tracheids, and libriform fibers, the entire matrix of cellulose is firmly coherent, and can be dissected only by forcibly tearing or rupturing the structural pattern. In *Siparuna bifida* the more obvious planes of weakness in the cellulosic matrix are radio-longitudinal or radio-helical; whereas in cotton hairs or in *Poraqueiba sericea* they are concentric-longitudinal.

B. "Fibrils" and other "Units" of Cellulose

Since the pioneer days of Von Mohl, Valentin, and Th. Hartig, a succession of investigators have visualized the secondary wall as composed of visible units of cellulose — elementary fibrils, dermatosomes, etc. — that are held together by non-cellulosic material. It is essential to understand the relationship between these units and the visible structural patterns produced by different optical aggregates of cellulose.

We have shown in Part I of this paper that the orientation of the cellulose is correlated with that of the so-called fibrillar structure, as has been demonstrated by analyses of X-ray diagrams, of anisotropy, of dichroism, and of other physical properties of the cell wall. However, these physical correlations are concerned only with the orientation of the fibrillar structure and afford no conclusive evidence that fibrils obtained by chemical or mechanical treatments are discrete entities of constant length or cross sectional area.

Ritter (27) has discussed the length of the so-called fibril and concludes that it is variable. He states that "although fibril segments of only 230 microns in length have been isolated, it seems that some may be as long or longer than the fiber." Lüdtke (22), on the contrary, claims that the length of fibrils is determined by the presence and spacing of transverse plates of non-cellulosic material. Jancke, working with R. O. Herzog (15), measured the width of fibrils and obtained values of some 0.3–0.5 μ. Balls and Hancock (3), proceeding upon the assumption that lamellae[1] are composed of a single concentric row of fibrils, inferred that the width of both lamellae and fibrils in cotton is 0.4 μ. Frey-Wyssling (13) tabulates the dimensions of fibrils as $0.4 \times 0.4 \times 100$ μ.

Fibrils may be dissected by relatively drastic treatments with oxidizing agents or acids into short segments which are variously designated as dermatosomes, spherical units, ellipsoid bodies, etc. According to Frey-Wyssling (13), dermatosomes have dimensions of $0.4 \times 0.4 \times 0.5$ μ; whereas Farr and Sisson (11) state that ellipsoid bodies prepared from cotton have axes of 1.1 μ and 1.5 μ. Lüdtke (20) believes that dermatosomes are held together by his "Fremdsubstanz"; whereas Farr and Eckerson (9) maintain that the ellipsoid bodies of cotton are jacketed by a pectic cement.

We have demonstrated in Part II that the central layer of tracheary cells and fibers is composed of an extremely complex and firmly coherent matrix of cellulose and that the details of the structural patterns of this matrix grade down to the limits of microscopic visibility. There is no evidence, either in untreated or in carefully swollen fibers, of discrete entities of cellulose, i.e., of fibrils or dermatosomes, which may be liberated simply by dissolving non-cellulosic constituents. The matrix of cellulose is shredded and disrupted during the production of fibrils and dermatosomes, which are heterogeneous fragments of larger size than the finer visible complexes of the structural pattern. In cotton, *Fig. 17,* as in *Pinus, Fig. 18, Poraqueiba, Fig. 15,* and *Siparuna, Figs. 10* and *14,* the lamellae obviously are not composed of a single row of adherent fibrils, but are alternating layers of varying width, porosity, and birefringence. The finer, visible, elongated complexes of the lamellae are 0.1 μ or less in thickness. As indicated at (a) in *Fig. 17,* the cross sectional area of an ellipsoid body of the size postulated by Farr and Sisson covers more than four lamellae and a relatively large number of the finer visible complexes.

The form and size of the fragments which may be dissected from the secondary wall are clearly dependent upon the structural pattern of the matrix of cellulose, and upon the type and severity of the chemical and

[1]Balls did not recognize two distinct categories of lamellae and evidently obtained the value of 0.4 μ by dividing the total width of the wall by the number of denser, strongly birefringent lamellae.

mechanical treatments to which the material is subjected. Splits or cracks develop in the more porous and weaker parts of the matrix, thus liberating the denser parts which contain a higher ratio of birefringent cellulose. In addition, there are submicroscopic, transverse, or oblique planes of cleavage, i.e., "slip planes," to which the work of Von Höhnel (16) and of Schwendener (29) has directed so much attention. It is these slip planes, rather than Lüdtke's hypothetical "Querelemente," which facilitate the dissection of the fiber and of the elongated complexes of its structural pattern into shorter segments.

It is of interest, in this connection, that a fibrillar structure is visible after the action of 72% sulphuric acid upon longitudinal sections of fibers which yield coherent "lignin" residues. By the use of mechanical pressure during the initial stages of the action of the acid, the walls of tracheary cells, *Fig. 12,* and fibers may be resolved into long "lignin" threads, similar to fibrils. These shreds of the originally coherent framework of "lignin" may be dissected by more drastic chemical and mechanical treatments into nearly isodiametric fragments resembling dermatosomes. As previously stated, the amorphous non-cellulosic constituents are deposited within the elongated, intercommunicating interstices of the cellulose matrix, resulting in two continuous, interpenetrating systems. Neither system is composed of discrete entities of visible dimensions, but each may be disrupted into fragments of varying size and form. If there are actual discontinuities in the systems, they must occur in the submicroscopic field, e.g., in the realm of micelles or of molecular chains. It should be emphasized, in addition, that so-called fibrillar structures are not visible in the secondary walls of parenchyma, of sclereids, or of other cells which exhibit statistical isotropy in surface view. The structural pattern of the cellulose matrix in such walls is of a fundamentally different type from that which occurs in fibrous cells.

Dermatosomes, spherical units, and ellipsoidal particles are difficult to homologize, either as regards their size or their form. They are obtained by the action of oxidizing agents or of acids which tend to modify the cellulose. Neale (24) has summarized the modifying effects of oxidation and hydrolysis as follows: "The loss of strength and fall in viscosity which accompany the hydrolysis or oxidation of cellulose are quite irreversible, and the general term degradation is applied to these changes. The degradation of cellulose is accompanied by the appearance of chemical properties foreign to the original material. The hydrolysis of the glucoside-oxygen bridge causes the appearance of reducing sugar properties which may be quantitatively, though arbitrarily, expressed as 'copper number' or 'iodine number.' The reducing sugar properties also arise as a result of oxidation and may be accompanied by the development of acidic properties, so that oxidized cellulose may retain traces of caustic alkali or absorb basic dyes. This latter property has been put on the quantitative basis so essential in the chemistry of cellulose in the form of the methylene blue absorption test."

Thus, it may be seen that the action of acids, which are supposed to dissolve some cementing substance and to liberate integral units of cellulose, may actually result in partial degradation of the cellulose. We have found that the staining of hydrocellulose and oxycellulose with ruthenium red is similar to the methylene blue absorption values as listed by Dorée (8). Ruthenium red behaves, in some respects, as a basic dye, and the staining of ellipsoidal particles, obtained by treating cotton with relatively strong acid (10), may be interpreted as an indication of the degradation of the cellulose rather than as evidence for believing that the particles are coated with a pectic cement. Ruthenium red is not a specific test for pectic compounds, as botanists have frequently assumed. It is removed from dilute aqueous solutions by coagulated protoplasm and other nitrogenous substances, by gums, mucilages, hemicelluloses, oxycelluloses, hydrocelluloses, and certain lipoids, as well as by pectic compounds.

Any hypothesis concerning the visible structure of the secondary wall must account not only for the varying structural patterns of a wide range of cells, but also for well known facts regarding the physical and chemical properties of cellulose. In the case of the hairs of the cotton plant, the constituents which do not yield glucose upon hydrolysis are small in amount, and are confined chiefly to the so-called cuticle or primary wall and to the lumen of the cell. There obviously is not a sufficient volume of cutinlike substances or of pectic compounds in the secondary wall to serve as a cementing substance of the type postulated by Lüdtke (21) or by Farr and Eckerson (9). Furthermore, when cotton is treated with solvents of such constituents, without degrading the cellulose, the structural pattern is not affected. It persists as a firmly coherent matrix of cellulose.

It is now generally admitted that the cellulose molecule is a long chain of glucose residues bound together by oxygen bridges. Furthermore, there is evidence from X-ray analyses, from anisotropy, dichroism, etc., to indicate that cellulose is built up of submicroscopic, crystal-like aggregates of these chains. The length of the cellulose chain and its arrangement within the crystallite are still subjects of dispute. Thus, it is uncertain whether the chain is shorter or longer than the crystallite or of equivalent length, and whether micelles are discrete and separate entities, or merely parts of a continuous system of overlapping chains.

Estimates of the length of cellulose molecules range from 100–3500 glucose residues. The highest value of 3500 units, i.e., that of Kraemer and Lansing (19), is based upon measurements of viscosity. Such molecules would have a length of approximately 1.8 μ, and would be visible microscopically if they were of sufficient thickness, which they obviously are not. Since the cellulose chains are arranged parallel to the so-called fibrillar orientation, and since there are no visible structures which transect this axis, it is possible to conceive of chains of the length postulated by Kraemer and Lansing arranged in an overlapping manner along the fiber axis.

Our investigations indicate that the cellulosic matrix of the secondary wall is composed of complexes of cellulose of varying birefringence which grade down to the limits of microscopic visibility, and that the fundamental units of cellulose are of submicroscopic dimensions. In the case of cotton, the available chemical and physical data make it appear improbable that the variations in birefringence are due to differences in chemical composition. Correns (5) recognized, more than 40 years ago, that cellulose is heterogeneous and attempted to explain the visible striations and certain types of lamellae as due to differences in water content. This hypothesis originated with Nägeli (23), who postulated water rich and water poor layers as a means of explaining concentricities and still permitting growth by intussusception. Differences in water content apparently do exist, and may be a factor influencing the intensity of birefringence in different lamellae. However, it is difficult to evaluate such differences by a study of dried material. Drying the walls shrinks the cell so that structures just within the limits of microscopic visibility when the preparation is in water, may be contracted to invisible dimensions. Furthermore, differences in water content must be explained in terms of submicroscopic differences in the cellulose which permit varying degrees of hydration. The question whether the variation in birefringence of different complexes of the cellulosic matrix is due to fluctuations in the size, number, or orientation of submicroscopic units of cellulose is one which must be attacked from the physical and chemical, rather than from the botanical, side.

C. Significance of Biological Variables in Physical and Chemical Investigations

Our survey of a wide range of gymnosperms and angiosperms indicates that the secondary wall is a very complex structure, and that the structural pattern of the cellulose matrix varies greatly, not only in different groups of plants but also, at times, in homologous cells of the same plant, and even in different parts of the same cell. There is a similar variability in the distribution of "lignin" and of other non-cellulosic constituents. Therefore, since all types of secondary walls can not be homologized in a single structural model, there are grave dangers in generalizing from intensive investigations of isolated species, e.g., cotton, spruce, bamboo, or ramie.

Deductions concerning the structure of the cell wall based upon physical or chemical analyses, should be checked by microscopic investigations and by accurate information concerning the numerous biological variables. This is particularly necessary in the interpretation of X-ray diagrams, where the investigator of necessity must deal with complex aggregates of plant material. Van Iterson (31) has shown that certain misconceptions regarding *Valonia* might have been avoided by an acquaintance with the work of Correns (6) and others upon the visible structure of the walls of algae. Preston (25) undoubtedly errs in concluding, from an examination of X-ray diagrams, that there is a single plane of orientation of "fibrils" in the secondary wall of the tracheids of *Sequoia* and of other conifers. Accurate interpretations of X-ray diagrams of growing cells and of differentiating tissues are especially difficult, and such conclusions regarding structural changes as those of Clark and Farr (4) and Ritter and Stillwell (28) must be carefully verified from the histological side.

Although "lignin" residues of thick sections exhibit rod double refraction, as demonstrated by Freudenberg and his co-workers (12), a careful study of the residues of thin sections shows that a considerable proportion of the secondary wall "lignin" is isotropic. Similarly, there are parts of the cellulosic matrix which do not exhibit a clearly defined dichroism when thin sections are stained with chloro-iodide of zinc or congo red. The woods of certain dicotyledons leave no coherent structural residue when subjected to standard treatments with 72% sulphuric acid, as shown by Harlow (14); whereas others leave compact residues such as have been considered to be typical of conifers. In the wood of certain plants, the bulk of the "lignin" is confined to the so-called middle lamella, as Ritter (27) maintains; whereas in others, there is a relatively large proportion in the secondary wall.

It should be emphasized, in conclusion, that most of our own data were obtained from a study of tracheary cells and fibers, and that many additional types of cells must be investigated before it will be possible to visualize the full range of structural variability of the secondary wall. In a succeeding paper, we shall discuss methods that have been perfected for studying the small-celled, lightly lignified woods of dicotyledons of temperate regions.

SUMMARY AND CONCLUSIONS

1. An extensive survey of a wide range of gymnosperms and angiosperms has shown that the structural pattern of the secondary wall is clearly visible in the large fiber-tracheids and libriform fibers of various dicotyledons.

2. By using untreated sections of such cells as controls, it is possible to observe the exact effects of specific chemical and mechanical treatments upon normal structures, and thus to extend the scope of investigation to cover a wide range of less favorable material.

3. The cellulosic matrix of the swollen secondary wall of cotton, as of normal tracheids, fiber-tracheids, and libriform fibers, is an extremely heterogeneous but firmly coherent structure, the finer details of which grade down to the limits of microscopic visibility.

4. There is no reliable evidence to indicate that the matrix is composed of discrete entities of visible size — e.g., elementary fibrils, dermatosomes, ellipsoidal bodies, etc. — that are bound together by non-cellulosic material. On the contrary, our data demonstrate that such putative entities actually are heterogeneous fragments that are shredded or disrupted from an originally continuous and coherent matrix. If there are discontinuities in the structural pattern of the cellulose in normal tracheary cells, they are confined to the submicroscopic field, e.g., to the realm of micelles or molecular chains.

5. The visible structural pattern of the cellulosic matrix varies greatly in form and texture, not only in different plants, but also in homologous cells of the same plant, and even in different parts of the same cell.

6. There are at least two optically different elongated complexes of cellulose which may be segregated into radio-helical, radio-longitudinal, or concentric-longitudinal lamellae, or into various radio-concentric patterns.

7. The orientation of the elongated complexes of the structural pattern fluctuates more or less in successively formed parts of the secondary wall. In the case of normal tracheids, fiber-tracheids, and libriform fibers, there are three layers due to varying orientations: narrow inner and outer layers, in which the orientation is more nearly at right angles to the longitudinal axis of the cell, and a central layer of varying width, in which the orientation is parallel to this axis or does not deviate excessively from it.

8. "Lignin" and other non-cellulosic constituents may be deposited in the elongated, intercommunicating interstices of the cellulosic matrix, thus resulting in two continuous, interpenetrating systems. In heavily

lignified forms, either system may be dissolved without seriously modifying the structural pattern of the remaining system. The purified cellulose and the "lignin" residue reveal positive and negative images of the original structural pattern.

9. Deviations from the typical 3-layered type of secondary wall are of not infrequent occurrence. Thus, many thick-walled libriform fibers and fiber-tracheids have no clearly differentiated inner layer; whereas others have more than three layers of varying "fibrillar" orientation.

10. Conspicuous discontinuities in the structural pattern of the cellulose commonly occur in the multiple-layered walls of so-called gelatinous fibers, in certain types of bast fibers, and in sclereids. They are due to narrow layers of truly isotropic material which contain little, if any, cellulose.

11. There are five different types of visible concentricities which occur in varying combinations, and may be associated at times with radio-helical or radio-longitudinal lamellae. Therefore, it is misleading and fruitless to attempt to homologize all types of fibers in a single structural model.

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DESCRIPTION OF PLATES

Figs. 1–6 and 13 were made from unstained sections and were photographed in polarized light between crossed nicols. All the remaining photomicrographs were made with an arc-light and Zettnow's filter. Figs. 1–6, 8, 10, and 21 were made from sections mounted in diaphane ($N = 1.47$).

PLATE 140

Fig. 1. *Myodocarpus simplicifolius* Brong. & Gris. Transverse section of the xylem, showing a fiber-tracheid and parts of seven adjoining ones. The thick secondary walls are composed of three distinct layers: a narrow brilliant outer layer, a brilliant narrow inner layer, and a wide intervening dark layer. In a section of this thickness, 15 μ, the isotropic intercellular substance and the feebly anisotropic primary walls are more or less completely fogged or obscured by the brilliant outer layers of the secondary walls (compare *Fig. 3* for a section 5 μ in thickness). × 1750.

Fig. 2. *Urandra corniculata* Foxw. Radial longitudinal section of the xylem, showing the walls of adjacent fiber-tracheids in sectional view. The broad central layers of the secondary walls are brilliant. The intercellular substance, the feebly birefringent primary walls, and the inner and outer layers of the secondary wall are dark. A bordered pit is shown in the center of the photomicrograph. × 1750.

Fig. 3. *Trochodendron aralioides* Sieb. & Zucc. Transverse section of the xylem, showing a tracheid and parts of seven adjoining cells. In a section of this thickness, 5 μ, the outer brilliant layers of the secondary walls of adjacent cells are clearly separated by a narrow intervening dark layer, which actually consists of two feebly birefringent primary walls and a truly isotropic layer of intercellular material. × 1400.

Fig. 4. *Myodocarpus simplicifolius.* Transverse section of the xylem, showing a fiber-tracheid and parts of seven adjoining ones. The thick secondary wall of the central cell consists of a series of alternating brilliant and dark layers. × 1750.

Fig. 5. *Urandra corniculata.* Thick secondary wall of a sclerenchymatous cell in sectional view, showing alternating brilliant and dark layers. × 1750.

PLATE 141

Fig. 6. *Pandanus odoratissimus* L. Transverse section of a group of lignified fibers, showing secondary walls composed of regularly alternating brilliant and dark layers. × 1150.

Fig. 7. *The same.* Transverse section of a fiber after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in balsam, showing residue of secondary wall. The brilliant layers of *Fig. 6* are split and embossed. × 1300.

PLATE 142

Fig. 8. *Siparuna bifida* (P. & E.) A. DC. Transverse section of a fiber-tracheid and of parts of several adjoining cells, stained with Haidenhain's haematoxylin and safranin, showing zones of varying intensities of lignification. × 2000.

Fig. 9. *The same.* Transverse section of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's

haematoxylin and mounting in aniline oil, showing finely radio-reticulate pattern and zones due to varying intensities of lignification. Dark zones heavily lignified, light zones less intensely lignified. × 1300.

PLATE 143

Fig. 10. *Siparuna bifida.* Transverse section of a fiber-tracheid and of parts of several adjoining cells, stained with Haidenhain's haematoxylin and safranin. The broad, unswollen central layer of the secondary wall is radially striated. × 2000.

Fig. 11. *The same.* Transverse section of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing radially striated and finely reticulated residue of the central layer of the secondary wall. In the outer part of the central layer, there is a concentricity due to an abrupt transition from coarse to fine texture. The inner concentricity is due to varying intensities of lignification. × 1900.

PLATE 144

Fig. 12. *Tetramerista glabra* Miq. Tangential longitudinal section of the central layer of a fiber-tracheid after treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing longitudinal pattern of fine anastomosing threadlike components. The longitudinal orientation has been somewhat distorted during swelling. × 1900.

Fig. 13. *Siparuna bifida.* Tangential longitudinal section through the central layer of a fiber-tracheid mounted in water and photographed with polarized light between crossed nicols, showing alternating birefringent and isotropic striae. × 1900.

Fig. 14. *The same.* Transverse section of a delignified fiber-tracheid, after treatment with diluted cuprammonium hydroxide and staining with congo red. The denser, darker radii of the purified cellulose correspond to the lighter radii of *Figs. 10* and *11.* × 1200.

PLATE 145

Fig. 15. *Poraqueiba sericea* Tul. Transverse section of the secondary wall of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing concentrically lamellated residue of the central layer. × 3200.

Fig. 16. *Siparuna bifida.* Transverse section of the secondary wall of a fiber-tracheid after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin and mounting in aniline oil, showing finely radio-reticulate residue of the central layer. × 3200.

PLATE 146

Fig. 17. *Gossypium hirsutum* L. Transverse section of a cotton hair after swelling with diluted cuprammonium hydroxide and staining with congo red, showing alternating lamellae of varying width and porosity in the inner part of the secondary wall. A particle 1 μ in diameter in the untreated wall would expand to the size of the circle at (a). × 1200. Owing to swelling, the original width of the lamellae has been increased 7500 times in this photomicrograph.

Fig. 18. *Pinus ponderosa* Dougl. Transverse section of the secondary wall of a tracheid after treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline oil, showing concentrically laminated residue of the central layer. × 1900.

PLATE 147

Fig. 19. *Tetramerista glabra.* Transverse section of a fiber-tracheid and of parts of several adjoining cells, mounted in a dilute aqueous solution of iodine potassium iodide and photographed with a Zeiss 70-water-immersion lens. The broad central layer has a coarsely radio-concentric pattern which is complicated by zones of varying intensities of lignification. × 2000.

Fig. 20. *The same.* Transverse section of a fiber-tracheid after treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in balsam, showing finely radio-concentric pattern and broad zones due to varying intensities of lignification. × 1300.

PLATE 148

Fig. 21. *Homalium luzoniense* F. Villar. Transverse section of a libriform fiber stained with Haidenhain's haematoxylin and safranin, showing alternating broad cellulosic and narrow non-cellulosic layers. The radio-reticulate structure of the former layers is vaguely visible. × 3200.

Fig. 22. *The same.* Transverse section of a libriform fiber after standard treatment with 72% sulphuric acid, staining with Haidenhain's haematoxylin, and mounting in aniline, showing residue of both the cellulosic and the non-cellulosic layers. × 1300.

PLATE 149

Fig. 23. *Rhizophora mangle* L. Isolated, delignified, libriform fiber, swollen in diluted Schweizer's reagent, showing beadlike swelling of the central layer of the secondary wall. The outer layer of secondary wall is resolved into a series of constricting rings and helical bands. × 650.

Fig. 24. *Olmediella Betschleriana* (Goepp.) Loes. Isolated, delignified, libriform fiber, swollen in diluted Schweizer's reagent. The outer layer of the secondary wall is resolved into constricting helical bands. × 325.

Fig. 25. *Pandanus odoratissimus.* Isolated delignified fiber, swollen in diluted Schweizer's reagent, showing that each of the internal brilliant layers in *Fig. 6* may be resolved into constricting rings and helical bands. × 650.

Fig. 26. *Olmediella Betschleriana.* Segment of a libriform fiber isolated from a thick transverse section of the xylem after delignification and treatment with 50% sulphuric acid. The concentric cylinders of cellulose are slipping apart. × 650.

Fig. 27. *Olmediella Betschleriana.* Isolated, delignified, libriform fiber, swollen in diluted Schweizer's reagent. The outer layer of the secondary wall is resolved into a series of constricting rings and helical bands. × 400.

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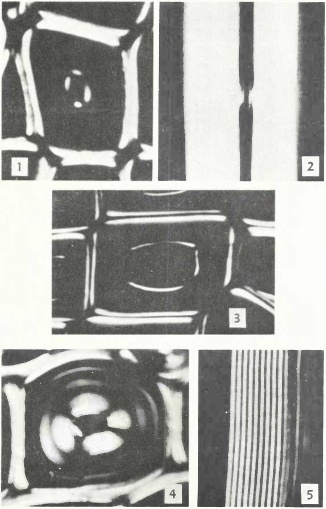
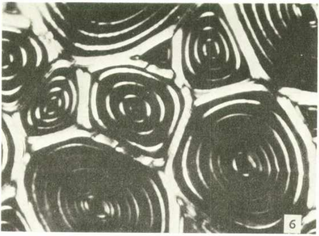
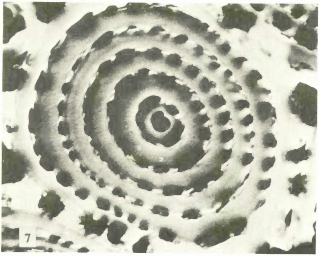


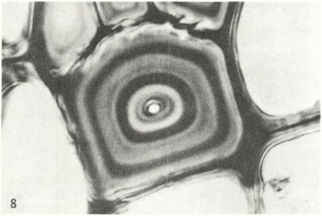
VISIBLE STRUCTURE OF THE SECONDARY WALL

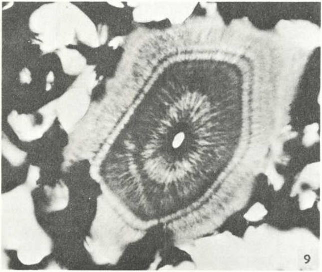
FULL-TONE—MERIDEN





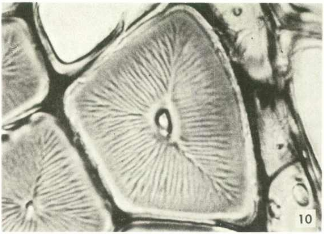
Visible Structure of the Secondary Wall

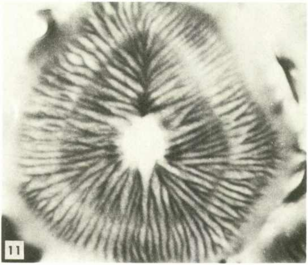




Visible Structure of the Secondary Wall

FULL-TONE — MERIDEN





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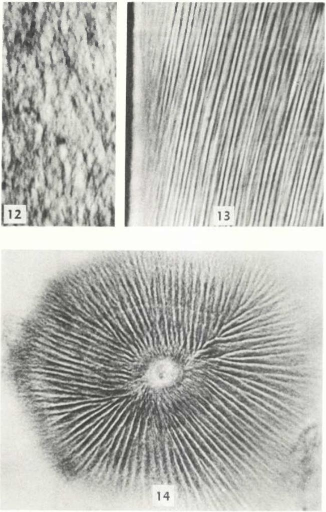

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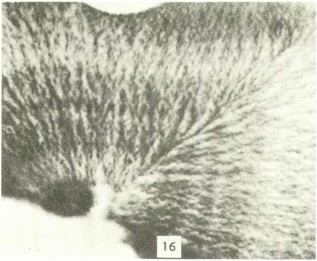
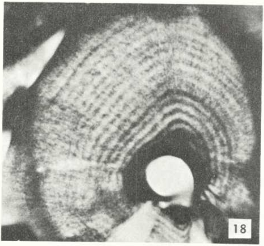


Visible Structure of the Secondary Wall



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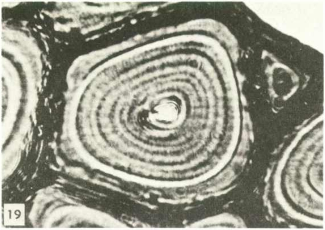

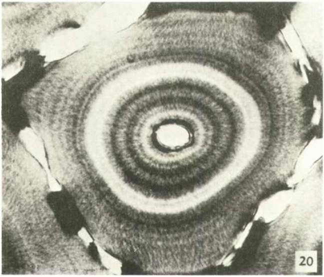

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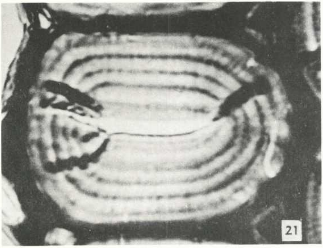

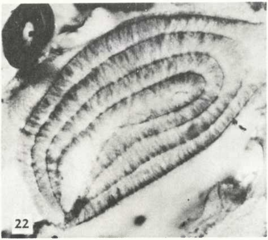

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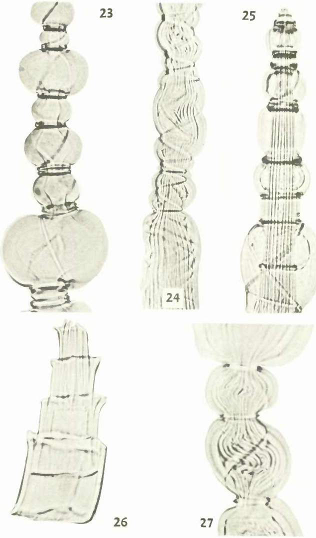


VISIBLE STRUCTURE OF THE SECONDARY WALL

THE EFFECT OF TEMPERATURE ON NUCLEAR DIFFERENTIATION IN MICROSPORE DEVELOPMENT

Karl Sax

With one text figure and plate 150

"Heredity is effected by the transmission of a nuclear preformation which, in the course of development, finds expression in a process of cytoplasmic epigenesis" (Wilson, 1925). The evidence from genetic and cytological investigations has proven conclusively that nuclear preformation is dependent upon the genic constitution of the chromosomes. The mechanism of expression in cytoplasmic epigenesis is more obscure. The problem is difficult because it is not subject to direct attack. A comparison of induced and hereditary effects has provided a method for studying certain developmental processes in *Drosophila*. An analysis of the effect of temperature on developing microspores has provided some information regarding nuclear cytoplasmic relations in differentiation and development, and has some bearing on the problem of genic expression.

Normal microspore development in *Tradescantia* has been described in detail by Sax and Edmonds (1933). The young microspore contains a centrally located nucleus surrounded by cytoplasmic granules. The granules disappear, and the nucleus migrates to the end of the oval-shaped microspore. The cytoplasm is massed around the nucleus, and at the other end of the cell there is a large vacuole. There is then a migration of cytoplasm and vacuole so that two vacuoles are formed, one at each end of the cell. Most of the cytoplasm lies between the vacuoles so that the longer axis of the cytoplasmic mass lies in the short axis of the cell. The nucleus at this time lies toward the heavy or dorsal wall of the microspore, — originally the inner wall at the time of tetrad formation. When the nucleus divides, the daughter nucleus near the heavy wall of the microspore is enclosed by a thin temporary wall which includes little cytoplasm. This nucleus does not pass into the typical resting stage, but retains its chromaticity and finally elongates to form the generative nucleus. The other nucleus formed near the center of the cytoplasmic mass enlarges to form the inactive tube nucleus. Shortly after the division of the microspore nucleus, the vacuoles disappear, and the cytoplasm appears to be rather homogeneous.

The normal development of the microspore of *Pseudolarix amabilis* resembles that of *Pinus*, described in detail by Coulter and Chamberlain (1901). Soon after the release of the microspore from the wall of the microsporocyte, the wings develop rapidly on opposite ends of the spore towards the ventral side of the cell, while the dorsal side of the spore, which was formed during meiosis, becomes thickened. At the time of the first nuclear division, the nucleus lies near the dorsal wall surrounded by most of the cytoplasm, and the region towards the wings and the ventral side of the spore are more vacuolate. The first division occurs across the short axis of the microspore, and the nucleus near the dorsal wall is cut off and degenerates. The other nucleus divides again in the same axis, and another prothallial cell is cut off. The third division produces the generative nucleus and the tube nucleus of the mature pollen grain. The generative nucleus lies near the inner or dorsal wall of the pollen grain and is cut off by a thin wall which encloses little cytoplasm, while the large tube nucleus lies free near the center of the cell.

THE EFFECT OF TEMPERATURE ON NUCLEAR DIFFERENTIATION

Both high and low temperatures are effective in producing abnormal development in the microspores of *Tradescantia*. Plants were placed in a constant temperature chamber where the temperature was maintained at about 6° C. for the cold treatment, or at about 35° C. for the heat treatment. Three days' treatment was sufficient to produce abnormal development at either temperature range, and doubtless a shorter time would be effective at the higher temperature. The microspores were examined soon after exposure to abnormal temperatures, and for several subsequent days after they had been placed in the normal greenhouse environment.

Three types of abnormalities were produced. Under normal conditions, only two nuclei are formed in the pollen grain,—the generative nucleus and the tube nucleus. The tube nucleus normally does not divide and is inactive in further development. The heat treatment occasionally causes the tube nucleus to divide in *Tradescantia* (Figs. 1 and 2). The subsequent fate of the daughter nuclei is not known. Apparently no great deviation from normal environment is required to produce a second division, since this behavior was observed by Mr. R. H. Goodwin in Tradescantia plants grown in the greenhouse at the Biological Institute of Harvard University.

The second type of abnormality is produced by either cold or heat treatment. The polarity of the microspore is disturbed so that the nuclear division is no longer oriented across the short axis of the cell.

In extreme cases the division is at right angles to the normal axis, the daughter nuclei are not differentiated, and the temporary cell wall is formed across the center of the microspore (Fig. 3). In most cases there is partial differentiation of the daughter nuclei, but the more compact nucleus does not elongate to form the typical generative nucleus (Fig. 4). The degree of differentiation of the two nuclei is closely associated with the angle of division. With a smaller degree of variation from the normal axis of division there is increased differentiation of the generative nucleus (Fig. 5). In a single anther all degrees of differentiation are found, including the normal condition (Fig. 6).

In order to determine more accurately the relation between the angle of division and the differentiation of the nuclei, a statistical study was made. All microspores measured were from a single flower taken from a plant which had been kept at a temperature of about 36°C. for three days. Camera lucida drawings were made of 163 microspores selected at random among those which showed the two nuclei in the same focal plane. The angle between the normal axis of division across the short diameter of the microspore and the line drawn through the centers of the two nuclei was taken as the angle of division. The length of the outline of the "generative" nucleus was measured in millimeters. This work, as well as the tabulation and analysis of the data, was done by my wife, Dr. Hally Jolivette Sax. The relation between the angle of division and the length of the generative nucleus is shown in Table 1. The high correlation of $-.81 \pm .02$ shows that the degree of nuclear differentiation is closely associated with the angle of division.

A third type of aberrant development was found in microspores which began to "germinate" before the division of the nucleus. In some cases one of the daughter nuclei was found in the original microspore and the other in the newly-formed outgrowth (Figs. 8 and 10). In these cases a thin cell wall divided the cytoplasm into approximately equal parts, and there was no indication of nuclear differentiation. The division may occur so that neither daughter nucleus remains in the original microspore (Figs. 7 and 9). If the division is oriented lengthwise of the cytoplasmic mass, there is no nuclear differentiation, but if it is oriented across the short diameter of the outgrowth, so that one daughter nucleus is near the cell wall, there is a differentiation which resembles that following normal division in a normal microspore (Fig. 7).

The precocious growth of the microspores of *Tradescantia* is unlike normal pollen-tube growth. The pollen-tube usually grows from the end of the pollen grain adjacent to the heavy dorsal wall, while the aberrant outgrowth occurs at the ventral side of the microspore. Perhaps this abnormal growth is the first stage in the development of an embryo-sac-like structure such as Stow (1930, 1933) has found in the anthers of *Hyacinthus*. Unfortunately, a study of the further development of the abnormal growth in Tradescantia microspores could not be continued because the anthers dehisced and disintegrated so soon. Possibly these peculiar microspores could be developed further in a nutrient solution.

TABLE I.

THE RELATION BETWEEN ANGLE OF DIVISION AND THE DIFFERENTIATION OF THE NUCLEI IN MICROSPORES OF TRADESCANTIA

Length of generative nucleus	Angle of division: 0	10	20	30	40	50	60	70	80	90
8–11	2		1	2		2	2	3	3	3
11				2	1	5	3	8	3	9
14	1	1	3	1	1	4	2	2	2	
17		5	4		3		3	2		
20	4	7	7	2	2	2	1	1		
23	10	4	5	1	1	1	1			
26	9	3	3			1			1	
29	3			1			1			
32	3			1						
35										
38–40	4	1								

$n = 163$

$r = -.81 \pm .02$

The development and differentiation of the microspores of *Pseudolarix amabilis* is also affected by environmental conditions. Branches containing male flowers were placed in a warm corner of the greenhouse for about two weeks. During this time meiosis occurred, and the microspores developed to maturity. Most of the microspores were normal in their development (Figs. 11 and 12), but various types of abnormalities were observed. If the first division occurs lengthwise of the cell in the axis of the wings, there is no differentiation of the nuclei if each is an equal distance from the cell wall (Fig. 13). If, however, one nucleus lies near the cell wall, regardless of the orientation of the division spindle, this nucleus tends to remain small and form a prothallial cell, while the nucleus near the center of the cytoplasmic mass remains large and divides again (Figs. 14 and 16). The first division may occur in the normal position, but the second division may be aberrant in orientation (Figs. 15 and 16). Several years ago Mrs. Sax found a mature pollen grain of *Picea* which contained four undifferentiated nuclei of approximately equal size. Apparently relatively slight changes in environmental conditions can cause abnormal development of conifer microspores. Nuclear differentiation in these microspores appears to be entirely dependent upon the orientation of the division spindles and the position of the nuclei in relation to the cytoplasmic mass.

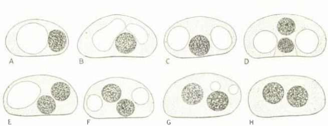
Nuclear differentiation in the microspores of *Tradescantia* and *Pseudolarix* appears to be determined by the nuclear cytoplasmic relationships. In *Tradescantia* it is possible to observe the relations of nuclei, vacuoles, and cytoplasm in the living microspores. Observations at various stages of development show that normal development is dependent upon the synchronization of cytoplasmic and nuclear activities.

In the microspores which develop under normal conditions, the cell contents show a gradual shifting in position before the nucleus divides. A large vacuole is formed at one end of the microspore, and the nucleus and most of the cytoplasm move to the opposite end. The vacuole then extends towards the opposite end, near the ventral side of the spore, and finally forms two vacuoles, one at either end of the cell. Meanwhile the cytoplasmic mass and the nucleus migrate towards the center of the cell. The cytoplasm extends between the ventral and dorsal walls so that the length of the cytoplasmic mass is across the short diameter of the cell. Some cytoplasm extends around the entire periphery of the cell. The nucleus lies near the dorsal wall at the time of division. After the division the nucleus near the dorsal wall is cut off by a thin temporary wall, and then develops into the elongated generative nucleus. The other nucleus enlarges, loses its chromaticity, and becomes the inactive tube nucleus. The sequence of early development of the normal microspore is shown in text figures a, b, c, and d, which are camera lucida sketches drawn from living material.

When the microspore develops at low temperatures, the same cycle of development begins, but the nucleus divides before the vacuole, cytoplasm, and nucleus reach their normal positions. (Text figure e.) Since the cytoplasm migrates towards the center of the cell along the dorsal wall of the microspore, the length of the cytoplasmic mass is at an angle to the normal axis of division. The nuclear spindle is oriented in the long axis of the cytoplasmic mass, and the daughter nuclei lie towards one end of the microspore and do not undergo complete differentiation.

The exposure to high temperatures for several days appears to accelerate the cytoplasmic movement without causing a corresponding activity of the nucleus. At the time the cell constituents are in the position usually associated with nuclear division (Text figure c), the nucleus may remain inactive. The vacuoles then become smaller or may disappear entirely before nuclear division. As a result, the long axis of the cytoplasmic mass is not oriented in the short axis of the cell, and the division may occur at various angles, depending in part upon the cytoplasmic distribution (Text figures f, g, and h).

In a single flower, following heat treatment, the angle of division may vary from 0 to 90 degrees. Camera lucida drawings were made from a random sample of these cells, and the angle of division was determined in relation to the distribution of cytoplasmic mass. The length of the



TEXT FIGURE. Development of the microspore under normal and abnormal conditions.

All figures are from camera lucida drawings of living microspores.

Figures a, b, c, and d show the movement of the cell contents during early development of the microspore under normal conditions. The vacuole becomes extended along the ventral wall and finally forms two vacuoles. The nucleus at the time of division becomes oriented near the dorsal or heavy wall of the microspore.

Figure e shows the nuclei formed by nuclear division before normal orientation of the cell constituents is attained. This microspore developed at a low temperature, which seems to retard cytoplasmic movement without retarding nuclear division.

Figures f, g, and h are drawings of microspores which had been subjected to a high temperature. The vacuoles are small or absent at the time of nuclear division, and the axis of division tends to occur in the long axis of the cytoplasmic mass.

cytoplasmic mass was determined for the long axis of the cell, and the width was measured across the short axis of the cell. For example, in a normal microspore (fig. d) the length of the cytoplasmic mass is the distance between the vacuoles, and the width is the distance across the microspore in the axis of division, and the angle of division is very small. In this cell the length-width ratio is about 0.5. In figure e the length-width ratio is about 1.0, and the angle of division is about 45 degrees, while in figure h the length-width ratio of the cytoplasmic mass is about 2.0, and the angle of division is about 80 degrees. The length-width ratio of the cytoplasmic mass correlated with the angle of division gave a value of $r = .66 \pm .03$. It is evident that there is a strong tendency for the nucleus to divide in the long axis of the cytoplasmic mass, although as the volume of cytoplasm increases, there is not a corresponding tendency for the nucleus to divide in the longer axis. In general, however, the direction of division in the microspore is controlled by the distribution of the cytoplasm in accord with Hertwig's rule, and the nuclear differentiation is controlled by the position of the daughter nuclei in relation to the cytoplasmic mass.

It is not possible to follow the cytoplasmic movements in the living cells of conifers, but judging from the description of normal development (Ferguson, 1904) and the behavior of the nuclei in abnormal microspores, the failure of normal differentiation is also based on the disturbed relations of nucleus, cytoplasm, and vacuoles.

A comparison of nuclear differentiation in *Tradescantia* and *Pseudolarix* microspores and in the embryo sacs derived from microspores in *Hyacinthus* shows a good deal of similarity in polarity. In both *Tradescantia* and *Pseudolarix* the center of activity in early microspore development is near the dorsal wall which was formed during microsporogenesis. If a second division occurs in the Tradescantia microspore, the nucleus nearer the center of the cell divides, as is the case in normal microspore development in the conifers. The vegetative nucleus is always the one nearer the ventral wall and is surrounded by a large amount of cytoplasm, while the generative or sexual nucleus lies near the dorsal wall and is enclosed by a thin temporary cell wall which includes little cytoplasm. The "embryo sacs" which develop from microspores of *Hyacinthus* (Stow, 1933) show the exine of the microspore at the egg or sexual end of the embryo sac, while the polar or vegetative nuclei lie in the center of the embryo sac, apparently surrounded by a relatively large amount of cytoplasm.

Stow was able to induce embryo sac-like structures in anthers of *Hyacinthus* by subjecting the bulbs to a temperature of 28°C. for 18 to 24 hours at the time of planting in the fall. The abnormal development observed in the following spring may have been induced either by the temperature treatment or by the effects produced by the large number of degenerating sterile microspores. At any rate the differentiation of the microspore to produce a normal pollen grain or an embryo sac appears to depend upon environmental conditions. We are inclined to believe that the precocious growth of Tradescantia microspores is the first stage in embryo sac formation, and that the complete structure could be developed, under temperature control, if the cells could be kept alive over a long period of time, as is the case in *Hyacinthus*.

FACTORS IN DEVELOPMENT AND DIFFERENTIATION

According to Osterhout (1921), life is dependent upon a series of reactions which normally proceed at rates which bear a definite relation to each other. If for life we substitute development and differentiation, we have an hypothesis which seems to explain development and differentiation. Certainly the differentiation of the microspore nuclei appears to be dependent upon the relative rates of cytoplasmic migration and nuclear activity. Less direct evidence indicates that the difference between a pollen grain and an embryo sac may be dependent upon the same type of timing relationships. If sex can be determined by the timing relationships of different reactions, effected either by environmental conditions or hereditary factors, we have indirect evidence that genic expression may be effected by differential reactions.

More direct evidence regarding the mechanism of genic expression is found in the behavior of the chromosomes at meiosis. A failure of chromosome pairing, or asynapsis, may be caused by genetic factors or by environmental conditions. Genetic asynapsis has been found in *Drosophila, Zea, Triticum, Rumex* and *Datura*. Induced asynapsis can be effected in *Rhoeo* and *Datura* by subjecting the plants to low temperatures for several days, and it has been obtained in *Tradescantia* following treatment at low and high temperatures. Both the hereditary and induced effects are similar in their expression. The chromosomes are unpaired at meiosis, the divisions are irregular, diploid gametes may be produced, and there is a high degree of pollen sterility in the asynaptic plants. Both types of asynapsis may be attributed to the same cause. If chromosome development is not synchronized with other cell activities, the chromosomes may not be effectively paired before nuclear division is initiated.

An exceptionally clear case of the timing factor in genic activity was found in *Aquilegia* by Anderson and Abbe (1933). The "compacta" mutant of *Aquilegia* is dependent on a single genetic factor. In the mutant type the branches are more erect and numerous, and the flowers are upright from the beginning. The dwarf type is caused by the precocious thickening of the cell walls, and the somatic expression is simply the result of disturbed timing relationships, — "the precocious initiation of a normal feature of normal development." Further aspects of the relation between genes and development in *Drosophila* have been discussed by Schultz (1935) and by Goldschmidt (1935), and similar work is being done on the cucurbits by Sinnott (unpublished).

The temperature chambers used in this work were paid for, in part, by a grant from the American Academy of Arts and Sciences.

SUMMARY

The subjection of Tradescantia plants to low and high temperatures may produce three kinds of abnormalities in microspore development. (1) The tube nucleus, which in normal microspores is inactive and ultimately degenerates, may divide. (2) The polarity of the cell may be disturbed so that the division of the microspore nucleus is not oriented in the normal axis. The angle of deviation is closely correlated with the differentiation of the daughter nuclei. (3) The microspore may become greatly extended on the ventral side, and the nuclear division may occur in this new outgrowth. This abnormality may be the first step in the transformation of a microspore to an "embryo sac," as found in *Hyacinthus* by Stow.

When Pseudolarix microspores are developed at a relatively high temperature, there is a failure of normal differentiation of the nuclei. The differentiation of prothallial cells and generative and tube nuclei is dependent upon the nuclear cytoplasmic relationships in the developing microspore.

The normal differentiation in Tradescantia microspores is dependent upon the synchronization of cytoplasmic movements and nuclear activity. There is some evidence that many differences in development and differentiation, induced either by genetic factors or by environmental conditions, are dependent upon differences in reaction rates of different processes.

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WILSON, E. B. (1925). The cell in development and heredity. (The Macmillan Co. New York.)

DESCRIPTION OF PLATE 150

Photographs of aceto-carmine preparations of abnormal microspores of *Tradescantia* and normal and abnormal microspores of *Pseudolarix amabilis*. Figures 1 to 6 inclusive, magnified $\times$ 800. The other figures are magnified $\times$ 600.

Tradescantia

Figures 1 and 2. Division of the tube nucleus of the microspore.

Figure 3. The division of the microspore nucleus has occurred at right angles to the normal axis of division, and the daughter nuclei do not become differentiated.

Figures 4, 5, and 6. The nuclear divisions have occurred at various angles followed by a corresponding amount of nuclear differentiation. These microspores were developed at a high temperature.

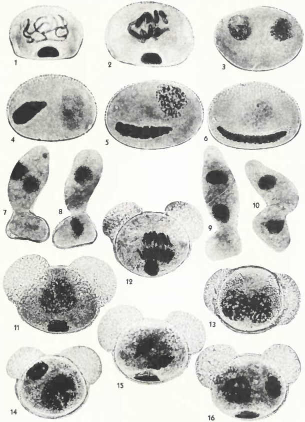
Figures 7, 8, 9, and 10. Abnormal microspores produced by heat and cold treatment.

Pseudolarix

Figures 11 and 12. Stages in the normal development of the microspore. All divisions are across the short axis of the cell, and the prothallial cells are always cut off near the heavy dorsal wall.

Figures 13, 14, 15, and 16. Abnormal development induced by heat treatment. The nuclei may divide at various angles followed by various degrees of differentiation of the daughter nuclei. The prothallial cells may be cut off at any point along the cell wall.

Cytological Laboratory, Arnold Arboretum,
Harvard University.



Temperature and Nuclear Differentiation

FULL-TONE — MERIDEN

NOTES ON THE LIGNEOUS PLANTS DESCRIBED BY LEVEILLE FROM EASTERN ASIA[1]

Alfred Rehder

LABIATAE

Leucosceptrum sinense Hemsley in Jour. Linn. Soc. Bot. **26**: 310 (1890). — Léveillé, Fl. Kouy-Tchéou, 209 (1914). — Dunn in Not. Bot. Gard. Edinb. **8**: 171 (1913); **6**: 192 (1915).

Elsholtzia Cavaleriei Léveillé & Vaniot in Fedde, Rep. Spec. Nov. **8**: 424 (1910).

Leucosceptrum Bodinieri Léveillé in op. cit. **9**: 224 (1911).

China. Kweichou: environs de Tsin-gay, au bord d'une rivière, *E. Bodinier*, no. 2709, Sept. 20, 1899 "sous -arbrisseau, fl. roses" (syntype of *Elsholtzia Cavaleriei;* photo. in A. A.); environs de Tou-chan, *J. Cavalerie* in herb. *Bodinier*, no. 2710, Sept. 1899 (syntype of *Elsholtzia Cavaleriei;* photo. in A. A.).

The name *Elsholtzia Cavaleriei* was changed by Léveillé to *Leucosceptrum Bodinieri* and later the two type specimens were enumerated by him in his Flore du Kouy-Tschéou under *L. sinense* without citation of synonymy, the reduction being based on identifications made by Dunn, to whom Léveillé had sent material of his Labiatae for revision, as it appears from a note in Léveillé's Flore du Kouy-Tchéou p. 203 under Labiacées which reads "(D. Dunn revisit)."

Leucosceptrum plectranthoideum (Lévl.) Marquand in Kew Bull. Misc. Inform. **1930**: 207.

Buddleia plectranthoidea Léveillé, Cat. Pl. Yun-Nan, 171 (1916).

China. Yunnan: pâtures des montagnes à Pé-long-tsin, 3200 m., *E. E. Maire*, Nov. 1912 (holotype of *Buddleia plectranthoidea;* merotype in A. A.).

This species seems nearest to *L. sinense* Hemsl. but can be at once distinguished by the shorter inflorescence, the yellowish closer tomentum of the calyx and the bracts, and the shorter elliptic or ovate-elliptic to oblong-elliptic leaves reticulate beneath and tomentulose above.

Colquhounia Seguini Vaniot in Bull. Acad. Intern. Géog. Bot. **14**: 165 (1904). — Rehder in Sargent, Pl. Wilson. **3**: 380 (1916). —

[1]Continued from Vol. **15**: 326; for preceding parts see Vol. **10**: 108–132, 164–196; **12**: 275–281; **13**: 299–332; **14**: 223–252; **15**: 1–27, 117.

Léveillé, Cat. Ill. Seu-Tchouen, 92, pl. 44 (1918). — P'ei, Verben. China in Mem. Sci. Soc. China, **1** (no. 3): 180 (1932).

Colquhounia elegans Wall. var. *pauciflora* Prain in Jour. As. Soc. Beng. **62**: 38 (1893). — Dunn in Not. Bot. Gard. Edinb. **6**: 179 (1915).

Caryopteris fluminis Léveillé, Sert. Yunn. 3 (1916); Cat. Pl. Yun-Nan, 298 (1917). — P'ei, Verben. China in Mem. Sci. Soc. China, **1** (no. 3): 180 (1932).

CHINA. Kweichou: environs de Ou-la-gay (Tchin-lin), *J. Seguin* in herb. *Bodinier*, no. 2237, March 1898 "longues tiges sous-ligneuses, lianeuses" (syntype of *C. Seguini;* photo. in A. A.); rives du fleuve Bleu, alt. 450 m., *E. E. Maire*, June 1912, "petit arbuste, feuilles persistantes, fleurs roses" (holotype of *Caryopteris fluminis;* photo. in A. A.). Yunnan: environs de My-tsao, *Fr. Ducloux*, no. 110, March 4, 1897, "long tiges s'enlaçant aux arbres et buissons, fleurs coccinées, 4 graines ailées" (syntype of *C. Seguini;* photo. in A. A.).

By Dunn (l. c.) this species was referred to *C. elegans* var. *pauciflora* Prain, but as I pointed out in 1916 (l. c.) this variety is best considered a distinct species which becomes *C. Seguini* Vaniot.

Micromeria biflora Bentham, Labiat. 378 (1834). — Dunn in Not. Bot. Gard. Edinb. **6**: 157 (1915). — Léveillé, Fl. Kouy-Tchéou, 210 (1914); Cat. Pl. Yun-Nan, 138 (1916).

Thymus Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **11**: 298 (1912).

CHINA. Kweichou: Tin-lan, montagnes sablonneuses, *J. Cavalerie*, no. 3778, "blanc-rose" (syntype of *Thymus Cavaleriei;* photo. in A. A.). Yunnan: Pan-pien-kai, pâturages des coteaux calcaires, alt. 2550 m., *E. E. Maire*, Sept. 1911 "Thymus vivace, étalé, fl. roses" (syntype of *Thymus Cavaleriei;* photo. in A. A.).

Elsholtzia rugulosa Hemsley in Jour. Linn. Soc. **26**: 278 (1890). — Léveillé, Fl. Kouy-Tchéou, 208 (1914); Cat. Pl. Yun-Nan, 138 (1916). — Dunn in Not. Bot. Gard. Edinb. **6**: 149 (1915).

Elsholtzia Labordei Vaniot in Bull. Acad. Intern. Géog. Bot. **14**: 177 (1904).

CHINA. Kweichou: environs de Tsin-gay, à Tchao-see, abonde dans la mont. et bord de routes, *J. Laborde* in herb. *Bodinier*, no. 2711, Sept. 7, 1899 "fleurs d'un bleu très pâle" (holotype of *E. Labordei;* photo. in A. A.).

Elsholtzia fruticosa (D. Don) Rehder in Sargent, Pl. Wilson. **3**: 381 (1916).

Elsholtzia polystachya Bentham, Labiat. 116 (1832). — Dunn in Not.

Bot. Gard. Edinb. **8:** 161 (1913); **6:** 149 (1915). — Léveillé, Fl. Kouy-Tchéou, 208 (1914); Cat. Pl. Yun-nan, 138 (1916).
Elsholtzia tristis Léveillé in Fedde, Rep. Spec. Nov. **8:** 424 (1910).
Elsholtzia Dielsii Léveillé in op. cit. **9:** 441 (1911).
Elsholtzia Souliei Léveillé in op. cit. **9:** 248, non p. 218 (1911).

CHINA. Szechuan: Ta-tsien-lu, *J. A. Soulié*, nos. 781 and 1023, in 1893 (syntypes of *E. Dielsii* [*E. Souliei* Lévl. p. 248, non p. 218]; photos. in A. A.). Kweichou: environs de Kouy-yang, mont du Collège, *E. Bodinier*, no. 1944, Nov. 3, 1897, "tige 1 m., fleurs blanches" (holotype of *E. tristis*, photo. in A. A.).

Elsholtzia ochroleuca Dunn in Not. Bot. Gard. Edinb. **8:** 161 (1913).
Elsholtzia lampradena Léveillé in Bull. Géog. Bot. **25:** 25 (1915); Cat. Pl. Yun-Nan, 137 (1916). — **Synon. nov.**

CHINA. Yunnan: pâturages des collines à Tong-tchouan, alt. 2600 m., *E. E. Maire*, Sept. 1912 "arbrisseau rameux, haut 0.40 m., fleurs blanches en épis dressés" (holotype of *E. lampradena;* photo. in A. A.).

Elsholtzia lampradena has been identified with *E. ochroleuca* according to a note on the type specimen.

Pogostemon glaber Bentham in Wallich, Pl. As. Rar. **1:** 31 (1830). — Léveillé, Cat. Pl. Yun-Nan, 143 (1916).
Caryopteris Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **9:** 449 (1911); Fl. Kouy-Tchéou, 440 (1915). — **Synon. nov.**

CHINA. Kweichou: Tchou-ly, alt. 900 m., *J. Esquirol*, no. 2053, March 1, 1910, "fl. blanche, labelle rose" (holotype of *Caryopteris Esquirolii;* merotype in A. A.).

Pogostemon glaber has not yet been recorded from Kweichou, as far as I know, but it is known from Yunnan.

Plectranthus ternifolius Don, Prodr. Fl. Nepal. 117 (1825). — Léveillé, Fl. Kouy-Tchéou 214 (1914); Cat. Pl. Yun-Nan 143 (1916). — Dunn in Not. Bot. Gard. Edinb. **6:** 138 (1915).
Elsholtzia Lychnitis Léveillé & Vaniot in Fedde, Rep. Spec. Nov. **8:** 425 (1910).
Teucrium Esquirolii Léveillé in Bull. Géog. Bot. **22:** 236 (1912).

CHINA. Kweichou: Tchen-lin-tchéou, route de Lo-pie à Oula-gay, *L. Martin* in herb. *Bodinier*, no. 1937, Oct. 9, 1899, "tige de 1.50 m. de haut, fleur blanches, ou blanc-bleuâtre" (syntype of *Elsholtzia Lychnitis;* photo. in A. A.); route de Tou-tchéou à Pien-yang, *J. Cavalerie*, no. 2573, Nov. 1905 (syntype of *E. Lychnitis;* photo. in A. A.); coteaux de Lo-fou, *J. Esquirol*, no. 2576, Nov. 1910 (holotype of *Teucrium Esquirolii;* ex Léveillé).

Of *Teucrium Esquirolii* I have seen no specimen, but Léveillé enumerates it in 1916 (Cat. Pl. Yun-Nan, 143) as a synonym of *Plectranthus ternifolius*, probably on identification by S. T. Dunn, though Dunn does not cite it in 1915. It does not appear in the Flore du Kouy-Tchéou. *Plectranthus ternifolius* should probably not be classed as a ligneous plant, though Hooker describes it in his Flora of British India (**4**: 621) as a bush 3-5 ft. high.

Plectranthus coetsa Hamilton ex Don, Prodr. Fl. Nepal. 117 (1825). — Léveillé, Cat. Pl. Yun-Nan, 141 (1916).

Plectranthus Mairei Léveillé, Cat. Pl. Yun-Nan, 141 (1916), pro synon. *P. coetsa* Ham.

CHINA. Yunnan: pâturages des mont. derrière Tong-tchouan, 2700 m., *E. E. Maire*, Oct. (1912–13), "plante annuelle très-rameuse, fl. rouge vif" (type of *P. Mairei;* photo. in A. A.); haies, plaine de Tché-hay, 2550 m., *E. E. Maire*, Sept. [1912–13], "plante vivace, tumescente, en touffes, haut 1.40 m." (in herb. Léveillé with *P. Mairei;* photo. in A. A.).

Plectranthus Mairei is apparently an unpublished name and is cited only as a synonym of *P. coetsa* (l. c.). On Mairei's specimen from Tong-tchouan the name *Plectranthus Mairei* appears in Léveillé's handwriting; the specimen from Tché-hay is without any name, but placed in the cover of *P. Mairei.*

The majority of Labiatae described by Léveillé are herbaceous and most of them have been examined by S. T. Dunn. He published his identifications in his Notes on Chinese Labiatae (in Not. Bot. Gard. Edinb. **8**: 153–171. 1913) and in his Key to the Labiatae of China (op. cit. **6**: 127–208. 1915). The identifications and reductions made by Dunn were accepted by Léveillé and incorporated in his Flore du Kouy-Tchéou (p. 203–217) and in his Catalogue des plantes de Yun-Nan (p. 136–149).

SOLANACEAE

Solanum aculeatissimum Jacquin, Coll. **1**: 100 (1786); Ic. Rar. **1**: t. 41 (1781–86). — Merrill in Contr. Arnold Arb. **8**: 149 (1934).

Solanum Bodinieri Léveillé & Vaniot in Bull. Soc. Bot. France, **55**: 206 (1908).

Solanum Cavaleriei Léveillé & Vaniot, l. c. 207 (1908). — **Synon. nov.**

CHINA. Hongkong: plage sablonneuse de l'île Verte, *E. Bodinier*, July 31, 1895 (holotype of *S. Bodinieri;* photo. in A. A.). Kweichou: Ly-po-hien, *J. Cavalerie* in herb. *Bodinier*, no. 2722, Aug. 10, 1899 (holotype of *S. Cavaleriei;* photo. in A. A.).

Solanum Bodinieri represents a glabrescent form of this very variable species, while *S. Cavaleriei* is much more pubescent throughout. *Solanum Bodinieri* has been identified with *S. aculeatissimum* by Merrill (l. c.).

SCROPHULARIACEAE

Brandisia racemosa Hemsley in Kew Bull. Misc. Inform. **1895:** 114.

Deutzia funebris Léveillé, Sert. Yunn. 1 (1916). — Cat. Pl. Yun-Nan, 296 (1917). — **Synon. nov.**

CHINA. Kweichou: rives du fleuve Bleu à Kiang-pien, alt. 350 m., *E. E. Maire,* Aug. 1913, "arbuste un peu grimpant; fl. roses" (holotype of *Deutzia funebris;* merotype in A. A.).

BIGNONIACEAE

Incarvillea Delavayi Bureau & Franchet in Jour. de Bot. **5:** 138. (1891).

Tecoma Mairei Léveillé, Cat. Pl. Yun-Nan, 20 (1916). — **Synon. nov.**

CHINA. Yunnan: rochers sous brousse, mont. de Pe-long-tsin, alt. 3200 m., *E. E. Maire,* May 1911, "plante vivace, fl. roses grandes" (holotype of *Tecoma Mairei;* photo. in A. A.).

Though this is an herbaceous species, I am including it in this enumeration, because Léveillé has described it under the ligneous genus *Tecoma.*

ACANTHACEAE

Phlogacanthus pubinervis T. Anderson in Jour. Linn. Soc. Bot. **9:** 508 (1867). — Léveillé, Cat. Pl. Yun-Nan, 6 (1915).

Aeschynanthus Dunnii Léveillé in Fedde, Rep. Spec. Nov. **9:** 453 (1911); Fl. Kouy-Tchéou, 180 (1914). — **Synon. nov.**

Lonicera Menelii Léveillé, Fl. Kouy-Tchéou, 63 (1914). — **Synon. nov.**

CHINA. Kweichou: without precise locality, *J. Esquirol,* no. 737, "fleur rougeâtre" (syntype of *Aeschynanthus Dunnii;* photo. in A. A.); Lo-fou, *J. Cavalerie,* no. 3475, March 1909 "couleur jaunâtre" (syntype of *Aeschynanthus Dunnii,* in fruit; photo. in A. A.); Thingmei, 1100 m., *J. Esquirol,* no. 3540, Dec. 2, 1913 (holotype of *Lonicera Menelii;* merotype in A. A.).

Cystacanthus yangtsekiangensis (Lévl.), comb. nov.

Strobilanthes yangtsekiangensis Léveillé, Cat. Pl. Yun-Nan, 7 (1915).

CHINA. Yunnan: rives du fleuve Bleu, alt. 400 m., *E. E. Maire,* May 1912, "plante sous-ligneuse en touffes dressées, fl. bleues" (syntype of *Strobilanthes yangtsekiangensis,* photo. in A. A.); rives du fleuve Bleu à Ta-tchai, alt. 450 m., "plante vivace, sous-ligneuse, en touffes, fl. roses" (syntype of *S. yangtsekiangensis;* photo. in A. A.).

This species is very near *C. yunnanensis* W. W. Sm., but is easily distinguished by the closer and finer pubescence of the young branchlets, the inflorescence and the calyx, and by the numerous lateral 2–6-flowered inflorescences along last year's branches. To *C. yangtsekiangensis* apparently belong Rock 8049 from Yunnan, between Tengyueh and Likiangfu, and Schneider 671 from southern Szechuan, between Mo-so-ying and Kung-mu-ying.

RUBIACEAE

Oldenlandia Bodinieri (Lévl.) Chun in Sunyatsenia, **1:** 310 (1934).

Hedyotis Bodinieri Léveillé in Fedde, Rep. Spec. Nov. **11:** 64 (1912).

CHINA. Kwangtung: Tay-mo-chan, sommet de la mont., 3500 ft., *E. Bodinier,* no. 1158, May 7, 1895, "petit sous-arbrisseau croissant dans les rocailles, fleurs blanches" (holotype; photo. in A. A.).

I have not been able to identify this plant with any described species.

Oldenlandia macrostemon (Hook. & Arn.) Kuntze, Rev. Gen. **1:** 292 (1891). — Pitard in Lecomte, Fl. Gén. Indo-Chine, **3:** 138 (1922).

Hedyotis macrostemon Hooker & Arnott, Bot. Beechey Voy. 192 (1841). — Léveillé, Cat. Pl. Yun-Nan, 245 (1917).

Hedyotis Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **13:** 176 (1914); Fl. Kouy-Tchéou, 367 (1915). — **Synon. nov.**

Oldenlandia Esquirolii (Lévl.) Chun in Sunyatsenia, **1:** 310 (1934).

CHINA. Kweichou: without precise locality, *J. Esquirol* (holotype of *H. Esquirolii;* photo. in A. A.).

Ophiorrhiza japonica Blume, Bijdr. 978 (1826).

Ophiorrhiza Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **13:** 177 (1914).

Ophiorrhiza Labordei Léveillé l. c. (1914); Fl. Kouy-Tchéou, 370 (1915). — **Synon. nov.**

CHINA. Kweichou: district de Tsin-gay, rocailles, bois à Kao-tchay, *J. Laborde* in herb. *Bodinier,* May 15, 1898 (holotype of *O. Labordei;* photo. in A. A.); without locality, *J. Cavalerie* (holotype of *O. Cavaleriei;* ex Léveillé).

Ophiorrhiza Cavaleriei is cited by Léveillé in his Flore du Kouy-Tchéou as a synonym of *O. Labordei,* but Cavalerie's specimen is not cited, only Laborde's specimen from Tsin-gay. Cavalerie's specimen I have not seen.

Ophiorrhiza cantoniensis Hance in Ann. Sci. Nat. sér. 4, **18:** 222 (1862). — Léveillé, Fl. Kouy-Tchéou, 370 (1915).

Ophiorrhiza Seguini Léveillé in Fedde, Rep. Spec. Nov. **13:** 177 (1914). — **Synon. nov.**

Ophiorrhiza violaceo-flammea Léveillé in Bull. Géog. Bot. **25:** 47 (1915); Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. Kweichou: environs de Gan-pin, croissant dans les rocailles, les trous entre des rochers, *E. Bodinier*, no. 1549, April 29, 1897, "fleurs blanches" (holotype of *O. Seguini*, photo. in A. A.). Yunnan: vallée de Li-tse-pin, 2700 m., *E. E. Maire*, April 1912, "sous-arbrisseau toujours vert, fl. violettes" (holotype of *O. violaceo-flammea;* photo. in A. A.).

Ophiorrhiza Seguini is not mentioned by Léveillé in his Flore du Kouy-Tchéou, but its type is enumerated, together with another specimen, under *O. cantoniensis*, which shows that Léveillé had reduced it to *O. cantoniensis*. The color of the flowers on the specimen of *O. violaceo-flammea* said to be violet does not look at all different from the color of flowers of *O. japonica*.

Ophiorrhiza cantoniensis is closely related to *O. japonica* Bl., but it may be distinguished by its oblong leaves attenuate at the base and quite glabrous, broadest at or above the middle, while *O. japonica* has shorter generally ovate or oblong leaves less attenuate or even nearly rounded at base and puberulous on the midrib beneath.

Wendlandia ligustrina Wallich, Num. List. 6272 (1832), in part, nom. nud. — Don, Gen. Syst. **2:** 518 (1834). — Léveillé, Cat. Pl. Yun-Nan, 242 (1917). — Cowan in Not. Bot. Gard. Edinb. **16:** 242 (1932); **18:** 183 (1934).

Luculia gratissima Sw. sensu Léveillé, Fl. Kouy-Tchéou, 368 (1915), non Sweet (1826).

CHINA. Kweichou: bords du Hoa-kiang, *L. Martin* in herb. *Bodinier*, no. 2563, Feb. 18, 1899, "petit arbuste, fleurs blanches" (photo. in A. A.).

This collection extends the range of *W. ligustrina* into Kweichou. Martin's specimen was identified with *W. ligustrina* by J. M. Cowan according to a note on the specimen.

Wendlandia salicifolia Franchet in herb. ex Castello in Jour. de Bot. **9:** 208 (1895). — Cowan in Not. Bot. Gard. Edinb. **16:** 244 (1932).

Ligustrum Thea Léveillé & Dunn in Fedde, Rep. Spec. Nov. **10:** 147 (1911). — Léveillé, Fl. Kouy-Tchéou, 295 (1914).

CHINA. Kweichou: without precise locality, *J. Esquirol*, no. 327, Dec. 16, 1904, "sous-arbrisseau des bords du fleuve, submergé aux grandes eaux; les feuilles donnent une infusion theiforme assez employée; fleur blanc-rose" (holotype of *Ligustrum Thea;* photo. in A. A.); without precise locality, *J. Esquirol*, no. 239 (cited in Fl. Kouy-Tchéou; photo. in A. A.).

Ligustrum Thea was first referred to *W. salicifolia* by Cowan in his "The Genus Wendlandia" (op. cit. 233-316).

Wendlandia Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **10:** 434 (1912); Fl. Kouy-Tchéou, 373 (1915). — Cowan in Not. Bot. Gard. Edinb. **16:** 263 (1932).

Wendlandia Feddei Léveillé in Fedde, Rep. Spec. Nov. **10:** 434 (1912); Fl. Kouy-Tchéou, 373 (1915).

CHINA. Kweichou: Lo-fou, *J. Cavalerie*, no. 3297, April 1907, "fleurs blanches" (holotype of *W. Cavaleriei;* merotype in A. A.); route de Pin-fa à Lo-fou, *J. Cavalerie*, no. 2732, April 4, 1906 (holotype of *W. Feddei;* photo. and merotype in A. A.).

Wendlandia uvariifolia Hance subsp. **Dunniana** (Lévl.) Cowan in Not. Bot. Gard. Edinb. **16:** 287 (1932); **18:** 185 (1934).

Wendlandia Dunniana Léveillé in Fedde, Rep. Spec. Nov. **10:** 434 (1912); Fl. Kouy-Tchéou, 373 (1915).

CHINA. Kweichou: Lo-fou, *J. Cavalerie*, no. 3476, March 1908 (holotype of *W. Dunniana;* merotype in A. A.).

Wendlandia longidens (Hance) Hutchinson in Sargent, Pl. Wilson. **3:** 392 (1916). — Cowan in Not. Bot. Gard. Edinb. **16:** 301 (1932).

CHINA. Yunnan: à mi-mont de Siao-ho, alt. 2800 m., *E. E. Maire*, [1911–14] "arbuste buissonant, fl. roses" (in herb. Léveillé sub *Leptodermis Mairei;* duplicate in A. A.).

In the herbarium Léveillé there were in the cover of *Leptodermis Mairei* three specimens collected by Maire, of which two belonged to *L. Mairei* which was identified by Dr. H. Winkler as *L. pilosa* (Franch.) Diels var. *glabrescens* H. Winkl., while the third was not a *Leptodermis,* but represents the species cited above. From the Szechuan and Hupeh specimens before me it differs slightly in the smaller leaves not exceeding 14 mm. and somewhat more densely pubescent on both sides; the flowers also are slightly smaller and are rose-colored according to the collector, while Wilson under his numbers 3756 (Veitch Coll.) and 2359 gives the color of the flowers as white. Possibly the specimen cited by Cowan (l. c.) as Maire, no. 326, without locality, is of the same collection as the specimen cited above.

Emmenopterys Henryi Oliver in Hooker's Icon. **19:** t. 1823 (1889).

Mussaenda Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **13:** 178 (1914); Fl. Kouy-Tchéou, 368 (1915). — Hutchinson in Sargent, Pl. Wilson. **3:** 397 (1916). — **Synon. nov.**

Mussaenda Mairei Léveillé in Bull. Géog. Bot. **25:** 47 (1915); Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. Kweichou: sur des rochers à Touan-po près Pin-yue (Pin-ue), *J. Cavalerie*, no. 2481, Aug. 10, 1905, "petit arbre à fl. blanches" (holotype of *Mussaenda Cavaleriei;* merotype in A. A.). Yunnan: vallée de Long-ky, 700 m., *E. E. Maire,* July 1912, "arbre moyen, fl. blanches" (holotype of *Mussaenda Mairei;* merotype in A. A.).

Adina racemosa Miquel, Cat. Mus. Bot. Lugd.-Bat. **1:** 44 (Fl. Jap.) (1870).

Cornus Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **13:** 257 (1914); Fl. Kouy-Tchéou, 116 (1914). — **Synon. nov.**

CHINA. Kweichou: rivière, Tong-tchéou, *J. Esquirol,* no. 407, June 1905 (holotype of *Cornus Esquirolii;* photo. in A. A.).

Uncaria scandens (Sm.) Hutchinson in Sargent, Pl. Wilson. **3:** 406 (1916). — Léveillé, Cat. Pl. Yun-Nan, 248 (1917).

Cephalanthus Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **10:** 434 (1912); Fl. Kouy-Tchéou, 365 (1915). — **Synon. nov.**

CHINA. Kweichou: Ma-jo, *J. Cavalerie,* no. 3015, May and Nov. 1908 (holotype of *Cephalanthus Cavaleriei;* merotype in A. A.).

Besides the flowering specimen described by Léveillé there is a fruiting specimen under the same number in his herbarium which is probably the specimen collected in November. This specimen apparently represents *U. rhynchophylla* (Miq.) Miq. which is of wide distribution in Eastern Asia, but to my knowledge has not been previously collected in western China.

Neonauclea Navillei (Lévl.), comb. nov.

Cephalanthus Navillei Léveillé, Fl. Kouy-Tchéou, 365 (1915).

CHINA. Kweichou: ruisseau qui monte à Kiao-miay, alt. 800 m., *J. Esquirol,* no. 3631, June 5, 1913, "arbre, 6 m." (holotype of *Cephalanthus Navillei;* merotype in A. A.).

This species is very similar to *N. Griffithii* (Hook. f.) Merr. but easily distinguished by ternate heads on a rather slender peduncle about 3 cm. long, the slender pedicels being 3–4 cm. long with scars of bractlets near the middle. The leaves are identical with those of specimens of *N. Griffithii* from Yunnan (Henry, nos. 12676 and 12880) which are in flower while Esquirol's specimen is in fruit.

Mussaenda Esquirolii Léveillé, Fl. Kouy-Tchéou, 369 (1915).

Mussaenda Wilsonii Hutchinson in Sargent, Pl. Wilson. **3:** 393 (1916). — **Synon. nov.**

CHINA. Kweichou: forêts de Tong-tchéou, 1400 m., *J. Esquirol,* no. 3264, June 22, 1912 "couleur jaune pâle" (holotype of *M.*

Esquirolii; photo. in A. A.). H u p e h : Chang-lo-hsien, ravines, 650 m., *E. H. Wilson,* Arn. Arb. Exp. no. 3265, June 1907 "bracts white, flowers yellow" (holotype of *M. Wilsonii* in A. A.).

The name *Mussaenda Esquirolii* does not appear on the original specimen, but an unpublished name under another genus with the same specific epithet in Léveillé's hand. The specimen differs from the type of *M. Wilsonii* in the more conspicuous pubescence of the veins and veinlets of the under side of the leaf, but this may be due to the younger state of the leaves.

Mussaenda pubescens Aiton f., Hort. Kew ed. 2, **1:** 372 (1810).

Mussaenda Bodinieri Léveillé in Bull. Soc. Bot. France, **55:** 59 (1908); Cat. Pl. Yun-Nan, 246 (1917). — Hutchinson in Sargent, Pl. Wilson. **3:** 396 (1916). — **Synon. nov.**

CHINA. K w a n g t u n g : pied du Tay-mo-chan (Taiman-san), commun dans les haies près des villages, *E. Bodinier,* no. 1159, May 6, 1895, "arbrisseau à branches sarmenteuses, fleurs blanches; differs des autres Mussaenda de l'absence de grande bractée florale" (holotype of *M. Bodinieri;* photo. in A. A.).

In *Mussaenda pubescens* the enlarged calyx-lobe is sometimes much reduced in size or entirely absent. I find it entirely absent in Hongkong Herb. 2784, J. B. Norton 1475, and H. H. Chung 3391 from Fukien, and in R. C. Ching 5433 and 5435 from Kwangsi. The locality given by Léveillé as Cay-mo-chan is apparently a misprint for Tay-mo-chan as it is clearly spelled on Bodinier's label; the same locality appears on English maps as Taimau-san.

Tarenna mollissima (Hook. & Arn.) Merrill in Philipp. Jour. Sci. Bot. **13:** 160 (1918). — Metcalf in Jour. Arnold Arb. **13:** 29 (1932).

Ehretia Esquirolii Léveillé, Fl. Kouy-Tchéou, 54 (1914), non Léveillé (1913).

CHINA. K w e i c h o u : route de Tong-tchéou, 1200 m., *J. Esquirol,* no. 3775, June 1912 (holotype of *Ehretia Esquirolii* of 1914: photo. in A. A.).

The name *Ehretia Esquirolii* (in Fedde, Rep. Spec. Nov. **12:** 335. 1913) had been given by Léveillé to another specimen collected by Esquirol at about the same time and at the same locality and numbered 3214. This specimen cannot be found in the Léveillé herbarium and was probably identified by Léveillé with another plant and the name used again for Esquirol 3775. The number 3775 seems to have been a mixture, for Léveillé enumerates in his Flore du Kouy-Tchéou the same number under *Ehretia Dunniana, E. Esquirolii* and *E. macrophylla;* under the last named as 3775 p.p. and without locality.

Tarenna incerta Koorders & Valeton in Meded. Lands Plantent. **59:** 268 (Bijdr. Boomsort. Java, 8) (1902). — Merrill in Philipp. Jour. Sci. **17:** 469 (1920).

Tarenna zeylanica Koorders & Valeton, l. c. 82 (1902); non Gaertn.
? Webera pallida Franchet ex Brandis, Ind. Trees, 378 (1906).
Webera Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **9:** 323 (1911); Fl. Kouy-Tchéou, 372 (1915).
Webera Henryi Léveillé, Sert. Yunnan. 1 (May 1916); Cat. Pl. Yun-Nan, 296 (1917).
Tarenna pallida (Franch.) Hutchinson in Sargent, Pl. Wilson. **3:** 410 (Aug. 1916).

CHINA. Kweichou: Pin-fa, *J. Cavalerie,* no. 2342, June 8, 1905, "petit arbre" (holotype of *Webera Cavaleriei;* photo. in A. A.). Yunnan: Szemao, *A. Henry,* no. 11923A (holotype of *Webera Henryi;* photo. in A. A.).

The type of *Webera Cavaleriei* consists only of a year-old branch with a few leaves and a small fragment of an inflorescence with very young fruits. It differs somewhat from the type of *W. Henryi* in the manifestly truncate calyx without any indication of teeth, though in the latter specimen perfectly truncate calyces occasionally occur. The type of *W. Henryi* agrees exactly with Henry no. 10686 which was identified by Hutchinson with *Tarenna pallida* together with Henry, nos. 11923, 11923C and 11923F.

Tarenna incerta seems to be somewhat variable in the number of ovules. Koorders & Valeton state that there are two or sometimes only one ovule in each locule and refer to a tree in the garden which had in all flowers only one ovule in each cell. In the one ovary of *Webera Cavaleriei* which I examined I also found only one ovule in each cell. Merrill (l. c.) states that the usual number of seeds in each fruit is apparently two. Brandis (l. c.), however, describes the fruit of *W. pallida* as having 4–6 seeds. Two fruits examined of Henry 11923F had 1 and 3 seeds each. It, therefore, seems somewhat doubtful if *Webera pallida* Franch. of which I have not seen the type really belongs to *T. incerta.*

Gardenia jasminoides Ellis in Philos. Trans. **51**(2): 935, t. 25 (1761).

Gardenia florida Linnaeus, Spec. Pl. ed. 2, p. 305, 1679 (1762). — Léveillé, Fl. Kouy-Tchéou, 366 (1915); Cat. Pl. Yunnan, 245 (1917).
Gardenia Schlechteri Léveillé in Fedde, Rep. Spec. Nov. **10:** 146 (1911); Fl. Kouy-Tchéou, 366 (1915). — **Synon. nov.**

CHINA. Kweichou: without precise locality, *J. Esquirol,* no.

777, April 1905, "arbre, fl. blanche" (holotype of *G. Schlechteri;* merotype in A. A.).

Esquirol no. 777 represents a rather small-flowered form, but otherwise it does not differ from *G. jasminoides*.

Varneria augusta L. (in Amoen. Acad. **4**: 136, 1759) upon which Merrill based the new combination *G. augusta,* is a nomen nudum. The oldest available specific epithet is *jasminoides,* though *florida* has been generally adopted.

Ixora Henryi Léveillé in Fedde, Rep. Spec. Nov. **13**: 178 (1914); Fl. Kouy-Tchéou, 367 (1915); Cat. Pl. Yun-Nan, 245 (1917). — Pitard in Lecomte, Fl. Gén. Indo-Chine, **3**: 324 (1924). — Chun in Sunyatsenia, **1**: 306 (1934).

CHINA. Kweichou: Lo-fou, *J. Cavalerie,* no. 3496, March 1909 (syntype; merotype in A. A.). Yunnan: Szemao, s. mountain forests, 5000 ft., *A. Henry,* no. 11637A, "shrub 5 ft., red flowers" (syntype; photo. and isotype in A. A.).

Here also belong Henry nos. 10407 and 10407 A-C from Mengtze and 11637 and 11637A-D from Szemao, Yunnan.

Psychotria Henryi Léveillé in Fedde, Rep. Spec. Nov. **13**: 179 (1914). — Hutchinson in Sargent, Pl. Wilson. **3**: 415 (1916).

CHINA. Yunnan: Szemao, s. e. mountains, 4000 ft., *A. Henry,* no. 12146D, "shrub 4 ft., red fruit" (holotype; photo. and isotype in A. A.).

Psychotria rubra (Lour.) Poiret, Encycl. Méth. Suppl. **4**: 597 (1816).

Psychotria elliptica Ker in Bot. Reg. **8**: t. 607 (1822); non H. & B. ex Roem. & Schult. (1819).

Psychotria Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **10**: 435 (1912); Fl. Kouy-Tchéou, 371 (1915). — **Synon. nov.**

CHINA. Kweichou: Ouang-mou, *J. Esquirol,* no. 119, June 1904 "fl. blanchâtre" (holotype of *P. Esquirolii;* photo. in A. A.).

This species has apparently not yet been recorded from western China, but seems common in southeastern China west to Kwangsi.

Psychotria Prainii Léveillé in Fedde, Rep. Spec. Nov. **9**: 324 (1911): Fl. Kouy-Tchéou, 371 (1915).

CHINA. Kweichou: Ouang-mou, *J. Esquirol,* 76 (holotype; photo. in A. A.); Héou-hay-tse, *J. Esquirol,* no. 860, June 1906, "fl. blanche" (enumerated in Fl. Kouy-tchéou; photo. and merotype in A. A.).

This species resembles in its capitate sessile or subsessile inflorescence *P. morindoides* Hutchins., but the inflorescence, branchlets and leaves beneath are covered with a ferrugineous pubescence similar to that of *P. pilifera* Hutchins., though shorter; besides it differs from *P. pilifera* in the sessile inflorescence, the smaller more coriaceous leaves glabrous above and in the short petioles.

Lasianthus Hookeri Clarke ex Hooker, f., Fl. Brit. Ind. **3:** 184 (1880). — Léveillé, Cat. Pl. Yun-Nan, 246 (1917).

Lasianthus Dunniana Léveillé in Fedde, Rep. Spec. Nov. **11:** 64 (1912); Fl. Kouy-Tchéou, 368 (1915). — **Synon. nov.**

CHINA. Kweichou: Lo-fou, *J. Cavalerie,* no. 3459, Oct. 1908 (holotype of *L. Dunniana;* photo. and merotype in A. A.).

Léveillé's description of the species is taken from a note on the type specimen which reads "aff. L. trichophlebus Hemsley, sed margine foliorum dense ciliata distincta," and is signed S. T. D(unn). It agrees exactly with Yunnan specimens referred by Hutchinson to *L. Hookeri* (in Sargent, Pl. Wilson. **3:** 402. 1916).

Lasianthus Biermanni King ex Hooker f., Fl. Brit. Ind. **3:** 190 (1880). — Léveillé, Cat. Pl. Yun-Nan, 246 (1917).

Lasianthus Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **11:** 295 (1912); Fl. Kouy-Tchéou, 368 (1915). — **Synon. nov.**

CHINA. Kweichou: without precise locality, *J. Esquirol,* no. 648 (holotype of *L. Esquirolii;* photo. in A. A.).

Esquirol's specimen agrees well with Henry no. 11148, identified by Hutchinson with *L. Biermanni* (in Sargent, Pl. Wilson. **3:** 402. 1916).

Lasianthus Labordei (Lévl.) Rehder in Jour. Arnold Arb. **13:** 340 (1932).

Canthium Labordei Léveillé in Fedde, Rep. Spec. Nov. **13:** 178 (1914); Fl. Kouy-Tchéou, 384 (1915).

CHINA. Kweichou: district de Tsin-gay, mont. de Kao-tchay, penchant escarpé des montagnes, *J. Laborde* in herb. *Bodinier,* no. 2109, March 7, 1898, "arbuste" (holotype of *Canthium Labordei;* photo. in A. A.).

Lasianthus Hartii Franchet in Bull. Soc. Bot. France, **46:** 209 (1899).

Canthium Dunnianum Léveillé in Fedde, Rep. Spec. Nov. **9:** 324 (1911); Fl. Kouy-Tchéou, 364 (1915). — **Synon. nov.**

CHINA. Kweichou: without precise locality, *J. Esquirol* (holotype of *Canthium Dunnianum;* photo. in A. A.); Pin-fa, montagnes, *J. Cavalerie,* no. 3226, May 20, 1907, "1 m. de h., fl. blanches" (cited in Fl. Kouy-Tchéou; merotype in A. A.).

In Flore du Kouy-Tchéou Léveillé cites only Cavalerie, no. 3226, which is in bloom, while the type, which is not cited, is a fruiting specimen.

This species is apparently related to *L. japonicus* Miq. from which it differs in the glabrous branchlets, glabrous calyx and glabrous or nearly glabrous leaves, and to *L. longicauda* Hook. f. from which it differs in the more coriaceous leaves with the veinlets less prominent beneath and in the five corolla-lobes being densely bearded inside up to the tip. The only flowering specimen of *L. longicauda* I have seen is Henry no. 10633 which has a 4-lobed corolla; this agrees with Hooker's original description of the flowers as "usually 4-merous." The flowers are also 4-merous in *Lasianthus Labordei.*

Lasianthus spec.

Canthium Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **10:** 434 (1912); Fl. Kouy-Tchéou, 364 (1915).

CHINA. Kweichou: Ma-jo, *J. Cavalerie,* no. 3350 (holotype of *Canthium Cavaleriei;* photo. and merotype in A. A.).

This species I am unable to identify with any species of *Lasianthus* and in the absence of flowers an exact determination is not possible. It can not be a *Canthium,* since the fruit is a several-seeded berry.

Paederia scandens (Lour.) Merrill in Contr. Arnold Arb. **8:** 163 (1934).

Paederia foetida Thunberg in Nov. Act. Soc. Sci. Upsal. **4:** 32 (1783); Fl. Jap. 106 (1784). — Léveillé, Fl. Kouy-Tchéou, 376 (1915). — Non Linnaeus (1767).

Paederia tomentosa Blume, Bijdr. 963 (1826).

Paederia chinensis Hance in Jour. Bot. **16:** 228 (1878).

Paederia Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **10:** 146 (1911).

Paederia Dunniana Léveillé, l. c. (1911).

Paederia Mairei Léveillé in Fedde, Rep. Spec. Nov. **13:** 179 (1914).

Paederia tomentosa Bl. var. *Mairei* (Lévl.) Léveillé, Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. Kweichou: Ky-che-ten, *J. Esquirol,* no. 184, Aug. 1904 (holotype of *P. Esquirolii;* photo. in A. A.); without precise locality, *J. Esquirol,* no. 775, April 1905, "fleur à gorge rouge" (holotype of *P. Dunniana;* photo. in A. A.). Yunnan: broussailles des collines à Siao-ou-long, 2550 m., *E. E. Maire,* July 1911, "arbuste grimpant, odeur fétide, fl. roses" (holotype of *P. Mairei;* photo. in A. A.).

The specimens cited above represent the typical glabrous form of

P. scandens; Paederia Esquirolii and *P. Dunniana* have narrow generally oblong leaves cuneate at base, while *P. Mairei* has larger and broader generally ovate leaves rounded to truncate at base.

This species which is the most widely distributed of the genus has been generally called *P. tomentosa* Bl. which is described by Blume as having the leaves tomentose beneath. I have seen no specimens from the type region, but as long as I have no evidence to the contrary, I accept *P. tomentosa* Bl. as a synonym of *P. scandens,* representing the form with leaves pubescent beneath which occasionally occurs also in China.

Paederia Wallichii Hooker f., Fl. Brit. Ind. **3:** 196 (1881).

Paederia tomentosa Bl. var. *purpureo-caerulea* Léveillé & Vaniot in Bull. Soc. Bot. France, **55:** 59 (1908).

Paederia Bodinieri Léveillé, Fl. Kouy-Tchéou, 371 (1915); non Léveillé (1914). — **Synon. nov.**

Cynanchum yunnanense Léveillé, Cat. Pl. Yun-Nan, 13 (1915). — **Synon. nov.**

CHINA. Kweichou: environs de Hoang-ko-chou, rochers, etc., *J. Seguin* in herb. *Bodinier,* no. 2501, Sept. 8, 1898, "liane grimpante, fleurs, atro-pourpre, avec bordure bleu-rouge, inodore" (holotype of *P. tomentosa* var. *purpureo-coerulea* and *P. Bodinieri;* photo. and merotype in A. A.). Yunnan: brousse des montagnes à Tcha-ho, alt. 2800 m., *E. E. Maire,* Nov. 1911, "arbuste grimpant, tomenteux, fl. violettes"; rives du fleuve Bleu à Siao-ho, 400 m., *E. E. Maire,* July 1912 "arbuste grimpant, feuil. blanches, velues en dessous" (syntypes of *Cynanchum yunnanense;* photos. in A. A.).

Paederia Bodinieri was described by Léveillé without reference to his earlier *P. tomentosa* var. *purpureo-caerulea,* but it is based on the same specimen which bears only the name var. *purpureo-caerulea* in Léveillé's hand. The name is a later homonym of his earlier *P. Bodinieri* (in Fedde, Rep. Spec. Nov. **13:** 179. 1914) which he referred the same year to *Marlea* as *M. Cavaleriei* and which turns out to be identical with *Gardneria multiflora* Mak. (see Jour. Arnold Arb. **15:** 309). *Cynanchum yunnanense* is not different from Seguin's specimen except that it has shorter inflorescences.

The specimens enumerated above are identical with Henry's nos. 9126 and 12442 and, judging from the description, seemed conspecific with *P. Wallichii* Hook. f. I am indebted to Sir Arthur W. Hill for a comparison of the Henry numbers with the type specimens of *P. Wallichii* in the Kew Herbarium; he writes me that Mr. C. E. C. Fischer reports on these specimens as follows: "the only difference between these numbers and the type of *P. Wallichii* Hook f. that I can see is that the basal lobes of the leaves are rather more rounded and the sinus slightly deeper and also the buds rather shorter. I doubt that this would suffice for even a variety." With the material at hand *P. Wallichii* Hook. f. may be characterized by cordate to subcordate leaves densely scabrid above with setulose appressed hairs somewhat bulbous at base and densely villous-pubescent or tomentose beneath, and by the lateral branches of the inflorescence bearing one or several capitate flower clusters. In the capitate or subcapitate flowers it resembles *P. microcephala* Pierre from which it differs in the short calyx-teeth and in the dense pubescence of the leaves.

Paederia Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **13:** 179 (1914).

Paederia tomentosa Bl. ex Léveillé, Fl. Kouy-Tchéou, 371 (1915).— Non Blume (1826).

CHINA. Kweichou: bois des montagnes, *J. Cavalerie*, no. 2058, Aug. 1904, "plante très puante" (holotype of *P. Cavaleriei;* photo. in A. A.).

This species is similar to the preceding, but differs in the long hirsute ferrugineous pubescence of the branches, the petiole and the inflorescence, in the petiole being 7.5–8 cm. long and in the 1–1.5 mm. long fairly straight hairs thinly covering the underside of the leaves, but dense on the midrib and veins, also in the glabrous narrower calyx-teeth. According to the original description it resembles *P. pilifera* Hook. f. in the long pubescence, but Pitard (in Lecomte, Fl. Gén. Indo-Chine, **3:** 412) describes the leaves as very tomentose beneath, the calyx-tube as very tomentose and the petiole as 1–2.5 cm. long.

A specimen collected in Kweichou at Sanhoa by W. Y. Chun (no. 6301) agrees in the pubescence of the stem and the leaf and in the thin texture of the leaf very well with *P. Cavaleriei*, but the lateral branches of the inflorescence end in cincinnate cymes, as is the rule in *P. scandens*, and not in subcapitate or capitate cymes, characteristic of this and the preceding species.

Leptodermis Potanini Batalin in Act. Hort. Petrop. **14:** 319 (1898).— H. Winkler in Fedde, Rep. Spec. Nov. **18:** 152 (1922).

Leptodermis Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **9:** 324 (1911); **13:** 179 (1914); Fl. Kouy-Tchéou 368 (1915); Cat. Fl. Yun-Nan, 246 (1917).

CHINA. Kweichou: Hin-y-fou, *J. Cavalerie*, no. 3930, July 1912 (cited in Fl. Kouy-Tchéou; duplicate in A. A.). Yunnan: Ouan-tse, *J. Esquirol*, no. 1503, May 22, 1909 "blanche à l'interieur, rouge à l'exterieur" (holotype of *L. Esquirolii;* photo. in A. A.).

Léveillé published *L. Esquirolii* a second time in 1914, but with a briefer description, both based on Esquirol no. 1503 which is a flowering specimen. Cavalerie no. 3930 from Kweichou is a fruiting specimen and owing to its fully developed broader leaves looks somewhat different, but apparently belongs to this species. *Leptodermis Esquirolii* was first identified with *L. Potanini* by H. Winkler (l. c.).

Leptodermis Potanini var. **glauca** (Diels) H. Winkler in Fedde, Rep. Spec. Nov. **18**: 153 (1922).

Leptodermis motsouensis Léveillé in Bull. Géog. Bot. **25**: 47 (1915); Cat. Pl. Yun-Nan, 246 (1917). — **Synon. nov.**

CHINA. Yunnan: collines arides de Mo-tsou, 800 m., *E. E. Maire,* May 1912, "sous-arbrisseau en touffes, fl. blanches" (holotype of *L. motsouensis;* merotype in A. A.).

The identification of *L. motsouensis* with *L. Potanini* var. *glauca* was communicated to me by Dr. H. Winkler in a recent letter as were the identifications of the following species of *Leptodermis.*

Leptodermis Potanini var. **tomentosa** H. Winkler in Fedde, Rep. Spec. Nov. **18**: 153 (1922).

Leptodermis tongchouanensis Léveillé in Bull. Géog. Bot. **25**: 47 (1915); Cat. Pl. Yun-Nan, 246 (1917), *"tongtchouanensis"* — **Synon. nov.**

CHINA. Yunnan: rochers des coteaux autour de Tong-tchouan, 2550 m., *E. E. Maire,* May 1912, "arbrisseau, feuilles velues blanchâtres, fl. blanches soyeuses" (holotype of *L. tongchouanensis;* merotype in A. A.).

Leptodermis pilosa (Franch) Diels var. **glabrescens** H. Winkler in Fedde, Rep. Spec. Nov. **18**: 160 (1922).

Leptodermis Mairei Léveillé in Fedde, Rep. Spec. Nov. **13**: 179 (1914); Cat. Pl. Yun-Nan, 246 (1917). — **Synon. nov.**

CHINA. Yunnan: plaine de Long-tang, 2500 m., *E. E. Maire,* Aug. 1912, "arbuste non grimpant, en touffes, fl. violet" (holotype of *L. Mairei;* merotype in A. A.); haies, plaine de Tong-tchouan, 2500 m., *E. E. Maire,* in 1912 "arbuste buissonant, écorce blanche, fl. roses" (in herb. Léveillé in cover of *L. Mairei;* duplicate in A. A.).

Only the specimen from Long-tang bears the name *L. Mairei* in Léveillé's hand. As Maire no. 21 Winkler (l. c.) enumerates under his *L. pilosa* var. *glabrescens* a specimen apparently of the same collection as Léveillé's type of *L. Mairei.*

Another specimen "à mi-mont de Siao-ho, 2800 m." in herb. Léveillé under *L. Mairei* belongs to *Wendlandia longidens* (Hance) Hutch. (see p 318.).

Leptodermis oblonga Bunge in Mém. Sav. Etr. Acad. Sci. St. Pétersb. **2:** 108 (Enum. Pl. Chin. Bor. 34) (1833).

Leptodermis Chaneti Léveillé in Bull. Géog. Bot. **25:** 47 (1915).

CHINA. Hopei: montagnes de Ping-chan, *L. Chanet*, no. 538 bis, Aug. 1910; without precise locality, *L. Chanet*, no. 574, June 1904 (syntypes of *L. Chaneti;* merotypes in A. A.).

Prismatomeris Henryi (Lévl.), comb. nov.

Canthium Henryi Léveillé in Fedde, Rep. Spec. Nov. **13:** 178 (1914); Cat. Pl. Yun-Nan, 245 (1917). — **Synon. nov.**

Prismatomeris brevipes Hutchinson in Sargent, Pl. Wilson. **3:** 413 (1916). — Léveillé, Cat. Pl. Yun-Nan, 247 (1917). — **Synon. nov.**

CHINA. Yunnan: Meng-tsę, S. E. mountains, 5000 ft., *A. Henry*, no. 9040F, "shrub 6 ft., fruit red" (holotype of *Canthium Henryi;* photo. in A. A.; paratype of *P. brevipes;* isotype in A. A.).

There is also an isotype of the holotype of *P. brevipes*, Henry 9040E, in the herbarium of the Arnold Arboretum and of another paratype, Henry 9040D.

CAPRIFOLIACEAE

Sambucus javanica Bl. var. **Argyi** (Lévl.), var. nov.

Sambucus Argyi Léveillé in Bull. Géog. Bot. **24**(no. 3301): 292 (1914); in Mem. Acad. Ci. Arts Barcelona, ser. 3, **12:** 545 (Cat. Pl. Kiang-Sou, 5) (1916).

CHINA. Kiangsu: Ka-se-dao, trouvé venant de Tou-ka-dou, *Ch. d'Argy* [1848–66] (holotype of *S. Argyi;* photo. in A. A.); Sê-hom, (jardin), *Ch. d'Argy* [1848–66] "fruit rouge" (with *S. Argyi* in herb. Léveillé; photo. in A. A.).

This variety differs from the type in the shorter and comparatively broader more coarsely serrate leaflets, the lateral ones ovate-oblong to oblong (5×1.8), the terminal elliptic or elliptic-obovate (6×3), and slightly scaberulous on the veins.

Sambucus Argyi was first referred to *S. javanica* by H. K. Airy-Shaw according to a note on the specimens.

Viburnum erubescens Wallich, Pl. As. Rar. **2:** 29, t. 143 (1830). — Léveillé, Cat. Pl. Yun-Nan, 28 (1916).

Viburnum botryoideum Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — **Synon. nov.**

CHINA. Yunnan: rochers, brousse de Kiao-me-ti, 3100 m., *E. E. Maire*, May 1913, "arbuste, fleurs roses" (holotype of *V. botryoideum;* merotype in A. A.).

Viburnum oliganthum Batalin in Act. Hort. Petrop. **13:** 372 (1894).

Viburnum Stapfianum Léveillé in Fedde, Rep. Spec. Nov. **9**: 443 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. Kweichou: Ma-jo, *J. Cavalerie*, no. 3002, May 1908, "petit arbre, fleurs roses" (holotype of *V. Stapfianum;* merotype in A. A.).

This species seems common in Szechuan; the specimen cited above is the first I have seen from outside of that province.

Viburnum sympodiale Graebner in Bot. Jahrb. **29**: 587 (1901). — Rehder in Sargent, Trees & Shrubs, **2**: 83, 108, t. 139 (1908).

Viburnum Martini Léveillé in Fedde, Rep. Spec. Nov. **9**: 443 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. Kweichou: Pin-fa, bois, rare, *J. Cavalerie*, no. 2272, April 4, 1905, "fl. blanches" (holotype of *V. Martini;* merotype in A. A.).

Viburnum Cavaleriei Léveillé in Fedde, Rep. Spec. Nov. **9**: 442 (1911); Fl. Kouy-Tchéou, 66 (1914).

CHINA. Kweichou: Pin-fa, montagnes, *J. Cavalerie*, no. 977, April 13, 1903, "h. 1 à 2 m., fl. blanches odorantes," (holotype; photo. and merotype in A. A.).

This species is closely related to *V. fallax* Graebn. and *V. chinchanense* Graebn. differing from the former in its coriaceous leaves rugulose and stellate pubescent above and from the latter in the glabrous ovaries and the leaves being sparingly stellate-pubescent and somewhat scabrid above. Both related species have been collected in Kweichou; *V. fallax* is represented in this herbarium from Kweichou by Steward, Chiao & Cheo 11, and *V. chinchanense* by Y. Tsiang 7419 and 9216 and also by another specimen, Tsiang 8424, which approaches *V. Rosthornii* Graebn. by its larger subcordate leaves sparingly stellate above.

Viburnum congestum Rehder in Sargent, Trees & Shrubs, **2**: 111 (1907). — Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — P'ei in Mem. Sci. Soc. China **1** (no. 3): 90 (Verben. China) (1932).

Hedyotis Mairei Léveillé in Fedde, Rep. Spec. Nov. **13**: 176 (1914); Cat. Pl. Yun-Nan, 245 (1917). — **Synon. nov.**

Viburnum Mairei Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — **Synon. nov.**

Premna Esquirolii Léveillé, Sert. Yunnan. 3 (1916); Cat. Pl. Yun-Nan, 298 (1917).

Oldenlandia Mairei (Lévl.) Chun in Sunyatsenia, **1**: 314 (1934).

CHINA. Yunnan: brousse du plateau de Ta-hai-tse, alt. 3200 m., *E. E. Maire*, May (1912 or 1913), "grande arbuste, feuilles caduques, fl. blanches" (holotype of *Hedyotis Mairei*, named *H. yunnanensis* on the label of the type specimen; photo. in A. A.); brousse au pied de Io-chan, 3200 m., *E. E. Maire,* May 1912, "arbuste haut 1.30 m.," (holotype of *V. Mairei;* merotype in A. A.); brousse des montagnes à Motsou, 800 m., *E. E. Maire,* May 1912, "arbuste, feuilles caduques, fl. blanches" (holotype of *Premna Esquirolii;* merotype in A. A.).

The three specimens cited above have the corolla tube somewhat shorter than in the type of *V. congestum,* the tube being only slightly longer than the lobes, but in the otherwise similar *V. utile* Hemsl. the tube is wide-campanulate and much shorter than the lobes. *Viburnum congestum* differs from *V. utile* also in the less dense grayish tomentum of the under side of the leaves, the individual hairs being distinguishable and usually have shorter rays, while in *V. utile* they are matted and the tomentum is whitish, brownish on the veins in young leaves. There are, however, specimens of *V. congestum* with a denser tomentum similar to that of *V. utile.* Geographically the two species seem to be well separated; *V. congestum* is common in Yunnan and extends into Kweichou and western Szechuan, while *V. utile* occurs in Hupeh and extends to eastern Szechuan.

Viburnum cylindricum Ham. var. **crassifolium** (Rehd.) Schneider in Bot. Gaz. **64:** 77 (1917).

Viburnum crassifolium, Rehder in Sargent, Trees & Shrubs, **2:** 112 (1908). — Léveillé, Cat. Pl. Yun-Nan, 28 (1915).

Viburnum pinfaense Léveillé in Fedde, Rep. Spec. Nov. **9:** 442 (1911); pro parte, quoad Cavalerie no. 1483; Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. Kweichou: Pin-fa, bois, *J. Cavalerie,* no. 1483, Oct. 12, 1903 (syntype of *V. pinfaense;* merotype in A. A.).

This variety has been collected in Kweichou in three different localities by Y. Tsiang (nos. 4121, 7558 and 9137). The leaves of Cavalerie's specimen are unusually small and narrow.

Under *V. pinfaense* Léveillé describes two different plants, of which the fruiting specimen belongs here, while the flowering one belongs to *V. sempervirens* K. Koch.

Viburnum ternatum Rehder in Sargent, Trees & Shrubs, **2:** 37, 112 t. 117 (1907).

Viburnum Chaffanjoni Léveillé in Fedde, Rep. Spec. Nov. **9:** 443 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. Kweichou: Pin-fa, bois presque à pic, *J. Cavalerie,* no. 3093, July 2, 1907 (holotype of *V. Chaffanjoni;* merotype in A. A.).

This very distinct species, differing in its ternate leaves from all other species, was known to me before only from Szechuan: banks of Min

River (Wilson 3736), Mt. Omei (W. P. Fang 2461, 2631, 3309, 3355 and F. T. Wang 23138), and Kuan-hsien (W. P. Fang 2021).

Viburnum Schneiderianum Handel-Mazzetti in Akad. Wiss. Wien Anzeig. **1925:** 66 (Pl. Nov. Sin. Forts. **33:** 4) (1925).

CHINA. Yunnan: rochers de Io-chan, alt. 3200 m., *E. E. Maire,* May (1911–13), "arbrisseau rampant, toujours vert," (in herb. Léveillé sub *Gaultheria crenulata;* duplicate in A. A.).

The specimen cited above was referred by Léveillé to *Gaultheria crenulata* Kurz and represents, at least partly, the plant enumerated under that name in his Cat. Pl. Yun-Nan, 86 (1916).

Viburnum sempervirens K. Koch, Hort. Dendr. 300 (1853). — Rehder in Sargent, Trees & Shrubs, **2:** 95, 113, t. 145 (1908).

Viburnum pinfaense Léveillé in Fedde, Rep. Spec. Nov. **9:** 442 (1911), pro parte, quoad specim. no. 1056; Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

CHINA. Kweichou: Pin-fa, montagnes, *J. Cavalerie,* no. 1056, June 11, 1903 (syntype of *V. pinfaense;* merotype in A. A.).

This species seems to be rare in western China. I have seen it only from Pin-fa, Kweichou (Cavalerie 1056 and Y. Tsiang 6385), and from Szemao, Yunnan (Henry 12753).

Viburnum foetidum Wallich, Pl. As. Rar. **1:** 49, t. 61 (1830). — Léveillé, Cat. Pl. Yun-Nan, 28 (1915). — P'ei in Mem. Sci. Soc. China, 1, no. **3:** 90 (Verben. China) (1932).

Viburnum ajugifolium Léveillé in Fedde, Rep. Spec. Nov. **9:** 441 (1911); Fl. Kouy-Tchéou, 65 (1914). — **Synon. nov.**

Premna Valbrayi Léveillé, Sert. Yunnan. 4 (1916); Cat. Pl. Yun-Nan, 299 (1917).

CHINA. Kweichou: environs de Kouy-yang, mont du Collège, c. dans les haies, bords des ruisseaux, *E. Bodinier,* no. 2231, May 18, 1898, "fl. blanches" (holotype of *V. ajugifolium;* merotype in A. A.). Yunnan: haies et brousses des montagnes, à Tong-tchouan, 2500-2700 m., *E. E. Maire,* July 1912, "arbuste grêle, feuill. caduques" (holotype of *Premna Valbrayi;* merotype in A. A.).

The two specimens cited above are similar to the form described as *V. ceanothoides* C. H. Wright.

Viburnum foetidum var. **rectangulatum** (Graebn.) Rehder in Sargent, Trees & Shrubs, **2:** 114 (1908), *"rectangulum."*

Viburnum Touchanense Léveillé in Fedde, Rep. Spec. Nov. **9:** 442 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

Hedyotis yunnanensis Léveillé in Fedde, Rep. Spec. Nov. **13:** 176 (1914); Cat. Pl. Yun-Nan, 245 (1917). — **Synon. nov.**

Oldenlandia yunnanensis (Lévl.) Chun in Sunyatsenia, **1:** 310 (1934).

China. Kweichou: environs de Tou-chan, bord de la route, *J. Cavalerie*, no. 2192, July 5, 1897, "arbrisseau aux fleurs odorantes" (holotype of *V. Touchanense;* merotype in A. A.). Yunnan: broussailles des collines à Long-ky, alt. 700 m., *E. E. Maire*, June 1911, "arbuste à feuilles caduques, fl. blanches" (holotype of *Hedyotis yunnanensis;* photo. in A. A.).

Viburnum setigerum Hance in Jour. Bot. **20:** 261 (1882). — Rehder in Jour. Arnold Arb. **12:** 77 (1931).

Viburnum theiferum Rehder in Sargent, Trees & Shrubs, **2:** 45, 113, t. 121 (1907).

Viburnum Bodinieri Léveillé in Fedde, Rep. Spec. Nov. **9:** 442 (1911); Fl. Kouy-Tchéou, 65 (1914).

China. Kweichou: environs de Kouy-yang, bois de Kin-linchan, *E. Bodinier*, no. 2193, April 14, 1898, "arbuste, fl. blanches" (syntype of *V. Bodinieri;* merotype in A. A.); Pin-fa, bois ombreux, *J. Cavalerie*, no. 1285, May, 1903, "fl. blanches, odorantes" (syntype of *V. Bodinieri;* photo. in A. A.).

Viburnum Bodinieri was identified with *V. setigerum* by the writer and the identification published in 1931 (l. c.). The species has been collected in Kweichou also by Y. Tsiang near Tsunyi (no. 5318) and on the Yun-fu-shan near Pin-fa (no. 5510) and near Tuyun (5942).

Viburnum corylifolium Hooker f. & Thomson in Jour. Linn. Soc. **2:** 174 (1858).

Viburnum Dunnianum Léveillé in Fedde, Rep. Spec. Nov. **9:** 442 (1911); Fl. Kouy-Tchéou, 66 (1914). — **Synon. nov.**

Viburnum barbigerum Léveillé, Fl. Kouy-Tchéou, 65 (1914). — **Synon. nov.**

China. Kweichou: route de Pin-yue à Kouy-yang, bords d'une rivière, *L. Martin* in herb. *Bodinier*, no. 2598, May 13, 1899, "grand arbuste, fl. blanches"; environs de Kouy-yang, mont du Collège, *J. Chaffanjon*, May 1, 1898, "arbuste, fl. blanches"; route de Pin-fa à Oug-lan, *J. Cavalerie*, Aug. 1908 "fruite rouge" (syntypes of *V. Dunnianum;* photos. of Martin's and Cavalerie's specimens, merotype of Chaffanjon's specimen in A. A.); Pin-fa, bois de hautes montagnes, *J. Cavalerie*, no. 1742, Aug. 1904 (holotype of *V. barbigerum;* merotype in A. A.).

Viburnum barbigerum agrees in all its characters with the other specimens cited, but the fruits are strikingly different in being densely covered with long setose hairs. I suspect, however, that this development of hairs is abnormal, since I have found a few other specimens of *Viburnum* namely R. C. Ching nos. 2826 and 2952 of *V. ichangense* (Hemsl.) Rehd. from Anhwei with some of the fruits densely covered with similar, though somewhat shorter, hairs, while the rest of the fruits was perfectly normal and glabrous.

Viburnum corylifolium is perhaps only a variety of *V. dilatatum* Thbg. differing chiefly in the long spreading hairs of the young branchlets, inflorescence and petioles, while in *V. dilatatum* these parts are covered by a short and close stellate tomentum. *Viburnum corylifolium* has been collected in Kweichou also by Y. Tsiang (no. 5779) near Tu-yun and by Steward, Chiao and Cheo, (no. 583) on Niu-tu-shan; *V. dilatatum* was collected by Y. Tsiang (no. 6270) on Yao-ren-shan, Sanhoa.

Viburnum erosum Thbg. var. **Taquetii** (Lévl.) Rehder in Sargent, Pl. Wilson. **1:** 311 (1912). — Nakai in Nakai & Koidzumi, Trees & Shrubs Jap. ed. 2, **1:** 609 (1927). — Makino & Nemoto, Fl. Jap. ed. 2, p. 1146 (1931).

Viburnum Taquetii Léveillé in Fedde, Rep. Spec. Nov. **9:** 443 (1911).
Viburnum erosum var. *punctatum* Franchet & Savatier ex Nakai, Fl. Sylv. Kor. **11:** 42, t. 12 c. d (1921) quoad synon. *V. Taquetii* Lévl., vix Franch. & Sav.

CHINA. Korea: Quelpaert, in silvis Yengsil, 1000 m., *E. Taquet,* no. 4281, Aug. 12, 1910 (holotype of *V. Taquetii;* photo. and isotype in A. A.).

This peculiar variety chiefly characterized by the narrow leaves partly with two basal lobes near the base has been collected in Quelpaert also by E. H. Wilson (no. 9406). Nakai in 1921 (l. c.) referred it to *V. erosum* var. *punctatum* Franch. & Sav., but that variety represents apparently the plant with broader leaves densely stellate-pubescent above which seems to be the most widely distributed form. The glabrous or glabrescent form, var. *laeve* Franch. & Sav., which seems much rarer must be considered the typical form, since Thunberg (Fl. Jap. 124) describes the leaves as glabrous.

Dipelta yunnanensis Franchet in Rev. Hort. **1891:** 246, fig. 62. — Léveillé, Cat. Pl. Yunnan, 27 (1915).

Cavaleriella Dunniana Léveillé, Fl. Kouy-Tchéou, 61 (1914). — **Synon. nov.**

CHINA. Kweichou: hautes montagnes, Long-ly, *J. Cavalerie,* no. 3023, May 1908 (holotype of *Cavaleriella Dunniana;* merotype in A. A.).

The leaves are pilose on the midrib and veins beneath, also the young branchlets and the inflorescence are pilose.

Abelia verticillata Léveillé, Fl. Kouy-Tchéou, 61 (1914).

CHINA. Kweichou: Pin-fa, ruisseau du sud, *J. Cavalerie*, no. 497, Sept. 1912, "fl. blanche-violette-pourprée" (holotype; photo. in A. A.).

This species appears to be closely related to *A. uniflora* R. Br. and *A. Graebneriana* Rehd., but differs from both in the pilose branches and in the ovary being pilose with rather long white hairs; it also differs from the former in the ciliate leaves and from the latter in the subcoriaceous leaves not bearded in the axils and without hairs alongside the midrib and the base of the lateral veins. On one of the branches of the type specimen the leaves are in whorls of threes, from which the specific epithet is derived, but the other branch has opposite leaves; branches with ternate leaves are also occasionally found in *A. uniflora* and in other species, e. g. in Wilson no. 747 of *A. parvifolia* Hemsl.

Abelia Schumannii (Graebn.) Rehder in Sargent, Pl. Wilson. **1**: 121 (1911). — Léveillé, Cat. Pl. Yun-Nan, 26 (1915).

Strobilanthopsis deutziaefolius Léveillé in Fedde, Rep. Spec. Nov. **12**: 20 (1913).

Abelia deutziaefolia (Lévl.) Léveillé, Fl. Kouy-Tchéou, 60 (1914). — **Synon. nov.**

Strobilanthes deutziaefolia, Léveillé, l. c. (1914), pro synon. *Abeliae deutziaefoliae*. — Ind. Kew. Suppl. **4**: 252 (1921).

Abelia Mairei Léveillé, Cat. Pl. Yun-Nan, 26 (1915). — **Synon. nov.**

CHINA. Kweichou: sous bois, *J. Esquirol*, no. 466, June 1905, "sous-arbrisseau, fl. blanches, panachées de rose," (holotype of *Strobilanthopsis deutziaefolius;* merotype in A. A.). Yunnan: rochers des collines à Siao-ou-long, 2250 m., *E. E. Maire*, June 1912, "arbuste delicat, buissonant, haut 0.80 m., fl. roses (holotype of *A. Mairei;* merotype in A. A.).

The leaves of Esquirol's no. 466 are rather large being up to 3.5 cm. long and resemble somewhat those of *A. Graebneriana* Rehd., though scarcely acuminate, but the branchlets are pubescent.

Abelia myrtilloides Rehder in Sargent, Pl. Wilson. **1**: 120 (1911).

Strobilanthopsis hypericifolius Léveillé in Fedde, Rep. Spec. Nov. **12**: 20 (1913), "*hypercifolia*."

Abelia Bodinieri Léveillé, Fl. Kouy-Tchéou, 61 (1914) pro synon. *A. parvifoliae*.

Abelia parvifolia Hemsl. sec. Léveillé, Fl. Kouy-Tchéou, 61 (1914), saltem quoad specim. Bodinier, no. 1607, vix Hemsley.

Strobilanthes hypericifolia Léveillé, l. c. (1914), pro synon. *A. parvifoliae*. — Ind. Kew. Suppl. **5**: 252 (1921).

CHINA. Kweichou: mont de Lou-tsong-koạn, 1500 m., Kienlin-shan çà at là dans les montagnes rocailleuses, *E. Bodinier,* no. 1607, June 1, 1897 and June 19, 1899, "petit arbuste à jolies fleurs roses" (syntypes of *Strobilanthopsis hypericifolius;* photo. and merotype in A. A.).

Léveillé cites in his Flore du Kouy-Tchéou (l. c.) under *A. parvifolia* as synonyms besides *Strobilanthes hypericifolia* the unpublished name *A. Bodinieri;* both names appear on the labels of the type sheet of Bodinier no. 1607. The two specimens on the type sheet are somewhat intermediate between *A. myrtilloides* and *A. parvifolia* Hemsl., but in the oblong-elliptic or oblong-ovate shape of the leaves glabrous above and nearly so beneath they seem closer to the former, only in the glandular under surface they approach *A. parvifolia* which typically has ovate leaves of thicker texture pilose and glandular on both surfaces. A form very similar to Bodinier's specimen was collected near Kwei-yang, Kweichou, by Handel-Mazzetti, (no. 10477) who determined it as "*A. parvifolia* Hemsl. trans. ad *A. myrtilloidem* Rehd."

Abelia Cavaleriei Léveillé, Fl. Kouy-Tchéou, 60 (1914).

China. Kweichou: sud de Tin-fan, mont. rocheuses, *J. Cavalerie,* no. 1909, Oct. 1904, "fl. blanches" (holotype; merotype in A. A.).

This is a very distinct species on account of its subcoriaceous leaves which recall those of *Ligustrum strongylophyllum* Hemsl. The species is apparently nearest *A. chinensis* R. Br., but is readily distinguished by the subcoriaceous perfectly glabrous quite entire leaves broadly ovate to orbicular-ovate, 1–2 cm. long, rounded or broadly cuneate at base, obtuse or rounded and apiculate at the apex. The branchlets and the many flowered terminal inflorescence are minutely puberulous. The specimen is in fruit but according to the collector the flowers are white.

Lonicera tangutica Maximowicz in Bull. Acad. Sci. St. Pétersb. **24:** 48 (1877); in Mél. Biol. **10:** 75 (1877).

Lonicera Rocheri Léveillé in Bull. Géog. Bot. **24**(no. 301): 289 (1914); Cat. Pl. Yun-Nan, 27 (1915). — **Synon. nov.**

China. Yunnan: brousse de Lan-mou-kiao, 3000 m., *E. E. Maire,* May 1912, "arbuste en touffes; fl. jaunes" (holotype of *L. Rocheri;* merotype in A. A.).

The species cited above differs somewhat from typical *L. tangutica* in the linear-lanceolate somewhat leafy bracts about twice as long as ovary, in the anthers being exserted about one-half and in the less slender corolla-tube, but in its other characters it agrees with this species.

Lonicera ligustrina Wallich in Roxburgh, Fl. Ind. ed. 2, **2:** 179 (1824). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera missionis Léveillé, Fl. Kouy-Tchéou, 63 (1914), pro parte, quoad specim. "Esquirol (May 10, 1906), Chaffanjon no. 2215"; Cat. Pl. Yun-Nan, 27 (1915).

CHINA. Kweichou: environs de Kouy-yang, mont. du Collège, à la cascade, *J. Chaffanjon* in herb. *Bodinier*, no. 2215, April 14, 1898, "arbuste" (syntype of *L. missionis;* photo. in A. A.); mont du Collège, grotte, *J. Esquirol*, May 10, 1906 "fl. blanches" (syntype of *L. missionis;* merotype in A. A.). Yunnan: sous bois de couteaux à Long-ky, 700 m., *E. E. Maire*, "arbuste toujours vert, fl. blanches," (in herb. Léveillé under *L. missionis;* duplicate in A. A.).

This species has been collected in Kweichou also by W. Tsiang (nos. 4580, 5972, 7640) and by Steward, Chiao & Cheo (no. 244).

Lonicera pileata Oliver in Hooker, Icon. Pl. **16**: t. 1585 (1887). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera missionis Léveillé, Fl. Kouy-Tchéou, 63 (1914) pro parte, quoad specimen "Laborde 2502"; Cat. Pl. Yun-Nan, 27 (1915). — **Synon. nov.**

Lonicera buxifolia Léveillé, Fl. Kouy-Tchéou, 63 (1914); Cat. Ill. Seu-Tchouen, t. 11 (1918) MS. — **Synon. nov.**

CHINA. Kweichou: environs de Tsin-gay à Kia-la-tchong, *J. Laborde* in herb. *Bodinier*, no. 2502, Nov. 1898 "les fruits sont des jolies perles bleu-tendre, pulpeuses" (syntype of *L. missionis;* photo. in A. A.); environs de Kouy-yang, mont du Collège, rochers de la cascade, au bords de l'eau, *J. Chaffonjon* in herb. *Bodinier*, no. 2169, April 12, 1898, "fl. jaunâtres" (syntype of *L. buxifolia;* photo. in A. A.); grotte du Collège, 1350 m., *J. Esquirol*, no. 2069, April 1910, "blanche" (syntype of *L. buxifolia;* photo. in A. A.); Pin-fa, ruisseaux, *J. Cavalerie*, no. 1319, April 9, 1902, "fl. blanche" (in herb. Léveillé under *L. buxifolia;* photo. in A. A.).

This species has been collected in Kweichou also by Y. Tsiang (nos. 4529, 4562, 7937) and by Steward, Chiao & Cheo (no. 803); the last named specimen is approaching in the shape of its leaves f. *linearis* Rehd. The specimens named *L. buxifolia* by Léveillé differ from typical *L. pileata* in their rather small leaves. The two species, *L. ligustrina* and *L. pileata*, are closely related and connected by intermediate forms in regard to shape of the corolla and of the leaves and to pubescence. Without flowers *L. ligustrina* may be distinguished by the leaves being generally ovate, rounded at base, acuminate, and with the midrib more or less impressed above at least toward the base and strigose, while *L. pileata* has generally elliptic to oblong leaves, narrowed at base, obtuse to acute at apex, with the midrib distinctly elevated above and glabrous. In regard to shape and pubescence of the leaves *L. nitida* Wils. seems intermediate between the two, but the leaves are much smaller and usually broader, generally ovate, but not acuminate. *Lonicera virgultorum* W. W. Sm. is very close to *L. ligustrina* and chiefly distinguished by the shape of the corolla.

Lonicera fragilis Léveillé in Fedde, Rep. Spec. Nov. **13:** 337 (1914); Cat. Pl. Yun-Nan, 37 (1915).

China. Yunnan: vallée de Li-tse-pin, 2800 m., *E. E. Maire*, April 1913, "arbuste cassant, haut de 1.20 m., fl. roses" (holotype; merotype in A. A.).

Frutex metralis ramis hornotinis sparse setosis vel glabris; gemma terminalis interdum evoluta perulis duabus exterioribus et 4–6 interioribus. Folia nondum plane evoluta, elliptico-oblonga, acuminata, basi cuneata, utrinque hirsuta, glandulis sparsis intermixtis, margine ciliata et stipitato-glandulosa. Flores praecoces in axillis bractearum ad basin ramulorum; pedunculi brevissimi glabri; bracteae late ovatae, 8–10 mm. longae, irregulariter eroso-denticulatae, basin versus ciliatae et sparsissime stipitato-glandulosae, apicem versus glabrae, ceterum extus intusque glaberrimae; ovaria subglobosa, glabra; calyx ovario circiter duplo longior, latus et plicatus, dentibus carnosulis inaequalibus 1.5–3 mm. longis, late ovatis apice rotundatis margine irregulariter erosulis glabris; corolla rosea (ex collectore), infundibuliformis, tubo 7–8 mm. longo basi manifeste gibboso supra paullo ampliato extus basi excepta sparse setoso-hirsuta, intus a medio ad faucem villoso-hirsuto, lobis late ovatis apice rotundatis 3 mm. longis glabris; stamina medio tubo affixa, antheris 2.5 mm. longis faucem non attingentibus, filamentis glabris brevissimis; stylus medium tubum non superans, glaber.

As Léveillé's description is very brief and inaccurate particularly in regard to the calyx which he describes "calyce ciliato," apparently taking the bracts for the calyx, I have given above a more complete description. The species seems nearest to *L. nubigena* Rehd., from which it chiefly differs in the bracts being quite glabrous except ciliate toward the base, in the large calyx, in the corolla being sparingly setose-hirsute outside, not short-pubescent and glandular, in the hirsute pubescence at the mouth with the anthers much below the mouth, not just reaching the mouth as in *L. nubigena,* and in the glabrous style.

Lonicera lanceolata Wallich in Roxburgh, Fl. Ind. ed. 2, **2:** 177 (1824). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera acrophila Léveillé in Bull. Géog. Bot. **24** (no. 301): 289 (1914); Cat. Pl. Yun-Nan, 27 (1915). — **Synon. nov.**

China. Yunnan: haut plateau de Je-ma-tchouan, 3200 m., *E. E. Maire*, July 1912, "arbre moyen, fl. roses" (holotype of *L. acrophila;* merotype in A. A.).

According to Maire this is a medium-sized tree, but by most collectors it is described as a shrub, 4–8 ft. tall.

Lonicera Koehneana Rehder in Sargent, Trees & Shrubs, **1:** 41, t. 21 (1902). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915).

Lonicera gynopogon Léveillé in Bull. Géog. Bot. **24** (no. 301): 289 (1914); Cat. Pl. Yun-Nan, 27 (1915). — **Synon. nov.**

CHINA. Yunnan: brousse derrière Tong-tchouan, alt. 2550 m., *E. E. Maire*, May 1912, "Lonicera non grimpant, rameaux courts et grèles, fl. blanc-jaune" (holotype of *L. gynopogon;* photo. in A. A.); haies, plaine de Tong-tchouan, alt. 2500 m., *E. E. Maire*, May [1912], "fl. de Lonicera, mi-blanche, mi-jaune" (in herb. Léveillé under *L. gynopogon;* photo in A. A.); haies de Tchéou-kia-tse-tang, alt. 2500 m., *E. E. Maire*, "arbuste buissonante, haut 2 m., feuilles molles, velues et blanches en dessous, fl. mi-blanches, mi-jaunes, inodores" (in herb. Léveillé under *L. gynopogon;* duplicate in A. A.).

Specimens from the same locality and partly apparently of the same collection have been distributed by the Arnold Arboretum under Maire, no. 142 and no. 286.

Lonicera Pampaninii Léveillé in Fedde, Rep. Spec. Nov. **10:** 145 (1911); Fl. Kouy-Tchéou, 64 (1914); Cat. Pl. Yun-Nan, 27 (1915).

Lonicera Henryi var. *setuligera* W. W. Smith in Not. Bot. Gard. Edinb. **10:** 47 (1917).

CHINA. Kweichou: mont de Lou-tsong-koan, Tsin-gay, rocailles à Ché-tiou-tchay, Gan-pin, buissons et rochers de la montagne, *L. Martin* in herb. *Bodinier*, no. 1623, June 10, 1897 and June 27, 1899, "fleurs jaunes" (syntypes; merotype in A. A.).

This species is similar to *L. Henryi* Hemsl., but is easily distinguished by the slenderer corolla-tube densely clothed with reflexed yellowish hairs; in the subsessile or sessile flowers with subulate pilose bracts exceeding the pilose calyx-lobes; the leaves which closely resemble those of *L. Henryi* are pilose on the midrib above and below otherwise glabrous even on the margin.

This species has been collected in Kweichou also by Y. Tsiang near Tsun-yi and Pin-fa; nos. 5277 and 5377; also Steward, Chiao & Cheo no. 271 from Tsun-yi is probably the same, but it has no flowers.

Lonicera macrantha Sprengel, Syst. Veg. 4^2: 82 (1827). — Léveillé, Fl. Kouy-Tchéou, 63 (1915).

Lonicera Guilloni Léveillé & Vaniot, in Bull. Soc. Bot. France, **51:** cxliv (1904).

CHINA. Kweichou: Pin-fa, *J. Cavalerie*, no. 1015, May 28, 1903, "fl. blanches et jaunes au veillisant, sans odeur" (holotype of *L. Guilloni;* photo. in A. A.).

Cavalerie no. 1015 is cited by Léveillé in his Flore du Kouy-Tchéou under *L. macrantha* (l. c.), but the name *L. Guilloni* is not mentioned. The specimen differs somewhat from typical *L. macrantha* in the shorter and slighter pubescence of the branches and in the scarcely ciliate leaves.

Lonicera Esquirolii Léveillé, Fl. Kouy-Tchéou, 63 (1914).

CHINA. Kweichou: without locality, *J. Esquirol,* no. 889, June 1903, "fl. jaunes après floraison" (holotype; photo. and merotype in A. A.).

This species seems most nearly related to *L. ferruginea* Rehd., but is easily distinguished by the shorter, not hirsute pubescence and the glabrous ovary. From *L. inodora* W. W. Sm. it differs in the glabrous style, the glandular pubescence of the corolla, the sessile or subsessile inflorescence and in the setulose pubescence extending over the whole under surface of the leaf.

Lonicera japonica Thunberg, Fl. Jap. 89 (1784). — Léveillé, Cat. Pl. Yun-Nan, 27 (1915); in Mem. Acad. Ci. Art. Barcelona, ser. 3, **12:** 545 (Cat. Pl. Kiang-Sou, 5) (1916).

Lonicera Fauriei Léveillé & Vaniot in Fedde, Rep. Spec. Nov. **5:** 100 (1908). — **Synon. nov.**

JAPAN. Nippon: in littore Shiogama, *U. Faurie,* no. 6823, Oct. 1905 (holotype of *L. Fauriei;* photo. and merotype in A. A.).

Léveillé compares his species with *L. bracteolaris* Boiss. & Buhse and describes the fruit as having 3 persistent hairy styles; he apparently mistook for styles the sepals which in one of the fruits appear to be only three, the other two not being clearly visible.

Lonicera yunnanensis Franchet in Jour. de Bot. **10:** 310 (1896).

Lonicera Mairei Léveillé in Bull. Bot. Géog. **24:** 289 (1914). — **Synon. nov.**

CHINA. Yunnan: collines herbeuses autour de Tong-tchouan, alt. 2550 m., *E. E. Maire,* fl. blanc-jaunâtre" (holotype of *L. Mairei;* merotype in A. A.).

The branches of Maire's specimen are apparently from different plants; one has the leaves quite glabrous beneath as in the type of *L. yunnanensis,* while in the other they are slightly pubescent beneath and are referable to var. *tenuis* Rehd., but there is no difference in the size of the leaves.

COMPOSITAE

Pertya Bodinieri Vaniot in Bull. Acad. Intern. Géog. Bot. **12:** 116 (1903). — Beauverd in Bull. Soc. Bot. Genève, sér. 2, **1:** 386, fig. 6 (1909). — Léveillé, Cat. Pl. Yun-Nan, 47 (1915).

CHINA. Yunnan: environs de Yunnan-fou, dans les ravines de la montagne, *E. Bodinier,* no. 10, Jan. 27, 1897, "tiges sous-ligneuses, de 0.6–1 m., fl. roses" (holotype; merotype [from herb. Léveillé] and photo. of isotype [in herb. Paris] in A. A.).

Though this is not one of Léveillé's species I have included it here, since the type is in the herb. Léveillé.

Pertya Esquirolii Léveillé (in Bull. Géog. Bot. **24:** 251 (1914); Fl. Kouy-Tchéou, 100 (1914) from Kweichou, based on Esquirol no. 3633 is an herbaceous plant and belongs to *Ainslea;* it seems very near or identical with *A. rubrifolia* Franch. which I have not seen.

(To be continued)

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

HUODENDRON, A NEW GENUS OF STYRACACEAE

Alfred Rehder

With plates 151 and 152 and one text figure.

Huodendron, gen. nov.

Flores hermaphroditi, actinomorphi, pentameri; calycis tubus ovario adnatus, dentibus 5 triangularibus vel ovatis circiter dimidium tubum aequantibus; petala 5, initio basi coherentia, demum libera, lineari-oblonga, anguste imbricata vel valvata, sub anthesi revoluta; stamina 7–10, uniserialia, libera, petalis subaequilonga, sed ob petala revoluta valde exserta, filamentis complanatis linearibus, antheris anguste oblongis introrsis, loculis distinctis, connectivo cum filamento continuo et supra antheras in appendicem conspicuum tri- vel rarius bidentatum elongato; ovarium inferum, triloculare; styli 3, triente inferiore vel fere ad apicem connati, stigmatibus capitellatis; ovula in quoque loculo numerosa, axi centrali affixa, erecta. Fructus capsularis, ovoideus, parva, triente infra apicem sepalis circumcincta, trilocularis, loculicide dehiscens, valvis interdum demum septicidis, endocarpio crustaceo, exocarpio tenui; semina numerosa, scobiformia, minuta, oblonga vel elliptico-oblonga, leviter complanata, testa tenui reticulata, basi et apice fimbriata et saepius ad marginem sparse breviterque fimbriata, albuminosa, embryo centralis, rectus. — Arbor vel frutex ramis gracilibus, gemmis parvis nudis pubescentibus; folia decidua, alterna, petiolata estipulata, ovato-elliptica vel ovato-oblonga, acuminata, basi cuneata, integra vel remote minuteque denticulata, glabra vel fere glabra, penninervia, nervis curvatis anastomosantibus; inflorescentiae terminales et axillares, paniculatae vel subcorymbosae, ebracteatae et ebracteolatae, floribus satis parvis albis graciliter pedicellatis; capsula parva, pedicello recurvo.

Ab aliis Styracacearum generibus, petiolis et staminibus liberis vel fere liberis, filamentis supra antheram in appendicem 3-vel 2-dentatum elongatis, stylo 3-fido, capsula valvis 3 dehiscente, seminibus scobiformibus numerosis bene distincta. Ob semina numerosa *Alniphyllo* affinis videtur, sed petalis et staminibus liberis, stylo trifido, connectiva appendiculato, capsula 3-loculari subinfera, seminibus scobiformibus circiter 1 mm. longis facile distinguitur.

Type Species: *Huodendron tibeticum* (Anthony) Rehd.

Distribution: The genus is restricted to southern China and extends northwest across the border into southeastern Tibet and northeastern Burma and south into northern Tonkin, where it occurs near Lao-kay, about 150 km. southeast of Mengtze. Within China it ranges from western Yunnan through southern Kweichou, to Kwangsi and Kwangtung. Of the two species *H. tibeticum* is restricted to southeastern Tibet, about N. Lat. 29°, while *H. biaristatum* ranges from northeastern Burma to Kwangtung and extends south into Tonkin; it does not seem to occur north of N. Lat. 25°.

The two species now known of the new genus were originally both referred to the genus *Styrax* to which the flowers bear a great resemblance, but the fruit is entirely different. In *Styrax* the fruit is indehiscent or irregularly dehiscent and contains only one or two rather large subglobose or ellipsoid seeds, while the fruit of *Huodendron* resembles strongly that of some Saxifragaceae-Hydrangeae, as *Deutzia* and *Hydrangea,* in shape and size and dehiscence of the capsule and in the numerous scobiform seeds; also the divided style recalls Saxifragaceae, and in some species of *Deutzia* the flattened filaments are elongated beyond the anther or are dentate at the apex. The petals and stamens fall off separately after anthesis, though in bud they are cohering at the very base; in Styracaceae free stamens and petals are very rare. Any doubt, however, one might have in regard to the affinity of *Huodendron,* is convincingly set at rest by the nodal structure of the stem, which shows the unilacunar nodes characteristic of all Ebenales, while the Rosales have trilacunar or quinquelacunar nodes, as pointed out by Dr. I. W. Bailey to whom I am indebted for the examination of the stem.

As type of the genus I have selected *Huodendron tibeticum,* because this species represents the distinctive characters from *Styrax* and other allied genera in a more pronounced degree, particularly by the deeply divided style and by the absence of stellate or fascicled pubescence and also in the distinctly corymbose inflorescence.

For the loan of additional specimens supplementing the material in the herbarium of the Arnold Arboretum (A. A.), I am indebted to Dr. E. D. Merrill of the New York Botanical Garden (N. Y.), Dr. H. L. Mason of the University of California (U. Calif.) and to Sir William Wright Smith of the Royal Botanic Garden of Edinburgh (Edinb.).

I take pleasure in associating with this new genus the name of Dr. H. H. Hu, director of the Fan Memorial Institute of Peiping, one of the foremost and active Chinese botanists, who has contributed and is still contributing extensively to our knowledge of the flora of China.

Huodendron tibeticum (Anthony), comb. nov.

Styrax tibeticus Anthony in Not. Bot. Gard. Edinb. **15:** 245 (1927).

Arbor vel frutex 6–25 m. altus, ramis gracilibus teretibus vel apicem versus leviter complanatis glabris; folia alterna, sed interdum apicem ramulorum versus subopposita, decidua, papyracea, elliptico-ovata vel oblongo-ovata vel ovato-lanceolata, 6–11.5 cm. longa et 2.5–4 cm. lata, longe acuminata apice mucronulata, basi late cuneata, integra, nervis utrinsecus 5–9 utrinque leviter elevatis, costa apicem versus supra leviter

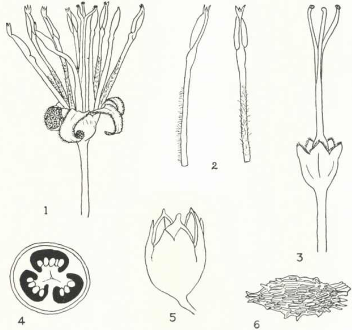


FIGURE 1. HUODENDRON TIBETICUM (Anth.) Rehd. 1. Flower. × 7. — 2. Stamens. × 8. — 3. Flower with petals and stamens removed. × 8. — 4. Cross-section of ovary. × 20. — 5. Capsule. × 10. — 6. Seed. × 35.

elevata basin versus plana, subtus manifeste elevata; petioli glabri, 5–10 mm. longi, supra leviter canaliculati. Inflorescentia glabra, corymboso-paniculata, terminalis 5–7 cm., lata, laterales cum pedunculo 1.5–3 cm. longo 4–8 cm. longa et 2.5–5 cm. lata; pedicelli graciles, 3–5 mm. longi, ut ramuli glanduloso-verruculosi; calycis tubus cupuliformis, glanduloso-verruculosus, 1 mm. longus, dentibus triangulari-ovatis dimidium tubum subaequantibus ciliolatis; petala valvata, lineari-oblonga, 6–7 mm. longa et 1–1.5 mm., lata, obtusiuscula, extus tomentosula, intus fere glabra, sub anthesi revoluta; stamina petiolis subaequalonga, filamentis 4–5 mm. longis intus triente inferiore excepto villosis extus glabris, antherae 1.25–1.5 mm. longae, glabrae, apice tridentato circiter 1 mm. longo, dente medio lateralibus plerumque breviore, styli in triente inferiore vel ad medium connati, graciles, glabri; discus glaber. Capsula pedicello plus minusve recurvo suffulta, ovoidea, 3 mm. longa, fusco-brunnea, subinfera; semina brunnea, circiter 1 mm., longa.

SOUTHEASTERN TIBET. Tsarong: Salween and Kiu-chiang divide, northwest of Si-chi-to, Lat. 28° 35′ N., Long. 98° 30′ E., alt. 10–11000 ft., *G. Forrest,* no. 21648, June 1922, "shrubby, 20–30 ft., flowers fragrant, white, in open thickets by streams" (holotype in herb. Edinb.); same locality, *G. Forrest,* no. 22882, Oct. 1922 (paratype in herb. Edinb.); Salween and Irrawaddi divide, near banks of Salween at Champutong, forests, alt. 7000 ft., *J. F. Rock,* no. 22020, May–July 1932, tree 70–80 ft. tall, flowers white (A. A., N. Y., U. Calif.); mountains west of Champutong, forests of upper Salween River, alt. 9000 ft., *J. F. Rock,* no. 22474, Oct. 1932 (A. A., N. Y., U. Calif.).

This species has a very restricted distribution and is apparently confined to the mountains of extreme southeastern Tibet between the headwaters of the Irrawaddi and Salween Rivers. In some of its characters, particularly by the deeply divided style and by the absence of stellate or fascicled pubescence is it farther removed from other styraceous genera than the more widely distributed *H. biaristatum.* The fruiting branch of this species has some resemblance to certain species of *Deutzia.*

Huodendron biaristatum (W. W. Sm.), comb. nov.

Styrax biaristatus W. W. Smith in Not. Bot. Gard. Edinb. **12:** 233 (1920).—C. E. C. Fischer in Kew Bull. Misc. Inform. **1933:** 365.

Frutex vel arbor 6–12 m. altus, ramis gracilibus hornotinis initio tomentosulis demum glabrescentibus, vetustioribus flavido-cinereis vel fusco-cinereis cortice demum rimoso vel fibroso vestitis. Folia alterna, papyracea, oblonga vel elliptico-oblonga vel obovato-oblonga, 8–17 cm. longa et 2.5–6 cm. lata, acuminata, basi cuneata, margine minute et remote denticulate vel integra, supra luteo-viridia, opaca, costa fasciculato-pilosula excepta glabra, subtus vix pallidiora, axillis saepe barbulatis exceptis glabra, costa supra leviter impressa subtus elevata, nervis utrinsecus 5–9 arcuatis margine anastomosantibus supra vix infra manifeste elevatis, venulis subtus elevatis; petioli 6–15 mm. longi, supra tantum vel undique fasciculato-pilosi. Inflorescentiae terminales et axillares, paniculatae, multiflorae, 3–10 cm. longae, ebracteolatae, cinereotomentellae; pedicelli 2–5 mm. longi; calyx cupuliformis, tomentellus, tubo 1–1.5 mm. longus, dentibus late triangularibus acutiusculis tubo brevioribus; petala imbricata, anguste oblonga, 6–9 mm. longa et 2–2.5 mm. lata, utrinque tomentella; stamina petalis subaequilonga, filamentis compressis utrinque dense pilosulis circiter 3 mm. longis, antheris glabris 2 mm. longis connectivo dorso puberulo in appendicem tridentatum vel rarius bidentatum elongata dentibus lanceolatis acutis medio plerumque minore; stylus staminibus paullo longior, crassus dense pilosulus, apice 3-lobata; ovarium semisuperum. Capsula ovoidea, resupinata, 4–5 mm. longa, cinereo-tomentella, in triente superiore sepalis persistentibus cincta; semina 1–1.25 mm. longa, flavo-fusca.

China. Yunnan: in thickets in ravines on the western flank of the Shweli-Salween divide, Lat. 25° 40′ N., alt. 9000 ft., *G. Forrest,* no. 18020, May 1919, "shrub 20–30 ft., flowers fragrant, creamy-yellow" (syntype in herb. Edinb.); side valleys of the Shweli-Salween divide, Lat. 25° N., alt. 8000 ft., *G. Forrest,* no. 17894, June 1919, "shrub 10–20 ft., flowers immature" (Edinb., A. A.); N'Maikha-Salween divide, at Ho-tou, in thickets and open forests, Lat. 25° 55′ N., alt. 7–8000 ft., *G. Forrest,* no. 18400, Aug. 1919, "shrub 12–18 ft., in fruit" (syntype in herb. Edinb.); same locality, *G. Forrest,* no. 18833, Nov. 1919 (syntype in herb. Edinb.); Mengtze, S. E. mountain forests, 6000 ft., *A. Henry,* no. 10764 "tree 15 ft." (syntype in herb. Edinb., A. A., N. Y.); Mengtze, *A. Henry,* no. 13662A, "shrub 10 ft." (syntype in herb. Edinb.; A. A., N. Y.); south of Red River, *A. Henry,* no. 13662, "tree 40 ft." (syntype in herb. Edinb.; A. A.); Shweli-Salween divide, Lat. 25° 10′ N., Long. 98° 50′ E., alt. 9000 ft., in open thickets and forests, *G. Forrest,* no. 26108, Dec. 1924, "tree 30–40 ft." (Edinb., N. Y.); without precise locality, *G. Forrest,* no. 26108, 1924–25 (Edinb., N. Y.). Kweichou: Waichai, Tuh-shan, near border of Kwangsi, alt. 330 m., in densely shaded ravine, *Y. Tsiang,* no. 6686, Aug. 25, 1930, "tree 6 m., diam. of trunk 12 cm., bark pale gray" (A. A.). Kwangsi: Chin-fong, Lin-yuin-hsien, valley forest, alt. 1300 m., *Steward & Cheo,* no. 336, May 6, 1933, "tree 7 m., flowers white, fragrant" (A. A., N. Y.); Ta-tse-shan, Yung-hsien, forest, alt. 540 m., *Steward & Cheo,* no. 843, Aug. 21, 1933, "tree 9 m., fruit gray" (A. A., N. Y.).

Burma: Myitkyina Distr., Htangan, 3100 ft., *Sukoe* per *C. E. Parkinson,* no. 9197; Pyet Pass, 7200 ft., *Sukoe* per *C. E. Parkinson,* no. 10115 (ex C. E. C. Fischer, l. c.).

Tonkin: route de Lao-kay à Chapa, alt. 1500 m., *A. Petelot,* no. 3803, Aug. 1930 (N. Y.); massif du Fan-tsi-pou, chemin du col de Lo-qui-ho, environs de Chapa, alt. 1400 m., *A. Petelot,* no. 4373, Sept. 1931 (N. Y.).

This species is readily distinguished from *H. tibeticum* by the pubescent inflorescence, the thicker texture of the leaves, the pubescent stout style 3-lobed only at the apex, the shorter filaments pubescent on both sides, the broader narrowly imbricate petals pubescent on both sides and the tomentulose capsules. The fact that the petals in one species of this genus are valvate and in the other imbricate is not unusual in Styracaceae, for both kinds of aestivation are found in *Styrax*. The stamens are mostly 3-toothed at the apex, but the middle one is often shorter than the lateral ones; two teeth, as implied by the specific epithet, are only occasionally found.

The leaves of *H. biaristatum* show some variation in dentation, texture, pubescence and in the number of veins. The Forrest specimens have remotely denticulate leaves and are of rather thin texture, the leaves of the Henry specimens are occasionally furnished with minute denticulations reduced to a mucro, but are mostly entire like the other specimens and like those are of thicker chartaceous or subcoriaceous texture. The midrib is usually impressed and puberulous like the petiole, but in Petelot 4373 from Tonkin the midrib is glabrous except slightly puberulous toward the base and slightly elevated and quite glabrous toward the apex, also the lateral veins are slightly elevated and number about 5 pairs, while the leaves of the other specimens have mostly 6 or 9 pairs; by these characters this Petelot specimen approaches the following variety and connects it with the typical form.

Huodendron biaristatum var. **parviflorum** (Merrill), comb. nov.

Styrax parviflora Merrill in Jour. Arnold Arb. **8**: 15 (1927).

A typo recedit praecipue ramulis foliis petiolisque glabris foliis magis coriaceis integris nervis utrinsecus 4–6, costa media nervisque supra glabris et elevatis, venulis subtus minus conspicuis.

CHINA. Kwangtung: Lung-t'au Mountain, near Iu, in forest, Canton Christian College, nos. 12070 (holotype in hb. N. Y.; A. A.) and 12349 (paratype in hb. N. Y.; A. A.).

The flowers and fruits of the Kwangtung specimens, as far as can be judged from the rather poor material, are identical with those of typical *H. biaristatum* and the difference in the leaves does not seem sufficient to separate the Kwangtung form as a distinct species, considering the fact that the leaves of *H. biaristatum* show considerable variation and transitions to this variety.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

HUODENDRON TIBETICUM (Anth.) Rehd.

HUODENDRON BIARISTATUM (W. W. Sm.) Rehd.

STUDIES IN THEACEAE, I
EURYA SUBGEN. TERNSTROEMIOPSIS

Clarence E. Kobuski

With plate 153

During the past year the author has been making a survey of the Old World Theaceae, starting with a critical study of the genus *Eurya*.

The genus as a whole has presented some rather difficult problems in specific delimitation and in synonymy which cannot be settled until more ample material or photographs of types deposited in various foreign herbaria can be had.

In Szyszylowicz's treatment,[1] *Eurya* comprises three sections: Cleyera (DC.), Freziera (Sw.) and Proteurya Szysz. In 1896, Urban[2] separated *E. sandwicensis* from Proteurya and made it the type of the new genus, *Ternstroemiopsis*. The following year Engler[3] united *Ternstroemiopsis* with *Eurya* as a new subgenus, elevating, at the same time, the three sections of Szyszylowicz to subgeneric rank. At present, however, *Eurya* is generally considered as containing but two subgenera, Proteurya and Ternstroemiopsis, while *Cleyera* and *Freziera* represent distinct genera, the former Asiatic and American, the latter exclusively American.

In this paper, the subgenus Ternstroemiopsis is considered. This is distinguished from the subgenus Proteurya by the spiral arrangement of its leaves, the thick glandular sepals, fleshy petals and stamens whose anthers are twice as long as the filaments. Proteurya is characterized by two-ranked leaves, petals more or less membranous and anthers as long as or shorter than the filaments. Geographically also Ternstroemiopsis is distinct being confined solely to the Hawaiian Islands while Proteurya, although found in nearly all the Pacific islands and Asia, does not invade the Hawaiian group with a single species.

The institutions from which material for this study was borrowed along with the abbreviations used in this paper, are as follows: herbarium of the Arnold Arboretum of Harvard University (AA), herbarium of Otto Degener (D), Gray Herbarium of Harvard University (Gr), herbarium of the New York Botanical Garden (NY).

[1]Szyszylowicz in Engler & Prantl, Nat. Pflanzenfam. III. **6**: 189 (1893).
[2]Urban in Ber. Deutsch. Bot. Gesell. **14**: 49 (1896).
[3]Engler in Engler & Prantl, Nat. Pflanzenfam. Nachtr. **1**: 247 (1897).

KEY TO THE SPECIES AND VARIETIES

A. Leaves subcordate or truncate at base, obtuse or rounded at apex
  B. Small trees or erect shrubs ....1. *E. sandwicensis*
  BB. Prostrate shrubs ....1a. *E. sandwicensis* var. *prostrata*
AA. Leaves cuneate at base, acute at apex
  C. Leaves 3.5–4.7 cm. long, 1.2–1.7 cm. wide.....2. *E. Degeneri*
  CC. Leaves either larger or smaller than C
    D. Leaves 5.3–8.7 cm. long, 2.5–3.5 cm. wide
    2a. *E. Degeneri* f. *grandifolia*
    DD. Leaves 3.0–4.5 cm. long, 0.7–1.2 cm. wide
    2b. *E. Degeneri* f. *stenophylla*

1. **Eurya sandwicensis** A. Gray, Bot. U. S. Expl. Exped. 1838–1842, **1**: 209 (1854). — H. Mann in Proc. Amer. Acad. Arts Sci. **7**: 156 (Enum. Hawaiian Pl.) (1867); Mem. Boston Soc. Nat. Hist. **1**: 534, 539 (1869). — Hillebrand, Fl. Haw. Isl. 41 (1888). — Drake del Castillo, Ill. Fl. Ins. Maris Pacif. 117 (1890). — Szyszylowicz in Engler & Prantl, Nat. Pflanzenfam. III, **6**: 190 (1893). — A. A. Heller in Minn. Bot. Studies, **1**: 856 (1897). — Rock, Indig. Trees Haw. Isl. 308 (1913). — Melchior in Engler & Prantl, Nat. Pflanzenfam. Ed. 2, **21**: 147 (1925).

Eurya sandwicensis A. Gray var. *sessilifolia* A. A. Heller in Minn. Bot. Studies, **1**: 856 (1897), as a synonym.

Ternstroemiopsis sandwicensis Urban in Ber. Deutsch. Bot. Ges. **14**: 49 (1896).

Small trees, 5–6 m. in height, occasionally shrubby in higher altitudes, 2–3 m.; branches crowded with leaves, ultimate branchlets strigose; leaves oblong, elliptical or obovate, coriaceous, glabrous, occasionally strigosely hairy on midrib, 4.5–9.0 cm. long, 1.5–3.7 cm. wide, on short petioles 2–3 mm. long, sometimes subsessile, obtuse or rounded at the apex, more or less cordate, occasionally truncate at the base, closely serrulate with inflexed mucronulate teeth, veins and veinlets finely reticulate beneath, reddish brown in color; flowers solitary, occasionally two in axils, nodding, ebracteolate, pedicels approximately 5 mm. long; calyx purplish brown, quite coriaceous, subtended by two small unequal bracts; sepals five, unequal, 3–4 mm. long, persistent, suborbicular, thick in central portion, membranous, lighter in color and slightly glandular on margin, occasional strigose hairs on external surface; corolla pale yellow or cream-color, imbricated; petals five, obovate, 5–6 mm. long, united at base, somewhat fleshy in central portion; stamens in staminate flowers 10–15, slightly adnate to base of corolla, filaments distinct, half as long as the oblong mucronate anthers; staminodia in pistillate flowers, five sometimes six, 2–3 mm. long; pistil having three or occasionally four styles, sometimes connate nearly to stigma, usually divided; stigmas three (or four); ovary glabrous, 3-celled, axial placentation; fruit a globose berry, 7–10 mm. across, dark blue-black, many-seeded; mature persistent, subcordate calyx-lobes 8 mm. long, 7.5 mm. across at widest portion, lobes at base lighter in color and more membranous.

Specimens Examined:

Hawaiian Islands. O a h u : Nuuanu-Pali, *U. Faurie*, no. 284, October 1909 (AA); on mountains behind town of Honolulu, *Wm Rich*, collected in 1840 (type) (Gr, NY); exact locality lacking, *M. J. Remy*, no. 562, collected 1851–1855 (Gr); data lacking, *M. J. Remy* (NY); exact locality lacking, *H. Mann & W. T. Brigham*, no. 524, collected 1864–1865 (Gr, NY); exact data lacking, *W. Hillebrand* (Gr); precise data lacking, *C. Gaudichaud*, collected probably 1836 (Gr); in rain-forest from Kahana church up ridge to summit of mountain southeast of Kahana Bay, *O. Degener*, no. 8680, July 3, 1932 (AA, D); Waipio, Waiawa Ridge, on Dicranopteris-covered ridge, *O. Degener & Dr. C. L. Shear*, no. 9838, March 5, 1928 (tree 15 ft.; fruit inky blue-black) (AA, D); open forest in Dicranopteris tangle, Manana Gulch ridge, *O. Degener, W. Bush & K. K. Park*, no. 8679, October 2, 1932 (AA, D); on and near the summit of Konahuanui, *A. A. Heller*, no. 2240, May 2, 1895 (NY); lower slopes of Konahuanui, above Manoa, *A. A. Heller*, no. 2311, May 13, 1895 (AA, NY, Gr); ridge west of Kalihi valley, *C. N. Forbes*, no. 1483.O, March 17, 1910 (NY); ridge between Pololo and Waialue iki, *C. N. Forbes*, no. 2408.O, January 30, 1917 (NY); Koolau Mts., Pumaluu, *J. F. Rock*, no. 627, December 3–10, 1908 (Gr); Pumaluu, *J. F. Rock*, no. 843, December 1908 (NY); precise data lacking; *J. F. Rock*, collected 1910 (Gr). K a u a i : Mt. Waialeale, alt. 5200 ft., *J. F. Rock*, no. 8864, October 20, 1911 (Gr, NY); along stream-beds, Kaholuamano, *J. F. Rock*, no. 5499, September 1909 (Gr, NY); Kaholuamano, *J. F. Rock*, collected March 3–10, 1909 (NY); Hanapepe, *U. Faurie*, no. 286, December 1909 (AA). M a u a i : Honakahau Drainage Basin, *C. N. Forbes*, no. 421.M, September 25–October 17, 1917 (NY). H a w a i i : Kilauea, near fern-forest, *O. Degener*, no. 8678, November 10, 1929 (AA, D).

In the whole genus this species is probably the most outstanding. Although confined to the Hawaiian group, it has been found in nearly all the islands from which material has been collected. The flowers and fruit are nearly twice the size of any other species. Along with this size character can be mentioned the distinct reddish reticulate veining of the lower surface of the leaf and the subcordate or truncate base of the leaf.

The collections of Otto Degener made during the last few years on the various islands of the group had great influence in the decision finally to place the majority of Hawaiian specimens in this species. His specimens were so ample that it was possible to make two and even three sheets of each for the herbarium of the Arnold Arboretum. These sets of material show great gradation in leaf-size — a character which might cause some, especially in this genus, to describe new species.

Faurie's specimen, no. 286, according to the collector, was made at Hanapepe, Oahu. This probably is a mechanical error made in transferring the field notes to the herbarium label. Hanapepe is on the island of Kauai and the collection date of no. 286 agrees with other material collected by Faurie on Kauai.

1a. **Eurya sandwicensis** A. Gray var. **prostrata**, var. nov.

A typo recedit habitu prostrato et foliis remotis.

SPECIMENS EXAMINED:

HAWAIIAN ISLANDS. Molokai: At edge of windswept forested pali, Ohialele Pali, *O. Degener*, no. 8676 (type, AA) May 10, 1928 (more or less trailing along ground with branches sometimes eight feet long; flowers yellow, difficult to distinguish plant from *Vaccinium*) (AA, D); Pelekunu trail, *C. N. Forbes*, no. 249.Mo, July 1912 (NY).

A quotation from a recent letter from Otto Degener, the collector of the cited type throws considerable light on this variety and the species *E. sandwicensis*: — "*Eurya*, as I have found it on Oahu, grows as an erect small tree with very dense foliage. It is rare, and where found, usually grows in openings in the lower forest, covered over with *Gleichenia*. Rainfall would be moderate."

"The Molokai specimen I have found nowhere except in a typical dense extremely rainy rain-forest, and curiously enough, not anywhere in that region but only on the brink of a cliff extending for several miles. In short, it grows on the very "backbone" of Molokai where the rain and fog drive violently over the mountain crest. I collected five months on Molokai and do not remember seeing any *Eurya* except in that one type of locality. The rain-forest reaches up to this cliff and it is among the shrubs and small trees immediately overlooking the cliff that the *Eurya* is to be found. The plant sprawls rather than creeps, producing slender branches of unusual length—possibly 12 feet—with its leaves spaced far apart."

The collector remarked further that at first on seeing sterile plants, he thought this variety to be a low-growing *Vaccinium*. However, later on finding flowering material, he discovered it to be an *Eurya*. He suggested it as a variety or possible new species.

The second cited specimen, Forbes no. 249.Mo, resembles the type in the remoteness of leaves. However the habit of the plant was not given by the collector, but it appears to be prostrate.

2. **Eurya Degeneri,** spec. nov.; a *E. sandwicensi* A. Gray foliis ellipticis 3.5–4.7 (2.5–6.5) cm. longis, 1.2–1.7 (1.2–2.2) cm. latis, apice acutatis et emarginatis, basi cuneatis recedit.

Branches covered with leaves especially at ends, ultimate branchlets sparsely strigose; leaves elliptic, coriaceous, 3.5–4.7 (2.5–6.5) cm. long, 1.2–1.7 (1.2–2.2) cm. wide, acute at the apex, emarginate, cuneate at the base, closely serrulate with inflexed mucronulate teeth, conspicuously reticulate on under surface, veins and veinlets reddish brown in color, especially near base of leaf where color spreads into the leaf; petiole 3 mm. long; mature flowers unknown, bud resembling *E. sandwicensis* sufficiently in coriaceous character and color of calyx with occasional strigose hairs, character and number of stamens and corolla to show it to be typical of the genus and closely related to *E. sandwicensis;* berry (probably not mature) blue-black, 5 mm. across with the persistent styles separate to near the base, 3-celled, axial placentation, many-seeded.

Specimens Examined:

Hawaiian Islands. Kauai: open forest, Waineke swamp Kokee, *O. Degener,* no. 8675 (type AA) July 1, 1926 (AA, D); high plateau of Waimea, Halemanu to Kaholuamano, *J. August Kusche,* nos. 28, 139, 140, collected in 1919 (AA); Kilauea, *U. Faurie,* no. 285, January 1910 (AA); west side Waimea Drainage Basin, Kanaikinaua, *C. N. Forbes,* no. 1016.K, July 3–August 18 (1917) (AA, NY).

This species is very closely allied to *E. sandwicensis*. The leaf characters are most distinctive between the two species. *Eurya Degeneri* has elliptical leaves, cuneate at the base, acute and emarginate at the apex. On the other hand, *Eurya sandwicensis* has leaves which are oblong or elliptic, subcordate or truncate at base and rounded or obtuse at the apex. *Eurya Degeneri* and its varieties are confined to the island of Kauai, while *Eurya sandwicensis* is found on nearly all the islands including Kauai.

Otherwise these two species belonging to this distinctive section of the genus are very similar. This is especially true in flower and fruit characters. Although the mature flowers and fruit were not available in *E. Degeneri,* the material such as it is shows conclusively that there is a great resemblance.

It is a pleasure to dedicate this species to Otto Degener of Hawaii, whose recent collections from the islands are extremely fine and whose material of *Eurya* aided tremendously in clearing up this section.

2a. **Eurya Degeneri** Kobuski forma **grandifolia** (Wawra), comb. nov.

Eurya sandwicensis A. Gray β var. Hillebrand, Fl. Hawaiian Isl. 41 (1888). — Drake del Castillo, Ill. Fl. Ins. Maris Pacif. 117 (1890).

Eurya sandwicensis A. Gray var. *grandifolia* Wawra in Flora, **56**: 168 (1873). — J. F. Rock, Indig. Trees Haw. Isl. 308 (1913).

A typo recedit foliis amplioribus, 5.3–8.7 cm. longis, 2.5–3.5 cm. latis.

Specimen Examined:

Hawaiian Islands: Kauai: Wainiha, *U. Faurie*, no. 298, January 1910 (AA).

This large-leaved form has seemed rather evasive to most collectors. Hillebrand, Del Castillo, Wawra and Rock have made reference to it in literature. The first three in their treatments were working with a single specimen, that of Wawra collected at Kealia on the island of Kauai. Incidentally we have only the single specimen collected by Faurie (no. 298) collected at Wainiha. The Faurie specimen was collected on the north coast of Kauai while Wawra made his collection on the west coast.

Rock, although having collected considerably on the islands, never encountered this large-leaved form. However, he collected the narrow-leafed form cited next.

These two forms like the species have distinctly cuneate leaf-bases and acute apices. Their variation from the species lies chiefly in the leaf size. Again, like the species, they are found only on the island of Kauai.

2b. **Eurya Degeneri** Kobuski forma **stenophylla,** forma nov.

A typo recedit foliis minoribus angustioribusque, 3.0–4.5 cm. longis, 0.7–1.2 cm. latis.

Specimen Examined:

Hawaiian Islands. Kauai: precise locality and date of collection lacking, *J. F. Rock*, no. 17274 (type) (AA).

Unfortunately, the Rock specimen cited above is sterile and was placed in this genus under *E. sandwicensis* with some hesitation by an earlier student. At first, I was quite dismayed because I felt that it belonged to a species other than *E. sandwicensis*, but because of the lack of flowers or fruit I hesitated to describe it as new. It was not until more material came to my attention that its true affinity with *E. Degeneri* was discovered.

Herbarium, Arnold Arboretum,
Harvard University.

EURYA DEGENERI Kobuski

TWO NEW SPECIES OF CRATAEGUS FROM MISSOURI

Ernest J. Palmer

With two text figures

Crataegus hannibalensis, sp. nov. Arbor 6–8 m. alta vel frutex arborescens 4–6 m. altus, ramulis annotinis gracilibus vel paulo validis glabris fusco-viridibus, spinis numerosis. Folia ovata vel obovata vel oblongo-ovata, serrata, apice acuta, basi cuneata in petiolum 8–12 mm. longum attenuata, 2.5–4 cm. longa, 2–3 cm. lata, surculorum validorum ad 5–6 cm. longa, 4–5 cm. lata, matura firma, crassa, glabra, dentata, nervis superne manifeste impressis. Inflorescentiae glabrae, laxae, plerumque 5–16-florae; flores 14–16 mm. lati, staminibus circiter 10, stylis 1–3 plerumque 2; sepalis lanceolatis integris vel sparse dentatis. Fructus ovoideus, obovoidea-oblongus vel rare subglobosus, 8–10 mm. longus, 7–8 mm. latus, firmus, viridis denique rubro-luteus raro pruinosus, seminibus 2–3 plerumque 2 ovalibus dorso sulcatis.

A tree 6–8 m. tall, or sometimes an arborescent shrub 4–6 m. tall, with intricate ascending or horizontal branches and slender to stoutish flexuous branchlets, glabrous and olive-green or olive-brown at the end of the first season, usually armed with numerous stout, straight or curved purplish thorns 3–6 cm. long. Bark gray or pale brown, slightly scaly. Leaves obovate, oblong-obovate or oval, acutely pointed, short-acuminate or rarely rounded at apex, cuneate at the base and attenuate into the short 8–12 mm. long petioles, sharply serrate usually nearly to the base, glabrous, firm to subcoriaceous at maturity, yellowish-green above and slightly paler beneath, with slender but prominent mid-rib and 5–7 pairs of parallel veins elevated on the under surface and conspicuously impressed above, those of the fruiting branches mostly 2.5–4 cm. long and 2–3 cm. broad, on vigorous sterile shoots often 5–6 cm. long and 4–5 cm. broad, and with margins coarsely serrate or dentate. Flowers in loose glabrous compound 5–16-flowered corymbs, 14–16 mm. in diameter; pedicels slender, often glandular, 1–2 cm. long; stamens about 10; anthers in specimens examined pale yellow; styles 1–3, usually 2; calyx-lobes lanceolate, entire or slightly serrate towards the base, glabrous without and glabrous or slightly villous within. Fruit oval, oblong-obovoid or rarely nearly globose, 8–10 mm. long, 7–8 mm. thick, hard and green until late in the season, turning dull red or orange-red and becoming mellow when fully ripe late in September, rarely with a slight pruinose bloom. Fruiting calyx sessile or slightly elevated, with a broad shallow cavity; calyx-lobes often persistent and appressed, flesh thin; nutlets 1–3 but usually 2, relatively large, oval or elliptic in outline, blunt or rounded at the ends, and with broad shallow ridges and grooves on the dorsal surface.

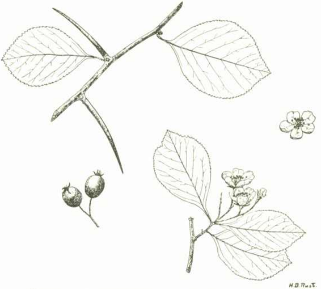


FIGURE 1. CRATAEGUS HANNIBALENSIS E. J. Palmer. × 2/3

Thickets and borders of woods, in fertile soil, on limestone hills or often along bluffs and banks of streams. *Crataegus hannibalensis* is rather abundant in northern Missouri and southeastern Iowa, and it is probably more widely distributed. A specimen collected in western Ohio seems to belong here.

This species is conspicuous and easily distinguishable on account of its rather large (for the group) yellowish-green leaves with deeply impressed veins, the pale olive branchlets and comparatively small oval or oblong fruit. In their deeply impressed veins the leaves resemble somewhat certain species of the Punctatae group, but the characters of the fruit and flowers and the entire absence of pubescence seem to place it clearly in the Crus-galli group. The type specimen is in the herbarium of the Arnold Arboretum.

Missouri: Hannibal (Marion Co.), *John Davis*, no. 177, Oct. 6, 1911, May 14, Oct. 10, 1912, Oct. 13, 1913; *E. J. Palmer*, no. 20381, Sept. 7, 1921; no. 20382 (type), Sept. 7, 1921; no. 20405, Sept. 8, 1921; no. 22337, Oct. 24, 1922; south of Hannibal (Ralls Co.), *John Davis*, no. 1645, Oct. 4, 1916; Eolia Pike Co., *John Davis*, no. 25, Sept. 30, 1912; no. 2147, Sept. 20, 1913; no. 2149, Sept. 22, 1913; no. 2153, Sept. 21, 1913; Dumas, Clark Co., *B. F. Bush*, no. 10139, July 28, 1923; between Renick and Clark, Macon Co., *E. J. Palmer*, no. 35943, May 21, 1929; between Lancaster and Downing, Schuyler Co., *Palmer & Steyermark*, no. 40970, June 30, 1933; Mill Grove, Mercer Co., no. 41270, July 4, 1933; Shelbina, Shelby Co., no. 40865, June 28, 1933; Eagleville, Harrison Co., no. 41340, July 6, 1933; St. Francois Co., *C. S. Sargent*, Oct. 5, 1899. Ohio: Springfield, *R. E. Horsey*, no. 338, May 17, Oct. 25, 1915. Iowa: Keokuk, Lee Co., *E. J. Palmer*, no. 21829, Sept. 6, 1922; no. 21831, Sept. 6, 1922; no. 40595, June 25, 1933; Burlington, Des Moines Co., *E. J. Palmer*, no. 21800, Sept. 6, 1922.

Crataegus Danielsii, sp. nov. Arbor 6–7 m. alta vel frutex arborescens 4–6 m. altus. Folia oblongo-ovata, elliptica vel rhombica, grosse serrata, saepe supra medium obscure inaequaliter incisa, apice acuta vel acuminata, basi cuneata in petiolum gracillimum 8–15 mm. longum attenuata, matura papyracea sed firma, superne glabra, infra paulo villosa, 2.5–4 cm. longa, 1–2.5 cm. lata, ramulorum sterilium ad 5–6 cm. longa 3–5 cm. lata. Inflorescentiae laxae, ramosae, paulo villosae, 6–15-florae, bracteis linearibus glanduloso-serratis. Flores 14–16 mm. lati, staminibus circa 12–15, antheris rubicundis, stylis 2–4, plerumque 3, sepalis lineari-lanceolatis integris vel paulo glanduloso-serratis. Fructus subglobosus, 8–12 mm. latus, maturus rubicundus; seminibus 2–3 dorso sulcatis.

A tree 6–7 m. tall, or sometimes an arborescent shrub 4–6 m. tall, with erect or ascending intricate branches and slender branchlets, more or less villous when young in the typical form, and armed with slender thorns 2–3 cm. long. Leaves oblong-elliptic, oblong-obovate or narrowly rhombic in outline, sharply and irregularly serrate, often obscurely incised above the middle with one or more pairs of shallow lobes or unsymmetrical with one or more odd lobes, pointed or acuminate at the apex, attenuate at the base into the slender 1–1.5 cm. long petioles, usually red as they unfold, and then villous on both surfaces, thin but firm at maturity, glabrous above and more or less villous along the veins beneath, those of the fruiting branches mostly 2.5–4 cm. long and 1–2.5

cm. broad, and up to 5–6 cm. long and 3–5 cm. wide on vigorous sterile shoots; petioles usually sparsely villous, sometimes with a few scattered glands. Flowers 14–16 mm. in diameter, in loose slightly villous compound corymbs; pedicels slender, 8–15 mm. long, glabrous or sparsely villous; bracts numerous and conspicuous, narrowly linear, finely glandular-serrate on the margins; stamens usually 12–15; anthers pink or rose-color in specimens examined; styles 3–4, usually 3; calyx-lobes linear-lanceolate, entire or somewhat glandular-serrate towards

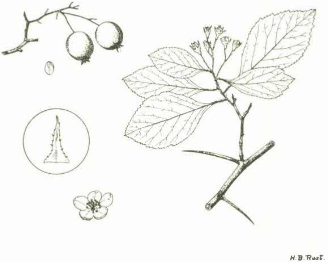


FIGURE 2. CRATAEGUS DANIELSII E. J. Palmer. × 2/3

the base. Fruit subglobose, 8–12 mm. in diameter, pruinose, becoming dull crimson when ripe in late September or October, flesh thin and hard; nutlets 2–3, usually 3, oblong, rounded at the ends and with broad shallow grooves and ridges on the dorsal surface.

Limestone glades and hillsides in the vicinity of Columbia, Missouri.

Several trees referable to this species have been found, all so far as known within a few miles of the type locality. The extremely local distribution, the variable and often asymmetrical outline of the leaves and the sparse and variable pubescence, nearly or quite absent in some specimens, all suggest the possibility of a hybrid origin, and it may have originated as a cross between *Crataegus crus-galli* and *C. verruculosa*, both of which are growing in the immediate vicinity. The specific name is for Dr. Francis Daniels, author of a Flora of Columbia, Missouri, and vicinity, who first collected it there.

Missouri: near Columbia, Boone Co., Hawthorn glades, north of Columbia, *Francis Daniels*, Sept. 26, 1902; May 3, 1903; *W. H. Rickett*, no. 8 (Crat. #8), 50 yds. west of Balanced Rock, May 3, 1931; no. 36 (Crat. #35), north side of Walnut St., west of highway 63, May 6, 1931; *Francis Drouet* (Crat. #8, W. H. R. #107), 50 yds. west of Balanced Rock, Oct. 4, 1931; (Crat. #8, W. H. R. #69), west of Balanced Rock, Sept. 15, 1931; (Crat. #35, W. H. R. #71), north side of Walnut St., west of highway 63, Sept. 22, 1931; *E. J. Palmer*, no. 39265 (type), May 4, 1931; near Hinton, Boone Co., *W. H. Rickett*, no. 40 (Crat. #39), 4.4 miles north of Hinton, May 17, 1931; no. 43 (Crat. #42), 1.3 miles south of Hinton, May 17, 1931; 84 (Crat. #54), 3.6 miles north of Hinton, Sept. 31, 1931; no. 86 (Crat. #56), north of Hinton, Sept. 30, 1931; no. 88 (Crat. 42), 1.3 miles south of Hinton, Sept. 30, 1931; no. 91 (Crat. #43), 2.3 miles south of Hinton, Sept. 30, 1931. Type in the herbarium of the Arnold Arboretum. All other specimens examined are in the herbarium of the University of Missouri.

In a few specimens examined the young foliage, branches, and inflorescence are quite glabrous and in others there is only the slightest trace of pubescence in the form of a few scattered hairs on either the pedicels, petioles or veins of the leaves. This may be distinguished as *Crataegus Danielsii* f. **glabra**, f. nov.[1]

Thickets, limestone hills and glades, Boone County, Mo. With the type.

W. H. Rickett, no. 39 (Crat. #38), 4.4 miles north of Hinton, Mo., May 17, 1931, in the herbarium of the University of Missouri, may be taken as the type of this form.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

[1]A typo differt ramulis foliis inflorescentiis glabris vel raro leviter pilosis.

NEW HYBRIDS FROM THE ARNOLD ARBORETUM

Edgar Anderson and Alfred Rehder

× **Akebia pentaphylla** (Mak.) Makino in Tokyo Bot. Mag. **16:** 30 (1902) = *A. quinata* Dcne. × *trifoliata* (Thbg.) Koidz.

Akebia trifoliata var. *pentaphylla* Makino in Tokyo Bot. Mag. **5:** 329 (1891).

Artificial hybrids between *Akebia trifoliata* Koidz. and *A. quinata* Dcne. were produced at the Arnold Arboretum in 1932 by Dr. Karl Sax.[1]

Though they have not yet flowered the hybrid seedlings have now reached a stage where their intermediate character is clearly evident and is in close agreement with Makino's description (l. c.) of × *A. pentaphylla,* a putative hybrid widely distributed in Japan. The hybrids, on the whole, resemble *A. trifoliata* somewhat more closely than they do *A. quinata*. As yet many of the leaves are three-foliolate, although leaves with four and five leaflets have been produced. It is of interest that Makino originally considered × *A. pentaphylla* as a variety of *A. trifoliata* (l. c.). In this connection one might speculate as to the origin of *A. trifoliata* Koidz. var. *australis* (Diels) Rehd. Diels[2] in describing the variety commented on its extreme variability, and it occurs in a region where both *A. trifoliata* and *A. quinata* are native. Furthermore, it is intermediate between the two species in both leaf and flower, though resembling *A. trifoliata* more closely. It seems not impossible that it has resulted through extensive hybridization between *A. trifoliata* and *A. quinata* in a region where the former is relatively more abundant.

It should be remembered that the consequences of hybridization between two species may be quite different in different parts of their ranges, depending upon the relative frequency of the two species, the presence of polyploid races within either parent, the adaptability of the hybrid to local conditions, etc. Such matters are usually highly speculative. The production of an artificial hybrid will make it possible, ultimately, to study such questions experimentally in the genus *Akebia*.

E. A.

Prunus Juddii E. Anderson, hybr. nov. = *P. Sargentii* Rehd. ♀ × *yedoensis* Mats. ♂.

[1]Arnold Arb. Bull. ser. iv. **2:** 17–20 (1934). — They are growing in the Arboretum under no. 624–32 and specimens collected June 3, 1935 are preserved in the herbarium.

[2]Bot. Jahrb. **29:** 344 (1900).

Intermedia inter parentes, et ab utroque differt praecipue inflorescentiis 2–6-floris breviter racemosis et breviter pedunculatis, calycis lobis sparse et leviter glanduloso-serratis, stylo basi sparse piloso.

Growing in the Arnold Arboretum under no. 22489 and type specimens collected May 5 and 10 and June 3, 1935, are preserved in the herbarium.

An upright tree with spreading branches. Branchlets glabrous. Leaves ovate, acuminate, doubly serrate, dull brownish green when unfolding, glabrous throughout. Flowers before the leaves in very short-peduncled racemes of two to six, subtended by greenish bracts. Pedicels with weak scattered hairs at the base. Petals oblong, white or whitish, flushed with deep rose pink (Ridgway). Calyx-tube cylindric to sub-urceolate, glabrous. Calyx-lobes weakly and irregularly glandular-serrate. Style with scattered hairs at the base. Fruit black.

Among the seedlings of *Prunus Sargentii* Rehd. (*Prunus serrulata* Lindl. var. *sachalinensis* [F. Schmidt] Mak.) which have been raised from the original trees at the Arnold Arboretum were certain plants which are evidently hybrids between that species and other cherries which were flowering at about the same time. In the case of one of these specimens the evidence for its exact parentage is so clear and the hybrid tree promises to be of such horticultural importance for New England that it seemed desirable to provide the hybrid with a scientific name.

I take pleasure in naming the hybrid after the propagator for the Arnold Arboretum, Mr. W. H. Judd, whose precise record of the material which has passed through his department is of great scientific importance.

The hybrid originated in 1914 at the Arnold Arboretum as a seedling of one of the original trees of *Prunus Sargentii* raised from seed sent from Japan by Dr. W. S. Bigelow in 1890. *Prunus yedoensis* was acquired in 1902 and for many years a large specimen stood adjacent to *Prunus Sargentii*, no. 5777. Since their flowering dates usually overlapped it is not at all surprising that cross-fertilization should have taken place. Mr. Edwin L. Hillier of the West Hill Nurseries, Winchester, England, writes me that he has obtained similar hybrids from seed sent him from the Arnold Arboretum. Since seed of both *Prunus yedoensis* and *P. Sargentii* have been distributed very widely for a number of years by the Arnold Arboretum, it is quite possible that the hybrid may have turned up in a number of nurseries and gardens.

× *Prunus Juddii* has proved hardy during the last two phenomenally cold winters though it is planted at the edge of one of the coldest spots in the Arnold Arboretum. It furthermore holds its flowers longer than does *P. Sargentii* and is a thrifty quick-growing tree. From *P. Sargentii* it can most easily be distinguished by the greener young leaves, by the scattered hairs at the bases of the style and the pedicel, and by the glandular serrations of the calyx. From *P. yedoensis* it can be distinguished by its brighter flowers and by its glabrous calyces and leaves. A more complete comparison of the hybrid and the parental species is given in Table I.

TABLE I. COMPARISON OF × PRUNUS JUDDII WITH ITS PARENTS

P. yedoensis	× *P. Juddii*	*P. Sargentii*
branches spreading to horizontal	branches spreading	branches upright
leaves greenish when unfolding	leaves dull brownish green when unfolding	leaves bright bronze green when unfolding
flowers in 2–6-flowered short-peduncled racemes	flowers in 2–4-flowered very short peduncled racemes	flowers in sessile or sub-sessile clusters
pedicels finely pubescent	pedicels with weak scattered hairs at the base	pedicels glabrous
petals broadly oblong, nearly white	petals oblong, flushed with rose pink	petals narrowly oblong, typically bright rose pink
calyx tube urceolate-cylindric, finely pubescent	calyx tube sub-urceolate, glabrous	calyx tube cylindric-campanulate, glabrous
calyx-lobes strongly glandular-serrate	calyx-lobes weakly and irregularly glandular serrate	calyx-lobes entire
style pubescent	style with scattered hairs at the base	style glabrous

Since it has not been found wild, ***Prunus yedoensis*** has itself been thought to be a hybrid between ***Prunus Lannesiana*** and ***Prunus subhirtella***.[1] The fact that it comes true from seed[2] makes this hypothesis less likely, though such true-breeding hybrids are not unknown in the genus ***Prunus***.[3]

E. A.

× **Viburnum Juddii** Rehder, hybr. nov. = *V. Carlesii* Hemsl. ♀ × *bitchiuense* Mak. ♂.

A *Viburno Carlesii* praecipue differt foliis supra minus dense pilosis, petiolis paullo brevioribus, corymbo laxiore magis multifloro, corolla extus magis roseo suffusa graciliore, limbo paullo minore, lobis angustioribus filamentis quam antherae longioribus; A *V. bitchiuensi* differt praecipue foliis supra magis pilosis, petiolis paullo longioribus, 5–7 mm. longis, corymbo 6–7 cm. diam. magis florifero, corollis majoribus tubo

[1]Wilson, E. H. The Cherries of Japan, p. 19. Cambridge (1916).
[2]Russell, Paul. The Oriental Flowering Cherries, p. 19. Washington (1934).
[3]C. D. Darlington in Jour. Genet. 19: 213–256 (1928).

9–10 mm. longo, limbo 14–15 mm. diam., lobis paullo latioribus circiter 5 mm. latis, staminibus medio tubo affixis antheris faucem attingentibus.

Growing in the Arnold Arboretum under no. 447–20; type specimens collected May 14, 1929, May 9, 1930, May 14, 1931 and May 14, 1935.

This hybrid is in almost all characters intermediate between the parent species which are closely related and very similar, the chief difference being in the stamens which in *V. bitchiuense* are inserted in the lower fourth or third of the corolla-tube with the filaments about twice as long as the anthers and the tips of the latter 1.5–2 mm. below the mouth of the corolla-tube, while in *V. Carlesii* the stamens are inserted above the middle with the filaments as long or shorter than the anthers which reach the mouth of the corolla-tube. Table II shows the chief characters by which the hybrid may be distinguished from the parent.

TABLE II. COMPARISON OF VIBURNUM JUDDII WITH ITS PARENTS

	V. bitchiuense	× *V. Juddii*	*V. Carlesii*
Leaf	broad ovate to ovate or elliptic, sparingly furcate-pilose above, slightly lustrous above and usually rugose	ovate to ovate-oblong or elliptic, furcate-pilose above, bright green, not rugose	ovate to oblong-ovate, rather densely furcate-pilose and grayish green when young, not rugose
Petiole	2–7 mm. long	4–9 mm. long	5–12 mm. long
Inflorescence	4–5 cm. across, rather loose, rays 7–12 mm. long, slender	6–8 cm. across, rather loose, rays about 1.5 cm. long, slender	4.5–6 cm. across, compact, rays 5–8 mm. long, stout
Corolla	pink outside, tube 7–8 mm. long, limb 12–14 mm. across, lobes 4–5 mm. broad	pink outside, tube 9–10 mm. long, limb 15–16 mm. across, lobes about 5 mm. broad	corolla faintly flushed pink outside, tube 7–8 mm. long, limb 15–16 mm. across, lobes 5–6 mm. broad
Filaments	inserted in the lower third of the corolla tube, about twice as long as anthers	inserted about or slightly below the middle, about 1–½ as long as anthers	inserted above to near the middle as long or slightly longer than anthers
Anthers	tips 1.5–2 mm. below the mouth	tips reaching the mouth	tips reaching the mouth

As shown by the table above, the hybrid holds the middle between the two parent species except in the size of the inflorescence and the length of the corolla-tube, in which it exceeds both parents. In its general appearance it resembles more *V. bitchiuense* on account of its looser habit and the looser inflorescence and more brightly pink flowers. As an ornamental plant it is superior to either parent.

Viburnum Juddii was raised in 1920 by Mr. William H. Judd of the Arnold Arboretum staff from seed of *V. Carlesii*. The largest plant of the hybrid is now 2 m. tall and flowered for the first time in 1929. Like the parent species it has stood the severe cold of the last two winters without injury to its flower-buds.

A. R.

× **Syringa diversifolia** Rehder, hybr. nov. = *Syringa pinnatifolia* Hemsl. ♀ × *oblata* Lindl. var. *Giraldii* (Lemoine) Rehd. ♂.

A *Syringa pinnatifolia* differt praecipue foliis partim integris, partim basi pinnatifidis pinnis 1–4 ovato-oblongis vel anguste ovatis 2–3 cm. longis acuminatis basi anguste decurrentibus leviter ciliolatis ceterum glabris, foliolo terminali ovato-oblongo sensim acuminato 3.5–5 cm. longo, foliis integris ovato-oblongis, 3.5–5 cm. longis, 1.4–2.2 cm. latis, basi rotundatis, inferioribus interdum fere ovatis, inflorescentia ad 12 cm. longa et laxiore, corolla coeruleo-lilacina, tubo circiter 8 mm. longo, limbo circ. 1 cm. diam., lobis apice leviter cucullatis, antheris faucem paene attingentibus; a *S. oblata* var. *Giraldii* recedit praecipue foliis partim pinnatifidis minoribus et angustioribus, gemma terminali ramorum evoluta et ramum foliiferum emittente, inflorescentia minore, corollae tubo breviore et limbo angustiore, antheris faucem attigentibus.

Growing in the Arnold Arboretum under no. 148–30; type specimens collected May 17 and 21, 1935, preserved in the herbarium.

A comparison of the chief characters by which the hybrid differs from its parents are given in Table III.

TABLE III. COMPARISON OF SYRINGA DIVERSIFOLIA WITH ITS PARENTS

	S. pinnatifolia	*S. diversifolia*	*S. oblata* var. *Giraldii*
Leaf	pinnate with 7–11 leaflets, 3–6 cm. long, leaflets 4–10 mm. broad, finely ciliate when young	partly entire and partly pinnatifid with 3–5 leaflets 4–6 cm. long, lateral leaflets 5–14 mm. broad, entire leaves 2–2.5 cm. wide, glabrous	always entire broad ovate 4–10 cm. long, and 3–6 cm. broad, glabrous
Branches	with terminal bud	with or without terminal bud	without terminal bud
Panicles	4–7 cm. long, usually several pairs along the branches, sessile	to 11 cm. long, usually one pair at end of branches, sessile	to 15 cm. long, usually one pair at end of branches, peduncled
Corolla	white, usually tinged pale lilac, tube 5–6 mm. long, limb about 7 mm. across, lobes oval-ovate, not cucullate	whitish or bluish lilac, fading to whitish, tube about 8 mm. long, limb about 1 cm. across, lobes oval, slightly cucullate	lilac or purple lilac, tube 15–18 mm. long, limb about 1.5 cm. across, lobes oblong, strongly cucullate
Anthers	slightly exserted	anthers just reaching the mouth	anthers about 1.5 mm. below the mouth

This hybrid was raised in 1929 from seed collected in 1929 from *S. pinnatifolia* Hemsl. the flowers of which were apparently pollinated by a plant of *S. oblata* var. *Giraldii* (Lemoine) Rehd. not very far from *S. pinnatifolia*. In the same year, Dr. K. Sax fertilized *S. pinnatifolia* with pollen of *S. oblata* var. *Giraldii* and plants were raised from this pollination; these plants have not yet flowered, but in their vegetative characters agree with the plant described above. The pollen of *S. pinnatifolia* is defective, at least that of our plant, and self-pollinated flowers produce no seeds. The hybrid is clearly intermediate between these two species, readily distinguished from both species by the partly pinnatifid and partly entire leaves. In the partly entire and partly pinnatifid leaves the hybrid resembles *S. persica* L. var. *laciniata,* which can be distinguished by the broadly decurrent often obtusish lobes of the leaves and by the narrower and generally smaller entire leaves, by the smaller panicles usually in several to many pairs along the branches, the absence of the terminal leaf-bud, and by the anthers not reaching the mouth.

A. R.

HERBARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

HYPODERMELLA HIRATSUKAE, A NEW SPECIES OF HYPODERMATACEAE FROM JAPAN[1]

GRANT D. DARKER

With plate 154

FIVE SPECIES of Hypodermataceae have been reported on conifers in Japan by Shirai and Hara (1927). Only one species, *Lophodermium pinastri* (Schrad. ex Fr.) Chev., was listed as occurring on pines. The present paper describes a new Japanese species of Hypodermataceae of unusual interest which was encountered during a hasty examination of the Hypodermataceae in the Mycological and Pathological Herbarium of the United States Department of Agriculture in Washington, D. C. Grateful acknowledgment is made to Dr. C. L. Shear and Mr. John A. Stevenson for the privileges extended to the writer.

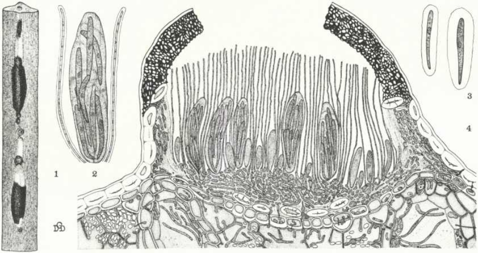
Hypodermella Hiratsukae, sp. nov.

Hysterotheciis in uno ordine epiphyllis oblongis ellipticisque atronitidis, 0.54–1.30 × 0.26–0.34 mm., longitudinali incisura aperientibus; hysterotheciis in transversali sectione in medio subcuticularibus sed ad marginem subepidermalibus, 0.16–0.22 mm. profundis; basilari plectenchymate achroö 20–35 μ crasso; tegente strato atri pseudoparenchymatis 28–34 μ crasso; hymenio 100–110 μ crasso. Ascis latis fusiformibusque octosporis 87–102 × 18–24 μ. Paraphysibus 100–110 × 1 μ simplicibus filiformibus muco involutis. Ascosporis clavatis fusiformibusque ad basin attenuatis hyalinis 35–56 × 3.5–5.0 μ, muco 8 μ crasso involutis.

In foliis *Pini pumilae* Regel, in monte Kuro-dake, provinciae Ishikari Japoniae, mense Augusto, 1927, *Naohide Hiratsuka* legit.

Hysterothecia in a more or less continuous row, epiphyllous, oblong and elliptical, shining black, 0.54–1.30 × 0.26–0.34 mm., opening by a longitudinal fissure; hysterothecia in cross section subcuticular in the middle but subepidermal at margins, 0.16–0.22 mm. deep (closed); basal layer colorless, plectenchymatous, 20–35 μ thick; covering layer of dark pseudoparenchyma 28–34 μ thick; hymenium 100–110 μ thick. Asci broad, somewhat fusiform, truncate to rounded at maturity at tip, 8-spored, 87–102 × 18–24 μ. Paraphyses 100–110 × 1 μ, simple,

[1]CONTRIBUTION FROM THE CRYPTOGAMIC LABORATORIES AND THE FARLOW HERBARIUM, HARVARD UNIVERSITY, NO. 138.



Hypodermella Hiratsukae Darker.

filiform, surrounded by a delicate gelatinous sheath. Ascospores clavate fusiform, tapering towards the base, hyaline, 36–56 $\times$ 3.5–5.0 μ, surrounded by a conspicuous gelatinous sheath up to 8 μ thick.

On needles of ***Pinus pumila*** Regel, Mt. Kuro-dake, Province Ishikari, Japan, August 12, 1927, collected by *Naohide Hiratsuka.*

Hypodermella Hiratsukae is of special interest because of certain morphological resemblances to ***Hypodermella Laricis*** v. Tub., the type species of the genus. As previously pointed out by the writer in 1932, the species of ***Hypodermella*** fall readily into four easily recognized groups named after the first described species in each as follows: (a) *H. Laricis* group, (b) *H. ampla* group, (c) *H. nervisequia* group, and (d) *H. sulcigena* group. Of nineteen species recognized in the genus, *H. Hiratsukae* approaches most closely *H. Laricis,* hitherto the only species in that group. The linear arrangement of the hysterothecia, the broad clavate asci and ascospores and the absence of a slit band along which the hysterothecium ruptures are common to both species. The position of the fruiting body of *H. Laricis* in the host tissue is difficult to determine even in microtome sections but is considered to be subcuticular by the writer. In the new species the hysterothecia are subcuticular in the centre and subepidermal at the margins as in *Lophodermium pinastri.* A prominently developed slit band, however, is characteristic of *L. pinastri.* Pycnidia with spores of the microconidial or spermatial type which are conspicuous and abundantly formed in the life cycle of *H. Laricis* are unknown in the case of *H. Hiratsukae* although in the material examined there are present certain small blister-like areas between the hysterothecia which may represent the remains of pycnidia.

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DESCRIPTION OF PLATE 154

Fig. 1–4. *Hypodermella Hiratsukae,* sp. nov., on *Pinus pumila* Regel.

1. Portion of needle with hysterothecia ($\times$ 17).
2. Ascus and paraphyses ($\times$ 500).
3. Ascospores ($\times$ 500).
4. Hysterothecium in cross-sectional view ($\times$ 270 approx.).

Farlow Herbarium, Harvard University,
Cambridge, Mass.

JOURNAL

OF THE

ARNOLD ARBORETUM

VOLUME XVI. OCTOBER, 1935 NUMBER 4

THE HOSTS, LIFE HISTORY AND CONTROL OF GYMNOSPORANGIUM CLAVIPES C. AND P.

IVAN H. CROWELL

With plates 155–160

TABLE OF CONTENTS

I. INTRODUCTION

GYMNOSPORANGIUM CLAVIPES C. and P., commonly referred to as the quince rust fungus, was one of the earliest species of the genus to be defined in North America. Schweinitz (1832) described it from the aecial phase occurring on *Crataegus* sp. as *Caeoma (Peridermium) germinale*. Later, Cooke and Peck (1871) described the telial phase of a rust on *Juniperus virginiana* L. as *Podisoma (Gymnosporangium) clavipes*. It was not until 1886, however, that Thaxter (1887) demonstrated by means of controlled cultures that these were but two phases of the same organism. Throughout the literature both specific names have been used. Some authors have followed Kern (1911) in calling the species *G. germinale* (Schw.) Kern. But Sydow (1915), Arthur (1934) and other mycologists adhere to the International Rules of Nomenclature and so designate the species *G. clavipes* C. & P.

The prevalence and destructiveness of the diseases caused by *G. clavipes* on ornamental pomaceous hosts and on many orchard varieties of apples, as well as on red cedars, have occasioned numerous inquiries regarding the pathogenicity and control of this rust. The information pertainable to these matters has been so meagre that comprehensive studies on the causal organism and the diseases produced by it were begun four years ago. The results obtained are presented in this paper. Certain phases of the investigations not yet completed are being continued.

The main lines of my investigations are as follows:

1. A determination by means of cultures and field observations of the pomaceous hosts of *G. clavipes* together with a discussion of their taxonomic position and geographic range.

2. Similar determinations and discussions of the Juniperus hosts of *G. clavipes*.

3. The symptomatology of the diseases caused by *G. clavipes*.

4. A thorough examination of the life history of *G. clavipes* on pomaceous and Juniperus hosts.

5. The practicability of fungicidal and of eradicative control measures of the diseases caused by *G. clavipes*.

II. THE POMACEOUS HOSTS OF GYMNOSPORANGIUM CLAVIPES C. AND P., THEIR TAXONOMIC POSITIONS AND THEIR GEOGRAPHIC RANGE

Contributions to our knowledge of the pomaceous hosts of *G. clavipes* as determined by artificial cultures are due chiefly to the work of Thaxter (1887), Arthur (1910, 1912), Thomas and Mills (1929) and Miller (1932). Numerous other investigators, by their field observations, have added several species to the list of pomaceous hosts. The total number previously reported is about thirty-six species in seven genera distributed as follows: *Amelanchier* (8), *Aronia* (3), *Chaenomeles* (1), *Crataegus* (20), *Cydonia* (1), *Malus* (2), *Pyrus* (1).

In my own studies on the pomaceous hosts, 701 species and varieties in 15 genera were inoculated, following essentially the same procedure described in a previous article (1934). These genera and the number of species of each inoculated are — *Amelanchier* (18), *Amelosorbus* (1), *Aronia* (4), *Chaenomeles* (2), *Crataegomespilus* (1), *Crataegus* (588), *Cydonia* (1), *Malus* (44), *Photinia* (1), *Pyrus* (19), *Sorbaronia* (1), *Sorbopyrus* (1), *and Sorbus* (17). One species of *Comptonia* and two of *Myrica* were also inoculated. From the results obtained the inoculated plants were placed in two groups. Those plants which developed no evidence of infection were classed as immune; while those plants on which infection was evident were classed as susceptible. The number of hosts determined by artificial inoculations was augmented by field observations in the Arnold Arboretum, on private estates about Boston and from the reports of former investigators.

The results showed that more than 480 species and varieties of pomaceous plants (including 48 varieties of orchard apples) scattered among eleven genera are susceptible. These hosts are presented in table 1.

TABLE I. POMACEOUS HOSTS OF GYMNOSPORANGIUM CLAVIPES C. AND P.[1]

Amelanchier alnifolia Nutt., *A. Bartramiana* Roem. (*A. oligocarpa* [Michx.] Roem.), *A. Bartramiana* × *laevis*, *A. Bartramiana* × *oblongifolia*, *A. canadensis* Med., *A. canadensis nana*, *A. erecta* Blanch., *A. florida* Lindl., *A. intermedia* Spach., *A. laevis* Wieg., *A. laevis* × *humilis*, *A. oblongifolia* (Torr. and Gray) Roem., *A. sanguinea* DC., *A. spicata* K. Koch, *A. stolonifera* Wieg.

Amelosorbus Jackii Rehd.

[1]For the taxonomy of the genus *Crataegus*, Palmer (1925) was used. Mr. Palmer has kindly checked the hosts of *G. clavipes* in the genus *Crataegus* against his revised but unpublished catalogue of *Crataegi*. For the taxonomy of the other genera, Rehder's Manual (1927) was followed as far as possible.

Aronia arbutifolia (L.) Ell., *A. floribunda* Spach (*A. arbutifolia atropurpurea* [Britt.] B. L. Robinson), *A. melanocarpa* Ell., *A. melanocarpa elata* Rehder, *A. monstrosa* Zabel.

Chaenomeles japonica Lindl., *C. lagenaria* Koidz., *C. lagenaria marmorata*, *C. lagenaria foliis rubris*, *C. lagenaria sanguinea semiplena*.

Crataegomespilus grandiflora Bean.

Crataegus

ANOMALAE: *C. affinis* Sarg., *C. asperifolia* Sarg., *C. Brockwayae* Sarg., *C. Coleae* Sarg., *C. cyclophylla* Sarg., *C. Dunbari* Sarg., *C. Egglestonii* Sarg., *C. errata* Sarg., *C. honesta* Sarg., *C. Ideae* Sarg., *C. improvisa* Sarg., *C. misella* Sarg., *C. pinguis* Sarg., *C. putata* Sarg., *C. repulsans* Sarg., *C. Saundersiana* Sarg., *C. scabrida* Sarg., *C. shirleyensis* Sarg., *C. urbana* Sarg.

COCCINEAE: *C. acclivis* Sarg., *C. arcuata* Ashe, *C. assurgens* Sarg., *C. aulica* Sarg., *C. caesa* Ashe, *C. chippewaensis* Sarg., *C. confinis* Sarg., *C. conspecta* Sarg., *C. cristata* Ashe, *C. delecta* Sarg., *C. densiflora* Sarg., *C. elongata* Sarg., *C. fluviatilis* Sarg., *C. fretalis* Sarg., *C. Hillii* Sarg., *C. Holmesiana* Ashe, *C. Holmesiana tardipes* Sarg., *C. lenta* Ashe, *C. Macounii* Sarg., *C. miranda* Sarg., *C. neolondinensis* Sarg., *C. pedicellata* Sarg., *C. perrara* Sarg., *C. polita* Sarg., *C. Pringlei* Sarg., *C. pura* Sarg., *C. sejuncta* Sarg., *C. sertata* Sarg., *C. Thayeri* Sarg., *C. vivida* Sarg.

CRUS-GALLI: *C. arborea* Beadle, *C. arduennae* Sarg., *C. armata* Sarg., *C. attenuata* Sarg., *C. barrettiana* Sarg., *C. Bartramiana* Sarg., *C. bellica* Sarg., *C. calophylla* Sarg., *C. Canbyi* Sarg., *C. cerasina* Sarg., *C. crus-galli* L., *C. crus-galli arbutifolia* Hort. ex Nicholson, *C. crus-galli exigua* Sarg., *C. crus-galli pyracanthifolia* Ait., *C. crus-galli rubens* Sarg., *C. crus-galli splendens* Ait., *C. effulgens* Sarg., *C. erecta* Sarg., *C. Farwellii* Sarg., *C. Fontanesiana* (Spach) Steudel, *C. geneseensis* Sarg., *C. insignis* Sarg., *C. Lavallei* Herincq, *C. lawrencensis* Sarg., *C. leptophylla* Sarg., *C. livoniana* Sarg., *C. macra* Beadle, *C. pachyphylla* Sarg., *C. Palmeri* Sarg., *C. parciflora* Sarg., *C. Pennypackeri* Sarg., *C. peoriensis* Sarg., *C. persimilis* Sarg., *C. phlebodia* Sarg., *C. Reverchonii* Sarg., *C. rivalis* Sarg., *C. robusta* Sarg., *C. rubrifolia* Sarg., *C. rudis* Sarg., *C. triumphalis* Sarg.

DILATATAE: *C. coccinoides* Ashe, *C. dilatata* Sarg.

DOUGLASIANAE: *C. colorado* Ashe, *C. columbiana* Howell, *C. Douglasii* Lindl., *C. Douglasii* f. *badia* Sarg., *C. Douglasii Suksdorfii* Sarg., *C. erythropoda* Ashe, *C. Piperi* Britt., *C. rivularis* Nutt. apud Torr. & Gray.

FLAVAE: *C. colonica* Beadle, *C. dispar* Beadle, *C. flava* Ait., *C. ignava* Beadle.

INTRICATAE: *C. Delosii* Sarg., *C. flavida* Sarg., *C. modesta* Sarg., *C. nemoralis* Sarg., *C. neobushii* Sarg., *C. scabra* Sarg., *C. straminea* Beadle.

MACRACANTHAE: *C. admiranda* Sarg., *C. aquilonaris* Sarg., *C. ardua* Sarg., *C. baccata* Sarg., *C. Beckiana* Sarg., *C. bristolensis* Sarg., *C. calpodendron* (Ehrh.) Med., *C. Calvinii* Sarg., *C. chadfordiana* Sarg., *C. corporea* Sarg., *C. Deweyana* Sarg., *C. divida* Sarg., *C. Emersoniana* Sarg., *C. ferentaria* Sarg., *C. ferta* Sarg., *C. fertilis* Sarg., *C. finitima* Sarg., *C. flagrans* Sarg., *C. fulgens* Sarg., *C. gemmosa* Sarg., *C. glabrata* Sarg., *C. Handyae* Sarg., *C. hystricina* Ashe, *C. laxiflora* Sarg., *C. macracantha* Lodd., *C. membranacea* Sarg., *C. microsperma* Sarg., *C. missouriensis* Ashe, *C. neofluvialis* Ashe, *C. occidentalis* Britt., *C. ogdenburgensis* Sarg., *C. peramoena* Sarg., *C. prunifolia* (Marsh.) Pers., *C. radiosa* Sarg., *C. rhombifolia* Sarg., *C. Robinsonii* Sarg., *C. Searsii* Sarg., *C. spatiosa* Sarg., *C. spinulosa* Sarg., *C. structilis* Ashe, *C. succulenta* Schrader, *C. tomentosa* L., *C. truculenta* Sarg., *C. vegeta* Sarg.

MICROCARPAE: *C. Phaenopyrum* (L. f.) Med., *C. spathulata* Michx.

MOLLES: *C. anomala* Sarg., *C. arnoldiana* Sarg., *C. champlainensis* Sarg., *C. contortifolia* Sarg., *C. digna* Sarg., *C. dispessa* Ashe, *C. Ellwangeriana* Sarg., *C. exclusa* Sarg., *C. Fulleriana* Sarg., *C. induta* Sarg., *C. invisa* Sarg., *C. lanuginosa* Sarg., *C. lasiantha* Sarg., *C. lauta* Sarg., *C. limaria* Sarg., *C. mollis* (Torr. & Gray) Scheele, *C. nutans* Sarg., *C. pennsylvanica* Ashe, *C. peregrina* Sarg., *C. Robesoniana* Sarg., *C. sera* Sarg., *C. submollis* Sarg., *C. Tatnalliana* Sarg., *C. urbica* Sarg.

OXYACANTHAE: *C. altaica* Lange, *C. hiemalis* Lange, *C. Heldreichii* Boiss., *C. intermedia*, *C. Maximowiczii* Schneider, *C. monogyna* Jacq., *C. monogyna albo-plena* Schneider, *C. monogyna inermis* Rehd., *C. monogyna laciniata* Loud., *C. monogyna pteridifolia* Rehd., *C. monogyna spectabilis*, *C. monogyna stricta* Loud., *C. monogyna versicolor*, *C. Oxyacantha* L., *C. Oxyacantha Gireoudi* Bean, *C. Oxyacantha alba* West., *C. Oxyacantha rubra* Schneider, *C. pinnatifida* Bunge, *C. sorbifolia* Lange, *C. Wilsonii* Sarg.

PRUINOSAE: *C. arcana* Beadle, *C. aridula* Sarg., *C. aspera* Sarg., *C. austera* Sarg., *C. beata* Sarg., *C. bellula* Sarg., *C. brachypoda* Sarg., *C. bracteata* Sarg., *C. cestrica* Sarg., *C. cognata* Sarg., *C. comparata* Sarg., *C. confragosa* Sarg., *C. delawarensis* Sarg., *C. disjuncta* Sarg., *C. dissona* Sarg., *C. divisifolia* Sarg., *C. Ferrissii* Ashe, *C. formosa* Sarg., *C. fusca* Sarg., *C. georgiana* Sarg., *C. glareosa* Ashe, *C. horridula* Sarg., *C. incisa* Sarg., *C. Jesupii* Sarg., *C. Kellermanii* Sarg., *C. latifrons* Sarg., *C. levis* Sarg., *C. macrocalyx* Sarg., *C. numerosa* Sarg., *C. patrum* Sarg., *C. pequotorum* Sarg., *C. perampla* Sarg., *C. perjucunda* Sarg., *C. philadelphica* Sarg., *C. platycarpa* Sarg., *C. pruinosa* (Wendl.) K. Koch, *C. pulchra* Sarg., *C. relicta* Sarg., *C. remota* Sarg., *C. rubicundula* Sarg., *C. sicca* Sarg., *C. tribulosa* Sarg.

PRUNIFOLIAE: *C. decorata* Sarg.

PUNCTATAE: *C. amnicola* Beadle, *C. angustata* Sarg., *C. barbara* Sarg., *C. Brownietta* Sarg., *C. calvescens* Sarg., *C. celsa* Sarg., *C. compacta* Sarg., *C. desueta* Sarg., *C. florifera* Sarg., *C. glabrifolia* Sarg., *C. incaedua* Sarg., *C. Lettermanii* Sarg., *C. notabilis* Sarg., *C. pausiaca* Ashe, *C. porrecta* Ashe, *C. praestans* Sarg., *C. pratensis* Sarg., *C. punctata* Jacq., *C. punctata aurea* Ait., *C. punctata canescens* Britt., *C. rigens* Beadle, *C. suborbiculata* Sarg., *C. succincta* Sarg., *C. tenax* Ashe, *C. verruculosa* Sarg.

ROTUNDIFOLIAE: *C. Bicknellii* Eggl., *C. Blanchardii* Sarg., *C. Brainerdii* Sarg., *C. Brunetiana* Sarg., *C. chrysocarpa* Ashe, *C. coccinata* Sarg., *C. cupilifera* Sarg., *C. Dodgei* Ashe, *C. inaudita* Sarg., *C. Jonesae* Sarg., *C. Kennedyi* Sarg., *C. kingstonensis* Sarg., *C. maligna* Sarg., *C. Margaretta* Ashe, *C. Margaretta xanthocarpa* Sarg., *C. Maribella* Sarg., *C. Oakesiana* Eggl., *C. praecoqua* Sarg., *C. Proctoriana* Sarg., *C. propria* Sarg., *C. rotundata* Sarg., *C. rotundifolia* Moench, *C. rotundifolia pubera* Sarg., *C. rotundifolia* f. *rubescens* Sarg., *C. varians* Sarg., *C. Websteri* Sarg.

SILVICOLAE: *C. allecta* Sarg., *C. Barryana* Sarg., *C. blairensis* Sarg., *C. compta* Sarg., *C. delectata* Sarg., *C. diffusa* Sarg., *C. dissona* Sarg., *C. effera* Sarg., *C. filipes* Ashe, *C. foliata* Sarg., *C. Fretzii* Sarg., *C. iracunda* Beadle, *C. iterata* Sarg., *C. Livingstoniana* Sarg., *C. luxuriosa* Sarg., *C. medioxima* Sarg., *C. opulens* Sarg., *C. promissa* Sarg., *C. prona* Ashe, *C. radina* Sarg., *C. recordabilis* Sarg., *C. ruricola* Sarg., *C. stolonifera* Sarg., *C. strigosa* Sarg., *C. tortuosa* Sarg., *C. xanthocarpa* Sarg.

TENUIFOLIAE: *C. acuminata* Sarg., *C. acutiloba* Sarg., *C. alnorum* Sarg., *C. apiomorpha* Sarg., *C. ascendens* Sarg., *C. asperata* Sarg., *C. bella* Sarg., *C. benigna* Sarg., *C. blandita* Sarg., *C. Boothiana* Sarg., *C. colorata* Sarg., *C. conferta* Sarg., *C. crudelis* Sarg., *C. cyanophylla* Sarg., *C. Damei* Sarg., *C. delucida* Sarg., *C. demissa* Sarg., *C. Edsoni* Sarg., *C. Eganii* Ashe, *C. firma* Sarg., *C. flabellata* (Bosc.) K. Koch, *C. florea* Sarg., *C. Forbesae* Sarg., *C. fucosa* Sarg., *C. genialis* Sarg., *C. glaucophylla* Sarg.. *C. gracilipes* Sarg., *C. Gruberi* Ashe, *C. Habereri* Sarg., *C. Hadleyana* Sarg., *C. heidelburgensis* Sarg., *C. insolita* Sarg., *C. leptopoda* Sarg., *C. lucorum* Sarg., *C. luminosa* Sarg., *C. macrosperma* Ashe, *C. marcida* Ashe, *C. matura* Sarg., *C. media* Sarg., *C. merita* Sarg., *C. miniata* Ashe, *C. modica* Sarg., *C. monstrata* Sarg., *C. Napaea* Sarg., *C. nescia* Sarg., *C. otiosa* Ashe, *C. Paddockeae* Sarg., *C. Paineana* Sarg., *C. pallidula* Sarg., *C. parviflora* Sarg., *C. pastorum* Sarg., *C. paucispina* Sarg., *C. pentandra* Sarg., *C. perlevis* Ashe, *C. populnea* Ashe, *C. pumila* Sarg., *C. retrusa* Ashe, *C. roanensis* Ashe, *C. rubicunda* Sarg., *C. rubrocarnea* Sarg., *C. rufipes* Ashe, *C. sarniensis* Sarg., *C. serena* Sarg., *C. sextilis* Sarg., *C. Slavini* Sarg., *C. Streeterae* Sarg., *C. suavis* Sarg., *C. taetrica* Sarg., *C. tarda* Sarg., *C. tenella* Sarg., *C. tenera* Sarg., *C. tenuiloba* Sarg., *C. trachyphylla* Sarg., *C. viridimontana* Sarg., *C. vittata* Ashe.

TRIFLORAE: *C. conjungens* Sarg.

UNIFLORAE: *C. uniflora* Moench.

VIRIDES: *C. abbreviata* Sarg., *C. blanda* Sarg., *C. penita* Beadle, *C. velutina* Sarg., *C. viridis* L., *C. vulsa* Beadle.

Cydonia oblonga Mill.

Malus angustifolia Michx., *M. floribunda* Sieb., *M. ioensis plena* Rehd., *M. pumila* Mill., *M. spectabilis* Borkh., *M. sylvestris* Mill.

Photinia villosa DC.

Pyrus communis L., *P. sinensis* Lindl.

Sorbus americana Marsh, *S. dumosa* Greene.

A complete enumeration of all species and varieties of inoculated plants on which the results were negative is as follows:

Amelanchier amabilis Wieg., *A. asiatica* Endl., *A. grandiflora* Rehd., *A. humilis* Wieg., *A. humilis* × *sanguinea*, *A. ovalis* Med., *A. sera* Ashe.

Malus arnoldiana Sarg., *M. asiatica* Nakai, *M. atrosanguinea* Schneid., *M. baccata* Borkh., *M. baccata costata* Hort., *M. baccata gracilis* Rehd., *M. baccata Jackii* Rehd., *M. baccata mandshurica* Schneid., *M. baccata microcarpa* Regel., *M. baccata pendula* Hort., *M. brevipes* Rehd., *M. flexilis* Hort., *M. florentina* Schneid., *M. Halliana Parkmanii* Rehd., *M. Halliana spontanea* Rehd., *M. Hartwigii* Koehne, *M. honanensis* Rehd., *M. hupehensis* Rehd., *M. kansuensis* Schneid., *M.* spec. (*Pyrus Malus laurifolia* Gibbs), *M.* spec. (*Pyrus Lemoinei* Hort.), *M. magdeburgensis* Schoch, *M. micromalus* Mak., *M. orthocarpa* Lavall., *M. Prattii* Schneid., *M. pumila Niedzwetzkyana* Schneid., *M. purpurea* Rehd., *M. purpurea aldenhamensis* Rehd., *M. purpurea Eleyi* Rehd., *M. robusta persicifolia* Rehd., *M. Sargenti* Rehd., *M. Scheideckeri* Zabel, *M. Scheideckeri "Excellenz Thiel," M. sikkimensis* Koehne, *M. spectabilis Riversii* Nash, *M. sublobata* Rehd., *M. toringoides* Hughes, *M. trilobata* Schneid., *M. Tschonoskii* Schneid., *M. yunnanensis* Schneid., *M. yunnanensis Veitchii* Rehd., *M. zumi* Rehd., *M. zumi calocarpa* Rehd.

Pyrus amygdaliformis Vill., *P. Balansae* Decne., *P. betulifolia* Bge., *P. Bretschneideri* Rehd., *P. denticulata* Hort. Angl. ex Dum.-Cours., *P. elaeagrifolia* Pall., *P. Korshinskyi* Litv., *P. Lindleyi* Rehd., *P. longipes* Coss. & Dur., *P. Michauxii* Bosc., *P. nivalis* Jacq., *P. pashia* Buch.-Ham., *P. phaeocarpa* Rehd., *P. salvifolia* DC., *P. serotina* Rehd., *P. serrulata* Rehd., *P. syriaca* Boiss., *P. ussuriensis* Maxim.

Sorbaronia alpina superaria, S. spec.

Sorbopyrus auricularis bulbiformis Schneid.

Sorbus Aria Crantz, *S. arnoldiana* Rehd., *S. Aucuparia* L., *S. commixta* Hedl., *S. discolor* Hedl., *S. hybrida* L., *S. intermedia* Pers., *S. japonica calocarpa* Rehd., *S. Matsumurana* Koehne, *S. Meinichii* Hedl., *S. pohuashanensis* Hedl., *S. rotundifolia* Hedl., *S. subpinnata* Hedl., *S. thuringiaca* Fritsch (*S. decurrens* Hedl.).

Other plants inoculated were *Comptonia asplenifolia* Ait., *Myrica carolinensis* Mill. and *M. Gale* L.

In addition to the pomaceous hosts just reported, several varieties of orchard apples have been found by former investigators to be susceptible. A compilation of these is presented in table 2. Mills (1929) gives the following account of the occurrence of *G. clavipes* on orchard apples in New York: "Counts in 14 orchards in 4 counties showed fruit infection on Delicious (3 counts) 60 per cent; Fameuse (1 count) 21 per cent; Hubbardston (1 count) 28 per cent; McIntosh (15 counts) 18 per cent average; Winesap (2 counts) 74 per cent; Yellow Transparent (1 count) 84 per cent. Specimens were from 6 or 7 counties. Not found on foliage or twigs." This account and the fact that many other varieties of orchard apples are susceptible serve to stress the economic importance of *G. clavipes* to orchardists. In several orchards visited in Massachusetts the disease caused by *G. clavipes* was found to be particularly abundant on the Delicious variety. As high as 90 per cent of the fruits were attacked. This disease, one of the most severe on the Delicious apple, is of much concern to orchardists because this variety is being grown in greater quantities to meet the steadily increasing demands for it on the market.

TABLE II. THE RELATIVE SUSCEPTIBILITY OF ORCHARD APPLES TO G. CLAVIPES

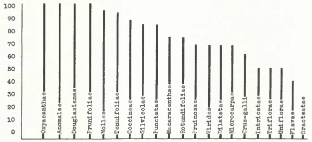
Variety	Susceptible	Immune
Alexander	N. Y.	
Baldwin	Ind., Me., N. Y., N. S.	
Bechtel's Crab	Mass.	
Bellflower	Me.	
Ben Davis	N. Y.	Ind.
Bishop	N. S.	
Black Twig	Va., W. Va.	
Cortland	Me., N. Y.	
Crimson Beauty	N. S.	
Delicious	Ind., Me., Mass., N. Y., Tenn., Va., W. Va.	
Duchess	Me., N. Y.	
Early Red McIntosh	Me.	
Fameuse	N. Y., N. S.	
Family	N. S.	
Gideon	Ind.	
Golden Delicious	Me.	
Gravenstein	Me., N. Y., N. S.	
Grimes	Ind., Tenn.	
Hubbardston	N. Y.	
Jonathan	Ind., Me., N. Y.	Tenn.
King David	Ind.	
Maiden Blush	——	Ind.
McIntosh	Me., N. Y., N. S.	
Northern Spy	N. Y.	
Northwestern Greening	Ind., N. Y.	
Red Delicious	Me., N. Y., Tenn.	
Red Winesap	Tenn.	
R. I. Greening	N. Y., N. S.	
Ribston	N. S.	
Rome	Md., N. Y., Tenn., Vt., Va.	Ind.
Roxbury	N. S.	
Russett	N. Y., N. S.	
Stark	N. S.	
Starkey	Me., N. S.	
Starking	Me.	
Stayman	Ind., N. Y., Tenn., Va., W. Va.	

TABLE II. (*Continued*)

Variety	Susceptible	Immune
Stayman Winesap	Tenn.	
Sweet Winesap	N. Y.	
Tolman	Me., N. Y.	
Tompkin's King	N. S.	
Twenty Ounce	Me., Mass., N. Y.	
Wagener	Me., N. S.	
Wealthy	Ind., Mass., Me., N. Y., Tenn.	
Winesap	Ind., Me., N. Y., Tenn., Vt., Va., W. Va.	
Winter Banana	Ind., Me., N. Y.	
Wolf River	N. Y.	
Yellow Bellflower	N. S.	
Yellow Transparent	Md., N. Y., Tenn., N. S.	Va.
York	——	Va.

The species and genera of pomaceous hosts recorded above show no simple relationship or correlation by which one can formulate a rule to encompass them and set them apart from related non-susceptible plants. Nevertheless, they possess several distinctive features chiefly with respect to their taxonomy and their geographic range. Pomaceous hosts of *G. clavipes* are found in eleven genera. So far as I am able to learn no other species of *Gymnosporangium* is known to have hosts in so large a range of genera. All of the host genera of *G. clavipes* are closely related, however, and confined within the family Rosaceae. The native geographic range of these hosts is more extensive than for those of any other species of *Gymnosporangium* known to me. Pomaceous hosts of *G. clavipes* are found throughout the whole of the temperate portion of the northern hemisphere.

One of the most outstanding of the introduced foreign host species to become parasitised is *Cydonia oblonga,* the quince. This plant is native over the greater portion of Asia but has been introduced into North America over a portion only of the range of the rust. In the genus *Chaenomeles,* also native to Asia, two of the three species listed in Rehder's Manual are attacked. Several varieties and forms of the Japanese quince (*Chaenomeles* spp.) are also parasitised. One European and one Asiatic species of the genus *Pyrus* are attacked, while all other species (Eurasian) have so far proved to be immune. Some native and some foreign species of *Malus* as well as many orchard varieties of apples are hosts to *G. clavipes*. In the genus *Sorbus* the two North American species are susceptible while all of the foreign ones inoculated remained immune. The hybrid genus *Amelosorbus* has but one species susceptible to *G. clavipes*. All of the species of the genus *Aronia*, native to North America, are hosts. With the exception of three or four species the genus *Amelanchier*, as represented in North America, is attacked by *G. clavipes*. A single species of the genus *Photinia*, the Eurasian species *P. villosa*, is liable to infection.



% suscept.	100	100	100	100	96	94	88	84	83	75	74	68	67	67	67	63	50	50	50	42	00
No. sp. with frt. tested	21	19	8	1	24	78	32	31	30	52	35	59	9	3	3	63	14	2	2	12	1
No. hosts.	21	19	8	1	23	73	28	26	25	39	26	40	6	2	2	40	7	1	1	5	0
Approx. no. sp. in group.	?	27	11	1	61	120	51	151	59	122	62	143	37	4	4	125	79	3	51	86	2

FIGURE 1. Data on Species and Varieties in Groups of the Genus *Crataegus* Susceptible to Attack by *Gymnosporangium clavipes* C. and P.

The susceptibility of each group of the genus *Crataegus* is presented as a graph in figure 1. The data for this graph were obtained by determining the percentage relationship between the number of species and varieties tested and the number that proved to be susceptible. While little significance can be attached to the results obtained from groups with a small number of species and varieties, nevertheless, reliable deductions can be made from those with large numbers as well as from the genus as a whole.

Susceptible species were found in all groups except the Bracteatae. Unfortunately this group was represented in the Arnold Arboretum by but a single tree. In these investigations, 79 per cent of the species that produced fruit when the tests were made proved to be susceptible. Many species and varieties have not yet been tested, either because they were not available or because they did not produce fruits in the years of my investigations. Therefore, the host list is far from complete. All of the foreign species and varieties available for testing (placed in the group Oxyacanthae) proved to be susceptible. Of the native *Crataegi,* the percentage of species susceptible in the several groups varied widely. In some groups, for example, the Anomalae and Douglasianae, all of the species and varieties tested were susceptible while in other groups, for example, the Molles, Virides and Flavae, the percentage of susceptible members was less. It is interesting to note that the relative susceptibility of species and varieties and of the groups of the genus is not the same for hosts of *G. clavipes* as MacLachlan (1935) found for hosts of *G. globosum,* though hosts for both of these fungi were in most cases determined from the same individual trees.

III. PRELIMINARY STUDIES ON THE PERIOD OF SUSCEPTIBILITY OF POMACEOUS HOSTS OF GYMNOSPORANGIUM CLAVIPES

It has been shown by several investigators that the leaves of pomaceous hosts of certain species of *Gymnosporangium* are susceptible during a limited period in their youth only. This interim is known as the period of susceptibility. Thomas (1933) showed that leaves of *Crataegus* spp. were susceptible in their youth only to the attack of *G. clavipes.* My preliminary investigations, with respect to this phenomenon on fruits of pomaceous hosts of *G. clavipes,* also indicate that their period of susceptibility is brief. In this connection inoculations were made every two days for a period of four weeks on different fruit clusters of two species of *Crataegus, C. tomentosa* and *C. fertilis.* Experimentation began when the flower buds of each species were opening. On *C. tomentosa* the ovaries, calyces, petals, pedicels, peduncles and twigs were attacked before the flowers opened. All but the ovaries and young fruit became immune within ten days. The fruits became decreasingly susceptible and by the time the petals fell they could no longer be infected. On *C. fertilis,* the young fruits only became infected. The flowers were immune up to the time the buds were opening and the petals began to expand; they then entered a brief period of susceptibility extending until the time when the petals began to fall, after which they again became immune.

A measure of susceptibility of the hosts of *G. clavipes* is here suggested. Those hosts that are susceptible for a longer period may be considered to be more susceptible than those that can be infected for a shorter period. No consistent difference was observed with respect to the abundance of aecia produced on susceptible as compared with resistant hosts.

The possibility of any relationship between immunity and fertilization was not investigated.

IV. THE JUNIPERUS HOSTS OF GYMNOSPORANGIUM CLAVIPES C. AND P., THEIR TAXONOMIC POSITIONS AND THEIR GEOGRAPHIC RANGE

Cultural studies for the purpose of determining the Juniperus hosts of *G. clavipes* have been very limited indeed. Arthur (1912) cultured *G. clavipes* on *J. communis depressa* Pursh (*J. sibirica* Burgsd.) and Dodge (1918) obtained heavy infection from sowing aeciospores of *G. clavipes* on *J. virginiana* L. Several other investigators have substantiated these reports and added other hosts from their field observations. In my own work I have repeatedly cultured this rust on the red cedar, *J. virginiana* L. The technique for this work followed essentially the same procedure as for culture work on pomaceous plants. A complete enumeration (to 1934) of the Juniperus hosts of *G. clavipes* together with data on their taxonomic position, as given by Rehder (1927), and their geographic range are presented in table 3. I have examined the rust on all of these species and varieties.

TABLE III. JUNIPERUS HOSTS OF G. CLAVIPES

Juniperus hosts	Taxonomic position	Geographic range
J. communis L.	Oxycedrus	North Amer., Eurasia
var. depressa Pursh.	"	" " "
var. hibernica Gord.	"	Europe
var. montana Ait.	"	North Amer., Eurasia
J. horizontalis Moench	Sabina	" "
J. Sabina L.	"	Europe
J. scopulorum Sarg.	"	Western North Amer.
J. virginiana L.	"	Eastern North Amer.

In 1933 each individual cedar in the collections at the Arnold Arboretum of Harvard University was examined for infection and the species and varieties were recorded in immune and susceptible groups. The species and varieties of *Juniperus* on which no infection was observed are as follows:

Juniperus chinensis L., *J. chinensis globosa* Hornibrook, *J. chinensis japonica* Lav., *J. chinensis mas* Gord., *J. chinensis pendula* Franch., *J. chinensis Pfitzeriana* Spaeth, *J. chinensis plumosa* Hornibrook, *J. chinensis plumosa aurea* Hornibrook, *J. chinensis pyramidalis* Beiss., *J. chinensis Sargentii* Rehd., *J. chinensis Watereri* Hort., *J. communis Ashfordii* Hort., *J. communis aurea* Nichols., *J. communis aureo-spica* Rehd., *J. communis compressa* Carr., *J. communis cracovica* Hort., *J. communis oblongo-pendula* Sudw., *J. communis oblonga* Loud., *J. com-*

munis pyramidalis Hort., *J. communis suecica* Ait., *J. conferta* Parl., *J. formosana* Hayata, *J. horizontalis alpina* Rehd., *J. horizontalis Douglasii* Rehd., *J. horizontalis glomerata* Rehd., *J. horizontalis plumosa* Rehd., *J. horizontalis variegata* Hort., *J. procumbens* Sieb., *J. rigida* Sieb. & Zucc., *J. Sabina cupressifolia* Ait., *J. Sabina pyramidalis* Hort., *J. Sabina tamariscifolia* Ait., *J. Sabina variegata* Carr., *J. scopulorum horizontalis* D. Hill, *J. scopulorum viridifolia* Hort., *J. squamata* Buch.-Ham., *J. squamata Fargesii* Rehd. & Wils., *J. squamata Meyeri* Rehd., *J. squamata Wilsonii* Rehd., *J. virginiana aurea* Hort., *J. virginiana Burkii, J. virginiana Canaertii* Senecl., *J. virginiana Chamberlaynii* Carr., *J. virginiana cinerascens* Hort., *J. virginiana elegantissima* Hochst., *J. virginiana fastigiata* Hort., *J. virginiana filifera* D. Hill, *J. virginiana glauca* Carr., *J. virginiana globosa* Beiss., *J. virginiana Hillii* Hort., *J. virginiana Kosteri* Beiss., *J. virginiana pendula* Carr., *J. virginiana polymorpha* Hort., *J. virginiana pyramidalis* Carr., *J. virginiana pyramidalis glauca* Hort., *J. virginiana plumosa* Rehd., *J. virginiana reptans* Beiss., *J. virginiana Schottii* Gord., *J. virginiana tripartita* R. Smith and *J. virginiana venusta* Rehd.

Usually the Juniperus hosts of species of *Gymnosporangium* are confined to a single section of the genus. Those of *G. clavipes* are exceptional in that they are classified in two sections of the genus, Sabina and Oxycedrus. Geographically the Juniperus hosts of *G. clavipes* are found throughout the greater portion of the temperate region of the northern hemisphere, an unusually wide distribution for telial hosts of any one species of *Gymnosporangium*.

V. SYMPTOMATOLOGY OF THE DISEASES CAUSED BY GYMNOSPORANGIUM CLAVIPES

1. On Pomaceous Hosts

(A) Morphological symptomatology

Morphological symptoms of disease caused by *G. clavipes* were first described from infected fruits on pomaceous hosts. Schweinitz (1832) gave a brief description of the gross morphological symptoms of the disease on the fruit of *Crataegus* sp. Farlow (1880) stated that *G. clavipes* (*Roestelia aurantiaca*) was "by far the most beautiful species of the genus which we have, at once attracting the popular eye by its brilliant orange or almost cinnabar colored spores and shining white peridium. It is generally found on young fruit, though it is occasionally found on the stems and petioles, but I do not recollect having seen aecidia on the leaves. — One sometimes sees a quince two inches in diameter more than half covered by the bright orange aecidia and occasionally small apples are affected in a similar way. *Roestelia aurantiaca* is generally found in midsummer. I have, however, seen it on *C. crus-galli* as late as October."

Weimer (1917) stated that "the veins alone (of quince leaves) are attacked and often become swollen to double their normal size." The swellings, he noted, caused the leaves to curl but the infected areas were not discolored. No aecia were found on the quince leaves. Adams (1921) reported that branches and buds of hawthorns were very severely injured by this rust. He stated that "the aecia on the branches always precede the appearance of aecia on the fruit of hawthorns." Thomas (1933) reported that symptoms on apple foliage appeared 10 to 18 days after inoculating and that on apple fruits the symptoms were predominately necrotic or hypoplastic. On artificially inoculated leaves of *Crataegus* he obtained numerous spermogonia "but aecia were produced only sparingly along the larger veins."

In the present study, data for the symptomatology of the disease caused by the aecial phase of *G. clavipes* were obtained from observations made on more than 400 pomaceous hosts. Data on the relationship between elapsed time and progressive stages of development of symptoms and signs were recorded from plants inoculated at various stages of development of the flowers, twigs and fruits. Comparisons of the symptoms and signs resulting from artificial inoculations made possible a more thorough understanding of the phenomena that occur in nature.

Gymnosporangium clavipes attacks primarily the fruits, less frequently the twigs and buds and rarely the leaves of its pomaceous hosts. The earliest observable symptom of disease on ovaries and young fruits is a pale yellowish green discoloration. This symptom was seen on certain species even before the petals fell. Occasionally the petals become infected and when they do they usually remain attached for the greater part of the season. In my experience, fruits are susceptible when in early stages of development only. After the petals drop the fruits of most species are no longer subject to infection. On the average, from 6 to 10 days after inoculating the diseased fruits begin to show evidence of infection by slightly pale swellings. From 4 to 5 days later the hypertrophied zone becomes dotted in its central portion with numerous, tiny, deep-reddish points — the developing spermogonia of the fungus. Within 1 to 5 more days, the first formed spermogonia begin to exude a pale-red, sweetish liquid. During further development the diseased area continues to increase in all dimensions and finally involves but a portion of, or, in many cases, the whole fruit. Occasionally, the infection spreads to the pedicels and even extends into the peduncles and twigs. Spermogonia are matured progressively over a large portion of the diseased tissue, and oozing of the young spermogonia continues for several days. The older spermogonia die and turn black.

Several irregularities or anomalies have been observed in the symptomatology of the disease during the life span of the spermogonia. Very frequently the infected tissues do not become hypertrophied, but quite cease development. During this time the adjacent tissues continue to expand, resulting in invaginated areas. This is particularly common in orchard apples where infection occurs most frequently at the blossom end. In many instances the spermogonia are few in number and do not reach full maturity. Tissues with this type of infection are usually green and firm. Fruits of hawthorns, shadbushes and chokeberries are found in which the swelling and discoloration involve the whole fruit, but in such cases no or few spermogonia are produced. Many of the fructifications exhibit various stages of abortion. Symptoms of this type were obtained from inoculation tests on *Crataegus* spp. and *Amelanchier oblongifolia* toward the close of the period of susceptibility of the fruits. Of course, in some instances it is possible that more than one kind of parasite is involved and that as a result the normal course of the Gymnosporangium disease is altered.

In 20 to 40 days after inoculating the second fructifications of the fungus, the aecia, begin to make their appearance within the diseased area. They are usually produced peripheral to, or to one side of, the spermogonia; but they are often found among them. Aecia, in progressive stages of development, are easily observed during their early appearance as is shown in plate 155, fig. 1. Often no aecia penetrate the surface of the infected fruits, yet internal ones are frequently formed. This is particularly true of orchard apples but has also been observed in many other hosts. Fruits that become infected late in the period of susceptibility are commonly observed to exhibit this phenomenon. Failure to fully develop aecia may be physiological — possibly a type of hypersensitivity — or it may be due to the development of a cuticle so tough as to prevent aecia from breaking through.

Many fruits were observed in which the lesions occupied by *G. clavipes* were browned or blackened and quite rotted. From such decayed areas imperfect fungi were repeatedly obtained by culture. It seems, therefore, that these are the real cause of the discoloration and decay noted. Some have ascribed such phenomena to *G. clavipes*, but it seems erroneously so. The fact that relatively few areas infected by *G. clavipes* become decayed strengthens this conclusion. A photograph of a rust-infected area that was parasitised by an imperfect fungus is in plate 155, fig. 2.

An anomolous symptom was frequently observed on fruits of *Crataegus monogyna* infected with *G. clavipes*. The whole of the fruits and the pedicels were infected, but from the blossom ends of these fruits numerous petals and abortive structures resembling stamens developed. Here again, more than one parasitic organism may have been active in causing these symptoms.

Twigs, including thorns, infected with *G. clavipes* are commonly found on certain species of hosts (plate 156). In my experience twigs of the current season only have become infected. The early symptoms of disease on twigs are pale, yellowish green, elongated areas occurring on the young bark. The infection spreads rapidly, however, usually girdling the stem and extending up to 3 inches longitudinally. The infected portion of the twig becomes hypertrophied. Frequently a fusiform swelling results, but irregularly swollen and cankered twigs are also common. Rarely, however, rotund galls are formed on the twigs. Thorns are also subject to infection and manifest similar symptoms. Spermogonia on infected twigs usually do not reach maturity until 9 to 12 days after inoculation. They follow the same course of development as on fruits. Aecia of the rust are produced among the spermogonia as well as outside the area occupied by them. Very often they are sparsely produced, but, on the other hand, twigs are sometimes found in which the aecia are very abundant. The first aecia reach maturity on the twigs and thorns in 30 to 40 days; others are produced progressively, as was described in the case of infected fruits, for a period of about a week.

In the longitudinal advancement of the fungus in a twig, it frequently encounters a terminal or lateral bud, which in turn usually becomes infected. Subsequently, the buds are forced to develop beyond the resting stage normal for the current season. Similar phenomena were observed on buds of ornamental apples infected with *G. Juniperi-virginianae* (Crowell, 1934). Forced growth of buds caused by *G. clavipes* has been observed on a large number of hosts. The early stages of infection, evidenced by a yellow discoloration and swellings of the buds, are not observable until late in June. The abnormal development of stunted twigs and leaves results. The photographs in plate 156 show some of these symptoms in forced buds. Spermogonia in all stages of development are produced along the deformed petioles and veins of the leaves. Rarely, however, are aecia produced on the forced buds. On *C. Phaenopyrum* several twigs were found in which the infection developed systematically, as shown in plate 156, fig. 5. It is possible that infection occurred on these twigs while they were in the stage of rapid elongation. That infection was confined largely to these malformations and did not extend into the main twig substantiates this supposition.

Many twigs infected with *G. clavipes* in the spring of 1934 were examined in the spring of 1935 to determine whether or not the fungus overwintered in its aecial hosts. No instance of overwintering was found. Thomas (1933), however, reported having observed the overwintering of this rust in pomaceous hosts. Dodge (1918) reported that the aecial phase of *G. biseptatum* Ellis (*G. Botryapites* [Schw.] Kern) and of *G. fraternum* Kern (*G. transformans* [Ellis] Kern) were observed by him to be perennial. Tubeuf (1906, 1907) also noted this phenomenon on pears infected with *G. Sabinae* (Dicks) Wint.

The leaves of the pomaceous hosts of *G. clavipes* are rarely infected. When such occurs the lesions are always small and few spermogonia develop on them. The spermogonia on leaf lesions are late in appearing, and on many hosts they never reach the oozing stage. Spermogonia have been observed on leaves of *Cydonia oblonga, Amelanchier* spp., *Craetegus* spp., and *Aronia* spp. *Amelanchier oblongifolia* is the only host, however, in which I have seen aecia of *G. clavipes* on affected leaves.

On its more susceptible pomaceous hosts *G. clavipes* is very destructive. The diseased fruits become misshapen and discolored, and often fall prematurely. In the case of quince and apples the loss is primarily a commercial one and frequently very great. Indeed, growing of quinces was impossible in many sections of eastern North America due largely to the ravages of this rust. Many varieties of orchard apples are also very susceptible. Thomas and Mills (1930) report instances in which as high as 95% of the fruits of the Delicious variety in New York were attacked. Ornamental plants, such as certain species of *Crataegus, Amelanchier*, etc., whose beauty and usefulness depend in a large measure upon an abundant production of colored fruits that persist long into the winter, sometime becomes worthless because so many of their fruits are spoiled by *G. clavipes*. Twigs killed beyond the infected portion are also unsightly and they tend to materially deform the trees and shrubs because of sequent prolific sprout growth. Hawthorns have been seen in which so many twigs were killed by the rust that death resulted.

(B) **Histological symptomatology**

Tissues of pomaceous hosts infected with *G. clavipes* are usually hypertrophied and the diseased portions of fruits and twigs are often greatly enlarged; infected parts of leaves, however, are changed but little. In the fruits chiefly the outer or cortical tissues are affected. They are often greatly enlarged and many of them are more or less filled with a deep-staining material while others, fully as hypertrophied, are often quite devoid of contents. Cells towards the center of the fruit, although they show no evident hypertrophy, contain much of the deeply staining material observed in the cortical cells. Exceptions to the hypertrophy of the fruit cells as noted have been observed in the infections of many orchard varieties of apples. In such infections the earliest stages of the disease are manifested as an hypertrophy of a small number of cells. The disease soon ceases to be an enlargement; indeed, the infected region becomes inhibited in its development. The surrounding uninfected tissues, however, continue to expand in their development while the diseased area remains stunted, depressed and usually greenish.

In twigs, mainly the cortical tissues are affected. The effects are similar to those in fruits. Occasionally, however, and always in the greatly enlarged twigs, the phloem and xylem are hypertrophied. Many of their cells contain much material that stains intensely with haematoxylin.

The mycelium of the aecial phase of *G. clavipes* is found in the cortical tissues of the fruits and twigs and in the palisade and mesophyll tissues of the leaves. Haustoria are abundantly formed in the cells of the fruits and twigs but are seldom seen in cells of the leaves. Frequently, haustoria are found in close association with the nucleus of its host cell.

The peridial cells and the aeciospores of *G. clavipes* are salient features for determination of the species. *Gymnosporangium clavipes* can also readily be identified from median longitudinal sections of the spermogonium. In my investigations of the spermogonia of the genus (to be reported in a separate article) three dimensions were averaged, namely, total width, total height and the depth to which the fructification is sunken in the host tissue. The measurements for *G. clavipes* were found to be 203 $\mu \times 207 \mu \times 163 \mu$ respectively. The spermogonia of *G. clavipes* are conspicuous because of their large size and their rotund form and they are almost completely sunken in the mesophyll. A photomicrograph of spermogonia of *G. clavipes* is shown in plate 156, figure 7.

Aecia of *G. clavipes* are found most abundantly in the fruits and twigs and are seldom produced in the leaves. Aecia develop in the outer cortex of fruits and twigs and in the mesophyll of leaves. They are sunken to a depth of approximately one millimeter and are of greater diameter near the base than at the apex. Fresh aeciospores of *G. clavipes* vary in color from bittersweet-orange to flame-scarlet (Ridgway, 1912). They are irregularly rotund, verruculose and measure $32.2 \mu \times 34.4 \mu$. Peridial cells are almost white in color; the inner wall is maked by coarse ridges forming an irregular mosaic pattern. The form of peridial cells varies widely, but on an average they measure 14.5μ in width $\times$ 55.6μ in length. They usually adhere in large numbers in water mounts.

2. On Juniperus Hosts

(A) **Morphological symptomatology**

Cooke and Peck (1873) gave a description of the symptoms of *G. clavipes* on *Juniperus virginiana;* they stated: "the younger branches are slightly swollen where attacked by this fungus and the bark is scaly." For many years, however, the fungus and the disease caused on its Juniperus hosts seem not to have been understood. Thaxter (1891) after an extensive series of cultural experiments clearly identified two species that were formerly confused with *G. clavipes,* namely *G. clavipes* proper and a new species, *G. Nidus-avis.* Kern (1911), in an account of the symptomatology of *G. clavipes,* stated that the telia were "caulicolus, appearing on slightly fusiform swellings, usually aggregated, roundish, one to four millimeters, often confulent, hemispheric — teliospores two-celled ellipsoidal 18 to 26 $\mu \times 35$ to 51 μ — pedicels carotiform. Dodge (1918) stated that small witches-brooms are sometimes formed on twigs of red cedars infected with *G. clavipes.* Dodge (1922) stated that needles as well as the main trunk are also infected, and that the bark over the infected portions of the trunk becomes much thickened and blackened.

The pertinent observations on the symptomatology of *G. clavipes* reviewed in the foregoing give a clear foundation for an appreciation of the disease caused by *G. clavipes* on its Juniperus hosts. My own findings and interpretations, while they add little to what is already known will, nevertheless, trace in sequence the development of the disease and its relative importance in the various organs attacked.

On its Juniperus hosts, particularly *J. virginiana* L., the disease induced by *G. clavipes* is perhaps one of the most destructive caused by any species of the genus *Gymnosporangium.* The needles, twigs, branches and even the main trunk are attacked. Very frequently the disease occurs on the needles but infected needles are relatively inconspicuous and are often overlooked. Usually but a single crop of teliospores is produced on needles, after which they die. From the needles, however, the fungus often migrates to the twigs and it is on these that the disease is most frequently found. Twigs may also become infected directly. On twigs the disease appears as slightly fusiform swellings covered by a flaky, darkened bark. Usually by the end of four to six years most of the infected twigs die. Occasionally, however, the infected twigs survive for a longer period and the larger limbs are distorted and covered with a heavy, cracked and blackened bark. If the diseased portion of a branch is near the main trunk the latter is liable to infection by the fungus advancing along the cortex. Infections of *G. clavipes* on the main trunk of red cedars are easily mistaken for one of the diseases caused by other species of the genus, because vertically elongated, often irregular, blackened, heavy-barked bulges are typical for diseases caused by several species of *Gymnosporangium*. Fructifications are, in my experience, necessary to identify the causal organism on trunk lesions.

That the disease caused by *G. clavipes* is very destructive to its telial host is evident since all organs attacked are killed usually in a few years. Trunk infections of many years standing are not uncommon, to be sure; but trees bearing such burdens show evident symptoms of poor health. Recently, I came upon a very striking demonstration of destruction of red cedars infected with *G. clavipes*. Several years ago, an estate owner cleared a natural grove of cedars of all other trees and shrubs. *Gymnosporangium clavipes* was very abundant on the twigs, branches and main trunks of certain of these cedars. Following the unusual cold of the winter of 1933-34 every tree that was heavily infected with *G. clavipes* died entirely or in large part, while all of the trees in this group that were not infected survived. An examination of the cedars in the surrounding uncleared lands revealed complete destruction of trees that were heavily infected with *G. clavipes*. As the only variable seemed to be the relative abundance of infections the loss seemed clearly attributable to the infection of *G. clavipes*.

(B) Histological symptomatology

Dodge (1922) gave a very complete account of the histological symptomatology of *G. clavipes*. A review of his paper is presented here. Dodge stated that "infection takes place on the proaxial side of the young leaf, or directly on the young stem at the base of the leaf — after entering the leaf, the mycelium invades the region between the cuticle and the cellulose walls of the epidermis on the proaxial side. The effect of the fungus on this part of the cell wall is usually marked by considerable swelling and the disorganized substances take the stains very readily — the fungus explores and feeds in the cuticularized layer, but it may go deeper and invade the palisade-mesophyll tissue. Haustoria are found in the epidermal cells, sometimes even in the guard cells of the stomata."

Young stems are "susceptible to infection, either directly or through the invasion of the fungus by way of the leaf axils." The mycelium occupies a cancellate portion of the periphery of the young cortex. The mycelial "strands actually interlace, weaving in and out around the veins [leaf traces] of the leaves and forming a closed network system in the cortical region of the young stem." After the leaves are shed the fungus, closing the gaps, may be found in the cortex around the entire circumference of every section. In the main trunk, infections are confined to a portion only of the circumference.

My findings with respect to the histological symptomatology agreed in detail with those of Dodge. My examination included the leaves and twigs of *Juniperus virginiana* as well as infected twigs of all other Juniperus hosts. Certain additional remarks with respect to the fructifications are also recorded.

The telia of *G. clavipes* arise at irregular intervals from aggregated masses of the mycelium on the phellogen. The telia first appear early in April in Massachusetts. In youth they are a deep-reddish color, expanding upon gelatinization to regular pulvinate sori. After two or three gelatinizations, however, the sori change their deep red color to a yellowish red and their shape is very irregular. Five to six gelatinizations occur during the season, after which the telia drop from their host.

VI. LIFE HISTORY STUDIES OF GYMNOSPORANGIUM CLAVIPES C. AND P.

The life history of *Gymnosporangium clavipes* is essentially the same as that of other species of the genus. It differs in certain details only from the life history of the more generally known species *G. Juniperi-virginianae*. A review of the extensive literature dealing with the life-history of *G. clavipes* shall be confined to the more pertinent reports of former investigators.

Schweinitz (1832) described the aecial phase of a rust which he found occurring "rarissime in germinibus Rosae" as *Caeoma* (*Peridermium*) *germinale*. Kern (1911) reported the determination of the host of this rust to be an error for a species of *Crataegus*. Cooke and Peck (1873) gave an account of the telial phase of a rust which they called *G. clavipes* occurring on *Juniperus virginiana* L. These two rusts were considered to be distinct species until Thaxter (1887) showed from the results of controlled cultural experiments that the spermogonial and aecial stages on pomaceous hosts were in reality genetically connected with the telia stage on red cedars. Following this basic step many observations have been reported with respect to details in the life history of *G. clavipes*.

In the development of the rust on pomaceous hosts Farlow (1886) and Thaxter (1887) found that 10 and 11 days respectively elapsed between the date of inoculating and the first appearance of spermogonia. Thomas (1933) stated that the first symptoms of disease on "relatively resistant" apple foliage were observed 10–18 days after inoculating but that spermogonia were never formed on the lesions. In contrast he found that symptoms appeared in 4–6 days and spermogonia in 13–15 days after inoculating "susceptible" foliage of *Crataegus* sp. and further that aecia were formed sparingly along the larger veins only of the infected leaves. Thaxter (1887) determined from his cultures that approximately 30 days were required for the maturation of aecia on young shoots of *Amelanchier canadensis*. Miller (1932) and other authors observed that spermogonia were frequently abortive in orchard apples and that aecia rarely matured in the fruits.

These observations while they differ greatly when considered separately are nevertheless in harmony when reviewed in the light of more complete knowledge of the behavior of the rust. From my cultural experiments on hosts in several genera, the same variations as reported in the foregoing were observed. These variations seemed to be correlated with two phenomena, — first, the relative susceptibility of the host plants and second, the stage of development of the diseased parts at the time of inoculating. The rust developed more rapidly on the more susceptible hosts and more slowly on less susceptible ones. In fact, on very resistant hosts, as certain orchard apples or on resistant organs as, for example, the leaves of nearly all hosts, longer time was required for the maturation of the fructifications; not infrequently these reached an imperfectly developed stage only.

The average time required for the maturation of spermogonia of *G. clavipes* on fruits and twigs was from 7 to 10 days. The beginning of spermogonial exudation was taken as the criterion of maturity. On individual lesions spermogonia continued to be produced for a period up to 3 weeks. The production of exudate by any one spermogonium continued up to about 7 days, after which the spermogonium became filled with long filaments, and soon died, usually turning black. Others in the lesion followed these developments. Spermogonia of *G. clavipes* were sub-epidermal in origin and position; they were reddish in color and among the largest of the genus. Details of average measurements of their size have been given on page 385.

The aecial primordium of *G. clavipes* is located deep in the cortical tissues of fruits and twigs and in the mesophyll of leaves. It is typical for the genus as is also the mycelium and haustoria. From thirty to forty days after inoculating, aecia of *G. clavipes* reached maturity and penetrated the epidermis of the host among or close by the spermogonia. Aecia were usually developed progressively over a period of a week or more. Upon their first appearance, about June 1 in Massachusetts, they had the form of short, blunt, white cylinders. One or two days later the white peridia were ruptured irregularly, usually with the loss of the cap cells, exposing and releasing the enclosed reddish aeciospores. Various stages of this phenomenon are shown in plate 155, fig. 1. The aecium of *G. clavipes* is broader at about midway between the hymenium and surface of the host than at the surface of the host itself. It is evident, therefore, that a crowding of the aeciospores occurs at the zone of constriction. Dodge (1924) associates these phenomena with a mechanism for the forcible discharge of aeciospores.

The peridial cells of *G. clavipes* are broadly rectangular and measure 14.5 μ × 55.6 μ with extremes of 33.4 μ to 83.5 μ × 10.4 μ to 23.4 μ. Their inner and thicker walls are ornamented with low interconnecting prominences forming irregular mosaic patterns. Peridial cells are of much diagnostic value as Fischer (1891) and Kern (1910) demonstrated. Those of *G. clavipes* may be easily identified by their markings, their size and their form. Peridial cells of *G. clavipes* usually remain flat in water mounts and adhere forming a large sheet of cells.

Aeciospores of *G. clavipes* are exceptional for the genus in their remarkably intense color. By comparisons of fresh aeciospores the color was determined as varying from bittersweet-orange to flame-scarlet according to Ridgway's (1912) color standards. With increase of age of the mature spores, however, their color gradually changes to orange and yellows. In old herbarium material they are frequently almost colorless. In many of the better preserved specimens the reddish color still is conspicuous. Aeciospores of *G. clavipes* are among the largest of the genus. They measure 32.2 μ × 34.4 μ with extremes of 28.4 μ to 42.3 μ × 26.7 μ to 37.4 μ. Their outer surfaces are ornamented with numerous, tiny, low papillae.

The problem of germinating aeciospores of species of *Gymnosporangium* has been given a great deal of attention. Difficulty has been experienced in germination of aeciospores of many species. Several investigators have shown that a period of rest at low temperature contributed greatly to the germinability of aeciospores of certain species of *Gymnosporangium* (Fukushi, 1925; Miller, 1932). Thomas and Mills (1929) reported moderate germination of aeciospores of *G. clavipes* stored for twelve weeks at 3° C. Thomas (1933) tested the germinability of aeciospores of *G. clavipes* that were precooled for various lengths of time at various temperatures as well as aeciospores that were not precooled. The highest germination was obtained from spores that "were mounted at 18° C. without precooling." Thomas also demonstrated that aeciospores kept dry at 3° C. rapidly lost the property of germination. It was found, however, that a small number of aeciospores remained viable in aecia in fruits throughout the winter. It should also be remarked that Professor J. C. Arthur observed internal aecia of *G. clavipes* in fruits of orchard apples. Dr. Arthur stated in a letter to Dr. Steinmetz, who forwarded the material to him, that aeciospores removed from internal sori germinated in the usual manner.

In my studies of the germination of aeciospores of *G. clavipes* it was found that they germinated readily in a moist atmosphere at room tem-

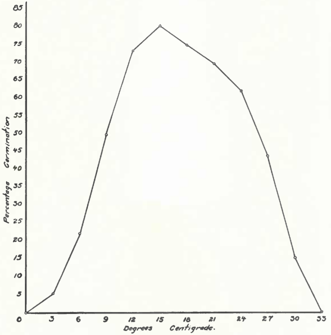


FIGURE 2. Graph showing the Germination of Aeciospores of *Gymnosporangium clavipes* C. and P.

perature at any time during the summer and fall seasons. Careful studies of germination revealed that they germinated over essentially the same range as did most species of the genus studied to date. Optimum conditions for germination in distilled water on glass slides were reached at about 15° C. The results of the tests are shown in figure 2 and in table 4.

TABLE IV. GERMINATION OF AECIOSPORES OF G. CLAVIPES

Temp.	No. of spores counted	No. of spores germinated	Percentage of germination
0° C.	1000	0	0
3	1000	53	5.3
6	1000	224	22.4
9	1000	506	50.6
12	1000	740	74.0
15	1000	807	80.7
18	1000	750	75.0
21	1000	698	69.8
24	1000	625	62.5
27	1000	413	41.3
30	1000	152	15.2
33	1000	0	0

Apart from the irregularities in the aecial phase that were discussed under the heading of symptomatology, an unusual development was observed in the aecia on fruits of *Crataegus* sp. collected by Prof. J. H. Faull in Pennsylvania. Some of these aecia and aeciospores appeared normal in all respects. Certain of the aecia were internal with the hymenia oriented in various directions. All of these latter and many of the aecia that developed in a normal position were filled with irregularly produced aeciospores and aeciospore chains. Cytologically either one or two nuclei were present in the cells. The cell contents were irregularly interspersed with vacuoles and deep-staining materials. Camera lucida drawings of two aeciospore chains are shown in plate 157, figure 2.

Aeciospores of *G. clavipes* are primarily wind borne. They are distributed throughout the growing seasons and probably germinate and infect the alternate hosts shortly after inoculation.

Previous to 1910, however, little investigative work had been conducted on the telial phase of *G. clavipes*. Arthur (1912) sowed aeciospores of *G. clavipes* on the common juniper and reported successful cultures. Dodge (1918) traced the life cycle of *G. clavipes* under controlled conditions from the telial phase on red cedars to the aecial phase on *Crataegus Oxyacantha*, thence back to the telial phase on red cedars. Dodge found that few telia were produced in the spring following inoculation but that many developed in the second spring. Inoculations made during the present investigations substantiated these findings. In addition it was shown that inoculations made on July 1, August 10 and October 3 all resulted in abundant infection, indicating that in nature aeciospores are a menace throughout their entire period of production.

Infection of the telial host was first described by Dodge (1922).

Dodge stated that entrance of the germ tube was gained through the adaxial surface of the leaves and tender epidermis of the twigs. In the leaves of its Juniperus hosts the mycelium of *G. clavipes* is confined almost exclusively to the epidermal cells. In twigs it is restricted to the phellogen cells — a most unusual limitation for the mycelium of a species of *Gymnosporangium.* Within the infected cells characteristic, binucleate, sac-like haustoria are formed. They are abundant, usually occurring singly but frequently in twos or threes. Telial sori of *G. clavipes* arise from masses of the mycelium. In leaves the mycelium usually dies after the production of one crop of spores, but in twigs the fungus is perennial for several years. After each successive crop of teliospores a new phellogen layer is formed immediately beneath the sorus. The surrounding vegetative mycelium then grows over this new tissue. It is from the mycelium on the older phellogen that the telium for the ensuing spring is produced. In certain microscopic sections it is possible to observe progressively (a) the dead mycelium on partially sloughed-off phellogens, (b) sori of the present season as well as (c) the primordia of sori for two seasons to come. The camera lucida drawing in plate 160, fig. 1 was made from such a section.

Telia of *G. clavipes* are produced on leaves and on the bark of various-sized branches and even the main trunk of red cedars. They were never observed on branches of red cedars more than one-half inch in diameter. Upon their early appearance telia of *G. clavipes* are aggregated, pulvinate in form, 2 to 5 mm. across and are distinctly bright reddish in color. During rains in the spring the telia swell to regular gelatinous forms as is shown in plate 159. After three or four gelatinizations the telia lose their regular form and deep-red color, becoming shapeless yellowish-red masses. After 6–8 gelatinizations the telia drop from the infected parts.

The development of teliospores of *G. clavipes* is essentially the same as Dodge (1918, 1922) reported for this and other species of the genus. Camera lucida drawings made during these investigations of teliospores in various stages of development are shown in plate 160.

Teliospores of *G. clavipes* are at once distinguished by the swollen pedicels near their bases. No other species of the genus in eastern North America has this characteristic. Certain data in regard to teliospores of *G. clavipes* are of interest. Both one- and two-celled teliospores are produced. In a count of 1000 spores, 94.8% were found to be two-celled while 5.2% were one-celled. Two-celled teliospores have one germ pore in each cell. In the upper cell the germ pore is apical while in the basal cell the germ pore is located near the pedicel. In other respects one-celled teliospores resemble the two-celled ones in all but the septum. One-celled teliospores have the germ pore at the apex. In the telium of *G. clavipes* both thick- and thin-walled spores were found. Thick-walled spores are more numerous and are always produced on the outer surface of the telium. Almost invariably one-celled teliospores are thick-walled. Thin-walled teliospores are located within or beneath the layer of thick-walled spores. Measurements were made of the lengths of the upper and basal cells, the total length and the width of teliospores of *G. clavipes*. The upper cell measured 23.0 μ with extremes of 16.5 to 33.0 μ, the basal cell 21.2 μ with extremes of 14.9 to 33.0 μ, the total length was 44.5 μ with extremes of 33.0 to 57.8 μ and the width 22.7 μ with extremes of 16.5 to 33.0 μ. Single-celled spores measured 19.7 μ in width by 33.4 μ in length with extremes of 26.4 to 51.2 μ × 14.9 to 29.7 μ.

When teliospores of *G. clavipes* first break through the cortical covering layer of the host, they expand but little when wetted and the teliospores do not germinate. From 1–3 weeks after their first appearance, however, the telia expands fully to a regular pulvinate form and the teliospores germinate in great abundance.

Several workers have reported the results of their investigations on germination tests of teliospores of *G. clavipes*. Weimer (1917) formulated a general curve of germination percentages obtained at various temperatures and stated that it applied to the germination of teliospores of *G. clavipes* as well as teliospores of other species of *Gymnosporangium*. The extreme temperatures found by Weimer were 7° C. and 29° C. and the optimum temperature was between 22° C. and 25° C. Miller (1932) found the extreme temperatures of germination to be 4° C. and 32° C. and the optimum germination at 25° C. He also investigated the phenomenon of the maximum rate of germination and found that when telia of *G. clavipes* were immersed in water for 25 minutes and removed to a moist atmosphere they discharged basidiospores in considerable numbers within two hours. It was also found that when telia were mounted in moist cotton and kept at 25° C. an abundant germination of the teliospores and the beginning of basidiospore formation occurred after an interval of eight hours.

Thomas also investigated the time required for and the rate of germination of basidiospores. He stated that basidiospores submerged in water at room temperature developed germ tubes equal in length to the spore in two hours and from four to six times their diameter in ten hours. Basidiospores were also mounted on a moistened leaf of *Crataegus* and held at 25° C. with the result that germ tubes reached a length of five to seven times their diameter in eight hours.

Farlow (1886) reported the production of secondary basidiospores from primary basidiospores of *G. clavipes*, a phenomenon that has frequently been reported for other species of the genus.

Beyond observing the usual germination of the teliospores of *G. clavipes*, a process common to other species, no further studies were made on the phenomenon. It was observed, however, that germination occurred in the field when the telia remained gelatinized for periods of

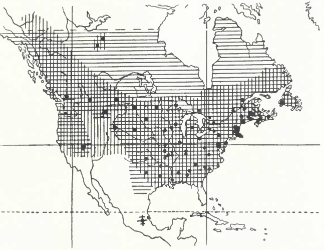


FIGURE 3. Geographical Distribution in North America of *G. clavipes* and its Hosts. The pomaceous hosts of *G. clavipes* shown as vertical lines. The Juniperus hosts of *G. clavipes* shown as horizontal lines. Stations for *G. clavipes* shown as dots. Note the extreme northern limit in northern Alberta, Canada, and the extreme southern limit near Mexico City, Mexico.

two hours or longer. Four to six gelatinizations were usual during the season and basidiospore dissemination occurred at most, if not at all, of these.

It is essential to the production of infection that the pomaceous hosts are within their period of susceptibility at the time of inoculation. As the period is very short in many species, the failure for the coincidence of basidiospore dissemination within this period may be held responsible for the variable abundance of spermogonia and aecia on certain pomaceous hosts in different years. Crowell (1935) reported unusual developments of the aecial phase of this and other species of *Gymnosporangium* in the very dry spring of 1935. In the spring of 1935, no rains sufficient to cause gelatinization of telia of *G. clavipes* occurred during the flowering period of most pomaceous hosts; most fruits becoming immune before inoculation took place. This resulted in a very limited number of infected fruits and the late appearance of the rust generally.

Although the host relationships for the perpetuation of *G. clavipes* are found over the greater part of the temperate northern hemisphere, nevertheless, so far as I am able to learn, this rust is not known outside of North America. Reported stations for this rust are most abundant in the eastern part of this continent as shown by dots on the outline map of North America in fig. 3. The rust has been collected, however, in widely separated stations outside the region of greatest concentration, an unusual feature in the distribution of any species of this genus.

Gymnosporangium clavipes has been reported from southern Newfoundland, from all the provinces of Canada except Prince Edward Island, from all the states of the United States except Arizona, California, Idaho, Kansas, Minnesota, Nevada, New Mexico, North Dakota, Oregon, South Dakota and Washington. It is also reported from Mexico State in Mexico. No other species of *Gymnosporangium* is known to have a longitudinal range extending from central Mexico State to northern Alberta in Canada. An even greater range is possible on the basis of host distribution. It would be very interesting as well as of much practical value to determine the phenomena responsible for the distribution of a rust within a portion of the territory occupied by both host groups.

VII. CONTROL MEASURES APPLICABLE TO GYMNOSPORANGIUM CLAVIPES ON POMACEOUS AND ON JUNIPERUS HOSTS

Prophylactic measures to control *G. clavipes* have been largely an adaptation of those practiced for the control of the cedar-apple rust diseases caused by *G. Juniperi-virginianae*. The results obtained in control work have been essentially parallel for both of these diseases, namely, fungicidal control as practiced was found unsatisfactory, while eradication of Juniperus hosts gave excellent protection to pomaceous hosts.

Halsted (1893) reported the destruction of quince, apple, hawthorn and shadbush fruit by *G. clavipes* in New Jersey and recommended remedial measures. Concerning the disease Halsted wrote: "an enemy is beyond the fence; therefore, go out and slay him with an axe." This was the earliest record that I found regarding the pathenogenicity and control of this rust. Bailey (1894) also recommended the destruction of red cedars as a control measure. He gave evidence to show that spraying thoroughly (with Bordeaux ?) was of considerable value. Many other authors stated that eradication of red cedars offered the most satisfactory solution to the control of this rust.

My own investigations on control measures applicable to *G. clavipes* were carried out simultaneously with those for the control of the cedar-apple rust fungus, *G. Juniperi-virginianae* (Crowell, 1934). Studies in this problem included an exploratory investigation of numerous fungicides with respect to their control value both on pomaceous hosts and on red cedars. The most promising of these fungicides were then tested on an extensive experimental scale on numerous trees under various weather conditions. The fungicides were applied to red cedars (a) to prevent germination of the teliospores, (b) to protect them from infection by aeciospores, and (c) to pomaceous hosts as a protection against basidiospore infection.

(A) Fungicidal applications on red cedars to prevent germination of teliospores

On the Lyman estate, Canton, Massachusetts, *Gymnosporangium clavipes* was in very great abundance and exploratory tests with several fungicides were made there. In table V are enumerated the sprays and dusts that were used in these tests.

TABLE V
SPRAY AND DUST MATERIALS USED IN EXPLORATORY TESTS

Bordeaux	3:3:50, 4:4:50, 6:6:50
Linco colloidal sulfur[1]	¼%, ½%, 1%, 2%, 3%
Lime-sulfur	1:30, 1:40, 1:50, 1:70
Soluble palustrex[2]	1%, 2%, 3%, 4%
" " A.	" " " "
" " B.	" " " "
" " C.	" " " "
Sunoco oil[3]	2%, 4%
50% Sunoco oil and 50% soluble palustrex	2%, 4%
50% Sunoco oil and 50% soluble palustrex B.	2%, 4%
80% Sunoco oil and 20% copper resinate	2%, 4%
80% Sunoco oil and 20% soluble palustrex	2%, 4%
Kolo base	
Kolo dust	
Pomo green	
Sulfur dust	

[1]Obtained from Linder and Co., 296 North Beacon St., Boston, Mass.
[2]Obtained from E. W. Coolidge, Jacksonville, Florida.
[3]Obtained from Sun Oil Co., Boston, Mass.

All of these spray and dust materials were first applied to potted red cedars in the greenhouse in the spring. None of them caused burning of the young foliage. In the field the sprays were applied to twig lesions as follows: (1) before the telia had emerged, (2) just after the telia had emerged, and (3) after one, two or three gelatinizations of the telia, but always when the telia were dry. Telia to which the sprays were applied were brought into the laboratory for examination; smear slides were made of the spores and examination was completed shortly after their arrival. It was not the purpose of this examination to determine the relative value of each spray, rather the purpose was to determine which ones would prevent germination of the teliospores. The most satisfactory sprays were soluble palustrex B. at 4% and Linco colloidal sulfur at 1%, 2% and 3%. In testing these sprays further it was found that this colloidal sulfur at 2% and 3% was the most constant in its reactions. Colloidal sulfur was, therefore, chosen for the experimental work that followed. It should be added, however, that colloidal sulfur at 1% greatly reduced the amount of germination; colloidal sulfur at 2% completely prevented germination of the teliospores of *G. clavipes*. Colloidal sulfur at 3%, therefore, was unnecessary.

In April 1933, many telia of *G. clavipes* were sprayed upon their first appearance with colloidal sulfur at 1% and 2%. The effect of the spray was determined by gathering several sprayed telia three days after the application and also unsprayed telia at the same time for controls, thoroughly wetting and keeping them in a moist chamber over night. When germination was abundant a spore print resulted, but when no spore print was formed a smear slide was made and the teliospores examined under the microscope. The unsprayed teliospores always germinated in abundance. Teliospores sprayed with colloidal sulfur at 1% strength germinated to some extent but few basidiospores germinated. Telia sprayed with 2% colloidal sulfur showed no germination of the teliospores.

After the rain following each spray application, telia were again gathered and immediately tested. The controls germinated in abundance. The telia sprayed with colloidal sulfur at 1% and 2% germinated to a slight extent. Some change, therefore, was called for in order to control this small amount of germination. Certain substances were used to lower the surface tension of the spray material which might aid its penetration into the telium. Spreaders were tried but with no success. Calcium casienate, a combined spreader and sticker, was next used in a series of experiments. A new lot of telia was sprayed with colloidal sulfur at the strength of 2% plus 2 pounds of calcium casienate per hundred gallons of water. Telia tested in the laboratory showed a high percentage of germination for those that were unsprayed and no germination for those that were sprayed. In subsequent rains none of the teliospores were observed to have germinated nor did the telia at any time regain the property of gelatinizing fully, although they did gelatinize to a slight extent.

(B) Fungicidal applications on red cedars as a protection against infection by aeciospores

Fungicidal protection to red cedars against infection by aeciospores of *G. clavipes* has been demonstrated on potted red cedars in greenhouse trials. In these tests Linco colloidal sulfur at the strength of ½% or 6 pounds per 100 gallons of water only was used. Twenty-five red cedars twelve to eighteen inches high were sprayed with the fungicide. These and twenty-five unsprayed red cedars were thoroughly wetted with a strong stream from a hose the following day. They were then heavily inoculated with fresh aeciospores of *G. clavipes* and kept in a moist chamber for five days. In the spring of the second year after inoculating, each of the unsprayed plants produced an abundance of sori — a total of more than one thousand separate infections — while but a single infection was found on the sprayed plants.

In field experimentation, three applications (one each in July, August and September) were made to a group of red cedar trees near heavily infected hawthorns. Examination of the twigs the second spring after spraying showed a very marked reduction in the number of lesions produced. It was estimated after comparing the amount of infection on unsprayed red cedars in the vicinity that about 75% control was obtained.

The use of fungicidal means of protecting red cedars in practice should be guided, along with other considerations, by two important factors, namely, (1) the date of maturity of the aecia and (2) the duration of aeciospore production.

The first of these will vary with the season and with the time of blossoming of the host. In Massachusetts aecia reach maturity early in June. The second and the more variable of the two is the period of active aeciospore production. The duration of this period is dependent upon the date of maturity of the fruit of the associated pomaceous hosts. As the fruit of *Amelanchier* ripen and drop about the middle of July in Massachusetts and aeciospore production ceases at this time, protective sprays, therefore, need be applied for but a brief period. Twig infections, if present on the shadbushes, should be carefully removed, because aeciospore production will continue on them throughout the entire growing season. On the other hand fruits of *Crataegi* and most other pomaceous hosts do not reach maturity until late fall and aeciospore production usually continues during this period.

(C) Fungicidal applications on pomaceous hosts as protection against infection by basidiospores

Fungicidal protection of pomaceous hosts from infection by *G. clavipes* has been conducted through field experiments only. Individuals of *Amelanchier oblongifolia* were sprayed with Linco colloidal sulfur at the strength of ½% or 6 pounds per 100 gallons of water after each of three rains during the early development of the flowers in the spring. Spraying was begun just before the first rain after the flower clusters began to unfold; the last application was made when about three-fourths of the petals had fallen. The protection afforded these plants was excellent. Counts of infected fruits showed that 98% of them remained free from infection, while 95% of the fruits on unsprayed plants nearby were infected. Certain other experiments with this same material on hawthorns and apples have not met with the same success. Excellent protection was afforded certain of the tested trees while practically none was obtained on others. It is believed that this irregularity can be overcome. It is not yet known just when infection occurs nor the limits of the period of susceptibility of many of the host species. A knowledge of these is necessary to satisfactory control. The value of thorough spraying cannot be over-emphasized.

Gymnosporangium clavipes is largely a fruit parasite on its pomaceous hosts, and a difficulty arises with respect to spraying while the hosts are in flower. Sprays may be applied at any time except for a few days immediately after the unfolding of the petals. It is at this time that pollination occurs. The problem of controlling the disease caused by *G. clavipes* on orchard apples has not as yet been given attention. A project to determine the limits of the period of susceptibility and modifications, if any, of the spray schedule now generally used in apple orchards is planned.

In addition to protective spray applications for the control of *G. clavipes*, other means of attack may be employed. In ornamental plantings of red or common cedars judicious pruning of infected branches and twigs is very effective. Not only will pruning remove the disease from infected trees but will afford a degree of protection to neighboring pomaceous hosts as well. The work is best done in the spring when infected parts are clearly marked by the presence of telial sori. Small twigs may be cut off below the nearest uninfected shoot, but it seems advisable that larger branches be removed well below visible lesions; in many instances this may be back to the main trunk.

The possibility of freeing infected trunks of red cedars from disease has been the subject of an, as yet, incomplete investigation. It will be recalled that the mycelium of *G. clavipes* is localized on the phellogen layer only of red cedars. Experimentation was conducted for the purpose of investigating the possibility of removal of the fungus by removing the outer bark. For this purpose a coarse wood rasp was used, and the bark, over and for about an inch around the lesion, was scraped off and painted with shellac and later with an antiseptic tree dressing. The work was done in March and no telia developed in the spring nor did the trees show visible symptoms of injury the following growing season. Only one season has passed since the undertaking and thus far the operation seems successful.

Eradication of Juniperus and of pomaceous hosts, while often limited in practice, is; nevertheless, a very effective adjunct or under certain conditions the most effective means of controlling this rust. The low growing types of junipers, such as *J. communis* and varieties and *J. horizontalis*, are frequently weed plants. In some localities in the Annapolis valley of Nova Scotia wild junipers have been eradicated for one-quarter to one-half mile around commercial orchards with the result of almost complete protection to the susceptible varieties of apples. From their observations in an apple orchard in Maine, Steinmetz and Hilborn (1934) state: "the approximate shortest distance between the infected junipers and infected apple trees is 3900 feet. The extreme distance between infected hosts is over 4500 feet." Various environmental factors, however, may influence the distance that the contagion will travel as I have already discussed in another paper (Crowell, 1934 pp. 202–209) and these should be considered in plans for eradication. As an expedient to the protection of either pomaceous or Juniperus hosts, all nearby hosts that can be dispensed with should be removed. Elaborate protective measures may be largely upset by a single weed-host plant located near valued plantings.

VIII. RECOMMENDATIONS

The problem of controlling the diseases caused by *G. clavipes* on pomaceous and on Juniperus hosts usually varies with the relative value of the infected plants and with the interest of the owner. The problem, however, merits wider attention. The moral obligation of consideration for a neighbor's earnest endeavors to improve a serious situation is too often thought of very lightly. Several practical control measures have been demonstrated. These are as follows:

1. *Selection of immune or highly resistant species and varieties for planting.* Attention should be given not only to avoiding hosts of *G. clavipes* but to avoiding hosts of other species of *Gymnosporangium* native in the vicinity. Host lists for all of the species of *Gymnosporangium* in eastern North America are now rapidly nearing completion. MacLachlan (1935) has shown that practically the whole of the genus *Crataegus* is more or less susceptible to attack by *G. globosum*. Many species and varieties of hawthorn are also susceptible to *G. clavipes* as shown in the present paper and to another widespread species common in this region, namely, *G. clavariaeforme*. (The presentation of results of investigations on this species is planned for an early publication.) Species and varieties of *Crataegus*, either native or foreign, cannot be planted in the vicinity of Juniperus hosts in eastern North America with expectation of their remaining entirely free from infection by one or more species of *Gymnosporangium*. In the genus *Malus*, Crowell (1934) has shown that all of the native species and varieties and one foreign species (*M. sylvestris*) can harbor and reproduce the cedar-apple rust fungus *G. Juniperi-virginianae*. The present paper and that of MacLachlan (1935) give but few additional species and varieties of *Malus* that are hosts to *G. clavipes* and *G. globosum*. All other Eurasian species and varieties do not harbor and reproduce the rusts native to this region. In the genus *Amelanchier* one species only, namely, *A. amabilis*, has proved to be highly resistant to all of the *Gymnosporangia* in this region. Other species and varieties are subject to infection by one or more species of *Gymnosporangium*.

Few hosts for the native *Gymnosporangia* were found in the genera *Pyrus* and *Sorbus* while practically all of the species and varieties tested in the genera *Aronia, Crataegomespilus, Cydonia* and *Photinia* were susceptible. Information as to the hosts in other pomaceous genera is too meagre for general recommendations at this time. For specific host lists together with the relative data of various hosts attention is directed to the present and the following publications now available. For hosts of *G. globosum*, (MacLachlan 1935). For hosts of *G. Juniperi-virginianae*, on ornamental apples (Crowell 1934); on orchard apples (Crowell 1935).

Of the telial hosts, with the exception of *Juniperus virginiana, J. horizontalis, J. scopulorum* and several of their varieties among the native species and *J. communis* and *J. Sabina* and several of their varieties among the foreign species, all other species and varieties tested (see p. 379) may be considered as desirable for plantings in this locality.

2. *Planting a screen of tall non-susceptible trees about groups of alternate host plants.* Groups of alternate host plants in close proximity may be effectively protected from infection by surrounding them with a screen of tall trees. Densely branching trees, as many of the conifers, are particularly effective. The corollary is also true. Groups of alternate host plants may be grown in close proximity if planted among taller non-susceptible trees. These phenomena have frequently been observed in nature. A fuller discussion is given on page 204 of an account of the cedar-apple rust disease by Crowell (1934).

3. *Eradication of pomaceous or Juniperus hosts.* To be most effective eradication of either pomaceous or Juniperus host plants should be complete over a radius of at least one-half mile. Even though eradication is carried out over this area, complete protection is not assured. Thus, the direction of winds during the time of spore production, continued humidity and the location of the source of inoculum are factors that may tend to offset or vary the results. A high degree of protection may be expected from eradication, however. If eradication cannot be complete, partial eradication of host plants will reduce the amount of inoculum and will therefore aid in controlling the rust. All wild or scrubby pomaceous as well as Juniperus hosts that can be dispensed with should be removed.

4. *Removal of infected parts of host plants.* As infections in Juniperus hosts are perennial for several years removal of diseased twigs and branches will contribute materially to control measures. Diseased twigs should be removed well below visible lesions. In the case of infected branches it may be necessary to remove them back to the main trunk. Similarly, on pomaceous hosts diseased fruits and twigs may be removed as an aid to control measures. Unless diseased parts are few in number and can be easily and thoroughly picked by hand, the undertaking is not recommended.

5. *Removal of the fungus from infected trunks of red cedars.* Incomplete experimentation has shown that infections on the main trunk of red cedars may be satisfactorily removed. This is done by rasping off the outer bark down to the living outer tissues, painting the wound with shellac and later with an antiseptic tree dressing. The practice is limited to trunk lesions and is not generally recommended. Removal of diseased parts or the disease from parts of Juniperus hosts is best accomplished when telia are present on infected areas to guide one in the work.

6. *Protective spray applications.* Protective spray applications to pomaceous plants for protection against infection by basidiospores of *G. clavipes* are of value during the early stages of development of flowers

and fruits. Linco colloidal sulfur was the only fungicide tested for this purpose. Applications at ½% strength or 6 lbs. per 100 gallons of water plus a casein sticker are recommended. The first application should be made before the first expected rain as the cluster buds are breaking. Subsequent applications of the same strength should be made at 7–10 day intervals until most of the petals have dropped. More frequent applications may be necessary if rain is unusually heavy or prolonged, or if flowers have expanded with unusual rapidity.

Spray applications to Juniperus hosts should be confined to the period of aeciospore production on neighboring pomaceous hosts, and should be made after each two or three rains. In Massachusetts aeciospores are first liberated about June first. In the case of most species of *Amelanchier* the fruits are ripened and dropped by the middle of July. Therefore, spray applications need not be continued longer than this time, provided that *Amelanchier* species are the only hosts in the vicinity. Care should be taken, however, to remove all infected twigs from these plants for aeciospore production on them continues throughout the entire growing season. On most other hosts, aeciospores continue to be liberated during the entire growing season. Under such conditions spray applications should be continued until the end of the growing season.

The telia of *G. clavipes* are fully exposed one to two weeks before susceptible parts of pomaceous hosts are released from their buds. This affords an opportunity to attack the telia before it is possible for them to cause infection. Two spray applications of colloidal sulfur at the strength of one percent or 10–12 pounds per one hundred gallons of water are recommended. The applications should be made before buds of pomaceous hosts burst. Each application should be made just after a rain in which the telia are fully expanded and are beginning to dry. At this time they expose the greatest surface and absorb water with much avidity. It should not be expected that the fungus in the twigs and branches will be killed by this means, the telia of the present season only will be destroyed.

The relative merits of each of the foregoing means of control for *G. clavipes* will vary with individual situations. Single or a combination of methods of control may be employed. Selective planting methods will doubtless give the most permanent results but are limited in their adaptation. Methods of eradication (3, 4 and 5) may be employed where the plants are of such high value, or are few, or the rust sufficient sparse as to make hand labor practical. Spray applications are perhaps most wide in applicability since the practice of spraying is so general.

IX. SUMMARY

1. Inoculations with *Gymnosporangium clavipes* C. and P. and examinations for infection were made on approximately seven hundred species and varieties in thirteen genera of pomaceous hosts. These genera were *Amelanchier, Amelosorbus, Aronia, Chaenomeles, Crataegomespilus, Crataegus, Cydonia, Malus, Photinia, Pyrus, Sorbaronia, Sorbopyrus* and *Sorbus*. The genera *Comptonia* and *Myrica* as represented in the Arnold Arboretum were also inoculated. The results show that hosts were distributed in eleven of these genera, namely, *Amelanchier, Amelosorbus, Aronia, Chaenomeles, Crataegomespilus, Crataegus, Cydonia, Malus, Photinia, Pyrus* and *Sorbus*. Although pomaceous hosts of *G. clavipes* are found over the entire temperate region of the northern hemisphere, the fungus is confined to North America.

2. Investigations made on the period of susceptibility of flowers and fruits of certain pomaceous hosts showed that the flowers and fruits were susceptible after they were released from their buds for a brief period only. The more susceptible hosts were susceptible for a longer period than less susceptible hosts.

3. Inoculations and examinations for infection on the genus *Juniperus* in the Arnold Arboretum and accounts in the literature showed that a total of eight species and varieties were susceptible to *G. clavipes*. Hosts were found in two sections of the genus *Juniperus*. These hosts occur over essentially the same geographical range as do the pomaceous hosts.

4. The disease caused by *G. clavipes* on pomaceous hosts was found to occur most frequently on fruits, less frequently on twigs and buds and but rarely on leaves. It was most severe on fruits, twigs and buds, usually causing marked hyperplastic distortion. Infected buds were not only swollen but were forced to develop beyond the usual for the current season. On certain fruits, particularly varieties of orchard apples the disease produced was limited to small hypoplastic lesions usually at the blossom end. On leaves the disease was limited to small, usually partially necrotic, spots.

5. On its Juniperus hosts the disease was most abundant on twigs from one to five years old but was also found on leaves, branches and the main trunk. Diseased leaves were discolored and slightly swollen. They were usually killed in one or two years. The disease was perennial for several years on twigs and branches. They were usually girdled and covered with a thick, flaky or furrowed blackened bark. On the main trunk the disease lived for many years but was usually confined to elongated swollen patches covered with deeply furrowed and blackened bark.

6. The life history of the aecial phase of *G. clavipes* was essentially the same on fruits and twigs. It was slower in its development in leaves and in fruits of very resistant hosts, in fact in the latter it was often aborted. In forced buds the mycelium was essentially systemic and developed spermogonia, rarely aecia, progressively as the buds elongated.

7. The mycelium of the telial phase of *G. clavipes* was confined to the epidermis of leaves and to the phellogen of twigs, branches and the main trunk of its Juniperus hosts. It remained in leaves for but one, occasionally for two years. It was perennial for several years in twigs, branches and the main trunk. Telia were produced annually on infected organs.

8. Several means have been demonstrated for the control of *G. clavipes* on pomaceous and on Juniperus hosts. Especial attention has been given to finding satisfactory fungicides and formulating practical spray programs. Of the fungicides tested Linco colloidal sulfur gave very promising results. It was the only one used in field experimentation.

9. Recommendations with respect to the control of this rust have been discussed under the headings of: selective plantings, eradication of hosts, removing infected parts from pomaceous and Juniperus hosts, removing infections from trunks of red cedars and spray applications on pomaceous and Juniperus hosts.

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EXPLANATION OF THE PLATES

Plate 155[1]

Fig. 1. Progressive stages are shown in the exposure and rupturing of aecial fructifications of *Gymnosporangium clavipes* on an orchard apple.

Fig. 2. The dark colored lesion was caused by an imperfect fungus. Aecial fructifications of *G. clavipes* are shown on the upper portion of the lesion.

Fig. 3. Infected twig and fruit of *Cydonia oblonga*, the quince.

[1]Figures 1, 2 and 3 were obtained through the courtesy of Mr. K. A. Harrison of the Dominion Experimental Farms, Kentville, N. S.

Fig. 4. This shoot of *Amelanchier oblongifolia* was inoculated with teliospores of *G. clavipes*. Infection occurred, however, on the fruits and pedicels only.
Fig. 5. Fruits of *Crataegus mollis* infected with *G. clavipes*.
Fig. 6. Fruits of *Malus floribunda* infected with *G. clavipes*.

PLATE 156

Fig. 1. Twig and thorns of *Crataegus* sp. infected with *G. clavipes*.
Fig. 2. Forced growth of infected buds of *Crataegus mollis*. The diseased buds on the twigs of this species have enlarged greatly. Compare with the normal buds on the twig shown on the extreme right.
Fig. 3. Another manifestation of the forced growth of infected buds on *Crataegus* sp. On this species the buds and stems have enlarged but little while the leaves, though small, have taken on features of normal maturity.
Fig. 4. Another manifestation of the forced growth of infected buds on *Crataegus* sp. On this host the buds have swollen considerably and the young stems have elongated but the leaves have remained quite stunted in their growth.
Fig. 5. Infected shoot of *Crataegus Phaenopyrum*. This type of symptom was also found on the English hawthorn, *C. Oxyacantha*.
Fig. 6. A globose gall-like swelling of an infected twig of *C. Oxyacantha*.
Fig. 7. Spermogonium of *G. clavipes*. Note its deep, sunken location and rotund form.

PLATE 157

Fig. 1. Normal aeciospore chain of *G. clavipes*. Note the regular occurrence of aeciospores and intercalary cells.
Fig. 2. Abnormal aeciospore chain. The aeciospores are irregular in shape as well as in their arrangement with respect to the intercalary cells.
Fig. 3. Outline drawings of aeciospores of *G. clavipes*.
Fig. 4. Camera lucida drawings of germinating aeciospores of *G. clavipes*.
Fig. 5. Face and side views of peridial cells of *G. clavipes*.
Fig. 6. Outline drawings of peridial cells of *G. clavipes*.
Fig. 7. Camera lucida drawings of haustoria of *G. clavipes* as seen in the cells of fruits and twigs of various pomaceous hosts. All forms shown may be found in the same organ of any specific host.

PLATE 158

Fully gelatinized telia of *G. clavipes* on branches of red cedar. The bright red sori are very conspicuous during spring rains.

PLATE 159

Fig. 1. Trunk lesion caused by *G. clavipes* on red cedar. Lesions are typically oval in outline and the bark over them is darker in color than normal bark. Note the former location of a branch near the center of the lesion.
Fig. 2. Several trunk infections on a red cedar tree. Note that the trunk lesions are found in connection with lateral branches; many of these have died and been removed.
Fig. 3. Telia of *G. clavipes* in their last stages of gelatinization. At this time they are almost shapeless masses.

Fig. 4. A slight swelling of the twig and a darker color of the bark are typical of the lesions on twigs of red cedars. These photographs were taken in mid-winter.

Fig. 5. Cross section of a telium of *G. clavipes* on *J. virginiana*. Note the pulvinate form of the sorus.

PLATE 160

Fig. 1. Shows diagrammatically the location of the telia and the course of extension of the mycelium of *G. clavipes* over the phellogen of its host. This is a camera lucida drawing.

Fig. 2. The mycelium of *G. clavipes* in an early stage of extension over the new phellogen that has recently connected with the existing one. Note that the mycelium is found on the phellogen only of its host.

Fig. 3. Formation of the telial sorus. Buffer cells are in various stages of development. It will be observed here also that the mycelium does not penetrate beneath the phellogen.

Fig. 4. Early stages in the development of teliospores. The teliospore initials are elongating into the buffer cells.

Fig. 5. Stages in the maturation of teliospores. These stages are similar to those for the maturation of teliospores of *G. Juniperi-virginianae*.

Fig. 6. Haustoria in the phellogen cells of red cedar. They stand out clearly in prepared sections. Two and three haustoria are commonly found in a single host cell.

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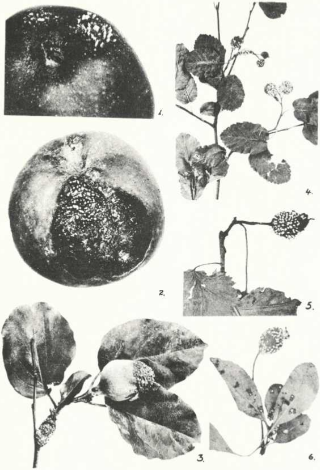
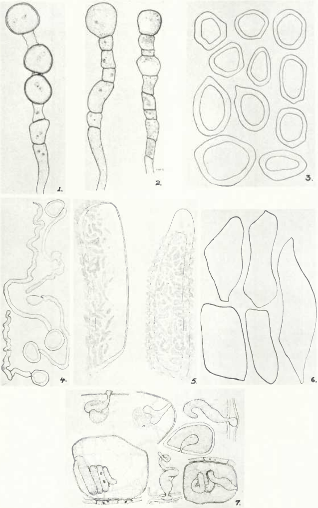


GYMNOSPORANGIUM CLAVIPES C. AND P.

GYMNOSPORANGIUM CLAVIPES C. AND P.

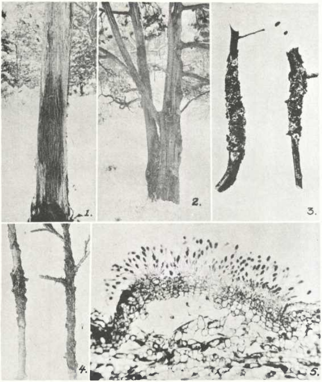


Gymnosporangium clavipes C. and P.

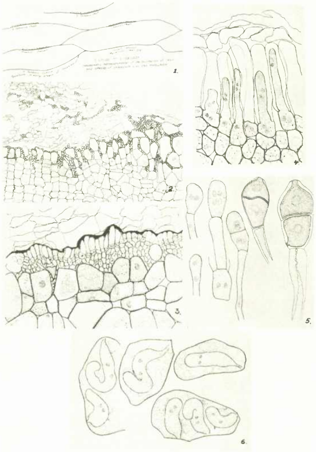
FULL-TONE — MERIDEN

GYMNOSPORANGIUM CLAVIPES C. AND P.

FULL-TONE — MERIDEN



Gymnosporangium clavipes C. and P.



GYMNOSPORANGIUM CLAVIPES C. AND P.

FULL-TONE — MERIDEN

THE DISPERSAL OF VIABLE BASIDIOSPORES OF THE GYMNOSPORANGIUM RUSTS

J. D. MacLachlan

With two text-figures

INTRODUCTION

The basidiospores of Gymnosporangium rusts are thin-walled and so are subject to rapid dessication. It would seem then that their effective range would be limited to a mile or less but instances have come to the attention of the writer which indicate that, under certain circumstances, the range may be as great as seven or eight miles. Three of such instances may be cited. The first was an observation made by Professor Roland Thaxter (1887) on basidiospores of *G. biseptatum* Ellis. He found infection on an island off the coast of Maine, eight miles distant from the only known source of inoculum. The second instance occurred at Lake Wentworth, New Hampshire, and was brought to the attention of the writer in the summer of 1933 by Mr. L. S. Mayo. In this locality infection by *G. clavipes* Cke. & Pk. and *G. globosum* Farl. on *Amelanchier* and *Crataegus,* respectively, was found on the northeastern side of the lake, while the nearest source of inoculum was from a stand of cedars on the opposite side of the same lake, more than six miles distant. The prevailing winds were from the southwest and had presumably carried the basidiospores across the lake. The third instance occurred in the Arnold Arboretum, where infection by *G. Juniperi-virginianae* Schw. and *G. globosum* Farl. on species of *Malus* and *Crataegus,* respectively, has been observed during the past three years. On both hosts the infection, while slight, was markedly uniform over the entire plantations, indicating that the sources of inoculum were considerably removed. A detailed scrutiny of the surrounding country revealed that no source of inoculum sufficient to produce this infection existed within a radius of more than six or seven miles.

In an effort to explain the occurrence of instances such as those that have been described, an airplane collection of basidiospores was made at different altitudes over infected cedar areas immediately following a rainy period in May, 1934; this was followed by laboratory tests on the duration of the viability of basidiospores of *G. Juniperi-virginianae* when subjected to varying temperature and humidity conditions.

AERIAL DISTRIBUTION OF BASIDIOSPORES AS INDICATED BY AN AIRPLANE COLLECTION

Two areas were selected in which an abundance of basidiospores were being discharged, namely, Waltham, Massachusetts, where heavy but restricted infections by *G. Juniperi-virginianae* and *G. globosum* existed, the other about seven miles distant from Waltham at Cochituate where there were approximately three acres of red cedars among which were scattered apple trees highly susceptible to *G. Juniperi-virginianae;* practically every cedar tree in the latter area was heavily loaded with galls of *G. Juniperi-virginianae*.

On May 5, 1934, ideal conditions prevailed for making such a collection. Prior to this date there had been intermittent rain, fog, and saturated humidity for approximately sixty hours; examination of the infected cedars showed that basidiospores were being released almost continually during this period and no high winds had occurred that would scatter the spores beyond the possibility of collection. As the plates revealed after the flight, the air had been washed relatively free of dust and smoke so that little trouble was experienced from such contaminations. At the time of flight, namely, 8.30 A. M., the clouds had just broken but the air was still saturated with moisture, evidenced by the fact that as we left the airport water was precipitated out of the air by the propellor and thrown on the windshield of the plane. It happened that a southwest wind was blowing directly over the area at Cochituate towards the Waltham area. Thus, optimum conditions existed for making the collection.

The spores were collected on petri-plates, each plate containing a thin layer of 2% pure bacto-agar. To prevent growths by other fungi no nutrients were added. Previous tests showed that the basidiospore would germinate freely on the agar alone and since they do not grow on artificial media, germination was taken as sufficient evidence that the basidiospores were viable. Crude but efficient holders for the plates were made by using circular lids, whose diameters were slightly greater than that of a petri-plate, attached to the ends of wooden rods two and one-half feet in length. Wire clamps that could be opened readily served to hold the plates in place while the exposures were being made.

Continuous exposures of one minute each, one overlapping the next by fifteen seconds, were made by removing the cover, clamping the open plate in the holder and immediately thrusting the latter out through the window the length of the handle so that the holder rested on a wind strut. Alternate exposures were made from each side of the plane on numbered plates. At the same time the course of the flight was outlined on a map and by marking the position of the plane at the end of each minute it was not difficult to determine afterwards the exact area over which the plate had been exposed.

Exposures were made from within about one mile of the first source of spores (the Waltham area) three times at an altitude of 200 feet, then directly into the wind at an altitude of 500 feet for seven miles to the Cochituate area. Over the latter area four flights were made at 100 ft. altitude, then two flights each at altitudes of 500 ft., 1000 ft., 1500 ft., and 2000 ft., respectively, finally directly with the wind at an altitude of 2000 ft. for ten miles, bringing us back again over the Waltham area. The average speed during the flight was about 85 miles per hour. Figure 1 illustrates the course of the flight.

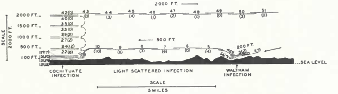


Figure 1. Illustration of the course of the flight over the areas of infected cedars.

Note: Each line represents a single exposure; the number in parentheses, below the plate number, indicates the number of spores caught on 20 sq. cm. of the plate. The topography of the land is shown in profile (from U. S. Geological Survey maps).

Five hours after the flight the plates were placed in the refrigerator at 0° C. and spore counts begun. An area enclosing twenty square centimeters was ruled off on the lower side of each plate prior to making the count. Within the area fine parallel lines were ruled, the distance between any two adjacent lines being slightly less than twice the diameter of the field covered by the low power of the microscope. The plates were examined from the upper side (lids removed). By moving the plate on the microscope stage so that a line (visible though out of focus) was just perceptible on one side of the field, and returning across the plate so that the next line was just in view on the other side of the field, the area enclosed was completely covered without the possibility of either overlapping or omitting any of the plate surface to be examined.

The basidiospores were distinguished from other spores caught on the plates by (1) the characteristic yellowish color of their protoplasm as seen under strong light, (2) the size and shape of the spores and (3) the characteristic germ tubes when present. As a means of comparison basidiospores of *G. Juniperi-virginianae* and of *G. globosum* were allowed to drop on similarly prepared plates from gelatinized telial masses; these two preparations were used for constant reference during the examination of the plates.

Table I gives, for the respective plates, the region over which each collection was made, the plate number, the number of spores found on twenty square centimeters of the plate and finally the number of spores exhibiting germ tubes.

TABLE I
DATA OBTAINED BY MEANS OF AN AIRPLANE COLLECTION OF BASIDIOSPORES OF THE GYMNOSPORANGIUM RUSTS

Region	Altitude in ft.	Plate No.	Total spores	No. spores germinated
Over Waltham	200	1	7	4
infection		2	4	1
		3	2	1
Between Waltham	500	4	0	0
and Cochituate		5	4	2
infections		6	0	0
		7	9	4
		8	3	0
		9	8	2
		10	10	5
		11	18	8
Over Cochituate	100	12	12	3
infection		13	29	9
		15	20	10
		17	17	5
	500	22	8	3
		24	12	5
	1000	27	2	0
		29	2	0
	1500	33	0	0
		35	0	0
	2000	40	0	0
		42	0	0
Between	2000	43	0	0
Cochituate		44	3	1
and Waltham		45	4	1
infections		46	1	0
		47	2	0
		48	0	0
		49	0	0
		50	3	1
		51	0	0

Total spores identified — 182
Total spores germinated — 65

The count included only those basidiospores of unquestionable identity. Spores that were embedded in the agar from the force of impact and could not be identified accurately due to the air spaces around them, as well as the spores which had burst when they hit the agar, were not considered. Certain plates exposed during turning or gaining altitude over the Cochituate area were omitted due to the difficulty in determining the exact location over which these plates were exposed (see Fig. 1).

As may be seen from Table I or Fig. 1, basidiospores were picked up almost continuously during the entire flight. Approximately one-third of them exhibited germ tubes at the time of examination. A sharp increase in the number of spores collected was evident as the large area at Cochituate was approached. Over this area there was a rapid decrease in the number of spores collected with increase in altitude, no spores being collected at 1500 ft. altitude; this may be accounted for by the fact that the wind was carrying the spores away from the immediate cedar area below a ceiling of 500 to 1000 ft. It is interesting to note, however, that spores were again picked up on the return flight (going with the wind) at an altitude of 2000 ft., a mile or so from this area (Fig. 1). The number of spores picked up over the Waltham area was much smaller than that over the Cochituate area; this coincided with a smaller amount of infection in the former area.

Before drawing any conclusion from the data obtained as to how far viable basidiospores may travel, the area over which the flight was taken was carefully examined to determine how much infection existed between the two main areas of infection. The survey revealed that scattered infection loci existed within less than one-half mile of each other over the entire area. Thus, although viable basidiospores were found over the entire flight it was impossible to determine the exact location of their source of dissemination and consequently the distance they had travelled.

DURATION OF THE VIABILITY OF BASIDIOSPORES OF G. JUNIPERI-VIRGINIANAE WITH RELATION TO THE FACTORS OF TIME, TEMPERATURE AND HUMIDITY

A knowledge of the length of time during which the basidiospores will live when they are subjected to varying temperature and humidity conditions should, indirectly, give an indication of the distance that the basidiospores may travel and still have the potential ability to produce infection. Reed and Crabill (1915) state that five to ten days is the life limit of basidiospores of *G. Juniperi-virginianae* in an air-dry condition. They also state that in direct sunlight the spores are killed within two to five hours; sunlight, then, may be a limiting factor in determining the longevity of the basidiospores. However, as has been stated previously, dispersal takes place during rainy weather, under which circumstances the basidiospores might travel many miles under the cloud line.

Laboratory tests were conducted in which fresh basidiospores were subjected to temperatures ranging from 0° to 35° C. at five degree intervals and humidities ranging from 0% to 100% at twenty-five percent intervals. After varying lengths of time samples of the spores were removed from the respective environmental combinations and tested for germination.

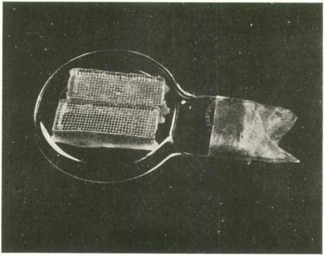


FIGURE 2. The type of humidity chamber used in testing the duration of the viability of basidiospores. (Explanation in text.)

Such an experiment required eight constant temperature chambers. Refrigerators kept in a warm room and equipped with thermostats that kept the temperature constant within 0.5° C. served for the 0, 5, and 10 degree chambers; temperatures of 15, 20, 25, 30 and 35 degrees were maintained in De Khotinsky ovens kept in a cold room at 4° C.

For humidity chambers Kolle culture flasks proved to be very efficient; they were of convenient size, exposed a large surface of the humidity controlling agent with respect to the volume of the flask and could be opened without altering the humidity within the flask to any great extent. Figure 2 illustrates a typical chamber.

Zero percent humidity was obtained by placing a layer of dry $CaCl_2$ in the bottom of the flask. Humidities of 25%, 50% and 75% were obtained by using aqueous solutions containing, respectively, 55.1%, 42.8% and 29.9% of H_2SO_4. These values were taken from data given by Wilson (1921) and are approximately half way between the values given for the respective humidities at temperatures of 0° C. and 25° C. The greatest difference in percentage of H_2SO_4 to maintain any of these humidities over a temperature range of 0° C. to 25° C. is 1.6, which would be insignificant when considering such wide humidity intervals. Enough H_2SO_4 solution was poured into each flask to cover the bottom to a depth of about one centimeter. The lip between the flask proper and the neck served to prevent the H_2SO_4 solution from running out. The mouths of the flasks were closed with covers made by cutting gum-rubber tubing of the appropriate diameter into four-inch lengths and sealing one end with rubber cement. Such flasks could not be used for 100% humidity as water of condensation would form inside the flask on the flat upper surface and drop on the spores. To eliminate this difficulty, small dome-shaped bell-jars were placed inside moist chambers containing distilled water; this type of chamber allowed any water of condensation to run down the sides of the dome.

Small trays of a size that two would conveniently slip into each flask and hold the cover glasses bearing the spores well above the humidity controlling agents were made out of wire screening. These were coated with paraffin (melting point 56° to 58° C.) to prevent the water or H_2SO_4 from coming in contact with the spores as well as prevent corrosion of the trays by the H_2SO_4.

A complete set of humidity chambers from 0% to 100% was placed in each of the respective temperature chambers twenty-four hours before the experiment started. In this way the temperature and the humidity within the flasks were brought to a definite equilibrium before the spores were introduced.

Telial material of *G. Juniperi-virginianae* was collected in the field, removed from the galls and soaked in water to form a thick gelatinous paste. This was smeared over the tops of the inside of large glass moist chambers, which were then set over clean cover glasses arranged in solid squares. Approximately five hundred cover glasses were placed under each chamber. The teliospores germinated and released an abundance of basidiospores, which fell on the cover glasses in a very uniform layer. Excess water was avoided in preparing the telial smears to prevent any condensation on the cover glasses; otherwise the basidiospores would germinate immediately. Ten hours after this experiment was set up the cover glasses bearing the basidiospores were removed and immediately placed on the trays within the series of humidity flasks in the respective temperature chambers. Fifteen cover glasses with the spores on the upper surfaces were placed in each unit. It is essential that the cover glasses are not inverted, as water of condensation in the 100% humidity chambers would form on the spore surfaces; no trouble was experienced from such condensation when the cover glasses were arranged so that the spores were on the upper surfaces.

At the same time three cover glasses bearing fresh basidiospores were inverted over Van Tieghem cells which were placed in a petri-plate lined with wet filter paper. Sufficient water of condensation formed on the lower (spore) surfaces of the cover glasses for optimum germination; the addition of more water causes irregularity in the rate of germination. This culture chamber was then placed in a temperature chamber maintained at 18° C. and the percentage germination was determined twenty-four hours later by counting five hundred spores on each cover glass. This count gave the percentage germination when the basidiospores were fresh and was used as the basis of comparison for all succeeding counts.

At intervals, given in Table II, one cover glass was removed from each unit of the complete series, set up for germination as described above, and the percentage germination of five hundred spores on each cover glass determined twenty-four hours later.

By this experiment the relative effect of the three factors, temperature, humidity and time on the potential viability of the basidiospores of *G. Juniperi-virginianae* was determined. Table II presents the data obtained.

Analysis of these data reveals certain significant facts:

(1) The basidiospores are killed at 0% humidity at all temperatures within at least twenty-two hours time. Practically speaking this is of no importance because such an environment is never attained in the field.

(2) Above a temperature of 30° C. the basidiospores died within twenty-two hours under all humidity conditions. This is also of little practical significance as such temperatures are rarely if ever attained during wet periods in early May.

(3) Above a humidity of 25% and below a temperature of 25° C. the spores could live a sufficient length of time to blow many miles and still remain viable; such humidity and temperature conditions prevail during the normal dispersal of basidiospores of the Gymnosporangium rusts. Below a temperature of 10° C., as far as humidity and temperature alone are concerned, the spores can remain viable for more than a

TABLE II

DATA ON THE PERCENTAGE GERMINATION OF BASIDIOSPORES OF G. JUNIPERI-VIRGINIANAE THAT MAY BE OBTAINED AFTER THE SPORES HAVE BEEN SUBJECTED FOR VARYING LENGTHS OF TIME TO DIFFERENT TEMPERATURE AND HUMIDITY CONDITIONS

TEMPERATURE of 0 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	73.0	82.2	81.6	70.6
30	0.0	64.6	78.0	78.0	57.4
52	0.0	53.4	73.4	74.2	74.2
77	-	50.6	72.4	59.8	60.0
108	-	47.2	53.6	56.0	42.4
138	-	44.8	51.4	50.6	44.2
176	-	0.0	53.0	42.4	42.8
215	-	.8	0.0	37.4	lost
239	-	0.0	0.0	0.0	0.0
625	-	0.0	0.0	0.0	0.0

TEMPERATURE of 5 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	82.6	88.0	89.6	81.2
30	0.0	80.2	86.8	84.6	80.4
52	0.0	73.4	85.6	79.0	79.6
77	-	64.0	60.6	61.4	45.8
108	-	61.6	61.4	63.2	50.2
138	-	lost	59.4	61.6	52.8
176	-	0.0	52.8	59.6	52.4
215	-	0.0	26.0	36.2	53.0
239	-	0.0	32.4	41.4	lost
625	-	-	0.0	28.8	45.0

TEMPERATURE of 10 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	83.6	88.6	88.2	88.6
30	0.0	72.8	78.4	82.4	79.4
52	0.0	lost	66.2	78.4	80.8
77	-	lost	56.6	52.2	70.6
108	-	58.2	62.8	60.4	73.2
138	-	25.2	55.8	44.4	71.6
176	-	0.0	57.6	1.6	53.0
215	-	0.0	10.2	5.2	59.2
239	-	0.0	1.6	.8	22.4
625	-	-	0.0	0.0	0.0

TEMPERATURE of 15 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	lost	lost	76.6	80.2
30	0.0	3.2	10.2	76.8	83.0
52	0.0	0.0	0.0	4.6	72.2
77	-	0.0	0.0	0.0	55.8
108	-	0.0	0.0	0.0	4.2
138	-	-	-	0.0	2.0
176	-	-	-	-	0.0
215	-	-	-	-	0.0
239	-	-	-	-	0.0
625	-	-	-	-	-

TEMPERATURE of 20 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	82.0	79.6	76.4	90.6
30	0.0	46.8	60.2	72.2	84.6
52	0.0	43.4	43.0	82.2	62.4
77	-	0.0	0.0	0.0	1.6
108	-	0.0	0.0	0.0	1.0
138	-	0.0	0.0	0.0	2.0
176	-	-	-	-	0.0
215	-	-	-	-	0.0
239	-	-	-	-	0.0

TEMPERATURE of 25 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	5.2	4.8	4.8	71.4
30	0.0	0.0	0.0	0.0	76.0
52	0.0	0.0	0.0	0.0	0.0
77	-	0.0	0.0	0.0	0.0
108	-	-	-	-	0.0
138	-	-	-	-	-
176	-	-	-	-	-
215	-	-	-	-	-
239	-	-	-	-	-

TEMPERATURE of 30 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	0.0	0.0	0.0	0.0
30	0.0	0.0	0.0	0.0	0.0
52	0.0	0.0	0.0	0.0	0.0
77	-	-	-	-	-

TEMPERATURE of 35 C.

Time in hours	% germination after subjection to humidities of				
	0%	25%	50%	75%	100%
22	0.0	0.0	0.0	0.0	0.0
30	0.0	0.0	0.0	0.0	0.0
52	0.0	0.0	0.0	0.0	0.0
77	-	-	-	-	-

week; while at high humidities and a temperature of 5° C. they can live for more than twenty-five days.

Whether the basidiospores of other Gymnosporangium rusts have the same potential viability exhibited by *G. Juniperi-virginianae* in this experiment is not known. Such may very well occur.

CONCLUSION

The data obtained from the airplane collection on the aërial distribution of the basidiospores and from the laboratory tests on the longevity of basidiospores of *G. Juniperi-virginianae* afford a possible explanation of the occurrences, described at the beginning of this presentation, of infection several miles from the source of inoculum. The infection that occurred in the first two instances described may have been facilitated by the fact that the basidiospores had an unobstructed passage over water where the humidity was relatively high and the temperature lowered to some extent.

BASIDIOSPORE DISPERSAL AND THE PRACTICE OF CEDAR ERADICATION

A tremendous number of basidiospores may be released from a large stand of infected cedars; moreover, as has been shown in this presentation the basidiospores, when subjected to the environmental conditions that are met during their dispersal, have the ability to live for a sufficient length of time to be carried many miles. The question then arises as to why effective control of the cedar-apple rust has been repeatedly obtained by the removal of the red cedar within a radius of one to two miles from the pomaceous host.

An explanation of this question may be afforded by certain factors that are necessarily involved before injurious infection of the pomaceous host can take place:

(1) The rapidity with which the area of any circle described around a locus of infection increases with increase in radius would dilute the spore population correspondingly; the area enclosed within a radius of one mile involves an area of more than eighty-seven and one-half million square feet, while a radius of ten miles would involve an area of one hundred times that or between eight and one-half and nine billion square feet.

(2) The infection resulting from a basidiospore is not systemic in the host but is restricted to a small area on a single leaf, fruit or twig. Several lesions per leaf are required to materially injure the tree and

when one considers the hundreds of thousands of leaves on a single large tree, a tremendous number of basidiospores must fall within the area occupied by that tree and successfully produce infection before the foliage is materially injured.

(3) So far as is known, aeciospores cannot reinfect the same host; consequently, the amount of infection on any one tree is limited to the number of lesions originating from the basidiospore infections in the spring. It is very fortunate that such a short cycle does not exist; otherwise it would be very difficult to grow a susceptible host in any region where these rusts are present.

(4) One cannot assume that every basidiospore that alights on a host tree will produce infection; many must die before the germ tubes can penetrate the proper host tissue.

When the factors outlined above are fitted into the picture one can readily see that, in spite of the tremendous output of basidiospores and the length of time that they are able to live under the conditions that are met during their dispersal, eradication of the red cedar within a radius of one to two miles would ordinarily be sufficient to amply protect the alternate host from any injurious infection.

SUMMARY

Instances have been recorded to show that the basidiospores of at least certain of the *Gymnosporangium* rusts can produce infection on alternate hosts that are removed from the source of inoculum by several miles.

Attempts were made to explain the occurrence of such instances; the investigations included an airplane collection of basidiospores over infected cedar areas as well as laboratory tests on the duration of the viability of basidiospores of *G. Juniperi-virginianae* Schw. with respect to the factors of time, temperature and humidity.

The results of these investigations revealed that viable basidiospores are present in the air during rainy periods in early May at altitudes of at least 2000 feet and that basidiospores of *G. Juniperi-virginianae* can live for many days under the environmental conditions that prevail during their normal dispersal. These results give a possible explanation of the occurrence of infection on pomaceous hosts that are removed by several miles from the source of inoculum.

Experience has shown that eradication of the red cedar within radii of one to two miles will, ordinarily, amply protect the pomaceous host from injurious infection by the Gymnosporangium rusts. Certain of the factors which make possible the efficiency of this means of control have been presented.

ACKNOWLEDGMENTS

To Professor J. H. Faull for guidance and supervision during the pursuance of this investigation; to Dr. A. E. Navez for helpful suggestions in the compilation of data and to the Department of Biology, Harvard University, for laboratory facilities and financial assistance, the writer expresses sincere gratitude.

The writer also wishes to thank Mr. L. S. Mayo, Assistant Dean of the Graduate School of Arts and Sciences, Harvard University, for bringing to attention the locus of infection at Lake Wentworth, and Drs. Ivan H. Crowell and P. A. Vestal for assistance in the airplane collection of spores.

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CHROMOSOME STRUCTURE AND BEHAVIOR IN MITOSIS AND MEIOSIS

Hally Jolivette Sax and Karl Sax

With plates 161–164

A study of chromosome structure and behavior at mitosis and meiosis has been made in order to compare the two types of divisions and to aid in the analysis of the mechanism of meiosis. This work is based on a comparison of chromosome lengths at different stages in the mitotic and meiotic cycles, and the relation of these changes to the internal structure of the chromosomes.

The chromosome cycle in mitosis and meiosis has been studied in *Tradescantia paludosa, Vicia faba, Lilium regale,* and in *Allium Cepa.* The length of the chromosomes at various stages was also obtained in somatic cells of *Trillium grandiflorum,* and some work was done on the meiotic divisions in *Secale cereale* and in *Zea mays.* Recent advances in cytological technique have made possible a fairly accurate study of the length and structure of the chromosomes at various stages in the mitotic and meiotic cycles.

The meiotic figures were obtained from microsporocytes which were smeared on a dry slide, pretreated with 30 percent alcohol containing about six drops of ammonia water per 50 cc., and fixed and stained with aceto-carmine, or fixed in Flemming's solutions and stained with crystal violet iodine. The best preparations of somatic divisions were obtained from young microspores. After smearing on a dry slide they were pretreated with the alcohol ammonia for about a minute and then fixed either in aceto-carmine or Flemming's solution. Root tips were fixed for 12 to 15 hours in a mixture of absolute alcohol (70 cc.) and glacial acetic acid (30 cc.) and then macerated in a drop of aceto-carmine. In all cases the aceto-carmine smears were heated to clear the cytoplasm and the cover glass pressed to flatten the cells. The preparations were then sealed or made permanent by McClintock's method. The aceto-carmine preparations showed almost as much detail of structure as those fixed in Flemming's solution, and since the cells fixed in aceto-carmine could be flattened, these preparations were used in measuring chromosome lengths and were photographed to illustrate the various stages in mitotic and meiotic cycles.

THE MITOTIC CYCLE IN TRADESCANTIA MICROSPORES

At anaphase of the second meiotic division each chromosome consists of two spiral chromatids. When the chromosomes pass into the resting stage the chromonemata tend to uncoil and form a loose spiral structure which completely fills the nucleus. Well fixed preparations show distinct chromatic threads loosely coiled in the resting nucleus rather than a reticulate network (Plate 161, photo 1). At early prophase the nucleus enlarges and the spiral chromosomes are more easily observed (Plate 161, photo 2). The chromatids of each chromosome are so clearly associated that the doubleness is hardly discernible, a condition also observed by Kuwada and Nakamura (1935). As the prophase continues the coils tend to straighten out and at the same time there is evidence of a new coiling in the closely associated chromatids (Plate 161, photo 3). At this stage there is little evidence of the double thread structure of the chromosomes even though they appear to be two-parted at the preceding anaphase. When the old coils are straightened out so that the spireme thread can be followed at all loci, there is clear evidence of a longitudinal split and each chromatid is independently coiled (Plate 161, photo. 4). These new coils apparently shorten the chromosomes and draw out the old coils persisting from the previous anaphase of the second meiotic division. The chromosomes continue to shorten during anaphase and the chromatids become thicker and more clearly separated (Plate 161, photo. 5). There is some tendency for the two chromatids of a chromosome to be twisted about each other, but at most only two or three twists occur. These are usually eliminated by metaphase although overlaps and an occasional twist is found at this stage (Plate 161, photo. 7).

In preparations fixed without pretreatment, there is little or no evidence of the coiled chromosome structure at metaphase (Plate 161, photo. 6). The two chromatids of each chromosome usually can be identified although with certain types of fixation and staining the metaphase chromosomes appear as single rods. After effective pretreatment of the microspores the coiled chromatids can be seen at early metaphase and at anaphase (Plate 161, photos. 7, 8, 9). The diameter of the chromatid is so near the limit of microscopic resolution that it has not been possible to determine the direction of coiling, nor can the number of coils be determined accurately, but there appear to be about twenty-five coils in each chromatid (Plate 161, photo. 8). When the chromatids are twisted about each other at early metaphase the chromosome appears to be constricted at the point of overlap as is shown in the chromosome at the right in photo. 7 of Plate 161.

Each chromatid at metaphase and at anaphase usually appears to consist of a single coil, but there is some evidence that these chromatids contain two threads which are coiled together. In the first meiotic division the major coils are so closely associated that they appear as a single coil unless lightly stained, but at late metaphase the two coils separate and lie parallel. In the somatic chromosomes the two coiled threads in the anaphase chromosome do not separate enough to appear as two parallel coils, and the diameter of the chromatids is too small to permit the direct observation of two chromatic threads coiled together, but there is apparently a tendency for the two coils to separate so that when a twist occurs in an anaphase chromosome there is a constricted locus at the twist (Plate 161, photo. 9). Such constrictions may be observed even in the chromatids at early metaphase (Plate 161, photo. 8).

The chromosomes at late telophase appear so compact that little detail in structure can be observed, but as they elongate at later stages the coiled chromonemata expand and irregular coils and corrugations may be observed. The chromaticity of the chromosomes is reduced so that it is not possible to follow the coiling in any single chromosome and the entire nucleus is filled with loosely coiled chromonemata in the resting stage.

The somatic divisions observed in aceto-carmine preparations of root tips did not show the detail of the structure found in the microspores, but the general behavior is the same, except that the root tip chromosomes are longer than those of the microspore at the metaphase stage of division.

THE MITOTIC AND MEIOTIC CYCLES IN VICIA FABA

The early prophase stages in root tips of *Vicia faba* show the irregular spiral chromonemata. At this stage the chromatic threads appear to be single at most loci. As the spireme threads tend to straighten their dual nature is easily observed at all points (Plate 162, photo. 1). The chromatids are twisted about each other to a greater extent than is found in *Tradescantia,* and as many as five or six twists may be observed in a single chromosome. The chromatids appear to be independently coiled in small loose spirals at this stage. During later development the chromatids thicken and shorten until metaphase, but we have been unable to observe the internal structure at this stage. The anaphase chromosomes seem to show a double spiral structure (Plate 162, photo. 2), but not as clearly as in the figures published by Sharp (1929).

The prophase stages in the microspore nucleus are more difficult to follow, presumably because of the rather thick wall of the microspore, and the metaphase and anaphase stages show little or no detail of structure (Plate 162, photos. 6, 7, 8). The lengths of the prophase spireme and of the metaphase and anaphase chromosomes can be obtained, and it was found that the microspore chromosomes are shorter than those of the root tip cells at metaphase and anaphase.

The early meiotic stages were not studied in detail, but measurements were made of the pachytene spireme. There is a great reduction in chromosome length between pachytene and the first meiotic metaphase. The meiotic chromosomes at the first meiotic metaphase are even shorter than the metaphase chromosomes of the microspore mitosis. The long "m" chromosome has an average chiasma frequency of about 6 while the average chiasma frequency of the short "m" chromosomes is about 3 (Plate 162, photo. 3). The chromonemata are coiled in major spirals at metaphase and at anaphase (Plate 162, photo. 4). A description of these coils will be presented in a later paper. At late anaphase the meiotic chromosomes contract considerably (Plate 162, photo. 5). During the second meiotic division the major coils may persist, but frequently they are completely eliminated at this time and the chromosomes at anaphase appear as straight rods.

THE MITOTIC AND MEIOTIC CYCLE IN LILIUM REGALE

The root tip preparations of *L. regale* showed only the more general features of chromosome behavior. The prophase and metaphase stages were clear enough to provide measurements of the mitotic chromosomes (Plate 163, photos. 3 and 4).

The pachytene stages of meiosis showed the association of chromomeres as described by Belling and others. The pachytene chromosomes are much thinner and longer than the chromosomes of the "spireme" in root tip cells (Plate 163, photo. 1). The chromosomes of the first meiotic division are much shorter than the somatic chromosomes (Plate 163, photo. 2). There is clear evidence of major coils in these meiotic chromosomes and the average chiasma frequency is about 3 per bivalent.

The microspores did not provide good preparations for prophase stages, but Dr. W. S. Flory obtained metaphase figures in another species which could be measured.

OBSERVATIONS OF CHROMOSOMES IN TRILLIUM, ZEA, ALLIUM AND SECALE

Root tip preparations of *Trillium grandiflorum* provided prophase and metaphase figures which could be measured for comparison with corresponding stages in other genera. The prophase spireme in somatic cells is not so clearly split as is the case in *Tradescantia* and *Vicia* (Plate

163, photo. 5). The contraction of the chromosomes from the prophase spireme to metaphase is less than it is in the other genera which have been studied, and the metaphase chromosomes are very long (Plate 163, photo. 6). There is some twisting of sister chromatids about each other even at metaphase.

We have made no detailed study of Zea chromosomes, but McClintock's figures (1933) show about an 11 to 1 reduction in length between pachytene and the first meiotic metaphase, and according to McClintock (personal communication) the ratio may be as great as 15 to 1.

The meiotic cycle in *Allium Cepa* is especially clear for a study of chromosome contraction from pachytene to metaphase (Plate 164, photos. 3–6). The association of chromomeres can be observed at pachytene and the number of nodes is greatly reduced from early diplotene to metaphase. Most of these points of contact seem to be twists or overlaps.

A few measurements of mitotic and meiotic chromosomes were obtained from *Secale cereale*. The structure of the meiotic chromosomes has been described in some detail in an earlier paper (Sax, 1930).

CHROMOSOME LENGTH AT VARIOUS STAGES IN MITOSIS AND MEIOSIS

We have obtained measurements of chromosome lengths at prophase and metaphase in mitotic and meiotic cells of the various species examined. The prophase measurements of root tip cells were made after the old coils were straightened out and the new coils were started, the so-called spireme stage of mitosis. The cells were flattened so that most of the spireme could be drawn in two focal levels. The measurements of the chromosomes were made from camera lucida drawings, and no attempt was made to determine the additional length caused by foreshortening of threads passing through several focal levels. The lengths of the pachytene chromosomes were easier to obtain, but even these are only approximate. The meiotic chromosomes at metaphase form loops between chiasmata and we have tried to include these in our measurements of Vicia and Lilium chromosomes. The anaphase chromosomes in both mitosis and meiosis are essentially the same length as the metaphase chromosomes in some species so that anaphase figures were occasionally included in determinations of metaphase lengths. In view of the technical difficulties involved in determining comparable stages and in obtaining the prophase measurements, the results are only approximate, but the differences in chromosome contraction in mitosis and meiosis are so consistent that they must be of some significance. The data obtained are shown in Table I.

TABLE I

Average chromosome length in microns at prophase (P) and metaphase (M) in meiotic and somatic divisions. The number (n) of cells measured is indicated.

	Root tip				Meiotic				Microspore			
Species	n	P	n	M	n	P	n	M	n	P	n	M
Vicia faba	4	48	5	13	2	98	2	9	4	36	2	11
Tradescantia sp.	5	56	8	21	3	81	9	9	8	61	8	12
Lilium regale	3	35	2	22	2	83	4	12			1	15
Trillium grandiflorum	1	91	2	40								
Secale cereale	1	37	1	14	1	61	1	8				
Allium Cepa					4	69	1	9				

In every case where meiotic and mitotic prophases are compared the meiotic pachytene chromosomes are much longer than those at the somatic prophase spireme. The ratios range from about 1.4:1 in *Tradescantia* to about 2.4:1 in *Lilium* and the average ratio for all species examined is about 2:1.

The reduction in chromosome length from prophase to metaphase is much greater in meiosis than in mitosis. The chromosomes at pachytene are from 7 to 11 times as long as the chromosomes at meiotic metaphase and the ratio may be even more extreme in certain species. In root tip cells the prophase chromosomes are shorter, but the metaphase chromosomes are longer than the corresponding stages of meiosis. Consequently the reduction in chromosome length from prophase to metaphase is much less in root tip cells, ranging from less than 2:1 in *Lilium* to about 4:1 in *Vicia*.

The metaphase chromosomes of the microspore are shorter than those of the root tip cells, but longer than the meiotic chromosomes at first metaphase. The technical difficulties in measuring microspore chromosomes probably is responsible for the shorter prophase measurements in microspores of *Vicia* as compared with corresponding stages in root tip cells.

The outstanding feature of these comparisons in chromosome length is the consistent and striking difference in the degree of chromosome contraction in mitosis and meiosis. For the species examined the average degree of chromosome contraction between pachytene and the first meiotic metaphase is about 8.6:1, while for comparable stages in mitosis in root tip cells the ratio is about 2.6:1. In view of the method of calculating chromosome lengths and the greater difficulty in measuring somatic prophases, these average ratios may be considered approximately as 9:1 and 3:1 respectively.

Another bit of evidence should be considered before discussing the possible significance of these observations. In general it is well known that the meiotic cycle is a leisurely process. The resting stage of the sporocyte may be of short duration in certain species, but the early prophase is prolonged, and in certain conifers the microsporocytes may remain in the early prophase stage for several months (Sax and Sax, 1933). The pachytene stage is prolonged in most species of plants and animals judging by the ease and frequency with which this stage is found. The development from pachytene to metaphase may be rather rapid, but the first metaphase stages, interphase, and second meiotic division are more prolonged. The meiotic cycle from early prophase to tetrad formation in the microsporocytes of *Tradescantia* requires about six days (Sax and Edmonds, 1933). The somatic cycle in the microspore of *Tradescantia* is much more rapid. The prophase stage is not initiated until vacuolation of the microspore cytoplasm, and the development from this stage to the formation of the daughter nuclei occurs in about three days at most. We have no data regarding the time required for the mitotic cycle in root tips of *Tradescantia*, but the duration of mitosis in stamen hairs of *Tradescantia* is less than two hours at normal temperatures (Tischler, 1922). Laughlin (1919) found that the entire mitotic cycle requires only four hours in *Allium Cepa*, at a temperature of 20 degrees C. The duration of the development from the time that a definite spireme can be observed until the separation of sister chromatids appears to be much longer in meiosis than it is in mitosis, and it seems probable that the mitotic cycle is more rapid in root tips than in microspores.

THE MECHANISM OF CHROMOSOME CONTRACTION IN MITOSIS AND MEIOSIS

The chromonemata of mitotic chromosomes in *Tradescantia* are in the form of minor spirals at anaphase in the second meiotic division, the division of the microspore nucleus, and presumably in all other mitotic divisions (Cf. Sharp, 1934). As the chromosomes pass into the resting stage the spirals tend to uncoil and fill the nucleus with loosely and irregularly coiled chromonemata. These old coils are never straightened out before the new coiling is initiated in the prophase for the next division. The new coils contract the chromonemata and apparently aid in drawing out most of the old spirals persisting from the previous division. At this point the chromosomes are in the typical "spireme" stage and their lengths can be measured approximately. The new coiling can be observed during the later prophase stages, and at metaphase there are about 20 to 25 minor spirals in each chromosome. The microspore chromonemata are compactly coiled at metaphase. Judging from the relative lengths of the metaphase chromosomes in microspores and root tips, the chromonemata of the latter are not so tightly coiled (Cf. Sharp, 1934). In general the development of the minor spirals reduces the chromosome length about 70 percent between the prophase spireme and metaphase in root tip cells, and even more in microspore cells. At no period in the mitotic cycle are the chromosomes uncoiled completely; the spirals from the preceding division persist until the new coiling begins at early prophase. Observations and measurements in several different genera seem to indicate that this behavior is of general occurrence in the somatic cycle of cell division (Cf. Kuwada and Nakamura, 1935).

The chromosomes of the meiotic prophase appear to be free from spirals persisting from the previous mitotic anaphase, and if remnant spirals occur they are so nearly straightened out that they can hardly be recognized as spiral structures at pachytene. There is a great amount of chromosome contraction between pachytene and the first meiotic metaphase in *Vicia, Tradescantia, Lilium, Trillium, Secale, Allium* and other genera. Belling (1928) found a 10:1 reduction in chromosome length in *Lilium* and Dark (1934) found an 11:1 reduction in *Bellevalia*. The average reduction in chromosome length between pachytene and metaphase in the genera which we have examined is about 9:1. An examination of published drawings of these stages in other genera of plants with large chromosomes indicates that a similar degree of chromosome contraction is of general occurrence.

The paired chromosomes at early pachytene are very slender, and even at late pachytene the diameter of the chromonemata is much less than it is at corresponding stages in mitosis. During the contraction between pachytene and metaphase the chromonemata become coiled in major spirals. The two chromatids of each chromosome are coiled together in single spirals at early metaphase in *Tradescantia* (Sax and Humphrey, 1934), *Secale* (Sax, 1930), *Rhoeo* (Sax, 1935) and *Vicia*, but two parallel coiled chromatids are found at this stage in *Gasteria* (Taylor, 1931), *Trillium* (Huskins and Smith, 1935) and *Fritillaria* (Darlington, 1935). These major coils are much wider and fewer in number than the minor spirals of the somatic chromosomes. In *Tradescantia* there are 5 to 6 major coils in each chromosome at meiosis, as compared with 20–25 coils in somatic chromosomes, and the gyres of the major coils are about twice as wide as those of the minor coils. Darlington (1935) finds from 8 to 15 major spirals in the meiotic chromosomes of *Fritillaria* and about 80 minor coils in the somatic chromosomes.

Minor spirals within the major coils have been observed in *Tradescantia* (Fujii, 1926; Ishii, 1931; Kuwada, 1932; Kuwada and Nakamura, 1933; Kato, 1934); in *Hosta* (Ishii, 1931); in *Sagittaria* and *Lilium* (Shinke, 1934), and in *Trillium* (Matsuura, 1934). (For these literature citations see Kato and Iwata (1935), who also describe the spiral within spiral structure of the meiotic chromosomes of *Lilium*.) Our observations and measurements of chromosome length in mitosis and meiosis seem to show that the relations of the major and minor coils differ in different genera. In *Tradescantia* the minor coils seem to be well established at early metaphase so that the separation of the major coils at late metaphase is associated with little change in the coiled chromatids. There is, however, some reduction in the width of gyres between early metaphase and anaphase, which can be attributed to the continuation of minor coiling. If the minor coils are well developed at metaphase the length of the meiotic chromonema of the major coil should be about the same at the somatic metaphase chromosomes. We have made wire models simulating the major coils in order to estimate the degree of contraction caused by the major spirals. The coiling is responsible for about a two-thirds reduction in length, so that the meiotic chromonemata of *Tradescantia,* including only the major coils, are about 27 microns long, as compared with an average length of 21 microns for the somatic chromosomes. If only coiling is responsible for chromosome contraction in *Tradescantia* the minor coils at meiotic metaphase are nearly as well developed as they are in root tip chromosomes.

In *Secale* we find a different relation between the major and minor coils at meiosis (Sax, 1930). The two chromatids of each homologue are coiled together in a single spiral at early metaphase, but at late metaphase the major spirals tend to straighten out and the chromatids separate with no elongation of the meiotic chromosomes. The average length of these coiled chromonemata at early metaphase is estimated to be about 24 microns, but after the major coils are reduced at late metaphase the chromosome length is about 8 microns. The somatic chromosomes at metaphase have an average length of about 14 microns. Apparently the minor coils are not well developed at early metaphase, but are formed during metaphase and are effective in reducing the major spirals. The relations of the major and minor spirals in *Vicia, Lilium* and *Rhoeo* are more or less intermediate as compared with the conditions found in *Tradescantia* and *Secale*.

If chromosome contraction is effected only by coiling of the chromonemata we would expect that the degree of reduction in length between pachytene and metaphase would be correlated with the relation between major and minor coiling. There does seem to be some correlation in certain genera. In *Tradescantia* where both major and minor coils occur together at meiotic metaphase, the ratio of chromosome length at pachytene and meiotic metaphase is about 9:1. All of this chromosome contraction might be attributed to major and minor coiling. In *Rhoeo* and *Zea*, however, the pachytene metaphase ratio may exceed 15:1, although there are no apparent major spirals in the meiotic chromosomes of *Zea*, and in *Rhoeo* the minor spirals appear to be most effective in chromosome contraction during late metaphase as the major spirals are reduced (Sax, 1935). Apparently there may be some linear contraction of the chromonema without coiling as Belling (1928) has suggested.

The major spirals may be observed at the second meiotic division, as is usually or always the case in *Gasteria, Trillium, Sagittaria* and *Fritillaria*, or only minor spirals may occur as is the case in *Tradescantia, Rhoeo*, and presumably in all genera in which the second meiotic division chromosomes resemble those of mitosis. In *Lilium* and in *Vicia* some chromosomes show major spirals and others only minor spirals at the second meiotic division. The nature of the coiling at this division appears to be associated to some degree with the length of the interphase.

The outstanding features of meiosis in relation to chromosome contraction are, (1) the almost complete elimination of the coils of the preceding anaphase chromosome at the pachytene spireme, (2) the great reduction in chromosome length between pachytene and metaphase, and (3) the occurrence of major spirals.

THE TIME OF THE CHROMOSOME DUPLICATION

The anaphase chromosomes at mitosis have been described as two parted in *Tradescantia* (Kaufmann, 1926); *Trillium, Allium, Tradescantia, Vicia, Podophyllum* (Sharp, 1929; Telezynski, 1930); *Galtonia* (Smith, 1932); *Scilla* (Hoare, 1934); *Narcissus* (Hedayetullah, 1931); *Drosophila* (Kaufmann, 1934) while four parted chromosomes at late anaphase or telophase have been described in *Tradescantia* (Nebel, 1932) and *Paeonia, Allium* and *Tulipa* (Stebbins, 1935). Two coiled chromatids in the anaphase chromosomes of the second meiotic division have been described in *Gasteria* (Taylor, 1929, 1931), *Galtonia* (Smith, 1932), *Allium* (Koshy, 1934), *Scilla* (Hoare, 1934), *Trillium* (Huskins and Smith, 1935), *Rhoeo* (Sax, 1935) and *Tradescantia* (Nebel, 1932; Kuwada and Nakamura, 1935). The anaphase chromonemata at mitosis are described as longitudinally single structures by Belar (1928), Darlington (1932, 1935) and Belling (1933), although Belar shows clearly the longitudinal split at late anaphase in *Aulacantha*.

The anaphase chromosomes of the second meiotic division in *Tradescantia* have been described as single structures (Sax and Humphrey, 1934), but further study tends to confirm the interpretation of Kuwada and Nakamura, who present photographic illustrations which show the dual nature of these anaphase chromosomes. We can observe both in the second meiotic anaphase and in the anaphase chromosomes of the microspore division, some evidence of two closely associated coiled chromatids and the constrictions apparently produced by the twisting of the partially separated spirals. The experiments conducted by Riley (Cytologia, in press) indicate that the split chromosome behaves as a unit in response to X-ray treatment, since the microspore nuclei rayed during the resting stage show only chromosome breaks at metaphase. X-ray treatment at the resting stage of microspore nuclei in *Trillium* produces only chromatid breaks at metaphase, indicating that the chromosomes are effectively split when they go into the resting stage (Huskins and Hunter, 1935). The differences in the response to X-ray treatment in these two genera may be caused by the degree of separation of the sister chromatids. In *Trillium* the chromatids are well separated at diplotene and form more or less independent major spirals at early metaphase, while in *Tradescantia* the two chromatids of each homologue are closely associated at early metaphase of the first meiotic division. A corresponding difference in the relations of the chromatids may exist during the later stages of meiosis and early microspore development.

The available evidence seems to show that the chromonemata are longitudinally split when they enter the resting stage, and they may be four parted as indicated by the careful work of Nebel and Stebbins. If they are four parted at this stage the split chromatids may behave as units during the next mitotic cycle, so that the chromosomes may be considered as composed of two chromatids when they enter the resting stage (cf. Nebel, 1933).

The time at which chromosome duplication is initiated is a question on which there is considerable difference of opinion. Some investigators believe that it occurs at very early prophase while others find the split at late prophase, metaphase or even at anaphase or telophase. We are inclined to associate chromonema coiling with the longitudinal split of the chromosome. The chromosomes are considered as two parted when they enter the resting stage. In mitosis the two chromatids are coiled together in loose spirals at the beginning of prophase. At early prophase each of the two chromatids is longitudinally split. This split causes each split chromatid to coil independently. This coiling pulls out the remnant coils of the previous anaphase and causes the chromatids to separate so that two more or less parallel strands are observed at the spireme stage. These shorten by coiling, separate at anaphase, and each anaphase chromosome contains two closely associated spiral threads.

The leptotene threads at meiosis are also split, as observed by McClung (1928) and Robertson (1931), although they usually appear to be single. The threads pair at pachytene, and at late pachytene each chromatid splits and the coiling of the chromonemata begins as in mitosis. At diplotene the homologous chromosomes separate except at chiasmata or where twists occur. The minor spirals at meiosis involve only two strands or half-chromatids, as in mitosis. The minor spirals appear to begin development before the major spirals, but they may develop so slowly that they continue to coil, or at least contract, after the major coils are established at early metaphase in certain species. The meiotic bivalent is an eight parted structure as described in *Tradescantia* (Nebel, 1932), in *Trillium* (Huskins and Smith, 1935) and as we have observed in *Tradescantia* (from a preparation made by Dr. Dermen).

The chromosomes separate at anaphase, the two chromatids of each chromosome appear as parallel coils, but the "tertiary split" can not be seen. The interphase is brief and even the major coils may persist at the second division. There is apparently no true resting stage at interphase and the chromosomes pass to the second metaphase as four parted structures. At second anaphase each chromosome contains two coiled chromatids as a result of the split which occurred at late pachytene or early diplotene. The number of strands and time of splitting in any one of the 2n chromosomes is essentially the same in both the mitotic and meiotic cycles.

THE MECHANISM OF MEIOSIS

According to Darlington (1932 "meiosis differs from mitosis in the nucleus entering prophase before the chromosomes divide instead of after they divide. The "precocity theory" is based on the assumption that there is a curtailed resting stage or earlier prophase and that the leptotene chromosomes are single. Evidence from many sources indicates that the chromosomes contain at least two coiled chromatids when they enter the resting stage in the mitotic cycle and at the completion of meiosis. There is little reason for assuming that the last premeiotic division differs from other mitoses.

There is good evidence that the meiotic cycle is a much more leisurely process than the mitotic cycle. This evidence, together with the observations on chromosome length at prophase in mitosis and meiosis, seems to indicate that meiosis is associated with a retardation in cellular activity rather than precocity in development (Cf. Stebbins, 1935). The prolongation of prophase at meiosis is associated with the straightening out of the old spirals of the preceding anaphase before the new coiling begins. The two chromatids of each leptotene chromosome are so closely associated that they appear as a single thread. At mitosis there often is a tendency for homologous chromosomes to be associated in pairs, but intimate gene by gene pairing is inhibited by the coiled structure of the chromonemata. As the remnant coils begin to straighten out the chromatids are split and the new coiling begins so that the chromonemata are always coiled during the mitotic cycle. In meiosis, however, no coils, or at least only very loose remnant spirals, are found at prophase, and an intimate association of homologous chromosomes is effected. The new split occurs in each chromatid at late pachytene, coiling begins, and homologous chromosomes begin to separate. At this stage of chromosome development, in both mitosis and meiosis, each chromosome (2n) contains four chromatids and there is no longer any strong affinity between homologues. In meiosis the homologous chromosomes usually appear to be held together by chiasmata, although other factors appear to be effective in the meiotic association of chromosomes in certain cases. At interphase the pairs of "sister" chromatids separate except at the fiber attachment, and at second metaphase they again become closely associated. The anaphase chromosomes pass into the resting stage as double spirals as in mitosis. The prolongation of the mitotic cycle in the microspore suggests that the retardation of meiosis tends to persist at the subsequent mitosis so that the microspore chromosomes are more compactly coiled than in root tip cells, but the retardation at early prophase is not sufficient to effect chromosome pairing even in autotetraploids.

The retardation theory of meiosis is in accord with the numerous observations that the anaphase chromosomes pass into the resting stage as two parted (or four parted) structures, and with the fact that the meiotic prophase chromosomes are much longer than those of the mitotic spireme. The primary difference between mitosis and meiosis is the longer prophase in meiosis which enables the residual coils of the chromonemata to straighten out and permit the homologous chromosomes to become intimately associated in pairs before the chromatids split and coil.

SUMMARY

A study of chromosome structure and behavior at mitosis and meiosis has been made in *Tradescantia, Vicia, Lilium, Secale,* and other genera.

The somatic chromosomes at the resting stage are in the form of loose spirals. At prophase the chromonemata form new coils which appear as the remnant coils are straightened out. The contraction of the chromosomes between prophase and metaphase is effected by coiling of the chromonemata. The average reduction in length of the chromosomes

between the "spireme" stage and metaphase is about 3:1 in the root tip cells of the species examined, and may be greater in microspores. As the chromosomes enter the resting stage the chromonemata tend to uncoil filling the resting nucleus with loose, irregular spirals. Thus the chromonemata are coiled at all stages in the mitotic cycle.

The chromosomes at meiotic prophase are practically free from remnant coils and the new coils do not appear until late pachytene. The chromosomes at meiotic prophase are about twice as long as those of the mitotic prophase. The average reduction in chromosome length between pachytene and meiotic metaphase is about 9:1. This reduction in length may be effected by linear contraction of the gene string, and by major and minor coiling of the chromonemata. The relation of these factors in chromosome contraction may differ in different genera.

A theory of the mechanism of meiosis has been proposed, based on the comparison of chromosome behavior in mitosis and meiosis, and the comparative duration of the mitotic and meiotic cycles. The chromonemata of mitotic chromosomes are in the form of spirals at all periods of the chromosome cycle and this coiling prevents any intimate association of homologous chromosomes. At prophase of meiosis the chromonemata are relatively free from coils and homologous chromosomes can become closely paired before the new coiling is initiated. The retardation theory of meiosis is in accord with the recent evidence regarding the time of chromosome duplication.

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DESCRIPTION OF PLATES

Plate 161

Photographs of Tradescantia microspores fixed and stained in aceto-carmine after pretreatment with ammonia alcohol. Magnification $\times$ 1200 except photo. 8 which is $\times$ 2000.

Photo. 1. Resting stage, nucleus filled with loose spiral chromonemata.

Photo. 2 and 3. Early prophase with remnant spirals from preceding anaphase.

Photo. 4. Prophase spireme with most of the remnant coils removed and the new spirals appearing in each chromatid.

Photo. 5. Late prophase after the chromatids have contracted and more clearly separated.

Photo. 6. The chromosomes at metaphase fixed without effective pretreatment.

Photo. 7. Early metaphase showing the coiled chromonemata in each chromosome and partial twisting of chromosomes about each other.

Photo. 8. Early metaphase showing approximate number of coils, and twists in chromatids.

Photo. 9. Anaphase chromosomes with two coiled chromatids in each chromosome.

Plate 162

Photographs of mitotic and meiotic chromosomes of *Vicia faba*. Aceto-carmine preparations. Magnification $\times$ 1200.

Photo. 1. Prophase spireme of root tip cell.

Photo. 2. Anaphase from root tip chromosomes showing secondary constrictions in the "m" chromosomes, and some evidence of internal spirals.

Photo. 3. Meiotic metaphase showing distribution of chiasmata.

Photo. 4. Meiotic anaphase showing major coils.

Photo. 5. Meiotic telophase showing extreme chromosome contraction.

Photo. 6. Prophase of microspore division.

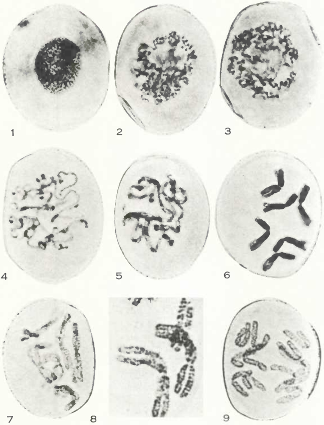
Photos. 7 and 8. Anaphase chromosomes of the microspore division.

Plate 163

Photographs of mitotic and meiotic cells from aceto-carmine preparations. Magnification $\times$ 800.

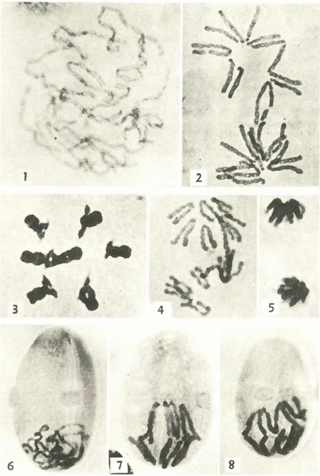
Photo. 1. Meiotic pachytene in *Lilium regale*.

Photo. 2. Meiotic metaphase in *Lilium regale*.



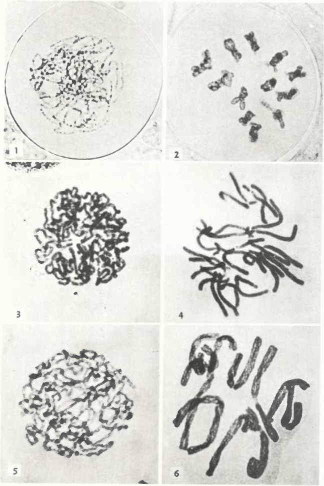
CHROMOSOME STRUCTURE AND BEHAVIOR

THE HELIOTYPE CORP. BOSTON



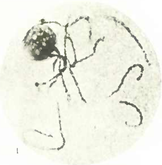
Chromosome Structure and Behavior

THE HELIOTYPE CORP. BOSTON



Chromosome Structure and Behavior

THE HELIOTYPE CORP. BOSTON



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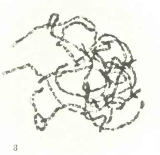

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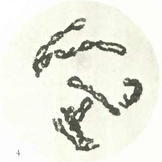

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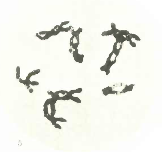

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6

Chromosome Structure and Behavior

THE HELIOTYPE CORP. BOSTON

Photo. 3. Somatic prophase in *Lilium regale*.
Photo. 4. Somatic metaphase in *Lilium regale*.
Photo. 5. Somatic prophase in *Trillium grandiflorum*.
Photo. 6. Somatic metaphase in *Trillium grandiflorum*.

PLATE 164

Photographs of meiotic chromosomes of *Zea* and *Allium* photographed at × 1200 and reduced in reproduction.

Photos. 1 and 2. Meiotic chromosomes of *Zea Mays* showing reduction in chromosome length between very late diakinesis or early diplotene and diakinesis.

Photos. 3–6. Meiotic chromosomes of *Allium Cepa* showing reduction in chromosome length between pachytene and metaphase.

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THE FLORA OF SAN FELIX ISLAND

IVAN M. JOHNSTON

With plate 165

THE ISLAND of San Felix, lat. 26° 16′ S., long. 80° 0′ W., lies over 800 kilometers off the north coast of Chile and about an equal distance north of the islands of Juan Fernandez. It is volcanic, apparently a portion of a disrupted crater, and is surrounded by depths of about 4000 m. The island is about 2.5 km. long. At the narrow west end there is an abruptly elevated hill of yellowish tuff called Cerro Amarillo, 183 meters high. The principal part of the island, however, is broad and flattish and is composed of a series of black lavas that form a platform which gently slopes towards the north and broadens towards the east end to a maximum width of nearly 1.5 km. It is bounded by sea-cliffs, 50–70 m. high on the south and 15–20 m. on the north side. This broad flattish part of the island is overlaid here and there with a thin covering of fine dry earth, and is strewn all over with fragments of lava of no great size. In appearance the island is extremely barren and desolate.

Most of the surface of San Felix is devoid of plants. Dr. Chapin informs me that on the flattish major part of the island the flora consists of three evident species, of which the scattered, depressed growths of the shrubby *Suaeda nesophila* are the most conspicuous. The other two species, members of *Eragrostis* and *Cristaria,* are ephemeral annual herbs of scattered occurrence. Two species can be attributed to Cerro Amarillo. On its lower slopes *Atriplex Chapinii* grows in the soft yellowish volcanic rock. The only erect shrub on the island, *Thamnoseris lobata,* grows in a few sheltered ravines on its upper slopes, where some adiabatic fogs supplement the extremely scanty rains of this desert island. The flora of San Felix is hence very poor in the number of its species, as well as in the number of individual plants. It is, however, high in endemism.

In the same small archipelago, about 18 km. east of San Felix, is the island of San Ambrosio. This is a slightly smaller island but is uniformly lofty, being surrounded by imposing cliffs and reaching an altitude of 450 m. Its high fog-bathed cliffs and crests are very much more favorable for plants than the low arid flats and slopes of San Felix. The very different environmental conditions have given it a flora almost completely different from that of its neighbor. Though San Ambrosio evidently has a much richer and more interesting flora, the difficulties of landing on the island and of climbing its precipitous sides have hindered its proper exploration. What is known of its flora today rests almost exclusively upon a few fragmentary specimens collected on its green crests by Simpson in 1869. These fragments, carried off the island in his hat (!), are all that has been collected of a number of very distinct endemic genera and species. The flora of San Ambrosio is obviously a remarkable one, high in endemism and still a promising source for new genera and species. No island off the west coast of America is in greater need of exploration.

The present paper is concerned only with the relatively small flora of the more accessible San Felix and is an account of the two collections from the archipelago preserved in North American herbaria. Its prime purpose is to put on record certain new species and new names for use in research growing out of the recent visit to the island by the yacht, *Zaca*.

The first botanical collections from San Felix and San Ambrosio appear to have been made by Enrique Simpson in August, 1869. The eight species represented were enumerated by R. A. Philippi, Bot. Zeitung, **28**: 496–502, tab. 8a (1870). Simpson had only one species from San Felix, a *Parietaria,* which has not since been collected in the archipelago.

The second and best existing account of the flora of San Felix and San Ambrosio is by Frederico Philippi, Anal. Univ. Chile, **47**: 185–194, cum tab. (1875). This paper reviews the collections of Simpson and discusses those made by Ramon Vidal in September, 1874. Simpson reached the crest of San Ambrosio, whereas Vidal got only the few plants he could obtain from the sides of that island. Vidal, however, did collect more carefully on San Felix. In publishing, the younger Philippi, unfortunately, treated the archipelago as a whole and gave only rare indications as to the particular island upon which Vidal made his several collections. From some notes which I made in the Philippi Herbarium at Santiago in 1926, from internal evidence within Philippi's report, and from mention of collections in Reiche's Flora de Chile, it is possible to state that Vidal obtained on San Felix specimens of *Suaeda, Cristaria, Lycapsus* and *Thamnoseris*. It is just possible that a *Tetragonia* and a *Frankenia* were also obtained. In his official report of his "Esploracion de las islas San Félix i San Ambrosio," Anal. Univ. Chile, **45**: 735–756 (1874), Vidal antedated the report of the younger Philippi and gave an atrociously misspelled list of 9 angiospermous species stated to represent the flora of San Felix. The determinations were attributed to

Philippi. The list evidently contains the species obtained by Vidal on San Ambrosio as well as San Felix. Among the species attributed to San Felix by Vidal, the following, to judge by the Vidal specimens in the Philippi Herbarium at Santiago, were collected on San Ambrosio only, — *Sicyos, Atriplex foliolosum, Heliotropium* (*Nesocaryum*), and *Frankenia*.

Subsequent to the report of Frederico Philippi accounts of the flora of San Felix and San Ambrosio have been largely compilation. Hemsley, Report Voy. Challenger, Bot. **3**: 97–100 (1884), apparently unaware of the report by the younger Philippi, translated and abridged the earlier and less complete report of the elder Philippi and recorded collections of *Lycapsus* and *Thamnoseris* made by Coppinger from rocks just south of San Ambrosio. Reiche, in Engler & Drude, Veg. Erde, **8**: 269 (1907), compiled a few general notes on the flora of the islands and mentioned the visit to the island by Johow. There is only the most general information recorded concerning the work accomplished by this latter botanist. According to the brief reports, Deutscher Wiss. Ver. Santiago, Verhandl. **3**: 525 and 529 (1898), Johow visited the island in October 1896. His collections, so long unenumerated, have only recently been placed in the capable hands of Prof. Carl Skottsberg for critical study and report.

The only other botanical collections from the islands known to me are those specially treated in this paper. Prof. Bailey Willis visited San Felix in May 1923 for geological observations and there obtained five specimens now preserved in the herbarium of Stanford University. An account of his visit to the islands, with numerous photographs, is to be found in the Publications of the Carnegie Institution, vol. **382**: 120–124, tab. 64–68 and 74–75 (1929). Dr. James P. Chapin visited San Felix for ornithological work on Feb. 18, 1935. He was a member of the "Templeton Crocker Pacific Expedition" of which there is an account in the Scientific Monthly, **41**: 281–285 (1935). His botanical collections consisting of nine numbers represent four species. The first set of them is in the New York Botanical Garden and a set of duplicates is in the Gray Herbarium. The collections represent plants from various parts of the island and are uncommonly ample. They are the best that have been made on San Felix. Through the courtesy of Dr. Chapin I am able to reproduce two of the photographs he made on the island.

In my list of the flora of San Felix there are seven species accredited to the island. Of this number two, *Eragrostis* and *Parietaria*, are non-endemic, occurring also on the arid coastal region of northern Chile and southern Peru. Of the remaining five, *Lycapsus* is known from San Ambrosio as well as San Felix. This is the only species accredited to both of the islands. The endemic species of San Felix belonging to non-endemic genera, *Atriplex, Suaeda* and *Cristaria*, are rather well marked but have their closest affinities with plants of the coastal hills of southern Peru and northern Chile. The archipelago has two genera of the Compositae, each of which has a species on San Felix. These genera are endemic and are so distinct that their natural position in their respective subfamilies is yet open to question. The genus *Thamnoseris* perhaps is nearest to *Dendroseris* of Juan Fernandez. The tribal position of *Lycapsus* is still undetermined. If we may judge from the relationship evident in all other members of the flora of San Felix and San Ambrosio, we may perhaps surmise that these two genera of Compositae had relationships, now lost or obscured, in western South America.

CATALOGUE OF THE SPECIES

Gramineae

Eragrostis peruviana (Jacq.) Trinius, Mem. Acad. St. Petersb. sér. 6, **1:** 396 (1831).

Collected in a mature condition by Chapin (1108). Not only a new species for the known flora of San Felix but also the first monocot to be reported from the archipelago. The species has heretofore been known only in the coastal hills from central Peru south to the Taltal region in northern Chile. A close comparison of Chapin's collections with abundant material from the continent has revealed no characters or even tendencies whereby it might be distinguished.

Urticaceae

Parietaria debilis Forster, Prodr. 73 (1786). — *Parietaria feliciana* Philippi, Bot. Zeit. **28:** 501 (1870); F. Philippi, Anal. Univ. Chile, **47:** 192 (1875).

This genus is known from San Felix only through a collection from Simpson. It was the only plant he obtained on that island. I have compared a fragment of his collection with the common and variable plant of western South America passing as *P. debilis* and can find no characters to separate them.

Chenopodiaceae

Atriplex Chapinii, sp. nov., perennis monoica fruticosa e caudice crasso lignoso erumpens depressa pallida 1–3 dm. alta, 3–12 dm. lata; caulibus prostratis vel decumbentibus ramosis, juventate summum ad apicem inconspicue evanescenter pubescentibus mox glabratis; foliis concoloribus glabris lanceolatis vel oblanceolatis numerosis confertis evidenter costatis sed inconspicue nervatis 8–15 mm. longis 2–7 mm.

latis apice subacutis basi in petiolum ca. 1 mm. longum gradatim attenuatis margine integerrimis; floribus staminatis in spicas terminales 2–3 cm. longas infra medium plus minusve interruptas et bracteatas flavescentas (maturitate plus minusve fuscas) aggregatis; floribus pistillatis in axillis foliorum superiorum dispositis; bracteis fructiferis ultra medium connatis in ambitu angulatis 6–7 mm. longis 5–6 mm. latis, corpore crassis induratis subobovoideis 2–3 mm. longis 2 mm. latis plus minusve verrucosis, margine prominente herbaceis planis sparse dentatis plus minusve trilobatis; seminibus erectis 1–1.5 mm. diametro, testa brunnescente, radicula verticali.

SAN FELIX: low bush about 2.5 dm. tall and 3–9 dm. broad, Feb. 18, 1935, *J. P. Chapin 1104* (Gray Herb., TYPE; NY); low bush, leaves grayish green, forming circular or oval clumps 3–12 dm. in diameter, 2.5–3 dm. high, *Chapin 1105* (NY); with male flowers, *Chapin 1106* (G, NY) and *1109* (G); a flat-growing plant keeping close to soil and rocks, May 2, 1933, *Bailey Willis 4* (Stanf.).

The material collected by Chapin and by Willis is quite similar and evidently conspecific. The island plant is most closely related to the poorly understood group of spreading monoecious perennials of the Chilean coastal region. Although collected by a busy geologist and by a busy ornithologist the species is curiously lacking in the collections of Vidal, who seems to have been the most energetic botanizer on the island, unless the report of *Tetragonia maritima*, by the younger Philippi, Anal. Univ. Chile, **47:** 88 (1875), may have been based upon a sterile specimen of it misidentified.

Atriplex Chapinii is evidently distinct from *A. foliolosum* Phil. which is known only from sterile specimens collected on the adjacent island of San Ambrosio. The latter endemic has crowded sessile ovate-triangular leaves only 2.5 mm. long and 2 mm. broad.

Suaeda nesophila, nom. nov. — *Suaeda divaricata* Moq. var. *microphylla* F. Philippi, Anal. Univ. Chile, **47:** 193 (1875); Reiche, Fl. Chile, **6:** 175 (1911), not *S. microphylla* Pallas.

This shrub was collected both by Willis (no. 2) and by Chapin (1107 and 1110). According to Dr. Willis it is the common bush growing on the flatter parts of the island in rounded masses up to 9 dm. in diameter and 5 dm. in height. Dr. Chapin notes that the leaves are at first a light grayish green which turns finally to a dull purplish red. The distal leaves are almost always reddish. He adds that the rounded clumps are 2.5–3.5 dm. tall and 9–12 dm. broad. This endemic species is evidently related to *S. foliosa* Moq. of the coastal hills of northern Chile and southern Peru, from which it is quickly distinguished by its very much more slender and more branched habit and very much smaller clavate leaves. It is certainly not closely related to *S. divaricata* Moq., which is a large bush confined to Argentina.

MALVACEAE

Cristaria insularis F. Philippi, Anal. Univ. Chile, **47:** 186 (1875); Reiche, Anal. Univ. Chile, **91:** 405 (1895) and Fl. Chile, **1:** 257 (1896).

Collected on San Felix by Willis (no. 3 a–b) and by Chapin (nos. 388, 1111). Their collections are very mature with the leaves mostly dried and weathered. There are some flowers and much good fruit. The plant is endemic though related to a group of small-flowered annuals occurring in the coastal hills from central Chile to central Peru.

COMPOSITAE

Lycapsus tenuifolius Philippi, Bot. Zeit. **28:** 499, tab. 8a, fig. 1–5 (1870); Philippi, Anal. Univ. Chile, **43:** 484 (1873), locality incorrect; F. Philippi, Anal. Univ. Chile, **47:** 188 (1875). — *Alomia tenuifolia* (Phil.) Benth. & Hook. ex Reiche, Anal. Univ. Chile, **109:** 10 (1901) and Fl. Chile, **3:** 260 (1902); Robinson, Proc. Amer. Acad. **49:** 439 and 453 (1913).

There are photographs and fragments in the Gray Herbarium of the original collections at Santiago made by Simpson and by Vidal. Simpson's collection is labeled as from San Ambrosio. Vidal's collection is given as from San Felix. Dissections of this authentic material shows conclusively that this endemic genus is not a Eupatorioid as has been supposed. The plant has fertile pistillate marginal florets with a 3-toothed ligule about once and a half the length of the tube. The tubular inner florets appear to be hermaphroditic and sterile. The style-branches are linear, flattened and abruptly contracted into a short triangular apex. The receptacle bears conspicuous slender scales which seem to separate the marginal florets from the inner ones. Except for the bracteate receptacle the plant is very suggestive of some of the Helenioids or even certain Asterioids. The bracteate receptacle suggests the Heliantholds but none of the other structures suggest that group of the Compositae. The same may be also said for the Madineae. *Lycapsus* has relations even more vague than *Thamnoseris,* the other endemic genus of the Compositae.

Thamnoseris lobata, sp. nov. — *Thamnoseris laceratus* sensu F. Philippi, Anal. Univ. Chile, **47:** 190, cum tab. (1875); Reiche, Anal. Univ. Chile, **116:** 580 (1905) and Fl. Chile, **5:** 6 (1910), as to shrub of San Felix.

The specimens from Prof. Willis (no. 1) which consist of leaves, flowering inflorescence and parts of stem, agree well with the collections from San Felix by Vidal which were described at length and illustrated by the younger Philippi. According to Willis' notes the plant grew in a sheltered ravine on Cerro Amarillo, 150 m. alt., and formed a low, abundantly lactiferous shrub with thick woody trunk and branches. The bark was light gray, smooth and "swollen looking."

Neither the collection by Vidal nor that by Willis matches the single leaf of the lactiferous shrub of San Ambrosio upon which the elder Philippi, Bot. Zeit. **28**: 499, tab. 8, fig. A6 (1873), based his *Rea ? lacerata*. This leaf from San Ambrosio is triangular in outline, broadest at the base, cut 9/10 of the way to the rachis and has the well spaced 3–4 pairs of lobes prominently and narrowly lobulate. In the San Felix plant, as given by the younger Philippi and later by Reiche, and as shown by the material collected by Bailey Willis, the leaves are lanceolate, broadest above the middle, gradually contracted towards the base, cut ½–⅔ to the rachis, and the crowded 3–5 pairs of lobes sparsely lobulate-toothed. The material from San Felix is consequently quite different in appearance from the scanty specimen originally described from San Ambrosio and so seems to merit a new name. The lengthy descriptions given by the younger Philippi and by Reiche are based upon the collection of Vidal illustrated by the former author. This collection and the mentioned descriptions and plate amply characterize *Thamnoseris lobata* of San Felix.

The imperfectly known plant that is correctly known as *Rea lacerata* Phil., *Thamnoseris laceratus* (Phil.) F. Phil. or *Dendroseris lacerata* (Phil.) Hemsley, is consequently known only from San Ambrosio where Simpson reported it as common on the crests and Hemsley, Report Challenger Voy. Bot. **3**: 99 (1884), reported it as occurring on a rock just south of that island. Until the flowers and inflorescence of this plant of San Ambrosio are described, its exact relationship with *T. lobata* of San Felix must remain a matter of surmise.

The lactiferous shrub of San Felix is evidently a member of the Cichorioideae. It has naturally been compared with *Dendroseris*, an endemic genus of Juan Fernandez having similar habit, for *Thamnoseris* and *Dendroseris* not only occur in adjacent archipelagos, but are unique among the Cichorioids in having a pronounced woody habit. Floral structures of these two genera, however, show many differences. I am inclined to the opinion that we must await the judgment of some future student who has mastered the complexities of the classification and interrelation of the Cichorioids, before we definitely select similarities of habit as indicative of direct relationship between the two insular endemic

WEST END OF SAN FELIX FROM THE LAVA CLIFFS ON THE SOUTHSIDE OF THE ISLAND; THE HIGH HILL OF TUFF IS CERRO AMARILLO.

SOUTHEAST PORTION OF SAN FELIX SHOWING THE TOPOGRAPHY OF THE PRINCIPAL PART OF THE ISLAND; THE ISLET OF GONZALES IS ON THE RIGHT AND TO THE LEFT, EASTWARD IN THE DISTANCE, IS THE ISLAND OF SAN AMBROSIO.

genera. The similarities of habit may be simply parallel evolution, the similar responses of two different stocks isolated under equitable insular climates. Many groups of angiosperms, prevailingly low and herbaceous on the continents, have produced woody forms on oceanic islands. The woody habits of *Dendroseris* and *Thamnoseris,* accordingly may be simply ecological and not indicative of immediate relationship. The exact relationship of the two insular genera with each other and with other Cichorioids is still uncertain. Their relationship does not seem to be Old Pacific, for the Cichorioids are very scantily represented in New Zealand and Australia and northward in the Pacific, and none of them in this region have structures suggestive of close affinity with our insular genera. In the past our genera have been associated with the genus *Fitchia,* a woody group of Polynesia, but as suggested by Drake del Castillo, Jour. de Bot. **12:** 176 (1898), that genus now proves to be a Mutisioid. Consequently the old hypothesis as to an Old Pacific relationship of our shrubs must seek new justification. Though I can find no evident relatives of them in South America, I suspect that, like other members of our insular florulas, the insular Cichorioids were probably derived from South American ancestors. The best development of the Cichorioid Compositae in the Southern Hemisphere is to be found in western South America. Our insular Cichorioid shrub may be merely aspects of the evolutionary activity centering on the adjacent continent.

Arnold Arboretum,
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SOME NEW TREES AND SHRUBS FROM MEXICO

ALFRED REHDER

Carya mexicana Engelm. forma **polyneura,** f. nov.

A typo recedit foliolis plerisque elliptico-lanceolatis margine penicillato-ciliolato excepto glabris vel fere glabris, nervis utrinsecus 15–20 tantum 3–6 mm. distantibus, exocarpio tenui 1.5–3 mm. crasso.

NUEVO LEON: Sierra Madre Oriental, Puerto Blanco to Taray, about 15 m. s.w. of Galeana, *C. H. and M. T. Mueller,* no. 1226, July 23, 1934, "shrub or small tree very abundant in more or less moist woods, practically all over the mountain" (type).

This form, at the first glance, looks very distinct with its closely and conspicuously veined leaflets, glabrous except the ciliate margin and a few hairs on the under side near the base, but among the numerous specimens under no. 1226 there are larger detached leaves, apparently from sterile vigorous branches, or from different trees, with more distant veins and thinly pilose over the whole under surface; these leaves do not differ at all from those of typical *C. mexicana.* Also the difference in the thickness of the husk does not seem to segregate the tree of the Sierra Madre Oriental from that of the type locality of the species, Alvarez, San Luis Potosi. A fruit of Palmer's no. 835½ which represents the type of *C. mexicana* has the husk in a dry state up to 6 mm. thick, while most specimens collected in the same locality by Dr. A. R. Goodman in 1910 have the husk only 2–3 mm. thick and a smaller nut resembling in shape that of *C. ovalis* var. *obcordata,* but one lot of seeds has the husk as thick as in the type.

It thus appears that *C. mexicana* varies as much in the thickness of its husk and in the pubescence of its leaves as *C. ovata* (Mill.) K. Koch, to which it is closely related: in fact, I cannot find any strong character to separate the two, and I believe that *C. mexicana* is only a southern climatic form of *C. ovata.* The buds are generally smaller, but in a specimen collected by Dr. E. Palmer in 1902 (no. 71) the terminal winter-bud is 1.5 cm. high. Nothing seems to be known of the character of the bark, and until we have more complete material, *C. mexicana* may be kept distinct. I also have before me a flowering specimen from La Jolla Ranch, Tamaulipas (Robert Runyon 1019) with nearly glabrous leaves. Thus the species seems to be restricted to three adjoining departments in northeastern Mexico, namely Nuevo Leon, San Luis Potosi and Tamaulipas.

Litsea Muelleri, spec. nov.

Frutex ramis gracilibus hornotinis ut petioli dense fulvo-villosis tertio vel quarto anno tarde glabrescentibus fuscis vel partim flavidis. Folia persistentia, coriacea, ovata, 2–4.5 cm. longa et 1.2–3.2 cm. lata, breviter acuminata vel acuta, basi rotundata vel subcordata, supra minute reticulata et tenuiter villosa demum glabrescentia, luteo-viridia, subtus tomentosa, glauca, nervis utrinsecus circiter 5 ut costa supra leviter vel vix elevatis, subtus distincte elevatis, costa flavescente; petioli 2–4 mm. longi, tomentosi. Inflorescentiae pleraeque 3-florae, axillares, solitariae vel 2–3 fasciculatae; pedunculi 1.5–3 mm. longi, fusco-pilosi ut pedicelli; pedicellus medius 1–1.5 mm. longus, laterales breviores; bracteae caducae, extus fusco-pilosae; perianthium tubo nullo, segmentis ovalibus 2.5–3 mm. longis basi extus strigosa exceptis glabris; stamina 9, filamentis glabris vix dimidias antheras subrectangulares truncatas aequantibus, ea seriei tertiae glandulis binis filamenta subaequantibus aucta; ovarium parvum, ovoideum, in stylum brevem attentuatum. Fructus tantum immaturi circ. 5 mm. diam. visi.

Nuevo Leon: Sierra Madre Oriental, east side of divide between San Francisco Canyon and Pablillo, 15 miles s.w. of Galeana; alt. 8500 ft., common in dense woods, *C. H. and M. T. Mueller,* no. 379, May 14, 1934 (type); Sierra Madre Oriental, cañon above Alamar, about 15 miles s.w. of Galeana, alt. 5000–6000 ft., common in open oak wood, *C. H. and M. T. Mueller,* no. 689, June 2, 1934 (with immature fruit).

This species seems to be most closely related to *Litsea Neesiana* (Schau.) Hemsl. which is easily distinguished by its larger and narrower leaves, cuneate or broadly cuneate at base, by the larger inflorescence, longer peduncles and filaments longer than the anthers; in the shape of the leaves it resembles *L. parvifolia* (Hemsl.) Mez, but that species is quite glabrous and the pedicels are long and slender.

Amelanchier paniculata, spec. nov. (§ Malacomeles).[1]

Frutex ramulis satis validis initio dense albo-tomentosi ut petioli et facies inferior foliorum, annotini tarde glabrescentes rubro-fusci, vetustiores griseo-fusci. Folia persistentia, chartacea vel subcoriacea,

[1]**Amelanchier** sect. **Malacomeles** (Dcne.), comb. nov.
Nagelia Lindley in Bot. Reg. **31**(Misc.): 40 (1845).
Nägelia Lindley, Veg. Kingd. 560 (1846). — Wenzig in Linnaea, **43**: 80 (1880) "Naegelia." — Non *Naegelia* Rabenhorst, Kryptog. **1**: 85 (1844).
Cotoneaster sect. *Malacomeles* Decaisne in Nouv. Arch. Mus. Hist. Nat. Paris, **10**: 177 (1874).
Cotoneaster A. *Naegelia* (Lindl.) Wenzig in Jahrb. Bot. Gart. Mus. Berlin, **2**: 304 (1883).
Amelanchier sect. *Nagelia* [Lindl.] Koehne, Gatt. Pomac. (in Wiss. Beil. Progr. Falk-Realgymnas. Berlin, p. 25. 1900). — Schneider, Ill. Handb. Laubholzk. **1**: 742 (1906).

oblongo-elliptica vel oblonga vel interdum obovato-oblonga, 3.5–7.5 cm. longa et 1.5–3 cm. lata, acutiuscula vel obtusiuscula, mucronulata, basi cuneata vel late cuneata, rarius fere rotundata, integra vel interdum remote et minute denticulata denticulis ad mucronem reductis, supra costa tenuiter villosa et margine dense villosula exceptis ab initio glabra, laete viridia, subtus dense albo-tomentosa, nervis utrinsecus 15–20 supra ut costa media leviter impressis, subtus prominulis et costa media manifeste elevata; petiolis 5–10 mm. longi, dense tomentosi. Inflorescentiae terminales, paniculatae vel simpliciter racemosae, pleraeque pedunculis inferioribus trifloris superioribus unifloris, rarius simpliciter racemosae, rarissime pedunculis inferioribus 7-floris et superioribus trifloris, 3–5 cm. longae, albo-tomentosae; pedicelli 3–10 mm. longi; calycis tubus 2.5 mm. longus, extus ut lobi leviter floccoso-tomentosus mox glaber, lobi triangulari-ovati, acuti, mucronulati; petala late ovalia, vel suborbicularia, basi abrupte contracta, circiter 6 mm. longa, glabra; stamina circiter 20, petalis dimidio breviora, antheris cordato-ovatis 1 mm. longis; carpidiis 3–5, dorso apice conico libero longe villoso excepto calycis tubo adnatis ventre fere ad basin liberis villosis; styli basi excepta glabri, staminibus paullo longiores. Fructus immaturus subglobosus, circiter 8 mm. longus, calycis lobis reflexis intus extusque glabris margine villoso-ciliolatis coronatus.

NUEVO LEON: Sierra Madre Oriental, San Francisco Cañon, about 15 miles s.w. of Galeana, alt. 7500–8000 ft., scattered on rocky soil in open or scrub wood, *C. H. and M. T. Mueller*, no. 282, May 9, 1934 (type).

This new species belongs to the section Malacomeles and seems most closely related to *A. nervosa* Dcne., but readily distinguished by the much larger, generally oblong and entire or nearly entire leaves and the usually paniculate inflorescence.

As Malacomeles is the earliest sectional name of this group, it must be maintained, when the section is transferred to *Amelanchier*. Moreover, *Nagelia* is an illegitimate name being a later homonym of *Naegelia* Rabenhorst. *Nagelia*, *Nägelia* and *Naegelia* must be considered orthographic variants of the same name, since both genera are named in honor of Karl Naegeli.

Arctostaphylos novoleontis, spec. nov. (§ Comarostaphylis).

Frutex ramulis hornotinis puberulis, secundo vel tertio anno glabrescentibus fuscis decorticantibus. Folia persistentia, lanceolata, 3–6 cm. longa et 6–12 mm. lata, interdum minora, acuta vel obtusiuscula, mucronulata, basi cuneata, margine integro cartilagineo et praesertim basin versus leviter revoluto, supra luteo-viridia, lucidula, tenuiter villosula, demum glabrescentia, subtus glauca, breviter villosula, costa media supra leviter impressa subtus elevata, nervis utrinque obsoletis; petioli 4–6 mm. longi, tenuiter villosuli. Panicula 3–6 cm. longa, interdum ad racemum reducta, minute canescenti-puberula, laxiflora; pedicelli graciles, 4–10 mm. longi; sepala 5, triangulari-ovata, acuminulata, 1.75 mm. longi, extus parce villosula, ciliolata, rubra; corolla cylindrico-urceolata, 8–10 mm. longa, extus glabra, intus sparse villosula; lobis latis rotundatis recurvatis; stamina dimidiam corollam aequantia, filamentis glabris ima basi dilatatis, antheris bi-aristatis; stylus corollam subaequans ut ovarium 5-loculare glaber. Fructus immaturus 4 mm. diam., granulosus, obscure fusco-ruber.

NUEVO LEON:. Sierra Madre Oriental, San Francisco Cañon, about 15 miles s.w. of Galeana, alt. 7500–8000 ft.; sparse on top of hill above the upper cañon, *C. H. and M. T. Mueller,* no. 319, May 12, 1934, (type); Sierra Madre Oriental, last hill on west side of lower San Francisco Cañon, about 15 miles s.w. of Galeana, common in shrub zones on slopes and tops, *C. H. and M. T. Mueller,* no. 1032, July 15, 1934, "fruit dark brownish red."

This species seems to be most closely related to *A. polifolia* H.B.K., *A. glaucescens* H.B.K. and *A. minor* (Small) Standl.; from the first two species it is readily distinguished by the glabrous ovary and from *A. polifolia* also by the glabrous filaments, from *A. minor* it differs in the larger and broader more pubescent leaves, the smaller corolla and the pubescent filaments. The fruiting specimen, no. 1032, differs somewhat in the smaller leaves 1.5–4 cm. long and 4–7 mm. broad and less densely pubescent.

Menodora Muellerae, spec. nov.

Suffrutex humilis, decumbens, ramosissimus, 15 cm. vix excedens, caulibus subteretibus viridibus, rima basibus foliorum decurrentibus formata hispidula excepta glabris. Folia opposita, crassiuscula, vix distincte petiolata, 4–10 mm. longa, lineari-oblonga vel anguste oblanceolata, inferiora interdum lineari-subulato, acuta et mucronata, basin versus sensim attenuata, basibus foliorum oppositorum contiguis rimam hispidulam ad par foliorum inferius decurrentem formantibus, margine setis brevibus leviter reflexis setoso-ciliolata, ceterum glabri, costa media subtus elevata. Flores in apice ramulorum solitaria; pedicellus 2–4 mm. longus, pilosulus; calyx campanulatus, tubo circ. 1.5 mm. longo glabro vel basin versus sparse pilosulo, lobis plerumque 10 subulato-linearibus 5–6 mm. longis ciliolatis; corolla hypocraterimorpha, tubo gracili apicem versus leviter ampliato 12–14 mm. longo, lobis oblongis 6–7 mm. longis acuminulatis; stamina exserta, dimidios lobos aequantia, filamentis glabris 5 mm. longis circiter 3 mm. infra faucem tubo affixis, antheris oblongis 2.5 mm. longis; stylus staminibus paullo longior; stigmate capitato lato. Fructus circ. 7 mm. diam.; pedicellis recurvatis, coccis circumcissilibus; semina plerumque 2 vel 3, rarius 4 vel 1, ovoidea vel oblongo-ovoidea, plus minusve compressa, circ. 4 mm. longa, atrofusca.

NUEVO LEON: Sierra Madre Oriental, cedar savannah above Encinal wheatfields, about 15 miles s.w. of Galeana, alt. about 7500–8000 ft., abundant over small areas, *C. H. and M. T. Mueller*, no. 463, May 19, 1934 (type).

This species seems to be most closely related to *M. longiflora* A. Gray on account of the salver-shaped corolla with a long slender tube, though not as long as in *M. longiflora*, but it is easily distinguished by the decumbent habit, smaller, much narrower leaves, exserted stamens and solitary flowers with the pedicels recurved in fruit. The species is named in honor of Mrs. Mary Taylor Mueller who accompanied her husband on his Mexican expedition.

HEBRARIUM, ARNOLD ARBORETUM,
HARVARD UNIVERSITY.

NEW FACTS CONCERNING CEPHALOSPORIUM WILT OF ELMS

D. B. Creager

One result of the experience of having to wage a campaign against the Dutch elm disease in America has been the calling of attention to the native wilt diseases of elms. Of these there are two; one is tentatively designated "Cephalosporium wilt" (or "Cephalosporium die-back"), the other "Verticillium wilt." They are widely spread and the first named is relatively frequent in nursery stock and on older trees of all ages. Both are being studied intensively at the Arnold Arboretum of Harvard University with the object of more clearly defining symptoms, discovering means of spread, determining the course of the infection and testing methods of control. My own investigations on the former are now sufficiently advanced to warrant the publication of certain findings which appear to point the way to control.

1. Two kinds of reproductive bodies, as recently noted by Dr. Curtis May, are produced by the fungus that causes Cephalosporium wilt. These are (a) naked spore heads such as are characteristic for the genus *Cephalosporium* and (b) pycnidia, a type of fructification not known for that genus. Both make their appearance in laboratory cultures and both occur in nature. The pycnidia are of special importance but no explicit statement of their occurrence in nature could be found in the literature. The significant feature to be emphasized, one hitherto unrecorded, is their natural abundance and their importance. They form profusely in the bark of infected twigs and branches as the bark tissues gradually die during the summer. These pycnidia contain myriads of small spores which remain viable over winter. The spores ooze out in a gelatinous matrix through ostioles to the surface of the bark. Apparently wind and rain play an important part in spore dissemination. Also, since spores are exposed to the outside, such agencies as insects and birds may serve an important rôle in transmission of the pathogene.

2. Wounds in the leaves provide the most common infection court. Large numbers of leaves injured by canker worms have been found to be infected in the vicinity of killed branches on the same and nearby trees. Any insect causing open wounds in leaves or stems such as the canker worms (*Alsophila pometaria* Harr. and *Paleacrita vernata* Peck), the spiny elm caterpillar (*Hamadryas antiopa* Linn.), the elm leaf beetle

(*Gallerucella luteola* Müll.). the small European elm bark beetle (*Scolytus multistriatus* Marsh) and numerous others, provide suitable wounds through which the fungus may enter the suscept.

3. An early symptom of the typically infected leaf is a yellowing near the infection court or wound. The yellowed area increases and the portion near the wound dies and becomes brown. Usually a brownish discoloration of the veins occurs in advance of the necrotic area in the mesophyll. Finally the discoloration extends through the vascular strands of the petiole into the stem, and the leaf drops off. The pathogene has been isolated from a large number of such leaves and from the stem in the vicinity of the leaf base.

4. Artificial inoculations made on seedlings in the greenhouse substantiate these facts observed in the field. Whether mycelium, spores from spore-heads, or spores from pycnidia were used as inoculum no infection resulted when unwounded leaves were inoculated. On the other hand, any one of these kinds of inoculum brought about infection when leaves were wounded. In stained serial sections of artificially inoculated leaves, the pathogene has been traced from the leaf wound into the stem through the vascular strands of lateral veins, midrib and petiole. The fungus has also been recovered from various regions of wounded leaves and stems of inoculated seedlings by culture methods.

5. Based on the foregoing facts, a number of experiments on control of the disease have been initiated. The first important step is to prune out all dead and infected branches in order to eradicate the disease from individual cases and to destroy the source of future inoculum. Spray tests are also in progress in which insecticides and fungicides are being used to prevent attacks of insects and fungi and to reduce possibilities for infection through wounds already present. Results of these preliminary tests are encouraging; they indicate that a combined pruning and spraying program offers promising possibilities for controlling Cephalosporium wilt.

It is with pleasure that acknowledgment is made of the excellent facilities afforded for this investigation by the pathological laboratory at the Arnold Arboretum and the adjunct laboratory of the North Country Garden Club at the Pratt Estate Oval, Glen Cove, Long Island, New York.

LABORATORY OF PLANT PATHOLOGY,
ARNOLD ARBORETUM, HARVARD UNIVERSITY.

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1935

THE WINTER of 1934–1935 was nearly as severe as that of the previous year.[1] Very little snow fell up to December 31, but a heavy fall of snow took place on January 23 and much of it remained all winter. In January temperatures varied, but low temperatures prevailed. This persistent cold, after the previous severe winter, caused considerable damage to trees and shrubs in the Arboretum. Some of this damage was not apparent until early summer. In the fall of 1934 several temperature stations were established in various parts of the Arboretum which recorded variations of as much as 12 degrees between different stations. Temperature records from these stations will be of much assistance in selecting favorable localities for new plantings.

Early in the spring, an extensive spraying program was carried through to combat a bad infestation of canker-worm. This was successful and prevented defoliation. Other successful spraying programs were carried out for leaf miner in hawthorns and for various other insect pests.

To facilitate the best growth in several groups of shrubs, it was necessary to move and rearrange a large number of plants. More of this work is to be carried out this fall; many large specimens which were badly damaged by winter conditions will have to be replaced.

The extensive collection of lilac varieties flowered exceedingly well last spring and attracted thousands of visitors, also the crab apples and later the mountain laurels flowered profusely, while most of the cherries and particularly the Japanese cherries showed the effects of the two preceding severe winters, as did many of the azaleas and rhododendrons.

During the year 1258 packages of seed were sent out, 782 in the United States, 476 to 12 foreign countries, also 2187 plants and 545 varieties of scions and cuttings. There were received from the United States and other countries 454 packages of seed, 1894 plants, and 592 cuttings and scions. Five hundred and ninety-five plants were added to the Arboretum collections. — L. V. S.

Pathological Laboratory.—The laboratory of plant pathology has now completed the first seven years of its existence. It was established through the efforts of the Supervisor, Professor Oakes Ames, in fulfill-

[1]Records of the effects of the low temperatures during the winter of 1933–34 on the trees and shrubs in the Arnold Arboretum have been published in the Arnold Arboretum Bulletin of Popular Information (Ser. 4, Vol. II, nos. 7 and 8).

ment of the expressed wish of the late Director, Charles Sprague Sargent, and as part of Dr. Sargent's conception of the Arboretum as an institution for the study of woody plants in all fundamental aspects. Professor Ames wisely housed the laboratory in quarters that facilitate cooperative effort and interchange of ideas with the Arboretum's propagator, superintendent and geneticist. The functions of the laboratory were defined as comprising interest in the Arboretum's living collections, extension services, instruction and research.

Naturally collections so extensive, so varied and of such diverse origins and requirements as are those of the Arboretum constantly present health problems of concern to the superintendent and much material of interest to the pathologist. Likewise from time to time pathological problems call for consultation or cooperative undertaking between the pathologist and the propagator or the geneticist. It should also be stated that control measures evolved in the laboratory are tested or applied in the Arboretum whenever possible.

The Arboretum has always exercised a generous attitude with respect to extension services; its plant stores and its knowledge are freely open to all. As might be expected many inquiries are referred to the laboratory of plant pathology and the number has increased yearly. They come from private individuals, nurserymen, arborists, city and town tree wardens, foresters, landscape architects, etc. An account in some detail of this phase of the laboratory's activities formed a part of the report for 1933–4.

Constituted as a unit of an educational institution, the Arboretum has felt that it should bear some instructional responsibility. So from the first the laboratory of plant pathology has assumed its share. A course in the pathology of the forest and of woody plants open to qualified undergraduates and graduates has been offered in Harvard University and from two to six appropriate research students each year have been directed in their special investigations. The Biological Laboratories and the Bussey Institution have provided suitable laboratory space for this work. Of the ability and the research accomplishments of these students I can speak highly. Five of them received travelling fellowships, including three Sheldon awards, at the conclusion of their undertakings at the Arboretum; and seven of them are now filling responsible positions in pathology, mostly research, here or abroad. While this participation in instruction has taken considerable time, most of it has been in connection with research and one result has been the enriching of the research activities of the Arboretum. This is of significance because research is the foremost function of the laboratory of plant pathology.

Statements covering the research accomplished by the laboratory during its first seven years have been included in the preceding annual reports. It will suffice here to report for the past year and merely to add that in the seven year period many problems have received attention and that many of these have been fruitfully solved.

For the year 1934–5 the laboratory reports progress with or completion of studies on the following topics: coniferous rusts, Gymnosporangium diseases, mycotrophy in *Pinus* and wilt diseases of elms. With respect to coniferous rusts particular mention should be made of the elucidation of life history connections, involving firs and spruces, in the genera *Chrysomyxa* and *Milesia,* and the working out of features of taxonomic value based on the morphology of spermogonia. The investigations of I. H. Crowell and J. D. MacLachlan on Gymnosporangium diseases, begun four years ago, are finished. From the results obtained lists have been compiled showing the immunity or grade of susceptibility of hundreds of pomaceous and Juniperus species to the more important species of *Gymnosporangium* found in eastern North America. Moreover, a new means of practical control has been demonstrated that obviates the necessity of eradication of either host, the only method practised up to this time. As a by-product of the research, about two thousand packets of culture materials have been added to the Arboretum's herbarium — a unique contribution. Dr. MacLachlan will spend the year 1935–6 on a Sheldon fellowship in Jamaica, B. W. I., working in a cooperative undertaking between the Arboretum and the Jamaican government on a devastating new rust disease of *Pimenta,* a genus of the economically important family Myrtaceae. This calls to mind the fact that so far no work has been done by our laboratory of plant pathology at the Arboretum's tropical branch in Cuba — almost certainly a fertile field. One of the most valuable results of the year's program has been the demonstration of the role of mycorrhizae in *Pinus* as collectors of certain of the tree's mineral requirements; thus an answer of far-reaching significance is afforded to long unanswered questions as to whether they are important and, if so, in what way.

The fate of America's elms, threatened as they are by the Dutch elm disease, is now the most important tree problem on this side of the Atlantic. The Arboretum's program in the campaign against the Dutch elm disease, as outlined in the report of 1933–4, has been continued vigorously. Distinct progress has also been made in our biological and control studies on a native wilt disease of elms the symptoms of which are almost the same as those of the Dutch elm disease. (See article by D. B. Creager in this number of the Journal of the Arnold Arboretum.)

An essential part of this work was done at our field laboratory on Long Island. That laboratory should be maintained for at least one more summer. Towards the end of 1934, when there was an alarming amount of wavering and pessimism over the possibility of successfully combatting the Dutch elm disease in America, the Arboretum took a strong public stand in support of the policy of complete eradication. It is gratifying to know that federal and state efforts towards eradication during 1935 afford justification for our optimism. With more reason than ever, we again express the belief that our elms can be saved if public support be maintained. — J. H. F.

Cytogenetic Laboratory.—The work on cytotaxonomic problems during the past year includes an analysis of *Robinia* by Dr. Whitaker, a cytological analysis of *Verbena* by Dr. Dermen, and a cytotaxonomic study of *Tradescantia* with the cooperation of Dr. Anderson.

A comparison of chromosome structure and behavior in mitosis and meiosis seems to explain the mechanism of meiosis. Other work on chromosome structure has been continued, especially the spiral structure of the chromonemata in meiotic chromosomes in *Tradescantia* and *Vicia*. The mechanism of development and differentiation has been studied in relation to environmental factors.

The breeding work has been continued with lilacs, roses, magnolias and azaleas. A plant breeding nursery has been established in which there are about a hundred first generation hybrids. A few of these hybrids flowered this year for the first time. — K. S.

The Herbarium.—During the past fiscal year, 16896 specimens have been added to the herbarium bringing the total number up to 408699 specimens.

Of these accessions about 3900 came from the United States and Canada, 4600 from Central and South America inclusive of Mexico, 1150 from Europe and western Asia, 2350 from China, 390 from Formosa, 1150 from India and Malaysia, 1800 from Australasia, and 530 were cultivated plants.

Among the more important collections received during the year may be mentioned: about 8000 specimens representing 1100 numbers from Mexico collected by C. H. and M. T. Mueller, 1350 numbers with many duplicates from Guatemala collected by A. F. Skutch, 290 specimens from Ecuador collected by H. J. F. Schimpff, 293 specimens from Peru collected by G. Klug, 1157 specimens from Brazil collected by A. B. Krukoff, 3100 specimens from Kwangtung and 701 specimens from Hainan received from Lingnan University, 2660 plants from western

China collected by J. F. Rock, 705 specimens from Hupeh collected by H. C. Chow and received from Wu-han University, 1296 specimens from Borneo collected by J. and M. S. Clemens, 1476 specimens from Sumatra collected by Rahmat Si Torroes, 215 specimens from Hawaii and 124 specimens from Samoa received from the Bishop Museum in Honolulu; 140 specimens from South Africa collected by Ecklon and Zeyher.

To the fruit collection, 395 specimens were added, bringing the total number up to 8379.

Additions to the wood collections consisted of 155 numbers, bringing the total up to 3786.

The collection of negatives of types and critical specimens, chiefly Chinese, amounts now to 3012 negatives, 268 having been added during the year.

For study outside of the Arboretum herbarium, 847 specimens were sent out on loan to 14 institutions and individuals in this country and in Europe.

The distribution of duplicates amounted to 19059 specimens sent to 44 institutions in the United States, Canada, Europe, Asia, Australasia and Africa.

Botanical exploration by members of the staff and by expeditions wholly or partly financed by the Arnold Arboretum, has been carried on in America, eastern Asia and Africa. During the summer of 1934, Dr. H. M. Raup continued the study of the flora of the Harvard forest and its neighborhood started the year before, and collected herbarium material. Mr. C. H. Mueller and Mrs. Mary T. Mueller returned in August, 1934, from their collecting tour to Mexico referred to already in last year's report. They collected chiefly in the Sierra Madre Oriental, Department of Nuevo Leon, and brought back about 8000 specimens, representing 1100 numbers. The collection is being identified chiefly at this institution and the Gray Herbarium, and already a number of new species has been described from this collection. About the middle of June, 1935, Mr. Mueller started on another collecting tour to the same locality. Mr. A. F. Skutch collected from July, 1934 to January, 1935, for the Arnold Arboretum in southwestern Guatemala in the Departments of Huehuetenango, Quezaltenango and Quiché; he collected about 1350 numbers with many duplicates, also wood specimens. His collection is being determined chiefly at the Gray Herbarium and the Arnold Arboretum.

In China, two institutions received financial support from the Arnold Arboretum in 1934 for carrying on botanical exploration. The Fan

Memorial Institute of Biology under the direction of Professor H. H. Hu sent an expedition to Yunnan to collect chiefly near the border of Cochinchina, and another to Szechuan which penetrated into the interior Lololand not yet visited by any botanical collector. From Lingnan University expeditions have been sent under the direction of Dr. Franklin P. Metcalf to the provinces of Kwangsi and southern Kiangsi.

Mr. M. Dinklage who had made before important collections in tropical west Africa for the Berlin Botanical Museum, went to Liberia in 1934 to collect in the hinterland of Monrovia for the Arnold Arboretum. As the rainy season prevented his starting soon after his arrival for the Nimba mountains, his final goal, he collected first in the neighborhood of Monrovia and toward the end of the year he started for the Nimba mountains which, however, he was destined not to reach. He was taken sick on the way and died of dysentery on February 2, at the Ganta Mission Station. — A. R.

The Library.—At the end of June 1935 the Library comprised 42,025 bound volumes, 10,917 pamphlets, and 17,573 photographs, a gain of 579 volumes, 432 pamphlets and 332 photographs. Many pamphlets and a few books have been received as gifts, including "Arbejder fra den Botaniske Have i København," Russian works, and miscellaneous articles. Important articles from periodicals and other works have been analyzed, and notice of all available obituaries of botanists have been filed in the author catalogue.

There has been an increase over last year in the number of photographs received, the largest accessions comprising those taken by Dr. Edgar Anderson during his trip to the Balkans, Mr. E. J. Palmer's taken on collecting trips in the western and southwestern United States, Prof. J. G. Jack's taken in Japan and Mrs. Susan D. McKelvey's in Jamaica.

The use of the collection has been extensive. Many photographs have been sold, including 700 taken by the late Dr. E. H. Wilson on his expedition to eastern Asia, 1917–18, purchased by Jardin Botanique de l'État, Bruxelles. Sixty-three lantern slides have been added, the majority of them being colored.

Cards filed during the year include 1,766 in the card catalogue of books in the Library, 336 in the catalogue of photographs, 4,617 in the "Card-index of New Genera, Species, and Varieties Published by the Gray Herbarium," and 5,625 in the manuscript "Index of Illustrations and of New Genera, Species and Varieties of Ligneous Plants Published Since 1915," prepared at the Arboretum, bringing the total of the latter to 106,675. For supplements to the author and subject "Catalogue of the Library" 2,589 slips have been filed. The subject slips now ready for publication number approximately 20,000.

Volumes bound number 229 and more than 100 smaller books and pamphlets were put into pamphlet binders. Clipping files and scrapbooks preserve much interesting material.

Approximately 225 visitors registered in the Library during the year. These include Ynes Mexia, University of California, Berkeley; Rev. and Dr. M. H. Rioch, India; J. J. Wilder, Honolulu; E. Percy Phillips, National Herbarium, Pretoria; Jan T. Byhouwer, Velsen, Holland; Chi-yian Chiao, University of Nanking; E. Lowell Kammerer, Morton Arboretum, Lisle, Illinois; Alfred Gundersen, Brooklyn Botanic Garden; Clara W. Fritz, Ottawa; Z. H. Hellwig, Warsaw; H. B. Haddow, Toronto; G. Weidman Groff, Lingnan University, Canton, China; T. Yamamoto, Taihoku Imperial University, Formosa; David D. Keck, Carnegie Institution Laboratory, Stanford University, California; G. E. Gates, Judson College, Rangoon, Burma; A. S. Thurston, University of Maryland, College Park; E. D. Merrill, New York Botanical Garden; Donald Wyman, Cornell University, Ithaca, N. Y.; Isabella Preston, Ottawa, and librarians attending the Convention of the Special Libraries Association held in Boston early in June. Dr. L. M. Ames of the U. S. Bureau of entomology and plant quarantine has spent more than a year studying Berberis and Mahonia.

The publications of the Arboretum, the "Journal of the Arnold Arboretum" and the "Arnold Arboretum Bulletin of Popular Information were issued regularly. "Contributions from the Arnold Arboretum of Harvard University," numbers vii and viii, and "Through the Arnold Arboretum" were published during the year. Of approximately 487 periodicals and reports currently received from all parts of the world, 220 are received in exchange for our "Journal" and "Bulletin" and 10 in exchange for our "Contributions." The subscription to 20 periodicals was cancelled with a saving of about seventy dollars. Reprints from the "Journal" were also sent out as a medium of exchange.

The following new periodicals have been received, a large number in exchange for our publications, some by gift and some by purchase. They are as follows:

Academy of natural sciences of Philadelphia. Proceedings. Vol. lxxxii → 1930 → Philadelphia. 1931 →

Academy of natural sciences of Philadelphia. Year book. 1930 → Philadelphia. 1931 →

Australia — *Council for scientific and industrial research.* Journal. Vol. viii, no. 1 → Melbourne. 1935 →

Black rock forest. Papers. Vol. i, no. 1 → April 1935 → Cornwall-on-the-Hudson. 1935 →

BLUMEA. Vol. i, no. 1 → August 25, 1934 → Leiden. 1934 →

BOTANICAL review, interpreting botanical progress. Vol. i, no. 1 → January 1935 → Lancaster, Pa. 1935 →

CHRONICA botanica. Vol. i → Leiden. 1935 →

INSTITUT J. B. CARNOY, *Louvain*. Travaux biologiques. No. 1 → January 11, 1929 → Lierre; Louvain. 1929 →

INSTITUTUL DE CERCETĂRI ȘI EXPERIMENTAȚIE FORESTIERĂ. Analele. Ser. 1. Anul i, nr. 1 → Bucarești. 1934 →

JAPAN — *Imperial forestry experiment station*. Bulletin. No. 31 → November 1931 → Tokyo. 1931 →

JOURNAL of South African botany. Vol. i, pt. 1 → January 1935 → Kirstenbosch. 1935 →

LEXINGTON BOTANIC GARDEN. Lexington leaflets. Vol. i, no. 1 → April 11, 1931 → Lexington, Mass. 1931 →

LISBON — *Instituto botânico de faculdade de ciências*. Trabalhos. i. 1925–32. Lisbôa. 1932?

NAŠ vrt; revija hortikulturnog društva. God. i, svezak 1–4, 7 → Zagreb. 1934 →

NEW ZEALAND journal of science and technology. Vol. xi, no. 5 → Wellington. 1930 →

PLANT science literature. Vol. i, no. 1 → Dec. 31, 1934 — Jan. 5, 1935 → Washington. 1935 →

REGENSBURG, *Germany — Königlich-baierische botanische gesellschaft*. Schriften. Bd. i. Regensburg. 1792.

REVISTA sudamericana de botanica. Vol. i, no. 1 → February 1934 → Montevideo. 1934 →

ROCZNIKA nauk ogrodniczych. (Annales des sciences horticoles.) Tom. i → Warszawa. 1934 →

ROSENJAHRBUCH. (Verein Deutscher rosenfreunde.) Berlin. 1934 →

SOVETSKIE subtropiki. No. 1–2. July–August 1929 → Sukhum. 1929 →

THARANDT — *Forstliche hochschule — Institut für ausländische und koloniale forstwirtschaft*. Mitteilungen. Nr. 1 → Dresden; Tharandt. 1932 →

ZEITSCHRIFT für weltforstwirtschaft. Bd. i, heft. 1 → Okt. 1933 → Neudamm; Berlin. 1933 →

Among other important accessions are:

AMERICAN GEOGRAPHICAL SOCIETY. New England's prospect. New York. 1933.

AUGUSTIN, Samuel. Prolegomena in systema sexuale botanicorum. Viennae. 1777.

BRITISH MUSEUM, *London*. A catalogue of the works of Linnæus, and publications more immediately relating thereto, preserved in the libraries of the British museum, Bloomsbury, and the British museum, Natural history, South Kensington. 2d ed. London. 1933.

BRITISH MUSEUM, *London — Natural history*. Catalogue of the books, manuscripts, maps and drawings in the museum. Vol. vii. Supplement J–O. London. 1933.

BUSSEY, Benjamin. Will of Benjamin Bussey (with four "codicils," 1835–41).

DEGENER, Otto. Flora hawaiiensis. [Book i. Honolulu. 1932.]

DIOSCORIDES, Pedanios. The Greek herbal of Dioscorides. Illustrated by a Byzantine, 512. Englished by John Goodyer, 1655. Edited and first printed, 1933, by R. T. Gunther. Oxford. 1934.

DOMIN, Karel. The beech forests of Czechoslovakia. Bern; Berlin. 1932.

FESTSCHRIFT Cornelius Osten. Montevideo. 1933.

GOEBEL, Karl. Organographie der pflanzen insbesondere der archegoniaten und samenpflanzen. 3^{e}, umgearbeitete aufl. Teil i-iii. Jena. 1928–33. — Ergänzungsband. [i, ii.] Jena. 1924–31.

INTERNATIONAL BOTANICAL CONGRESS, 5th, *Cambridge*, 1930. International rules of botanical nomenclature adopted by the International botanical congresses of Vienna, 1905, Brussels, 1910. Revised by the International botanical congress of Cambridge, 1930. Compiled by the Editorial committee for nomenclature from the Report of the subsection of nomenclature prepared by John Briquet. 3^{e} ausgabe. Jena. 1935.

LE CONTE, John B. Observations on the genera Viola, Utricularia and Gratiola. A reprint from the *Annals of the Lyceum of New York* (1824–1826), to which are appended photographs of the hitherto unpublished plates of the author, destined to illustrate these works. Edited by J. A. Nieuwland. Notre Dame. 1917.

MARIE-VICTORIN, frère. Flore laurentienne. Montréal. 1935.

PARSONS & SONS, co. Descriptive catalogue of hardy ornamental, flowering shrubs and vines; including rhododendrons, roses, magnolias, Chinese and Ghent azaleas, camellias, Japanese maples and other rare and choice plants [in Kissena nurseries]. Flushing, L. I., [1887?]

RAFINESQUE, Constantine Samuel. Monographie des coquilles bivalves et fluviatiles de la rivière Ohio contenant douze genres et soixante-huit espèces. [Avec] Remarques sur les rapports naturels des genres Viscum, Samolus et Viburnum. Bruxelles. [1820.]

SOWERBY, Arthur de Carle. The naturalist in Manchuria. 5 vol. Tientsin. 1922–30.

Books were sent out as inter-library loans to Field Museum of Natural History, Library of the United States Department of Agriculture, Smithsonian Institution, McGill University, United Fruit Company, Massachusetts State College, Wellesley College, University of Pennsylvania, Dartmouth College, New York Horticultural Society, Massachusetts Institute of Technology, Tufts College Library, Boston Society of Natural History, Massachusetts Horticultural Society and Michigan State College, as well as to many departments of Harvard University.

In addition to loans, photostats or typewritten copies of references have frequently been made when books could not be loaned.

Books were borrowed for the use of the members of the staff and students from the Boston Public Library, Massachusetts Horticultural Society, Library of the United States Department of Agriculture and from the University libraries.

A list of the forestry periodicals and reports prepared by the United States Forest Service was checked for our holdings, and additional material was prepared for inclusion in a supplement to "Index Londinensis."

At the invitation of the Committee on Binding Advertisements in Periodicals the Library has agreed to cooperate with some thirty-four other libraries to bind 12 of its periodicals entire, all advertisements included.

In the early spring Miss Margaret Hayes, under the direction of Mr. J. F. Ballard of the Boston Medical Library, spent more than two months in the Library indexing books and periodicals for a union list of the more important works to be found in special libraries in Boston.

The Librarian attended the Convention of the American Library Association in Denver from June 24–29, where she visited the public and university libraries. — E. M. T.

Bibliography of the published writings of the staff and students July 1, 1934—June 30, 1935

AMES, Oakes.

An addition to the genus Vanilla. (In *Harvard university, Botanical museum leaflets*, 1934, ii, 101–103.)

A contribution to our knowledge of the orchids of Spanish Honduras. Pt. ii. (In *Harvard university, Botanical museum leaflets*, 1934, iii, 17–36.)

Critical notes on Costa Rican orchids. By Oakes Ames, F. T. Hubbard and Charles Schweinfurth. (In *Harvard university, Botanical museum leaflets,* 1934, iii, 37–42.)

Epidendrum cystosum, a new species from the republic of Honduras, (In *Harvard university, Botanical museum leaflets,* 1934, ii, 105–109.)

A nomenclatorial note [Epidendrum neoporpax]. (In *Harvard university, Botanical museum leaflets,* 1934, ii, 112.)

Notes on Mexican epidendrums based largely on the Erik M. Ostlung collection. By Oakes Ames, F. T. Hubbard and Charles Schweinfurth. (In *Harvard university, Botanical museum leaflets,* 1934, iii, 1–16.)

Outline of lecture on economic botany given in Biology 115, formerly Botany 15, Nov. 1934. Material prepared in 1930. Broadside.

Studies in Stelis. iii–iv. (In *Harvard university, Botanical museum leaflets,* 1934–35, iii, 45–59, 134–135.)

A four polymorphic alliance in Epidendrum. By Oakes Ames, F. T. Hubbard and Charles Schweinfurth. (In *Harvard university, Botanical museum leaflets,* 1935, iii, 93–110.)

Nomenclatorial studies in Malaxis and Spiranthes. By Oakes Ames and Charles Schweinfurth. (In *Harvard university, Botanical museum leaflets,* 1935, iii, 113–133.)

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The above articles cover a total of about 1037 pages. — E. M. T.

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LOUIS VICTOR SCHMITT, Superintendent.

WILLIAM HENRY JUDD, Propagator.

ERRATA

Page 36, line 12 from below for (*C. macrostachia*) read (*V. macrostachia*).
" 42, line 3 *for* 5–10 cm. *read* 5–10 mm.
" 46, line 16 from below *for* east-northeast *read* east-northwest.
" 58, line 10 *for* style sessile *read* stigma sessile.
" 94, line 3 for *Ampelopsis humulifolia* Bunge read *Ampelopsis brevipedunculata* (Dipp.) Koehne var. *Maximowiczii* Rehd.
" 186, line 15 from below for **Heliotropium transandinum** var. **tiaridioides** read **Heliotropium transalpinum** var. **tiaridioides.**

INDEX

Synonyms are printed in *italics;* new names in **bold-face** type