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B. G. SCHUBERT
EDITOR

T. G. HARTLEY C. E. WOOD, JR.

LAZELLA SCHWARTEN
CIRCULATION

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COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, I. WOOD ANATOMY

WILLIAM C. DICKISON[1]

THE TAXONOMIC TREATMENT of the Dilleniaceae has been based, for the most part, on a limited number of characteristics which are not well defined nor thoroughly understood. As a result, a survey of the taxonomic literature reveals that there is little agreement on the proper phylogenetic position of the family (TABLE 1). This taxon has been included in as many as six orders and allied to no less than fifteen different families. Not only is there considerable controversy regarding its position in relation to other families, but there is still no satisfactory treatment to show intrafamilial relationships.

The early placement of the Dilleniaceae was in association with the ranalian complex, e.g., by Bentham and Hooker (1862) who divided the seventeen genera recognized by them as comprising the taxon into three tribes, based mainly on the form of the stamens. It is also interesting to note that these workers recognized the putative affinity of *Crossosoma* to the Dilleniaceae. Such an affinity was to be argued for many years.

On the basis of the supposed parietal placentation, Gilg (1893) in Engler and Prantl's *Die natürlichen Pflanzenfamilien*, placed the family between the Sterculiaceae and Eucryphiaceae in his large order Parietales. The artificiality of this order has been noted by Lawrence (1951) and by Standley and Williams (1961); their arguments have been supported by anatomical evidence described by T. K. Wilson (1960, 1964, 1965, 1966) in connection with his investigations on the Canellaceae. Within the family Gilg formed three subfamilies and six tribes and included the genera *Actinidia* and *Saurauia*. In a later edition of the *Syllabus*, Gilg and Werdermann (1925) removed the two above-mentioned genera to form a separate family Actinidiaceae. The four tribes within the Dilleniaceae proper were retained.

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[1] This study represents a portion of a thesis submitted to the Graduate School, Indiana University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. This investigation was supported by Grants GB 3820 and GB 4127 from the National Science Foundation to Dr. J. E. Canright.

TABLE 1. — **Systematic Treatment of the Dilleniaceae**

AUTHOR	PLACEMENT
DE CANDOLLE, 1824	Ranales; between Ranunculaceae and Magnoliaceae
LINDLEY, 1830	Ranales; between Magnoliaceae and Winteraceae
BENTHAM & HOOKER, 1862	Ranales; between Ranunculaceae and Calycanthaceae
BAILLON, 1871	between Ranunculaceae and Magnoliaceae
LE MAOUT & DECAISNE, 1873	Ranales; between Ranunculaceae and Calycanthaceae
KUNTZE, 1891	between Ranunculaceae and Calycanthaceae
GILG, 1893	Parietales; between Sterculiaceae and Eucryphiaceae
HALLIER, 1905	Rosales; near Brunelliaceae
WARMING, 1911	Cistiflorae; near Bixaceae
BESSEY, 1915	Ranales; between Ceratophyllaceae and Canellaceae
GILG & WERDERMANN, 1925	Parietales; near Actinidiaceae
RENDLE, 1925	Guttiferales; near Ochnaceae
HUTCHINSON, 1926	Dilleniales; near Connaraceae
WETTSTEIN, 1935	Guttiferales; near Actinidiaceae
GUNDERSEN, 1950	Theales; near Actinidiaceae
LAWRENCE, 1951	Parietales; near Actinidiaceae
TAKHTAJIAN, 1958	Theales; near Actinidiaceae
BOIVIN, 1956	Dilleniales; near Crossosomataceae
BENSON, 1957	Ranales; between Annonaceae and Cercidiphyllaceae
COPELAND, 1957	Guttiferales; near Theaceae
CRONQUIST, 1957	Dilleniales; near Crossosomataceae
CHADEFAUD & EMBERGER, 1960	Parietales; near Actinidiaceae
EAMES, 1961	Dilleniales; near Paeoniaceae
MELCHIOR, 1964	Guttiferales; near Paeoniaceae

Hoogland (1952, 1953) suggested the family should be divided into two subfamilies, the Tetraceroideae and Dillenioideae, again based primarily on stamen morphology. According to this author, the genera within the Dillenioideae show reticulate relationships with their arrangement depending on the principles employed.

At the present time, the most widely accepted treatment places the Dilleniaceae, Paeoniaceae, and Crossosomataceae in close alliance under the Dilleniales (Eames, 1961). Cronquist (1957, 1965) noted, however, that this association was not firmly established and suggested, furthermore, that the centrifugal stamen development of the Dilleniales is the only essential character by which the Dilleniales differed from the Ranales.

Since the Dilleniaceae possess a combination of characters particularly interesting to those concerned with the discipline of comparative morphology and phylogeny (see, e.g., C. Wilson, 1965), it appeared highly advisable to undertake a comprehensive comparative morphological and anatomical study of the family; not only to help clarify those characters already known to exist within the family, but also to attempt to uncover additional evidence which might help elucidate the phylogenetic relationships of the taxa in question. This initial paper concerns the features of phylogenetic value in the woods of the Dilleniaceae.

There are numerous descriptive works dealing with the wood anatomy of the Dilleniaceae, the most notable of which are: Moll and Janssonius (1906); Pearson and Brown (1932); Record and Hess (1943); Metcalfe and Chalk (1950); and Chowdhury and Ghosh (1958). Nevertheless, the wood of this family has neither been adequately described nor fully exploited in attempts to interpret phylogenetic relationships.

Vestal (1937) studied twenty-nine species representing seven genera of Dilleniaceae in reaching his conclusion, based entirely on wood anatomy, that the Guttiferales have a natural alliance with such families as Ochnaceae, Eucryphiaceae, Theaceae, Actinidiaceae, and Saurauiaceae, being derived through the dillenias. Bausch (1938), on the other hand, found no similarity in the wood of the Dilleniaceae and that of the Eucryphiaceae. The only other reference to the secondary xylem of this family from a phylogenetic viewpoint is that of Wilson (1960) who found some agreement with the Canellaceae.

The author respectfully acknowledges the assistance of Dr. James E. Canright, Arizona State University, for initially defining the scope of this research and for his continuing interest and guidance throughout.

MATERIALS AND METHODS

A total of seventy-one wood samples representing forty species in all ten genera of Dilleniaceae was examined. The writer is extremely thankful to Dr. William L. Stern for his generous personal gift of dilleniaceous wood slides. This collection included samples from the great majority of wood specimens of Dilleniaceae housed in the Samuel James Record Memorial Collection at Yale University. Special thanks are also given to Dr. P. S. Ashton, Kuching, Sarawak, for his contribution of wood from the monotypic *Didesmandra aspera* Stapf, without which this study would have been incomplete. Additional wood samples were obtained from the following sources: the Arnold Arboretum of Harvard University (Aw); Chicago Natural History Museum (Fw); Imperial Forestry Institute, Oxford University (FHOw); Division of Forest Products, Commonwealth Scientific and Industrial Research Organization, Melbourne (FPAw); Forest Research Institute, Kepong, Malaya (KEPw); personal collection of Dr. C. L. Wilson (WILSON); Division of Plant Anatomy, Department of Botany, Smithsonian Institution, Washington, D.C. (USw); Yale University, School of Forestry (Yw).

Woods of all ten genera considered by Hoogland (1951) to belong to the family were examined. However, the semi-herbaceous genera *Acrotrema* and *Pachynema* were represented only by twig material, and were, therefore, used simply for comparative purposes and not studied statistically. As suggested by Stern and Chambers (1960), a complete list of the woods studied, together with pertinent collecting information, is given in APPENDIX 1.

Transverse, radial, and tangential wood sections were cut on a sliding microtome at a thickness ranging from 15 to 30μ. The sections were stained by first being placed in a mordant of 2 per cent ferric ammonium sulphate (iron alum), after which they were transferred to 0.5 per cent aqueous Heidenhain's haematoxylin and then to a 1 per cent solution of safranin in 50 per cent alcohol. Slides of macerated wood were prepared by putting small slivers into vials containing Jeffrey's macerating fluid (equal parts 10 per cent aqueous nitric and chromic acids) and placing them in an oven at 60°C. The individual xylem elements resulting were washed and stained with a 1 per cent solution of light green in 75 parts clove oil and 25 parts absolute alcohol.

Wood features of phylogenetic value were selected from the compilations of Tippo (1941, 1946). Measurements of cell length were obtained exclusively from macerated material. All statistical data were derived by measuring twenty-five cells at random from each sample. Tippo (1941) and Rendle and Clark (1934) recommend that one hundred measurements be taken from each sample in order to get a truly accurate mean length. Because of the small number of wood samples available for study of *Tetracera*, *Schumacheria*, *Didesmandra*, and *Davilla*, the data given for these genera is indicative only of general size ranges. The statistical information on the remaining genera, however, should be considered as truly representative.

Rays are described in accordance with the system of Kribs (1935), as well as by giving a brief written description as advised by the Committee on Nomenclature of the International Association of Wood Anatomists in the *International Glossary of Terms used in Wood Anatomy* (1957). This classification was employed because of its ease of application and wide usage in the literature.

The descriptive terms for the wood parenchyma are those suggested by Hess (1950). In discussing relative cell size, the suggestions of Chattaway (1932), Chalk (1938), and the Committee on the Standardization of Terms of Cell Size (1937) are used. Those adopted in this investigation are given below:

PORE NUMBER	
Numerous	more than 40 per mm ^{2}
Many	20–40 per mm ^{2}
Rather many	10–20 per mm ^{2}
Rather few	5–10 per mm ^{2}
Few	2–5 per mm ^{2}
Very few	fewer than 2 per mm ^{2}

VESSEL DIAMETER	
Extremely small	up to 25μ
Very small	25–50μ
Moderately small	50–100μ
Medium	100–200μ
Moderately large	200–300μ
Very large	300–400μ
Extremely large	over 400μ

VESSEL MEMBER LENGTH	
Extremely short	less than 175μ
Very short	175–250μ
Moderately short	250–350μ
Medium	350–800μ
Moderately long	800–1100μ
Very long	1100–1900μ
Extremely long	over 1900μ

LENGTH OF IMPERFORATE TRACHEARY ELEMENTS	
Very short	up to 1000μ
Short	1000–1500μ
Long	1500–2000μ
Very long	over 2000μ

The remainder of the terminology is generally that advocated by the Committee on Nomenclature of the International Association of Wood Anatomists in the *Multilingual Glossary of Terms used in Wood Anatomy* (1964).

OBSERVATIONS

Description of the Wood of Dillenia. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 5, 7, 23, 24) solitary, or occasionally in pairs or small clusters, rarely as many as 4 in radial rows, very few to many (1–21, mostly 7–13 per mm^2), circular to angular in outline, very small to very large, usually medium-sized (diam. 45–330μ, mostly 113–228μ, mean 147μ); vessel member length medium to extremely long, usually very long (625–3062μ, mostly 687–2500μ, mean 1476μ); tyloses infrequently present. Intervascular pitting (FIG. 8) opposite to transitional, pits circular to elongate (diam. 7–35μ); pitting to rays similar to scalariform. Perforation plates exclusively scalariform with some branched bars, occasionally nearly reticulate; completely bordered, with 5–120 (mostly 15–40) bars. End wall inclination (FIG. 6) 25–72°. *Imperforate tracheary elements* (FIG. 7) of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and included or extended, slit-like, often crossed apertures; very short to very long, usually very long (625–4375μ, mostly 1875–3750μ, mean 2520μ). *Rays* (FIG. 6) heterogeneous, Type I, of two sizes; uniseriate rays 1–25 (mostly 4–12) cells high; multiseriate rays 1–18 (mostly 1–10) cells wide, 23 to more than 200 (mostly 52–183) cells high. Multiseriate rays often with long uniseriate wings composed of upright cells. Elongated upright cells in long series (2–19 cells) often running through multiseriate rays. Crystals in the form of raphides often numerous in ray parenchyma, as are enlarged secretory cells. Ray parenchyma sometimes containing dark, amorphous, gummy deposits. *Wood parenchyma* (FIG. 5) apotracheal diffuse and aggregate diffuse, often paratracheal diffuse to incomplete vasicentric.

The very close similarity of the wood anatomy in the two genera supports Hoogland (1952) in reducing *Wormia* Rottb. to *Dillenia* L.

Description of the Wood of Schumacheria. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 1, 22) solitary, apparent pairs due to overlapping ends, rather many to numerous (16–51, mostly 21–41 per mm^2); circular in outline, tending to angular, very small to medium, usually moderately small (diam. 30–140μ, mostly 70–120μ, mean 90μ); vessel member length moderately long to very long to extremely long, usually extremely long (1044–3074μ, mostly 1740–2610μ, mean 2047μ). Intervascular pitting scalariform to opposite to transitional, pits circular to elongate (diam. 7–35μ); pitting to rays opposite to transitional to scalariform. Perforation plates exclusively scalariform, bars commonly branched, completely bordered, with 34–135 (avg. 40–60) bars. End wall inclination 35–75°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and extended, slit-like, often crossed pit apertures; long to very long, usually very long (1160–3480μ, mostly 2030–2900μ, mean 2380μ). *Rays* (FIG. 2) heterogeneous, Type I, of two sizes; uniseriate rays 5–28 (mostly 10–15) cells high; multiseriate rays 1–5 cells wide, 35–68 (mostly 50–60) cells high; multiseriate rays often with extremely long uniseriate wings composed of upright cells. *Wood parenchyma* apotracheal diffuse.

Description of the Wood of Hibbertia. Growth rings present or absent, when present not well defined. Wood diffuse-porous; *vessels* (FIG. 3) mostly solitary, with some apparent pairs due to overlapping ends, very small clusters infrequently present, rather few to numerous (5–40, mostly 10–20 per mm^2); circular to angular in outline, very small to medium sized (diam. 30–165μ, mostly 60–135μ); vessel member length medium to very long, usually moderately long (625–1562μ, mostly 812–1437μ, mean 1074μ). Intervascular pitting opposite to transitional to scalariform, pits circular to scalariform (diam. 8–40μ), pitting to rays similar. Perforation plates exclusively scalariform, completely bordered to only bordered at the ends, with 15–88 (mostly 35–50) bars. Bars commonly branched to nearly reticulate. End wall inclination 45–85°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits with extended or included, slit-like, often crossed, pit apertures; very short to very long, usually long (625–2150μ, mostly 1250–1875μ, mean 1551μ). *Rays* (FIG.

4) heterogeneous, Type I, of two sizes; uniseriate rays 1–8 (mostly 2–7) cells high; multiseriate rays 1–5 (mostly 1–3) cells wide, 7–34 (mostly 15–30) cells high. Multiseriate rays often with long uniseriate wings. Ray parenchyma frequently contains dark, amorphous, gummy deposits. *Wood parenchyma* apotracheal diffuse; crystals in the form of raphides sometimes present in enlarged wood parenchyma cells.

Description of the Wood of Didesmandra. Growth rings absent. Wood diffuse-porous; *vessels* solitary, rarely in pairs, apparent pairs due to vessel overlap, rather many to numerous (13–65, mostly 25–45 per mm ^{2}); angular in outline, very small to moderately small, usually moderately small (diam. 30–90μ, mostly 45–70μ, mean 60μ); vessel member length medium to extremely long, usually very long (780–2600μ, mostly 1150–2250μ, mean 1574μ). Intervascular pitting scalariform to opposite; pitting to rays similar. Perforation plates exclusively scalariform. Bars commonly anastomosing to reticulate; completely bordered, with 25–160 (mostly 57–120) bars. End wall inclination 30–75°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, mostly thin-walled; fiber tracheids with distinctly bordered pits and included or extended, slit-like, often crossed, pit apertures; short to very long, mostly very long (1400–3050μ, mostly 1800–2870μ, mean 2292μ). *Rays* heterogeneous, Type I, of two sizes; uniseriate rays 2–33 (mostly 6–21) cells high; multiseriate rays 1–15 (mostly 3–10) cells wide, 14–83 cells high. Main body of multiseriate rays composed of both procumbent and upright cells, often with long uniseriate wings composed of upright cells. Crystals in the form of raphides infrequently present in ray tissue. Ray parenchyma sometimes containing dark, amorphous, gummy deposits. *Wood parenchyma* apotracheal diffuse.

Description of the Secondary Xylem of Acrotrema and Pachynema. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 9–12) solitary to rarely in pairs, apparent pairs due to vessel overlap; circular to angular in outline, extremely small to very small (diam. 11–34μ, mostly 20–27μ). Intervascular pitting (FIG. 13) scalariform to opposite to rarely transitional, pits circular to elongate (diam. 7–18μ). Perforation plates exclusively scalariform, with 16–48, completely bordered, bars. Bars sometimes anastomosing. *Imperforate tracheary elements* of the fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits with included, or extended, slit-like, often crossed, apertures. In *Acrotrema*, elements were found with greatly extended pit apertures and much reduced pit borders. *Rays* reduced to mostly uniseriate with occasional biseriate rays. Rays composed of both procumbent and upright cells, 1–14 cells high. *Wood parenchyma* apotracheal diffuse. Crystals in the form of raphides observable in the periderm of *Acrotrema*.

Description of the Wood of Doliocarpus. Growth rings absent. Two samples (*D. coriaceus* (Mart. & Zucc.) Gilg and *D.* sp., Yw 39903) exhibit successive cambial activity which resulted in concentric zones of included phloem, conjunctive tissue, and sclerotic cells. Wood diffuse-porous; *vessels* (FIG. 26) solitary, very few to rather many (2–20, mostly 4–9 per mm ^{2}); circular in outline, moderately small to extremely large, usually moderately large (diam. 50–555μ, mostly 150–450μ, mean 256μ); vessel member length medium to very long, usually moderately long (362–1812μ, mostly 687–1250μ, mean 917μ). Intervascular pitting (FIG. 21) opposite to transitional, pits circular to elongate (diam. 7–40μ); pitting to rays similar. Perforation plates mostly simple, scalariform in the smaller vessels. Scalariform plates with 1–15 bars, sometimes branched, completely bordered to bordered only at the ends. End wall inclination 35–90°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and extended, slit-like, often crossed, pit apertures, very short to very long, usually short (687–4000μ, mostly 1125–1562μ, mean 1471μ). *Rays* heterogenous, Type I and IIA, of two sizes; uniseriate rays 1–9 (mostly 3–7) cells high; multiseriate rays 1–41 (mostly 1–35) cells wide, 36 to over 500 (mostly 45–200) cells high. Crystals in the form of raphides often very numerous, as are enlarged secretory cells. *Wood parenchyma* mostly apotracheal diffuse, some paratracheal diffuse.

One sample studied, identified with an unpublished name (Yw *39903*), displayed features inconsistent with those of the other species examined. The radial pore chains and pore clusters, vasicentric parenchyma, and significantly different vessel member and fiber length suggest that it is not a member of this genus. The accompanying data stated it was taken from Fw *11189*. However, the two wood samples were clearly not taken from the same specimen.

Description of the Wood of Davilla. Growth rings absent. Wood diffuse-porous; *vessels* (FIGS. 15, 23) solitary, rather few to rather many (3–16, mostly 4–8 per mm ^{2}); circular in outline, very small to extremely large, usually moderately large (diam. 30–450μ, mostly 222–382μ, mean 284μ); vessel member length medium to moderately long, usually medium-sized (437–1062μ, mostly 625–937μ, mean 777μ). Intervascular pitting opposite to transitional, pits circular to elongate (10–25μ); pitting to rays similar. Perforation plates mostly simple, scalariform in the smaller vessels. Scalariform perforation plates with 5–10 bars, completely bordered to bordered only at the ends. End wall inclination 55–90°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin-walled; fiber tracheids with distinctly bordered pits with extended or included, slit-like, often crossed, pit apertures; very short to very long, usually long (938–2625μ, mostly 1250–2375μ, mean 1613μ). *Rays* (FIG. 15) heterogeneous, Type I and IIA, of two sizes; uniseriate rays 1–31 (mostly 15–30) cells high; multiseriate rays 1–38 (mostly 1–31) cells wide, 75 to over 500 (mostly 200–450) cells high. Large sclerotic cells infrequently present in ray tissue, quite common in bark. Ray cells often containing large secretory cells and dark, amorphous, gummy deposits. *Wood parenchyma* apotracheal diffuse to scattered paratracheal diffuse.

Description of the Wood of Curatella. Growth rings absent. Wood diffuse-porous; *vessels* (Fig. 14) solitary, or rarely in clusters of up to three vessels, very few to rather many (1–15, mostly 2–7 per mm ^{2}), circular to rarely angular in outline, very small to very large, usually medium-sized (diam. 45–360μ, mostly 145–200μ, mean 180μ); vessel member length very short to very long, usually medium-sized (250–1312μ, mostly 625–900μ, mean 725μ). Intervascular pitting opposite to transitional, pits circular to elongate (diam. 8–25μ); pitting to rays similar. Perforation plates mostly simple (Fig. 17), scalariform in the smaller vessels. Scalariform perforation plates completely bordered, with 1–12 (mostly 1–5) bars, branching of bars common, occasionally reticulate perforations are present. Inclination of end walls 55–90°. *Imperforate tracheary elements* of the tracheid and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits with extended, slit-like, often crossed, pit apertures; very short to very long, usually long (562–2750μ, mostly 1354–2208μ, mean 1805μ). Rays (Fig. 16) heterogeneous, Type I and IIA, of two sizes; uniseriate rays 1–20 (mostly 1–11) cells high; multiseriate rays 1–20 (mostly 1–15) cells wide, 32–279 (mostly 54–119) cells high. Crystals in the form of raphides often numerous, as are enlarged secretory cells. Ray parenchyma often containing dark, amorphous, gummy deposits. *Wood parenchyma* (Fig. 14) aggregate to narrow-banded apotracheal, some paratracheal diffuse.

Description of the Wood of Tetracera. Growth rings absent or present; if present, not well defined. One species (*T. volubilis* L.) exhibited successive cambial activity which resulted in concentric zones of included phloem, conjunctive parenchyma with scattered fibers, and sclerotic cells. Wood diffuse-porous; very weak ring-porosity in one species (*T. boiviniana* Baill.) as shown by larger vessel diameter in the spring wood. *Vessels* (Figs. 18, 27) solitary, rarely in pairs, few to rather many (3–11, mostly 5–8 per mm ^{2}); circular in outline, very small to very large (diam. 50–350μ); vessel member length very short to moderately long, usually medium-sized (220–1062μ, mostly 370–937μ, mean 565μ). Intervascular pitting opposite to transitional, pits circular to elongate (diam. 7–35μ); pitting to rays similar. Perforation plates mostly simple, scalariform in the smaller vessels. Scalariform plates completely bordered, with 1–20 (mostly 1–10) bars. Vessel members occasionally with reticulate or "multiperforate" perforation plates (Fig. 19). Inclination of end walls 35–90°. *Imperforate tracheary elements* of the tracheid, vasicentric tracheid, and fiber tracheid type, thin- to thick-walled; fiber tracheids with distinctly bordered pits and extended or included, slit-like, often crossed, pit apertures; very short to long, usually short (500–1625μ, mostly 625–1250μ, mean 1003μ). *Rays* (Fig. 20) heterogeneous, Type I and IIA, of two sizes; uniseriate rays 1–18 (mostly 3–11) cells high;

multiseriate rays 1–13 (mostly 1–10) cells wide, 20–152 (mostly 45–110) cells high. Multiseriate rays often containing large secretory cells. Crystals in the form of raphides numerous along with dark, amorphous, gummy deposits. Series of upright cells sometimes running through rays. *Wood parenchyma* apotracheal diffuse.

The small number of wood samples studied in this genus revealed a relatively large variability in anatomical structure. The extent and significance of this variation can only be determined by the examination of additional samples and species when they become available.

DISCUSSION

The woods of the Dilleniaceae reveal a rather low level of specialization. This is supported by the occurrence in all woods of the following primitive features: (1) wood diffuse-porous; (2) predominantly solitary pores; (3) opposite-transitional intervascular pitting; (4) fiber tracheids; (5) heterogeneous Type I or IIA rays; and (6) wood parenchyma mostly apotracheal diffuse. Despite this apparent homogeneity, it is quite obvious that considerable variation exists between genera in vessel member structure.

Since the trends of vessel specialization were initially discovered for dicotyledons by Bailey and Thompson (1918), Bailey and Tupper (1918), and Frost (1930, 1931), and for monocotyledons by Cheadle (1942, 1943a, 1943b, 1944), the vessel has been an invaluable tool for interpreting phylogenetic relationships. The importance ascribed to the vessel member in this regard results not only from a thorough understanding of vessel phylogeny, but more importantly from the fact that these clearly defined trends are both undirectional and irreversible.

It is of great interest, therefore, to find vessels within a single family which reveal salient irreversible trends of specialization. On the basis of vessel member structure, as well as more subtle wood characters, the Dilleniaceae are most conveniently segregated into the two subfamilies as suggested by Hoogland (1952, 1953). The anatomical features of the two subfamilies are summarized in TABLE 2.

I. COMPARISON OF THE TWO SUBFAMILIES OF DILLENIACEAE

The most primitive forms of vessel members are found in the subfamily Dillenioideae. In this group the vessels are angular to circular in outline, of very great length (mean 1532μ), possess exclusively scalariform perforation plates, with up to 160 bars, are mostly completely bordered, have very oblique end walls, and have scalariform to opposite to transitional intervascular pitting. The extremely tracheid-like vessel members of *Schumacheria* and *Didesmandra* are the least specialized in the family. The vessel members in the genera *Dillenia* and *Hibbertia* are, in general, only slightly more advanced.

The Tetraceroideae are characterized by certain salient trends of vessel

TABLE 2. — **Comparison of Averages of Characters of Wood Anatomy of the Two Subfamilies of Dilleniaceae**

CHARACTER	DILLENIOIDEAE	TETRACEROIDEAE
VESSEL MEMBERS		
1. Distribution	mostly solitary	mostly solitary
2. Shape in outline	circular to angular	circular
3. Type of perforation plate	scalariform only	scalariform and simple
4. Bars in perforation plate		
Lowest average	18	2
Mean averages	40	5
Highest average	123	9
5. End wall inclination	30–80°	50–90°
6. Length		
Range	625–3074μ	220–1812μ
Most frequent range	687–2610μ	370–1250μ
Mean	1532μ	766μ
7. Width		
Range	30–330μ	30–555μ
Most frequent range	60–228μ	145–450μ
Mean	124μ	240μ
8. Intervascular pitting	scalariform-transitional	opposite-transitional
WOOD FIBERS		
9. Type	fiber tracheid	fiber tracheid
10. Wall thickness	thin to thick	mostly thin
11. Length		
Range	625–4375μ	500–4000μ
Most frequent range	1250–3750μ	625–2375μ
Mean	2150μ	1473μ
WOOD RAY		
12. Type	Type I	Type I and IIA
13. Average width of multiseriate rays (no. of cells)	1–18 (avg. 9)	1–41 (avg. 22)
14. Average height of multiseriate rays (no. of cells)	7–200 (avg. 39–91)	20–500 (avg. 86–219)
WOOD PARENCHYMA		
15. Distribution	mostly apotracheal diffuse	mostly apotracheal diffuse

member specialization. The four genera included in this subfamily all possess vessel members with both simple and scalariform perforations. In all, simple perforations are considerably more numerous than the scalariform type, which are confined strictly to the smaller vessels of the secondary xylem. When scalariform plates do occur, they seldom have more than ten bars. A small number of vessel members were observed which bore scalariform and simple perforation plates at opposite ends. All gradations from porous-oblique to transverse-porous perforation plates are present. Correlated with the change in type of perforation plate is a significant decrease in length (mean 766μ) with a considerable increase in width. The transectional outline is predominantly circular. Whereas *Doliocarpus*, *Davilla*, and *Curatella* are intermediate in the above features, the genus *Tetracera* appears to be the most advanced of all Dilleniaceae in vessel structure. The last-named genus is also unique in its possession of so called "multiperforate" or reticulate perforations. The significance of this type of perforation plates is still a matter of controversy. Thompson (1923) suggested that they may represent modifications of scalariform types or retrogressions from simple plates. Gottwald and Parameswaran (1964), in describing their occurrence in the Dipterocarpaceae, believe they are intermediate forms between scalariform and simple perforations.

That all known trends of vessel specialization do not always occur simultaneously (Bailey and Howard, 1941; Bailey, 1944) is well exemplified by the existence of opposite-transitional, lateral-wall pitting in both subfamilies.

Bailey (1957) pointed out that in certain specialized cases, such as lianas, vessel members may become quite transformed as a result of their habit, and do not, therefore, indicate true phylogenetic advancement. Ayensu and Stern (1964) encountered such modification in their study of the scandent Passifloraceae, and so considered the presence of shorter, broader, solitary vessel members in this group to be related to the physiology of their habit rather than to their phylogenetic position. They indicate, however, that habit-related anatomical modification may be superimposed upon phylogenetic specialization and the separation of these facets is often difficult.

Since the Dilleniaceae range from large trees to scandent lianas, with all intermediate forms, it is quite possible that the advancement exhibited by certain species of *Davilla*, *Doliocarpus*, and *Tetracera* is actually coordinated with habit. However, the occurrence of scalariform perforation plates in these genera would also seem to indicate that they are really in an intermediate stage of advancement. Furthermore, similar advanced vessel types were observed in *Curatella*, which may be a small tree up to eight meters in height (Standley, 1928).

It is clear, therefore, that it would be erroneous to attempt to interpret phylogenetic position of the woods from vessel structure alone. It is necessary to correlate this evidence with that obtained from other features of the xylem.

The unspecialized nature of the Dillenioideae is indicated by the presence of the longest imperforate tracheary elements and by the exclusively heterogeneous Type I rays (except in the reduced *Acrotrema* and *Pachynema*). Both uniseriate and multiseriate rays are of extreme height. In addition, the multiseriate rays are often conspicuous by their long uniseriate wings composed of upright cells. Although the tremendously high and broad rays of the Tetraceroideae are the largest in the family, there is a marked tendency for reduction in the uniseriate wings and an increased uniformity in the ray cells to a point where more advanced Type IIA rays are present.

Both subfamilies have predominantly apotracheal diffuse parenchyma. Within the Dillenioideae, only *Dillenia* is characterized by paratracheal diffuse parenchyma, whereas in the Tetraceroideae both *Davilla* and *Doliocarpus* show this condition. Also, *Curatella* exhibits fairly specialized aggregate to narrow-banded apotracheal with some paratracheal diffuse parenchyma.

Crystals in the form of raphides are often quite numerous in the wood of the Dilleniaceae. Although Chattaway (1955) states that crystals have been reported in approximately 1000 genera of 160 families, the presence of certain types of crystals, such as raphides, is much less common and may, therefore, be of more taxonomic value (Metcalfe and Chalk, 1950; Chattaway, 1955). Raphides are undoubtedly diagnostic for the majority of genera within the family, but are of questionable taxonomic importance for the family as a whole. The only two genera in which raphides were not confirmed are *Davilla*, where they have been reported (cited by Chattaway, *loc. cit.*) and *Schumacheria*. In addition, any one genus may not possess raphides uniformly in all species (e.g., *Dillenia*). When present, these needle-shaped crystals are more commonly found in large, mucilage-containing ray cells. Enlarged, raphide-bearing wood parenchyma strands were observed only in certain species of *Hibbertia*. However, the occurrence of crystals in such a large number of unrelated plant families seems to negate any phylogenetic significance in this anatomical character.

Secretory cells were similarly encountered in all dilleniaceous genera except *Schumacheria* and *Didesmandra*. Stern (1954a) advised the term "secretory intercellular cavity" be used when the chemical composition of the secretion is not known. The darkly staining amorphous mucilage may be deposited either in ray parenchyma, axile parenchyma, or vessels (FIG. 18). The presence of this mucilage is apparently not uniform within genera or even in species. Canright (1955) considered oil cells to be of no phylogenetic significance in the wood of the Magnoliaceae. Stern (1954b), however, suggested they may represent a particular kind of specialization in lauraceous wood. The occurrence of secretory cells in the Dilleniaceae offers little evidence to support either concept. However, it is of importance to mention that secretory cells are common features of all organs of most families generally regarded as ranalian; on the other hand, this feature is relatively rare in families in the higher orders, e.g., Guttiferae.

II. COMPARISON OF WOOD OF THE DILLENIACEAE WITH THAT OF PUTATIVELY RELATED FAMILIES

The following discussion will attempt to evaluate, on the basis of wood anatomy, the relationships of the Dilleniaceae to many putatively related families. In the majority of cases, woods of the various families were actually examined. In addition to these personal observations, descriptions were obtained from the following sources: Canright (1955), Chattaway (1937), Keng (1962), Metcalfe and Chalk (1950), Swamy and Bailey (1949), Vander Wyk and Canright (1956), and Vestal (1937).

The Dilleniaceae have been placed, at one time or another, mainly on the basis of gross floral morphology, with the following ranalian families: Ranunculaceae, Magnoliaceae, Winteraceae, Calycanthaceae, Annonaceae, Canellaceae, Cercidiphyllaceae, and Ceratophyllaceae. Evidence from wood anatomy, for the most part, does not support such alliances.

The vesselless Winteraceae and aquatic Ceratophyllaceae may be readily dismissed as showing little similarity to the Dilleniaceae.

The presence of simple perforation plates, alternate intervascular pitting, libriform wood fibers and paratracheal parenchyma in the Ranunculaceae (excluding *Paeonia*) indicates that the xylem of this family is on a higher level of advancement than that of the Dilleniaceae.

The Calycanthaceae do possess fiber tracheids, heterogeneous Type I rays, and apotracheal diffuse to vasicentric scanty parenchyma, but, on the other hand, show pores mostly in radial multiples with exclusively simple perforation plates, alternate intervascular pitting, as well as uniformly occurring vasicentric tracheids.

The Magnoliaceae are characterized by wood which shows transitions from comparatively primitive to rather advanced. Although the most primitive genera do have some similarities with the Dilleniaceae, the family appears to be well placed near the Degeneriaceae and Himantandraceae (Bailey, Nast and Smith, 1943; Canright, 1955).

The Annonaceae, likewise, is anatomically advanced over the Dilleniaceae and accordingly, was considered by Vander Wyk and Canright (1956) to share more common features with the Myristicaceae.

Although Wilson (1960) did find several points of agreement between the Dilleniaceae and Canellaceae, he found the wood features in the latter family had the greatest degree of similarity with the Illiciaceae and Eupteleaceae.

The wood of the Cercidiphyllaceae approaches the Dilleniaceae in primitive vessel structure and the presence of fiber tracheids, but differs in the terminal wood parenchyma and heterogeneous Type IIB rays (Swamy and Bailey, 1949).

Due to the large degree of family overlap in ordinal concepts, it will be more meaningful for the remaining discussion to consider relationships of individual families irrespective of specific orders.

There is little similarity between the wood of the Sterculiaceae and that of the Dilleniaceae. Such features as exclusively simple perforation plates, alternate intervascular pitting, abundant parenchyma in uniseriate lines and in some cases together with distinct vasicentric sheaths, Type IIA or IIB rays, and libriform wood fibers, are much more advanced than those of the Dilleniaceae.

The Ochnaceae and Connaraceae are also anatomically on a higher level of advancement than the Dilleniaceae as evidenced by the occurrence in both families of the following features: typically simple perforation plates, alternate intervascular pitting, and libriform wood fibers (exclusively in the Connaraceae and partially in the Ochnaceae. The Connaraceae is further characterized by highly advanced heterogeneous Type III or homogeneous Type III rays.

Although the Eucryphiaceae and Brunelliaceae are not as advanced anatomically as the previous families, they are still more highly developed than the Dilleniaceae. Woods of both families contain both simple and scalariform perforation plates. The parenchyma of the Eucryphiaceae is diffuse or slightly banded to terminally banded, whereas wood parenchyma is absent from the Brunelliaceae. Both families have genera with occasional heterogeneous Type III rays. However, other lines of evidence, viz., floral morphology and chemical data, support placing these two families near the Cunoniaceae (Bausch, 1938).

The genera *Saurauia* and *Actinidia* have often been placed near, if not included in, the Dilleniaceae. Such wood features in *Saurauia* as mostly solitary pores, vessel members of extreme length and exclusively scalariform perforation plates (with up to 90 bars), scalariform to opposite to transitional intervascular pitting, long fiber tracheids, exclusively heterogeneous Type I rays, and apotracheal diffuse parenchyma, are very primitive; comparable features are found only in the most unspecialized members of the Dillenioideae.

Actinidia shows features more in common with the Tetraceroideae, such as solitary pores, both simple and scalariform perforation plates, fiber tracheids of similar mean length, and heterogeneous Type I or IIA rays. At the same time, however, *Actinidia* also has some wood characters not shared with any genera in the afore-mentioned subfamily. These include scalariform perforation plates which may have over 75 bars, and much reduced ray structure.

In contrast to the above, the alliance of the Dilleniaceae to the Theaceae is supported by anatomical considerations. Keng (1962) compared the wood of members of this family and found the wood of the Camellioideae to be, in general, more advanced than that of the Ternstroemioideae. Furthermore, although the wood of the Theaceae is considered to be relatively primitive, there are specific cases of high advancement. The greatest agreement between the Dilleniaceae and Theaceae exists between the Dillenioideae and tribes Adinandrieae and Ternstroemieae. This similarity is evident in the mostly solitary pores, exclusively scalariform perforation plates with many bars, similar mean vessel member length (Adinandrieae), scalariform to opposite intervascular pitting, uniform occurrence of fiber tracheids of similar mean length, heterogeneous Type I rays (significantly broader and higher in the Dillenioideae), and wood parenchyma mostly apotracheal diffuse.

The occurrence of spiral thickenings in the vessels of some Theaceae is a character of questionable phylogenetic significance (Canright, 1955; Keng, 1962; Stern, 1954b). This character was not encountered in any of the Dilleniaceae observed but does show up in the vessels of *Saurauia* and *Actinidia*.

Recent systems have repeatedly linked the monotypic family Crossosomataceae to the Dilleniaceae by the presence in the genus *Crossosoma* of free follicular carpels and strongly arillate seeds However, the semi-ring porosity, exclusively simple perforation plates, mostly alternate intervascular pitting, very short imperforate tracheary elements, heterogeneous Type IIB rays, very sparse to absent parenchyma are features clearly more advanced than those of the Dilleniaceae. If *Crossosoma* were closely related to the Dilleniaceae, it would seem that its secondary xylem should retain more of the primitive features found in that family.

Since being removed from the Ranunculaceae, the genus *Paeonia* is now most commonly placed as a monotypic family in close association with the Dilleniaceae. Examination of the wood reveals that it is more highly evolved than the Dilleniaceae in a number of characters: reduced ray structure (uniseriate or biseriate rays commonly occur), occasional alternate intervascular pitting, reduction in the number of scalariform bars in the perforation plates to 1 to 5, vessels occasionally in small clusters with semi-ring porosity. In spite of these features, wood anatomy does not negate the possible position of *Paeonia* as allied to, yet more highly advanced than, the Dilleniaceae.

Since a taxon which retains primitive wood characters cannot be derived from one which is uniformly advanced, Bailey (1957) has pointed out that the evidence obtained from wood studies are often more helpful in negations than in positive assertions of close alliance. Furthermore, structures often appear similar in quite distantly related groups owing to the frequent occurrence of parallel evolution (Bailey, *loc. cit.*). It would, therefore, be very unwise to speculate concerning phyletic relationships solely on the basis of wood anatomy. Bailey (1951, 1953, 1957) and Canright (1955, 1963) have stressed the need for comprehensive studies which take into account evidence from all organs and parts of the plant. Only when all the information has been gathered and carefully evaluated can meaningful phylogenies be constructed.

APPENDIX 1. — Dilleniaceous Wood Examined

SPECIES	COLLECTOR AND NUMBER	GEOGRAPHICAL ORIGIN	HERBARIUM VOUCHER	LOCATION AND CATALOG NUMBER
Acrotrema uniflorum Hook.	Thwaites 265	Ceylon	—	Aw 26224
Curatella americana L.	A. C. Smith 2185	British Guiana	Y	Yw 35484
C. americana L.	Zanderij 209	Surinam	Y	Yw 41257
C. americana L.	L. Williams 9842	Mexico	Y	Yw 35006
C. americana L.	A. J. Fors 96	Cuba	—	USw 21446
C. americana L.	H. Pittier	Venezuela	Y	USw 2773
C. americana L.	Forest Dept. 2185	British Guiana	—	FHOw 14636
C. americana L.	B. A. Krukoff	—	—	Fw 2055
Davilla aspera (Aubl.) Benoist	Cuatrecasas 17302	Colombia	F. VALLE	Yw 43186
D. aspera (Aubl.) Benoist	Cuatrecasas 17302	Colombia	F. VALLE	Fw 17302
D. aspera (Aubl.) Benoist	Woytkowski 5461	Peru	MO	USw 15527
D. rugosa Poir.	H. León	Cuba	—	Yw 40712
Didesmandra aspera Stapf	Banying anak Ludong	Sarawak	—	*s. n.*
Dillenia aurea Smith	—	Java	—	Yw 30030
D. biflora (A. Gray) Martelli ex Dur. & Jacks.	—	Fiji	—	Yw 25835
D. biflora (A. Gray) Martelli ex Dur. & Jacks.	A. C. Smith 3471	Fiji	NY	Yw 28327
D. biflora (A. Gray) Martelli ex Dur. & Jacks.	—	Fiji	—	Yw 25674
D. excelsa (Jack) Gilg	—	Java	—	Yw 30025
D. excelsa (Jack) Gilg	—	Java	—	Yw 30026
D. excelsa (Jack) Gilg	—	Java	—	Yw 30027
D. excelsa (Jack) Gilg	B. A. Krukoff 271	Sumatra	NY	USw 7127
D. excelsa (Jack) Gilg	B. A. Krukoff 271	Sumatra	NY	FHOw 8368

SPECIES	COLLECTOR AND NUMBER	GEOGRAPHICAL ORIGIN	HERBARIUM VOUCHER	LOCATION AND CATALOG NUMBER
D. excelsa (Jack) Gilg	D. E. Carver 20	Sarawak	—	FHOw 6655
D. eximia Miq.	—	Malaya	—	KEPw 7302
D. indica L.	—	Java	—	Yw 30028
D. indica L.	—	Malaya	—	KEPw 5968
D. ingens (B. L. Burtt) A. C. Smith	Waterhouse 25	Bougainville	Y	Yw 21156
D. ingens (B. L. Burtt) A. C. Smith	F. S. Walker 146	Solomons	—	FHOw 17958
D. luzoniensis (Vidal) Martelli ex Dur. & Jacks.	—	Philippines	—	Fw 272982
D. pentagyna Roxb.	—	Java	—	Yw 30032
D. pentagyna Roxb.	J. F. Kools 33	Indonesia	—	FHOw 18866
D. philippinensis Rolfe	—	Philippines	—	USw 5213
D. pulchella (Jack) Gilg	H. E. Desch. 41887	Malaya	KEP	Yw 38502
D. pulchella (Jack) Gilg	H. E. Desch. 41887	Malaya	KEP	KEPw 3675
D. pulchella (Jack) Gilg	—	Malaya	—	KEPw 6544
D. quercifolia (White & Francis ex Lane-Poole) Hoogl.	Holland	New Britain	—	USw 22228
D. quercifolia (White & Francis ex Lane-Poole) Hoogl.	—	—	—	FPAw 6437
D. reticulata King	Forest Dept. 422	Malaya	FHO	FHOw 7602
D. reticulata King	—	Malaya	—	KEPw 7261
D. reticulata King	—	Malaya	—	KEPw 5779
D. retusa Thunb.	—	Ceylon	—	Yw 9781
D. scabrella (D. Don) Roxb. ex Wall.	Forest Dept. 607	Burma	—	FHOw 1676
D. solomonensis (White) Hoogl.	—	Solomon Is.	—	FPAw 8226
D. solomonensis (White) Hoogl.	F. S. Walker 145	Solomon Is.	—	FHOw 17957
D. sumatrana Miq.	—	—	—	KEPw 403

D. sumatrana Miq.	—	—	—	KEPw 382
D. triquetra (Rottb.) Gilg	—	Ceylon	—	Yw 9807
D. triquetra (Rottb.) Gilg	—	Ceylon	—	USw 21889
D. turbinata Finet & Gagnep.	Sun Yatsen Univ. 0835	Hainan	SYS	Yw 29564
D. turbinata Finet & Gagnep.	Tang	China	Fan Mem. Inst. Chungking	USw 8597
Doliocarpus sp.	S. J. Record	British Honduras	—	Yw 8831
Doliocarpus sp.	A. Ducke 327	Brazil	Y	Yw 34091
Doliocarpus sp.	B. A. Krukoff 7020	Brazil	US	Yw 37027
D. coriaceus (Mart. & Zucc.) Gilg	Cuatrecasas 16556	Colombia	F, VALLE	Yw 43052
D. dentatus (Aubl.) Standl.	Stern et al. 549	Panama	US, MO	USw 16329
D. lasiogyne Benoist	Reitz & Klein 5776	Brazil	HBR	USw 15034
D. major Gmel.	Stern et al. 844	Panama	MO	USw 16485
D. olivaceus Sprague & Wms. ex Standl.	Stern et al. 11	Panama	MO	USw 16042
Doliocarpus sp.	B. A. Krukoff 11189	Bolivia	NY	Fw 11189
Hibbertia coriacea (Hook. f.) Gilg	—	New Caledonia	—	FPAw 23183
H. cuneiformis Sm.	—	Pemberton, W. Australia	—	FPAw 11684
H. lucens Brongn. & Griseb.	A. C. Smith 3546	Fiji	NY	Yw 28402
H. lucens Brongn. & Griseb.	A. C. Smith 3045	Fiji	NY	Yw 27903
H. lucens Brongn. & Griseb.	—	New Caledonia	—	FPAw 12037
H. saligna R. Br. ex DC.	—	New South Wales	—	FPAw 13034
H. tetrandra (Lindl.) Gilg	Wilson 848	—	US	Wilson 848
Pachynema complanatum R. Br. ex DC.	Von Mueller	New South Wales	A	Aw 26225
Schumacheria castaneifolia Vahl	—	Ceylon	—	Aw 2632
Tetracera boiviniana Baill.	H. J. Schlieben 5187	Tanganyika	Y	Yw 29962
T. scandens (L.) Merr.	—	Philippines	—	*s. n.*
T. volubilis L.	H. León	Cuba	—	Yw 40713

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. 1, *Schumacheria castaneifolia* Vahl, cross section of wood showing solitary, angular vessels and sparse apotracheal parenchyma, × 130. 2, the *same*, tangential section showing narrow heterogeneous rays and highly oblique end wall of vessel member, × 130. 3, *Hibbertia lucens* Brongn. & Griseb., cross section of wood illustrating mostly solitary pores, × 130. 4, the *same*, radial section, × 70.

PLATE II

FIGS. 5–8. 5, *Dillenia ingens* (B. L. Burtt) A. C. Smith, cross section of wood showing solitary vessels, apotracheal and paratracheal parenchyma, × 60. 6, the *same*, tangential section showing heterogeneous rays and oblique angle of many-barred scalariform perforation plate, × 60. 7, *Dillenia biflora* (A. Gray) Martelli ex Dur. & Jacks., cross section of wood illustrating solitary pores, thick-walled fiber tracheids, apotracheal parenchyma, and dark-staining deposits in ray parenchyma, × 100. 8, *Dillenia turbinata* Finet & Gagnep., longitudinal section of wood showing sparse opposite to transitional intervascular pitting, × 400.

PLATE III

FIGS. 9–13. 9, *Acrotrema uniflorum* Hook., cross section of stem with limited secondary xylem; note narrow rays, × 400. 10, *Pachynema complanatum* R. Br. ex DC., cross section of stem with limited secondary xylem, × 400. 11, *Acrotrema uniflorum*, longitudinal section of stem illustrating oblique angle of many-barred scalariform perforation plate, × 400. 12, the *same*, longitudinal section of stem showing scalariform perforation plate, × 400. 13, *Pachynema complanatum*, longitudinal section of stem showing scalariform to opposite intervascular pitting, × 400.

PLATE IV

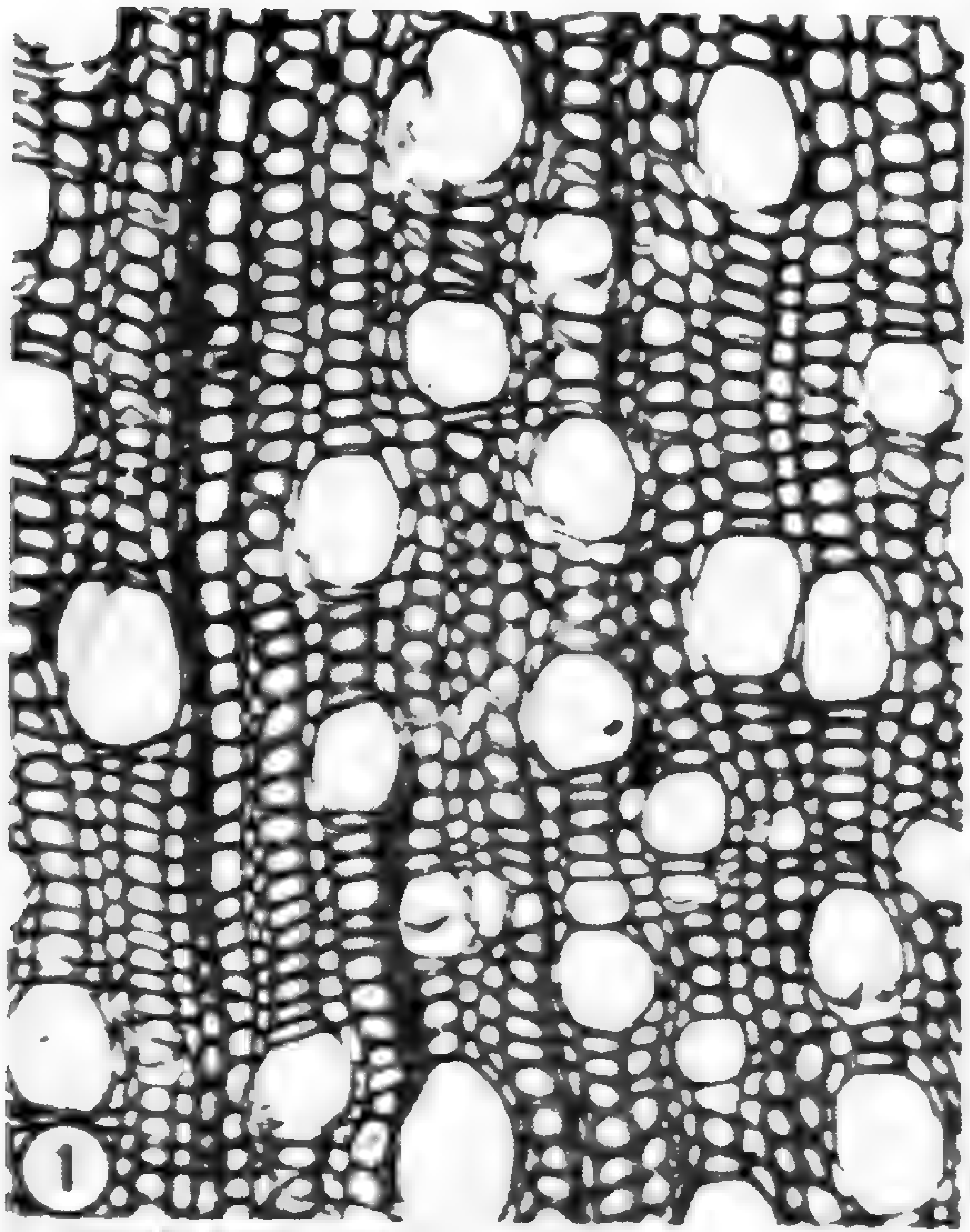
FIGS. 14–17. 14, *Curatella americana* L., cross section of wood showing solitary vessels, broad rays, aggregate to narrow-banded and paratracheal parenchyma, × 55. 15, *Davilla rugosa* Poir., cross section of wood showing very large circular vessels and broad rays, × 55. 16, *Curatella americana*, tangential section of wood, × 130. 17, the *same*, radial section illustrating obliquely oriented, simple perforation plate, × 400.

PLATE V

FIGS. 18–21. 18, *Tetracera volubilis* L., cross section of wood showing solitary pores and broad rays containing dark gummy deposits, × 60. 19, *T. boiviniana* Baill., cross section of wood depicting a multiperforate perforation plate, × 400. 20, the *same*, tangential section showing uniseriate and multiseriate rays, × 130. 21, *Doliocarpus* sp., longitudinal section of wood showing opposite to transitional intervascular pitting with very elongate pits, × 400.

PLATE VI

FIGS. 22–27. Vessel Member types in Dilleniaceae. 22, *Schumacheria castaneifolia* Vahl, × 400. 23, *Dillenia triquetra* (Rottb.) Gilg, × 400. 24, *Dillenia ingens* (B. L. Burtt) A. C. Smith, × 400. 25, *Davilla aspera* (Aubl.) Benoist, × 400. 26, *Doliocarpus dentatus* (Aubl.) Standl., × 400. 27, *Tetracera volubilis* L., × 400.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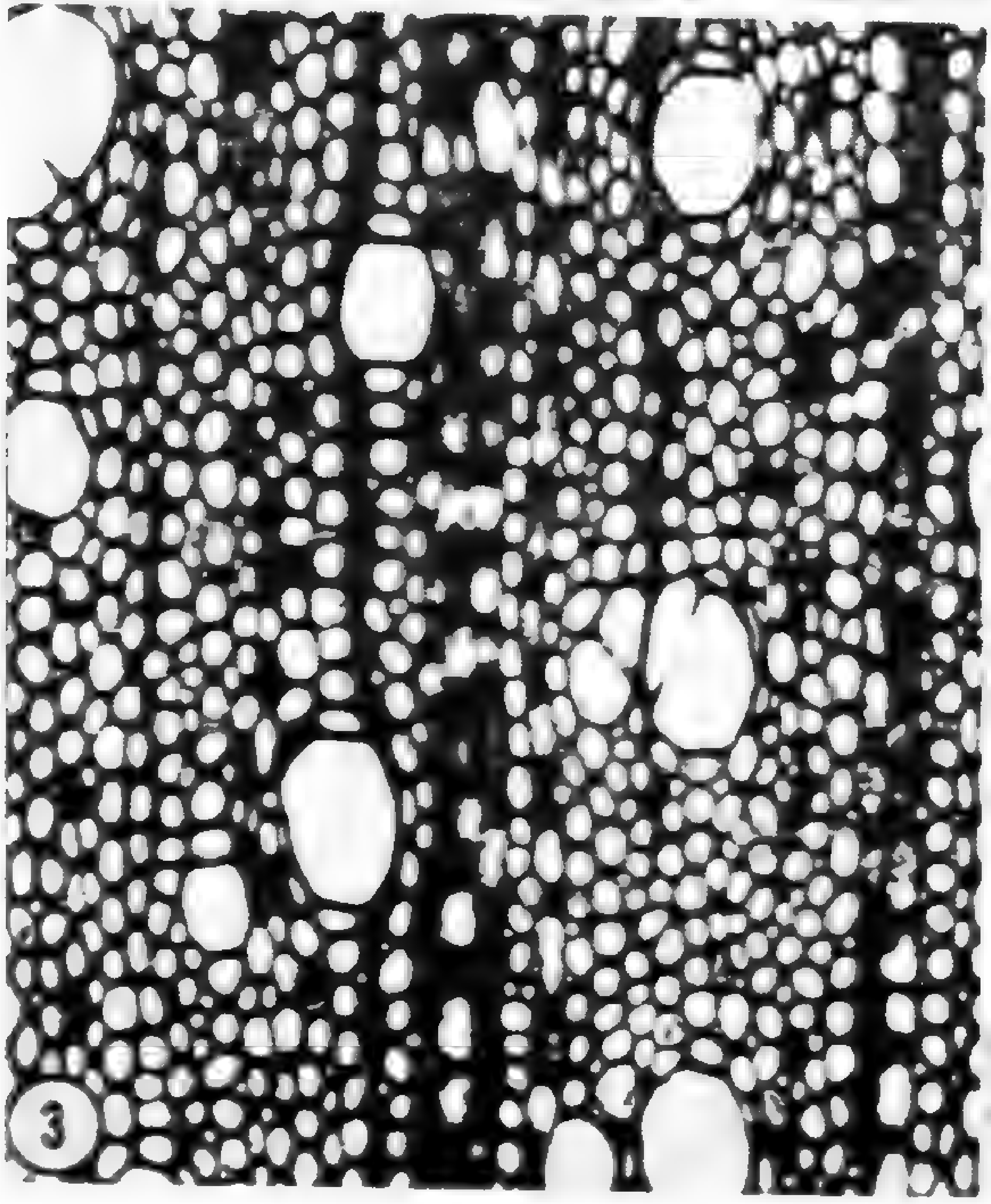
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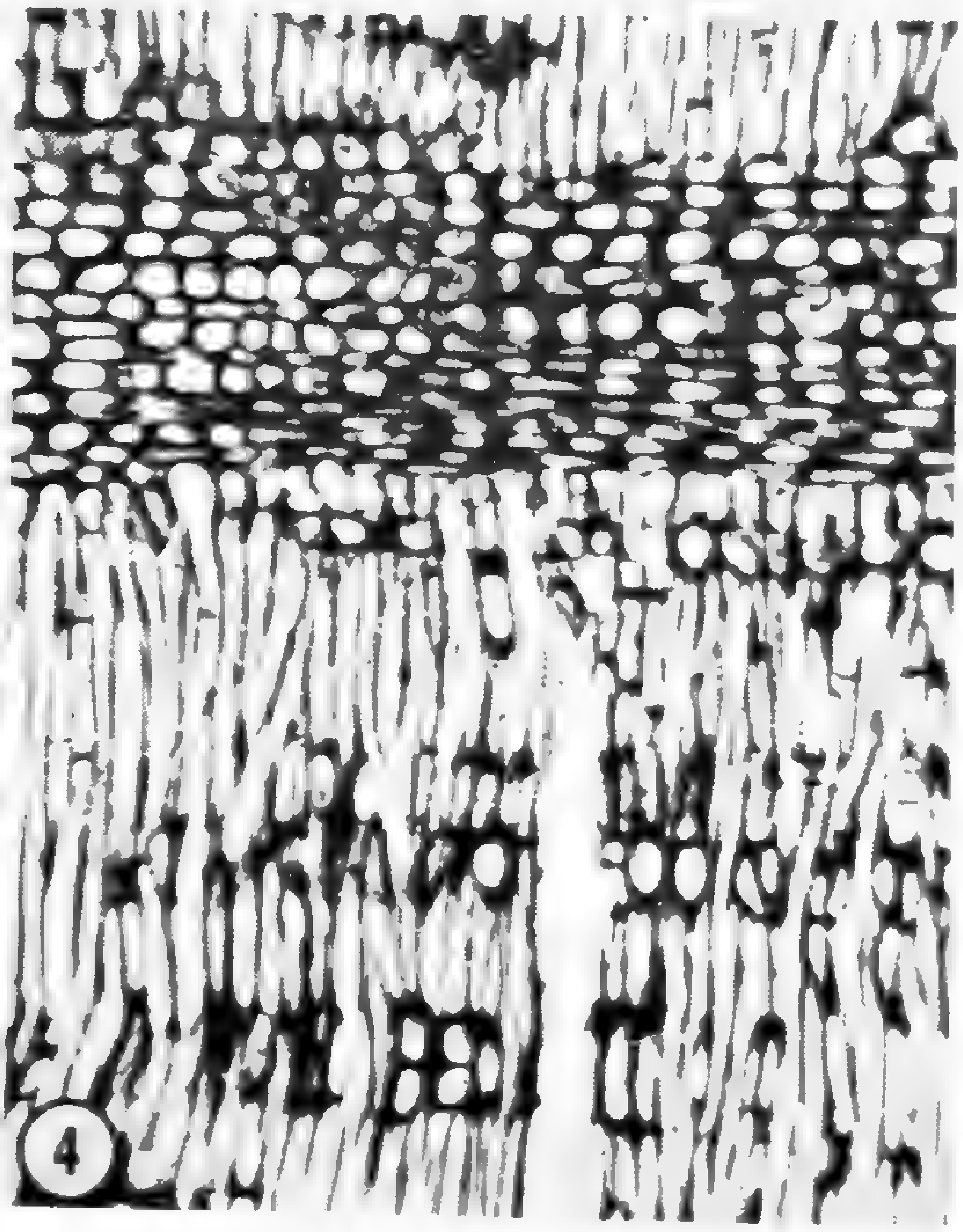
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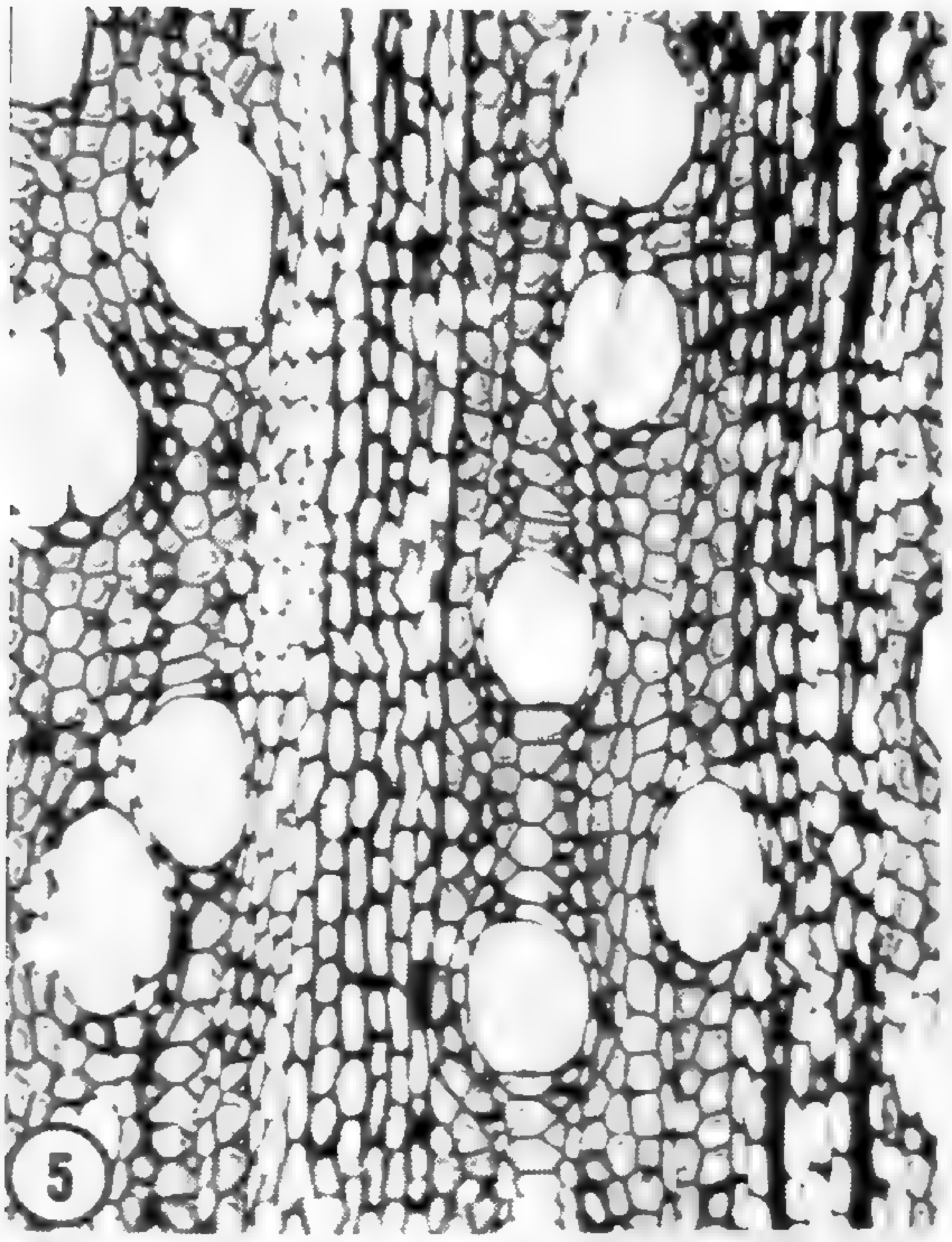
DICKISON, DILLENIACEAE. I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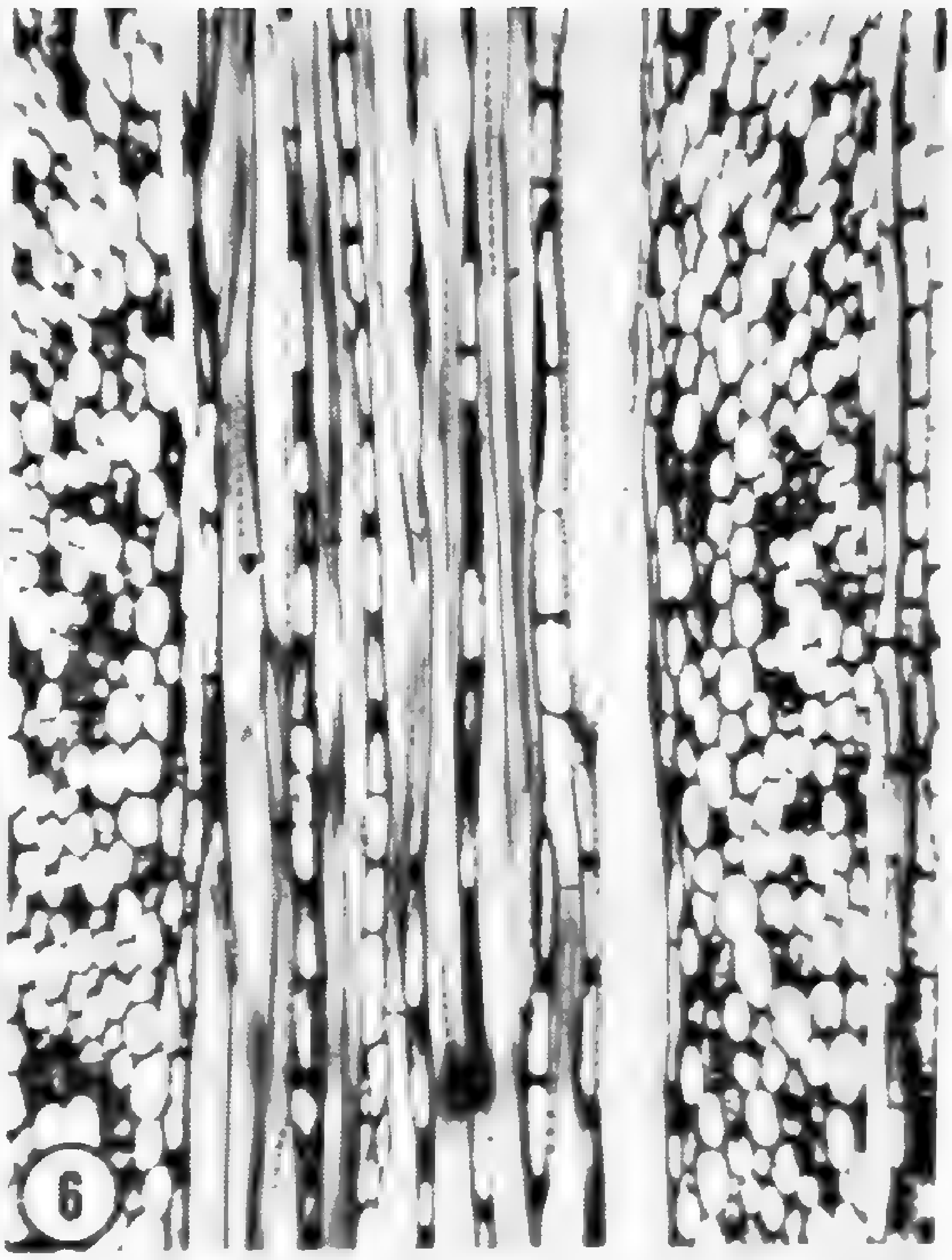
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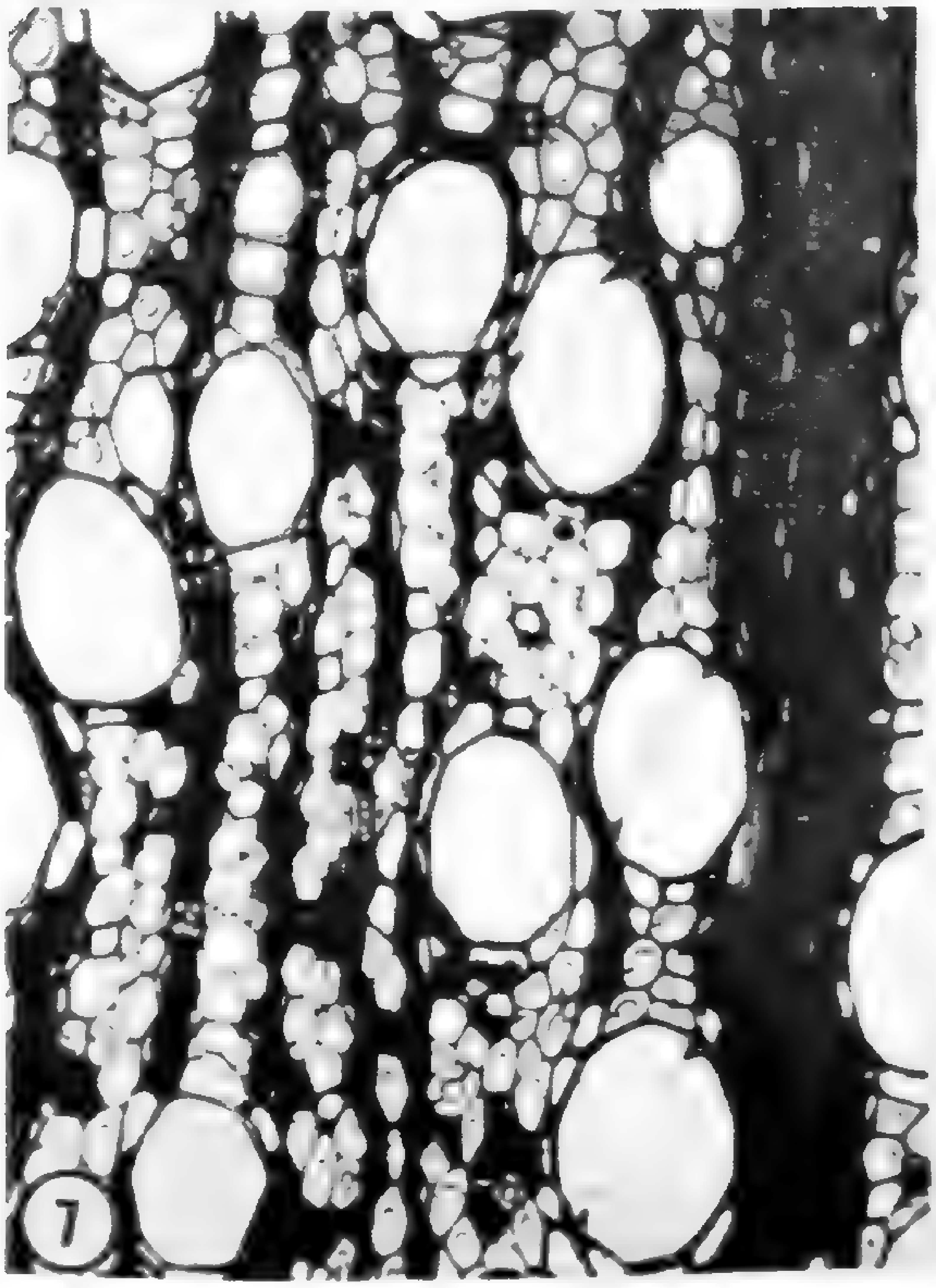
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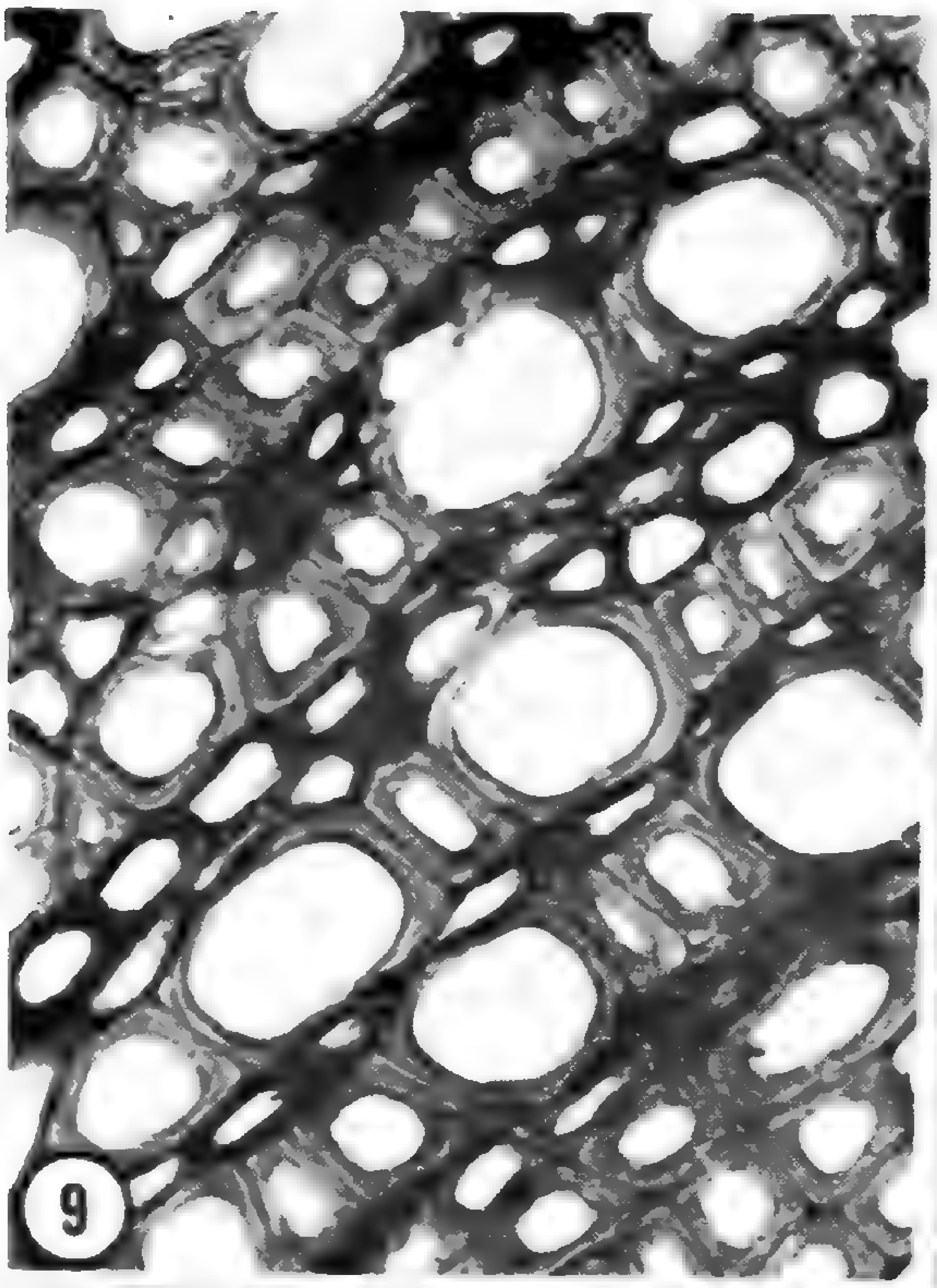
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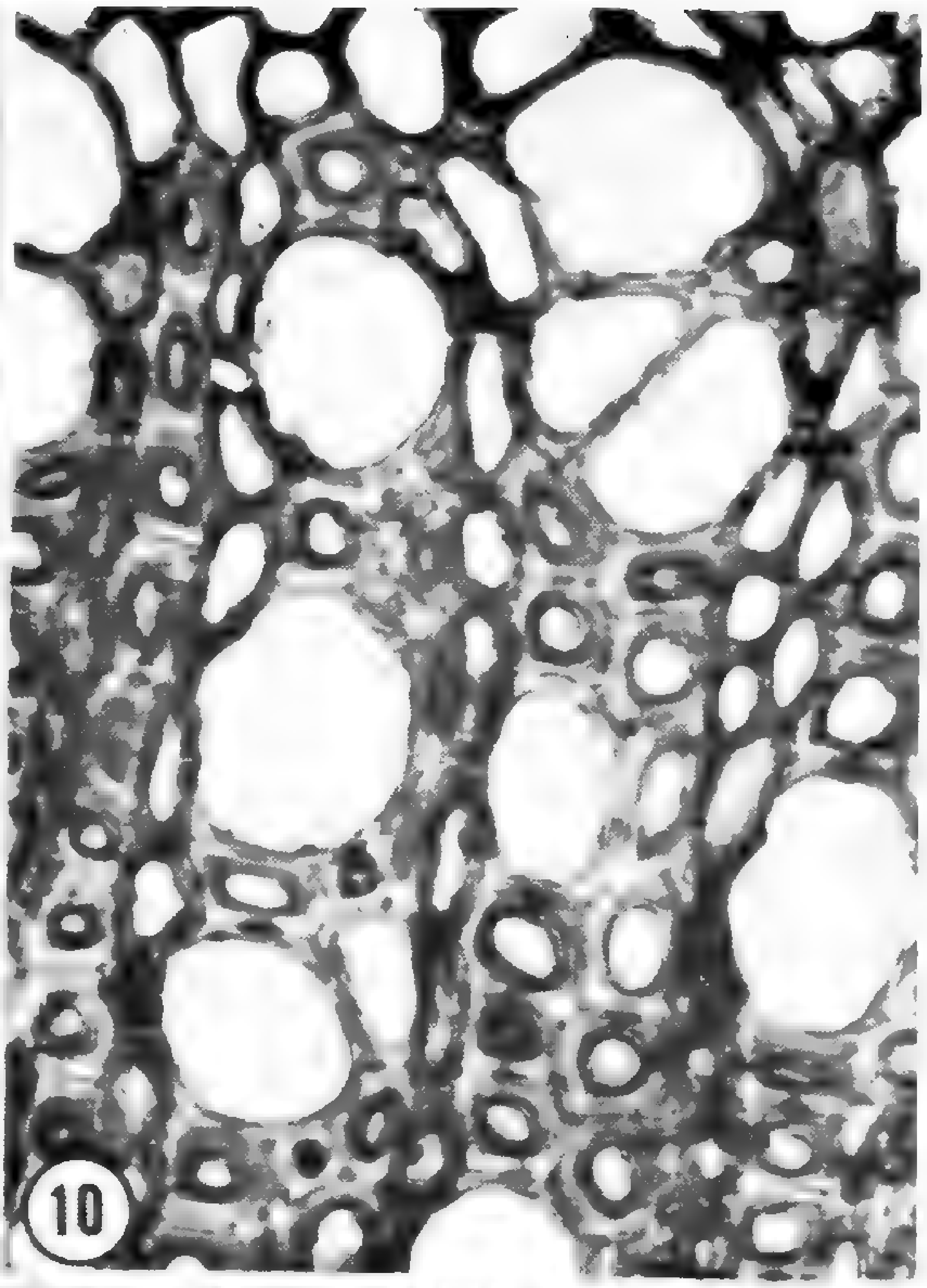
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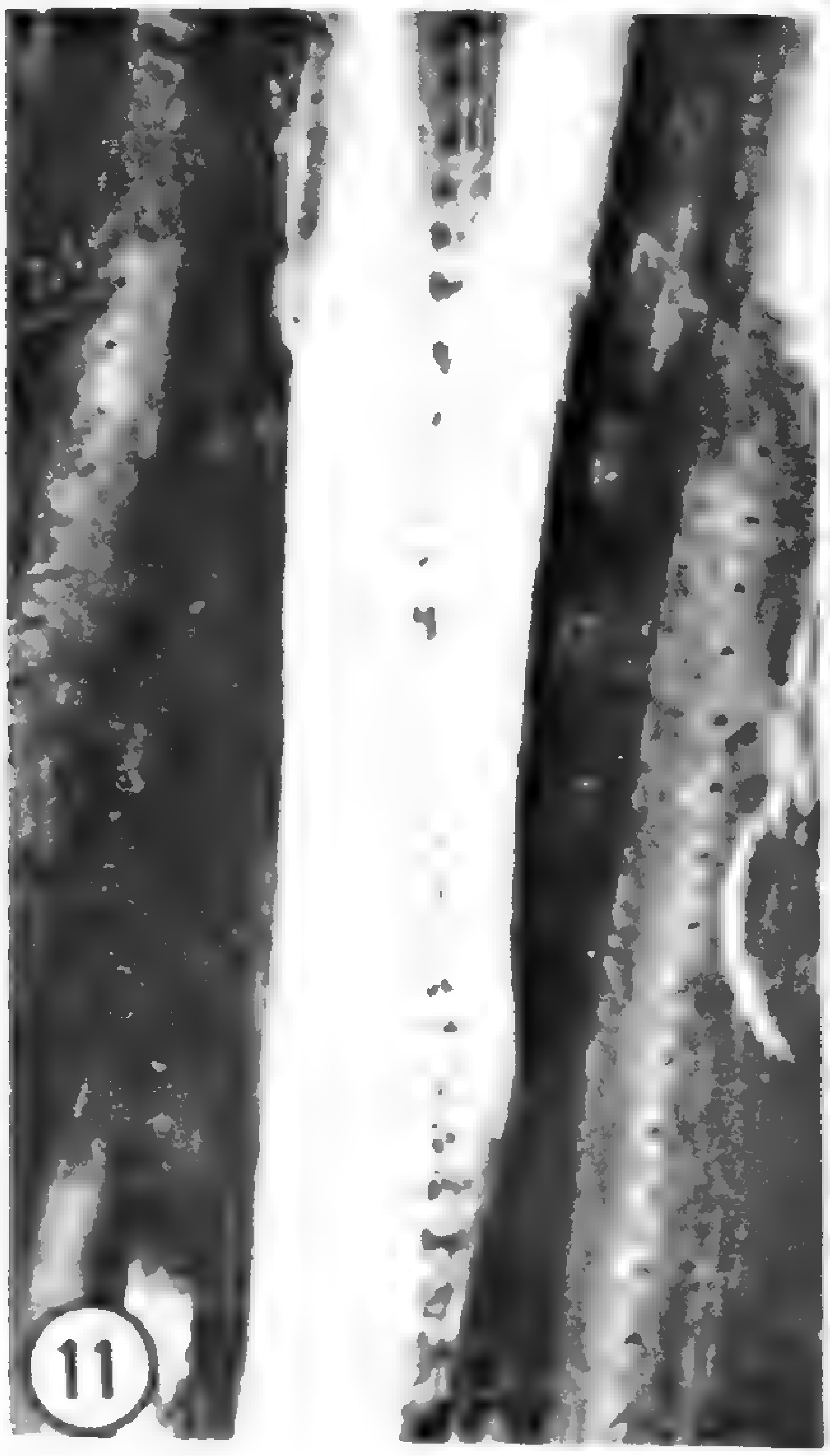
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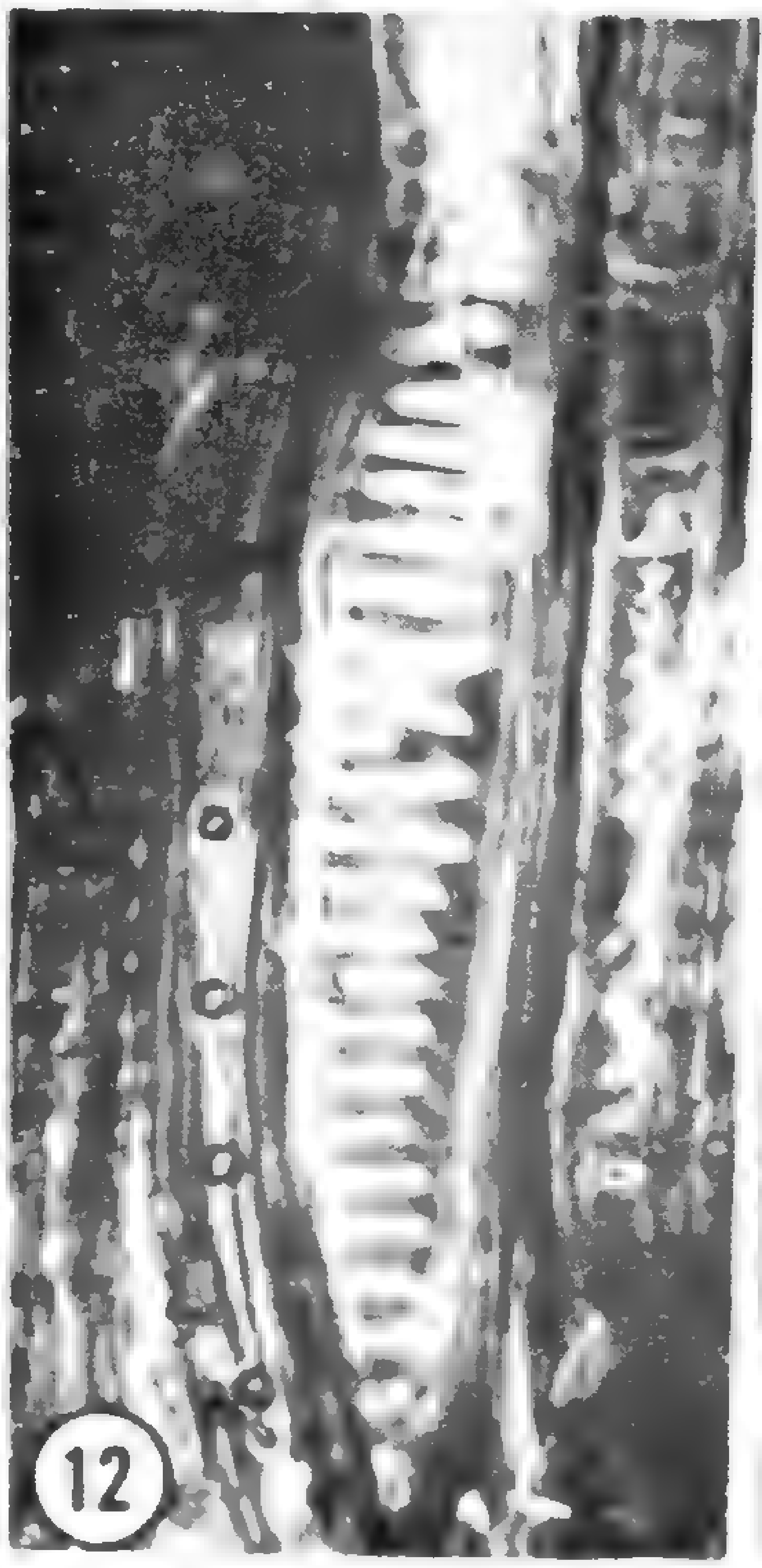
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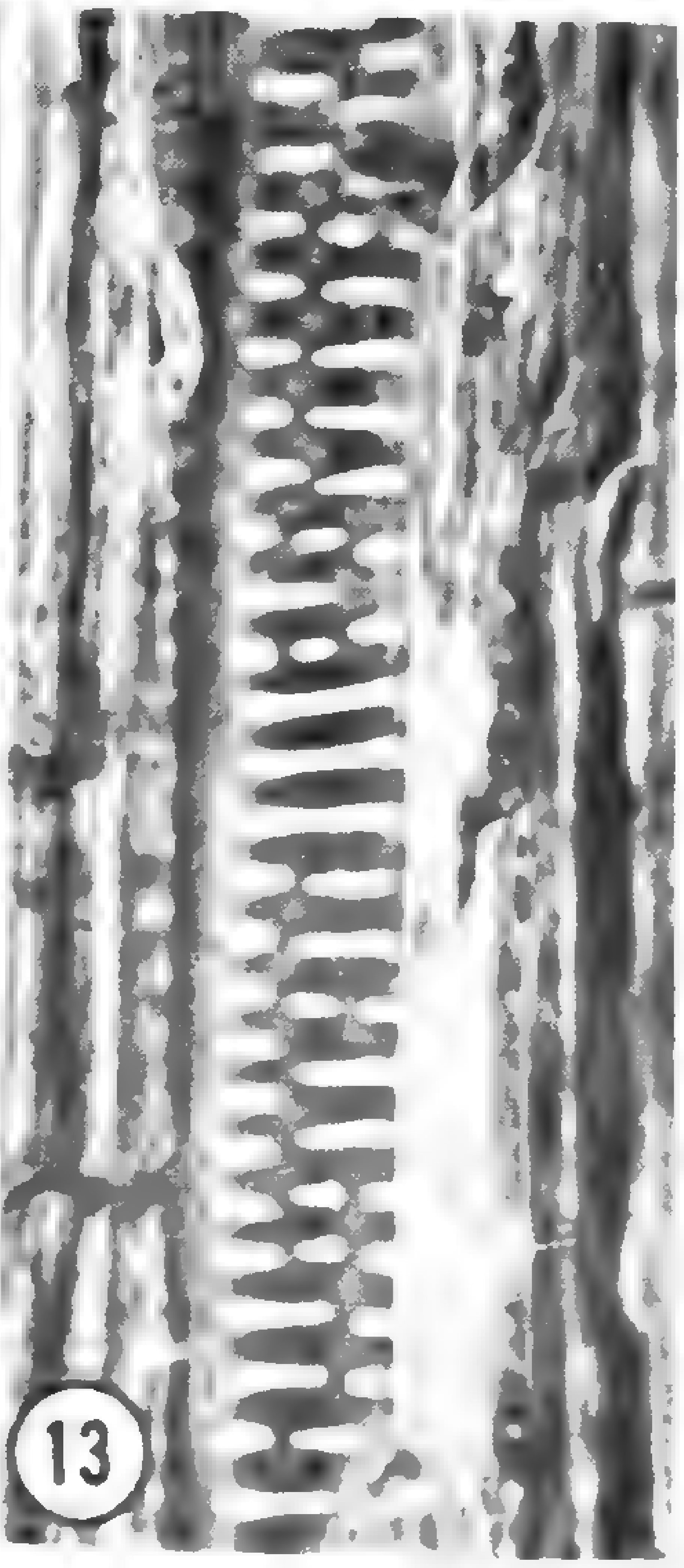
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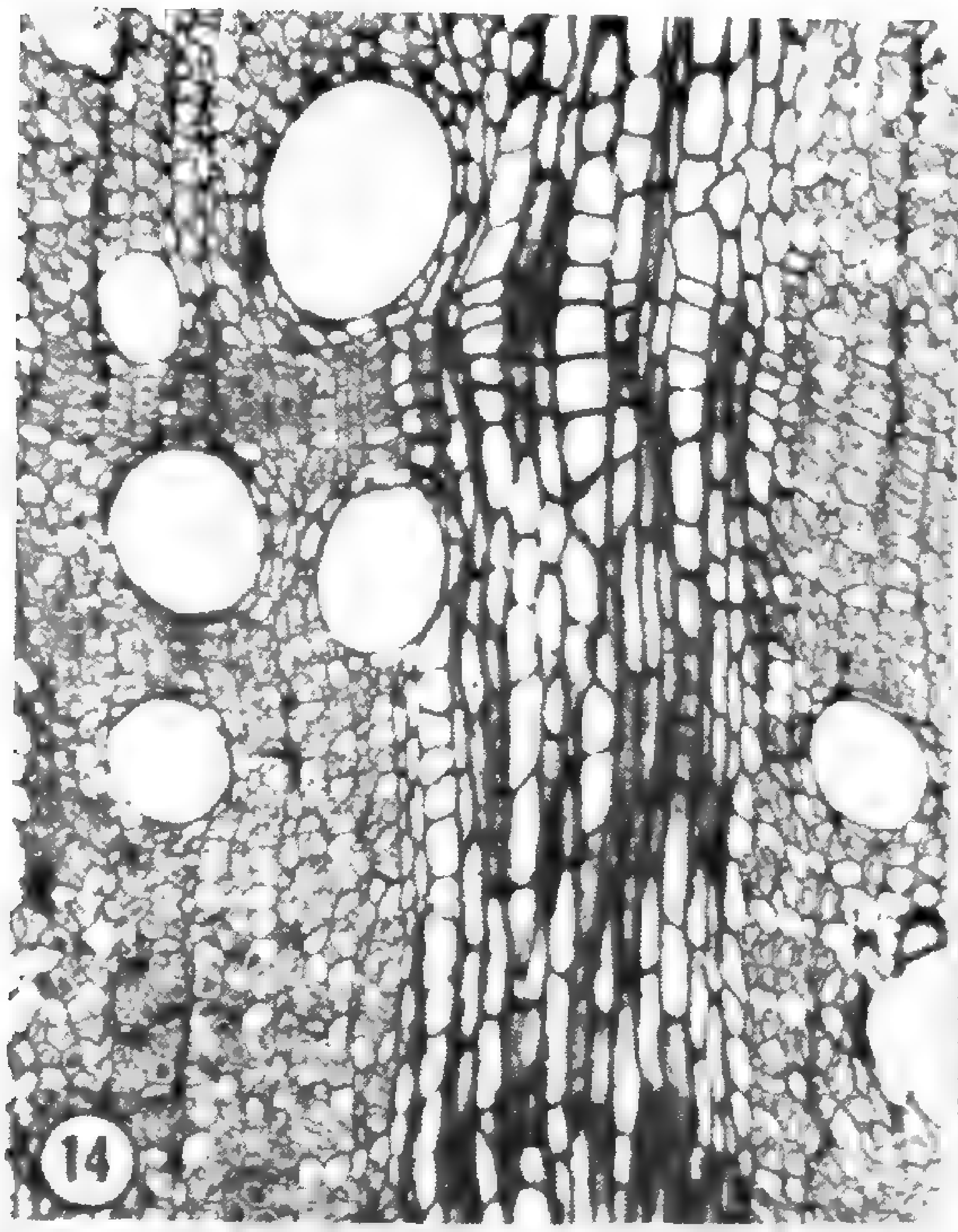
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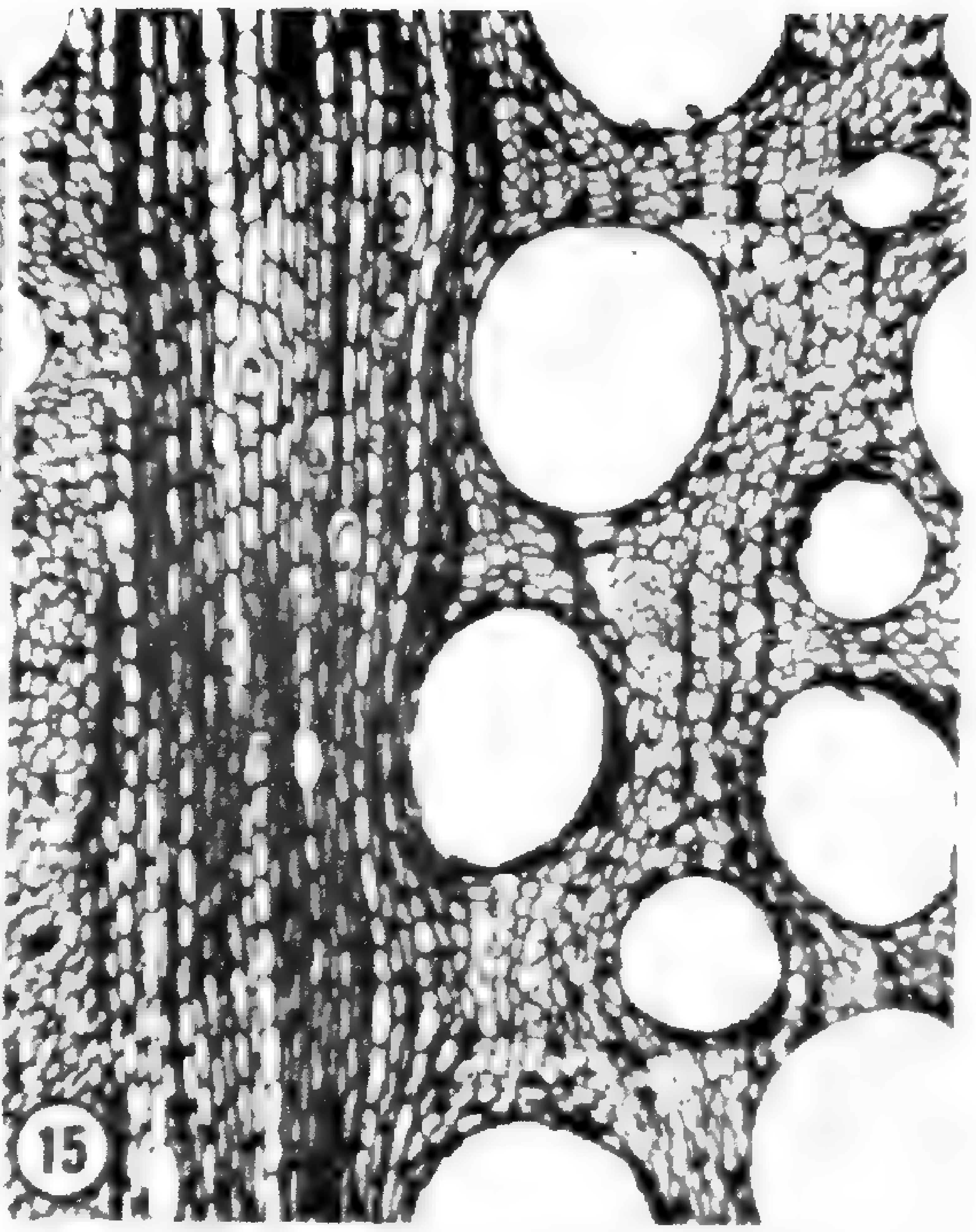
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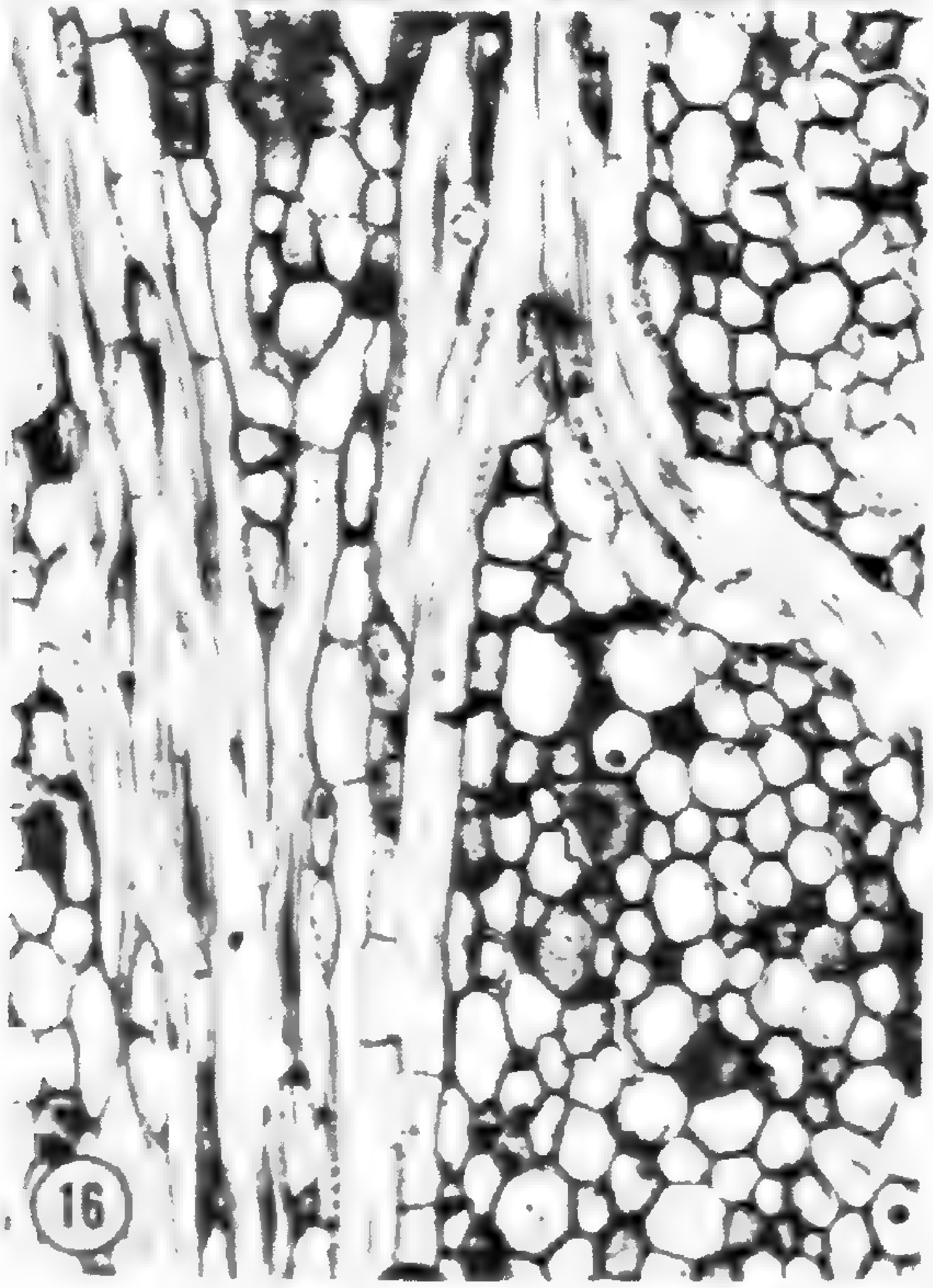
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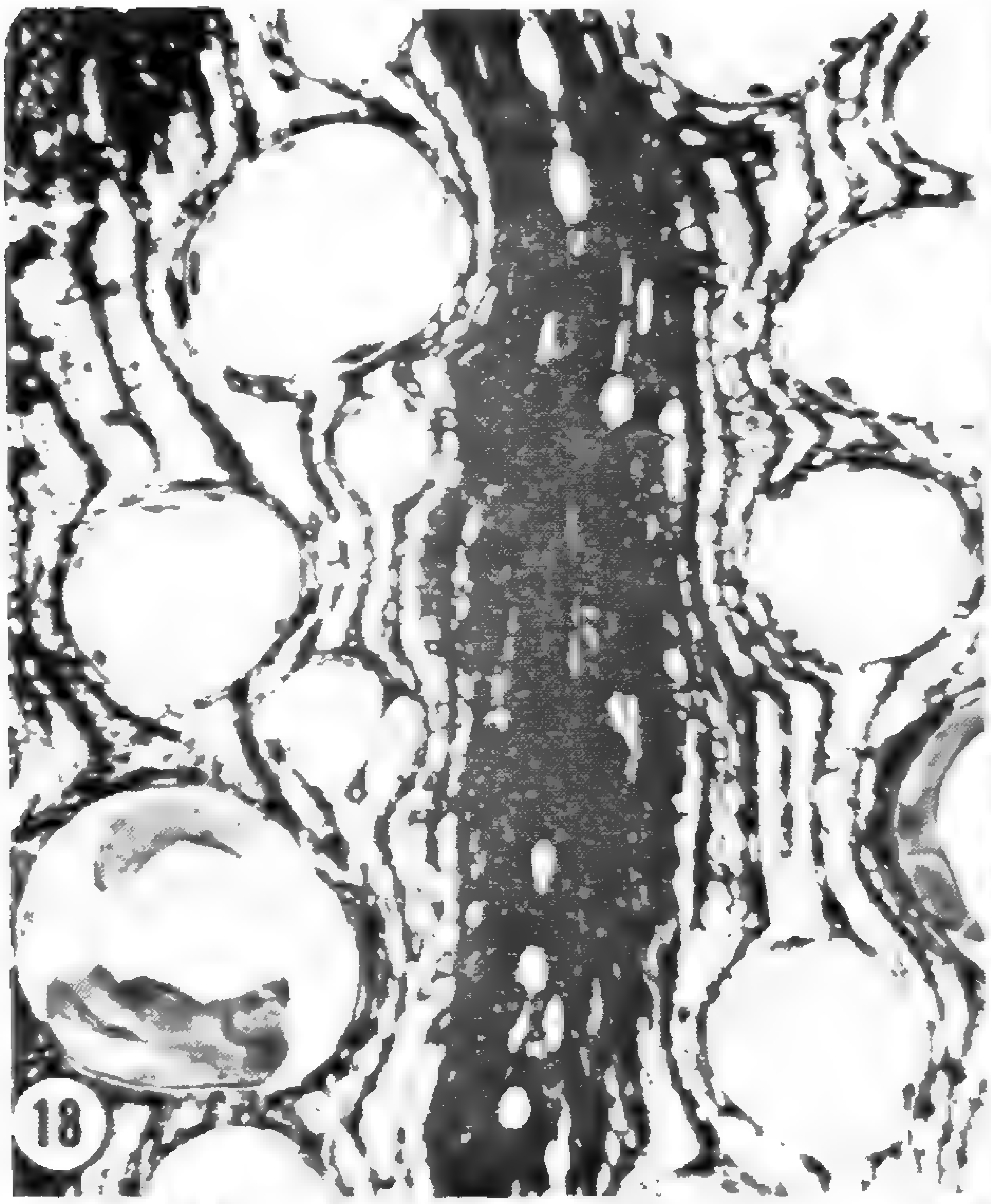
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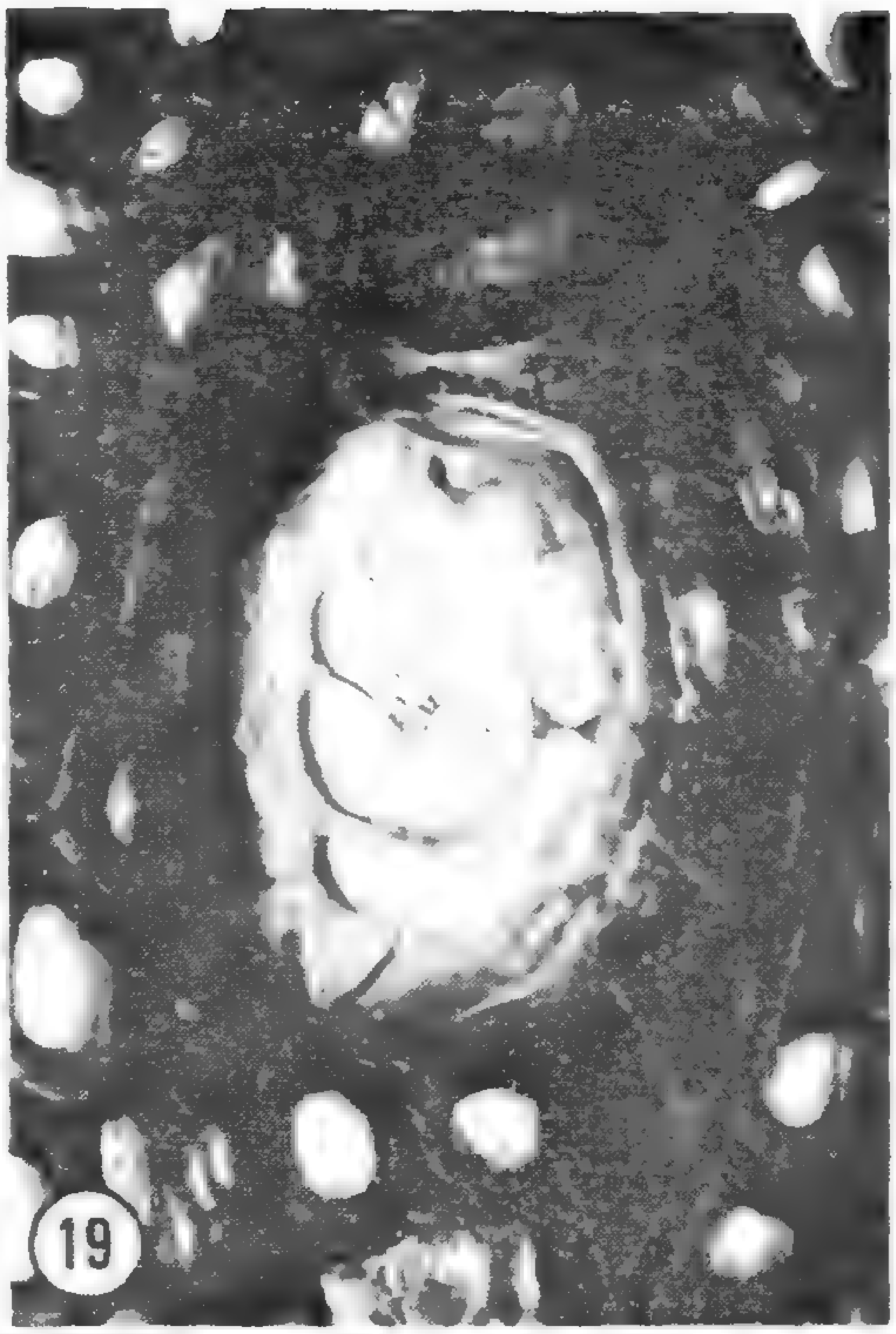
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Dickison, Dilleniaceae, I

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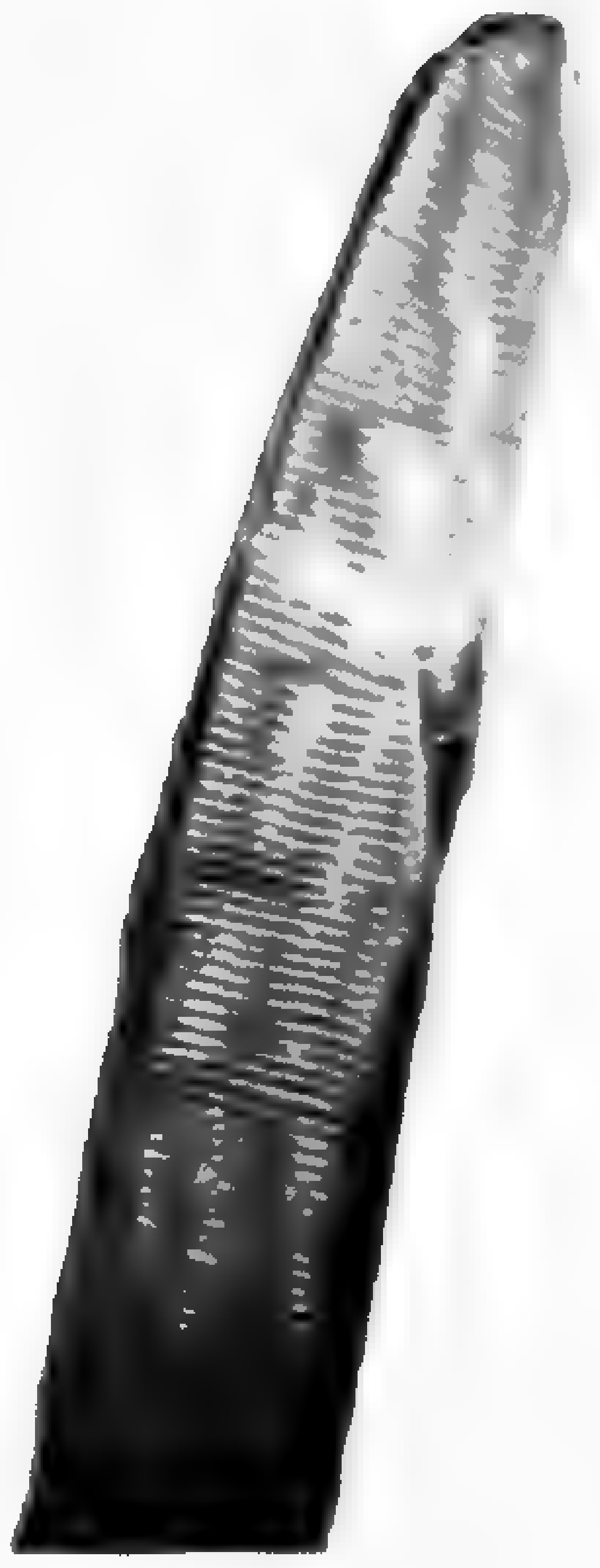

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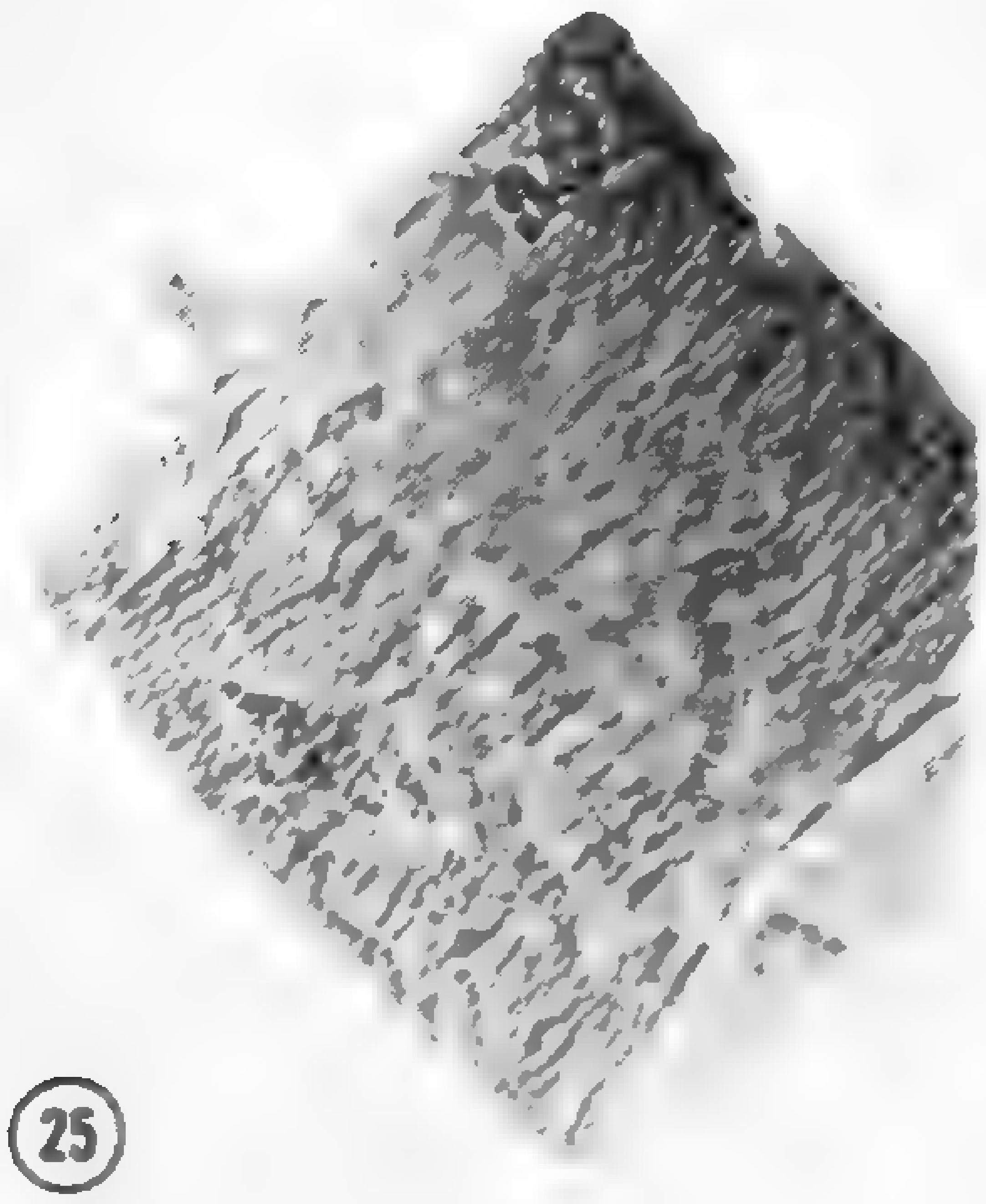

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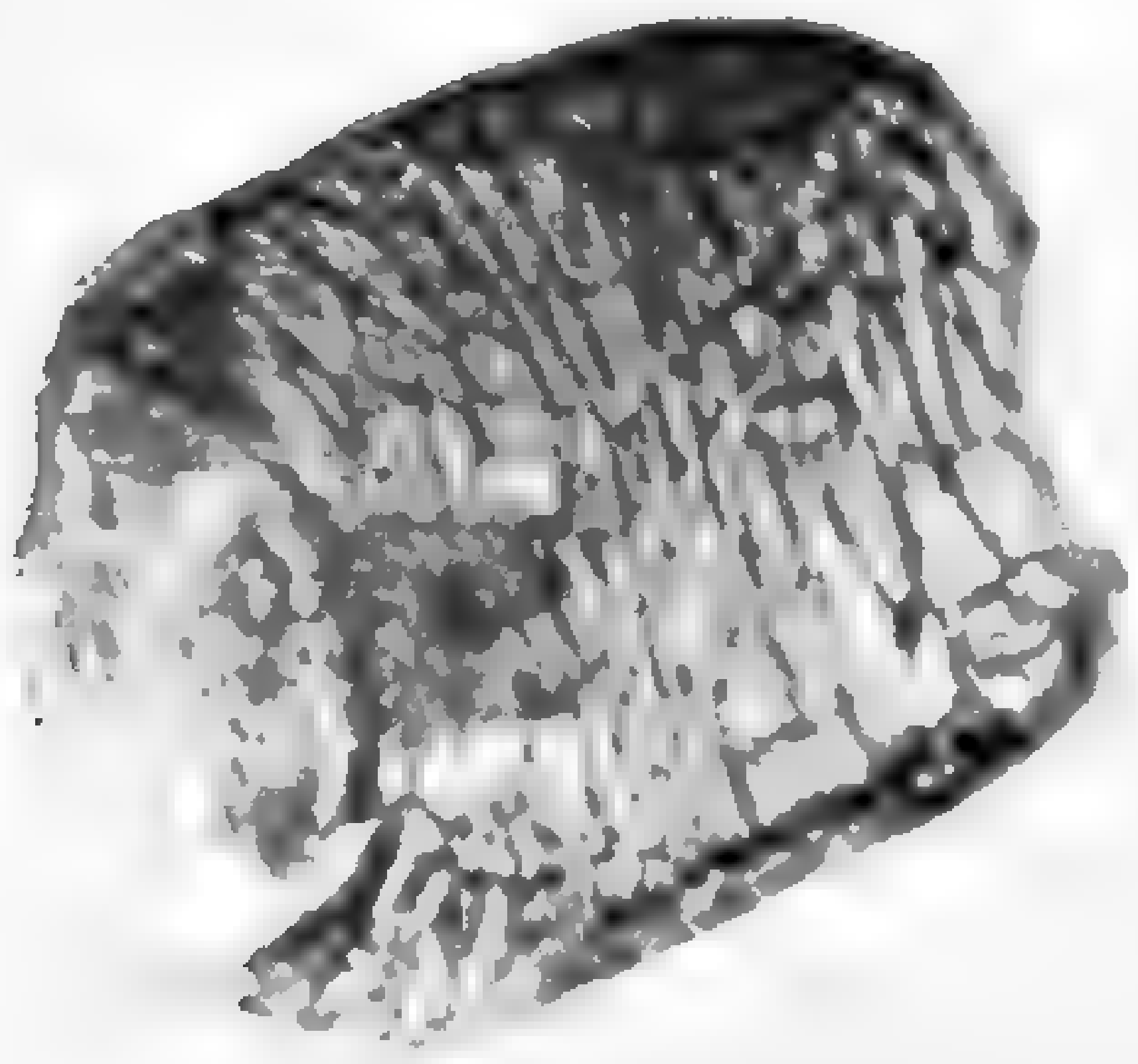

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DICKISON, DILLENIACEAE, I

A SYNOPSIS OF AFRICAN SPECIES OF DELPHINIUM AND CONSOLIDA

PHILIP A. MUNZ

LIKE SEVERAL OTHER HERBACEOUS GENERA of the Ranunculaceae, notably *Isopyrum, Coptis, Actaea, Aquilegia*, and *Aconitum* as examples, *Delphinium* is of the North Temperate Zone, but it differs remarkably in its far southern range on to the higher mountains, even, of central Africa. My interest in making some attempt to understand the species of this widespread group began when preparing a treatment of cultivated forms for *Hortus III*, since I had considerable misgiving as to the correct names and limits of some of the species involved.

With the American species fairly well understood (cf. EWAN, J. A., A synopsis of the North American species of *Delphinium*. Univ. Colo. Stud. D. **2**(2): 55–244. 1945; and LEWIS, H. & C. EPLING, A taxonomic study of Californian delphiniums. Brittonia **8**: 1–22. 1954), and with European species well summarized by A. O. CHATER & B. PAWLOWSKI (cf. Flora Europaea 1: 213–217. 1964), one turns naturally to Asiatic and African species as most needing study. The latter continent has the fewer and it seems well to treat these first, hence the present paper. The much more complex and larger Asiatic representation will be treated in subsequent articles.

In both the *Flora Europaea* cited above and in P. H. DAVIS, *Flora of Turkey* 1: 108–134. 1965, two genera are recognized: *Delphinium*, sensu stricto, and *Consolida*. The former is characterized by four separate petals (nectaries, honey-leaves), the two upper being spurred and secreting nectar, the spurs inserted into the sepal spur, the two lower petals not nectariferous, merely with a narrow claw and dilated lamina. Stamens in 8 spiralled series. Carpels 3, rarely 4 or 5. An almost entirely perennial group which includes the plants cultivated as "delphiniums."

Consolida, on the the other hand, has a single "petal" (nectary or honey-leaf), said to be formed by the union of the two superior petals of *Delphinium*, and one spur. The two lower petals are said to be lacking. Stamens in 5 series. Carpel solitary. Plants annual. Here fall the species known in gardens as "larkspurs."

I am following the above usage in my series of proposed papers. In his monograph of *Delphinium*, sensu lato, Huth (Bot. Jahrb. **20**: 322–499. 1895) has rather an elaborate scheme of sections and tribes, which in many cases do not seem to me to represent natural groups and which separate widely quite closely related species. I am not prepared to enter into any such scheme of subgeneric categories and can do no more than offer artificial keys for identification of species. Under each species treated synonymy is given at least for the geographic area involved, with a description and general distribution, and with mention of some representative illustrations in the literature. Where material has been available, there is shown a line drawing of the petals or "petal." Some of the principal exsiccatae are listed with the name of the collector and his collection number, by country, but without stating the exact locality or herbaria in which deposited.

To the curators of the herbaria at the following American institutions, from which material was borrowed, I express herewith my very great appreciation:

Arnold Arboretum (A)
Bailey Hortorium (BH)
California Academy of Sciences (CAS)
Field Museum, Chicago (F)
Gray Herbarium (GH)
Missouri Botanical Garden (MO)
New York Botanical Garden (NY)
Academy of Natural Sciences, Philadelphia (PH)
United States National Arboretum (NA)
United States National Herbarium (US)
University of California, Berkeley (UC)
University of Michigan (MICH)

I was given, also, the privilege of working for some months at the British Museum of Natural History (BM), at the Royal Botanic Gardens at Kew (K), and the Muséum National d'Histoire Naturelle at Paris (P). In addition, I have had loans from the Royal Botanic Garden at Edinburgh (E), the Komarov Botanical Institute at Leningrad (LE), the Conservatoire et Jardin botaniques at Geneva (G), the Naturhistorisches Museum at Wien (W), and the Botanisches Institut und Botanischer Garten der Universität Wien (WU). I am greatly indebted to all the officers in charge of these collections.

It is a pleasure also to acknowledge my obligation to the National Science Foundation for the financial aid received under Grant GB–2716.

The present series of papers cannot be monographic in nature, but merely synoptic, with the hope of presenting keys and means of identification as a useful step in our present knowledge. True monographic work must come later, when there is access to the regions inhabited by many of the species and observations can be made of them as living organisms.

1. **Delphinium** L.

Delphinium, as a genus, L. Sp. Pl. **1**: 530. 1753; Gen. Pl. ed. 5. 236. 1754. Huth, Bot. Jahrb. **20**: 322–499. *pls. 6, 7.* 1895. As a subgenus, *Eudelphinium* (Huth) Dalla Torre & Harms, Genera Siphonogamarum 165. 1901.

Mostly perennial, more rarely biennial or annual, herbs. Leaves alternate, palmately divided. Flowers zygomorphic, mostly in racemes or panicles. Sepals 5, petaloid, the posterior one normally spurred. Petals four, in two unlike pairs, the upper pair, sometimes called nectaries or honey-leaves, produced into nectariferous spurs inserted into the sepal spur; the lower pair with a basal claw and expanded lamina. Stamens in eight spiralled series. Carpels 3 (–5), free, becoming follicles.

TYPE SPECIES, *D. peregrinum* L.

KEY TO THE AFRICAN SPECIES OF DELPHINIUM, *sensu stricto*

a. Plants perennial.
- b. Petals glabrous, the upper with lateral wings on the limb. Morocco to Tunis. . . . . 2. *D. balansae*.
- b. Petals bearded and/or ciliate.
  - c. Spur 5–8 mm. long, ca. 4 mm. wide at base; upper petals short-pubescent toward the tips. Ethiopia southward. . . . . . 3. *D. dasycaulon*.
  - c. Spur longer; upper petals glabrous.
    - d. The spur 12–15 mm. long; flowers bluish.
      - e. Radical leaves 10–15 cm. in diameter; racemes many-flowered; carpels 3; seeds blackish, 2–3 mm. long. E. Algeria and Tunisia. . . . . 6. *D. sylvaticum*.
      - e. Radical leaves 3–7 cm. in diameter; racemes 4–10-flowered; carpels 5 (3, 4, or 6); seeds dark, 1.5–2 mm. long. Morocco to Tunis.
        - f. Carpels nearly always 5, divergent; sepals 12–16 mm. long. . . . . 7. *D. pentagynum*.
        - f. Carpels 3, erect; sepals 10–13 mm. long.
          - g. Sepals bright blue, distinctly shorter than the spur. . . . . 9. *D. nevadense*.
          - g. Sepals bluish lilac, about as long as or shorter than the spur. . . . . 8. *D. emarginatum*.
    - d. The spur 20–45 mm. long; flowers white to purplish, pinkish or bluish. Tropical Africa at higher elevations.
      - h. Spur slender, 3–4 mm. wide at the base, 30–45 mm. long; upper petals glabrous; sepals mostly 25–40 mm. long. . . . . 4. *D. leroyi*.
      - h. Spur thick, 5–7 mm. wide at base, 20–26 mm. long; upper petals pubescent; sepals mostly 10–15 mm. long. . . . . 5. *D. macrocentron*.

a. Plants annual or biennial.
- i. Middle cauline leaf blades 10–20 cm. long, 5–9-parted; blade of lower petal asymmetrically oblanceolate, gradually attenuate into the claw. . . . . 1. *D. staphisagria*.
- i. Middle cauline leaf blades mostly 2–3 cm. long; blade of the lower petals asymmetrically oblong to rounded.
  - j. Carpels 3; flowers few to several, the receptacle not inflated.
    - k. Limb of lower petals ovate to elliptic, cuneate at base, gradually narrowed into claw. Eastern Mediterranean.
      - l. The limb of lower petals more or less elliptic, often about as long as the claw; plant subglabrous to slightly pubescent, 2–7 dm. tall; racemes several- to many-flowered. . . . . 11. *D. peregrinum*.

1. The limb of lower petals almost round, shorter than the claw; plant grayish pubescent, 0.3–1.5 dm. tall; racemes mostly 2–3-flowered. . . . . 12. *D. nanum.*

k. Limb of lower petals abruptly contracted into the claw, not cuneate at the base. Western Mediterranean.

m. The limb of the lower petals not or little shorter than the claw, usually distinctly exserted, not cordate at the base. . . . . 13. *D. obcordatum.*

m. The limb of the lower petals ½–¾ as long as the claw, cordate or subcordate at the base.

n. Limb of lower petals oblong, 1½–2 times as long as wide, exserted. . . . . 14. *D. gracile.*

n. Limb of lower petals suborbicular, included.

o. The limb of the lower petals strongly cordate at the base. Uncommon. . . . . 15. *D. verdunense.*

o. The limb of the lower petals weakly cordate at the base. Common. . . . . 16. *D. halteratum.*

j. Carpels 5; flowers many, in a dense raceme to 4 dm. long. Morocco. . . . . 10. *D. cossonianum.*

1. **Delphinium staphisagria** L. Sp. Pl. **1**: 531. 1753. FIG. 1.

Staphisagria macrosperma Spach, Hist. Nat. Vég. Phan. **7**: 348. 1839. Sibth. & Sm. Fl. Graeca **6**: *pl. 508.* 1826.

Annual or biennial, usually 1-stemmed, simple or few-branched above, 3–12 dm. tall, leafy, soft hairy with fine, often long, spreading hairs and densely covered also with short retrorse hairs; leaves large, the blade rounded or broader, to 2 dm. in diameter, more or less finely strigose and with longer hairs, 5–9-parted, the segments entire or 2–3-lobed, these ultimate divisions broadly lanceolate, sharply acute, 3-veined, often entire or with few large teeth; petioles mostly longer than the blades, dilated at base, with both kinds of pubescence; racemes terminal, dense or lax, usually many flowered on main stem, few flowered on branches; lower bracts foliose, 3-parted or entire, sessile or petioled, from half as long to as long as pedicel; pedicels 0.5–5 cm. long, densely hairy and strigose, bibracteolate near the base; flowers mostly deep blue, 2–3 cm. in diameter; calyx fine-hairy without, the upper sepal oblong-ovate, 1–2 cm. long, the saccate spur 2–3 mm. long and wide; lateral sepals ovate, ca. 1.5 cm. long, rounded at apex, lower sepals similar but slightly shorter; upper petals white or bluish, pubescent, obtuse, simple or more or less bilobed at summit, 10–12 mm. long, short-spurred at base; lower petals glabrous or pubescent, more or less spatulate or obovate-cuneiform, somewhat asymmetrical, ca. 14–16 mm. long; stamens 8–10 mm. long, filaments ciliate above, glabrous and dilated below; carpels 3, long-pubescent, inflated and 12–20 mm. long at maturity; seeds few, 5–6 mm. long, blackish, obpyramidal, 3-angled, reticulate-foveolate.

Type not given; described as from Istria, Dalmatia, Apulia, and Calabria.

DISTRIBUTION. Mostly in woods and rocky places about the base of mountains; Canary Islands; Mediterranean region in Morocco, Algeria, southern Europe; Syria, Palestine, Turkey.

ILLUSTRATIONS. SIBTHORP & SMITH, Fl. Graeca **6**: *pl. 508*. 1826; COSTE, Fl. France **1**: 51. 1901; MAIRE, Fl. de l'Afrique du Nord **11**: 84. 1964.

REPRESENTATIVE SPECIMENS. **Canary Islands:** *Bornmüller 2013*; *Bourgeau 1231, 428*. **Morocco:** *Font Quer 107*. **Algeria:** *Alleizetti*, 1953; *Le Cesve*, 1938; *Cosson*, 1854; *G. Munby*, 1844, 1850; *Durando*, 1855.

Delphinium staphisagria is a species quite unrelated to any others. To begin with, there are few annual species in *Delphinium* and they differ widely from this one in appearance and technical characters. The leaves and terminal spikes of flowers give the general appearance of a lupine until they are examined more closely.

2. **Delphinium balansae** Boiss. & Reut. in Boiss., Diagn., II. **5**: 12. 1856. FIG. 2.

D. balansae formae *pallidum* and *caeruleum* Maire, Fl. de l'Afrique du Nord **11**: 83. 1964.

Perennial from a somewhat woody crown above a taproot system, but sometimes flowering in its first year; stems slender, several suberect, more or less strigulose to subglabrous, 2–7 dm. tall, simple or with some branching almost throughout, slightly angular; basal and lower leaves long-petioled, tripartite, the cuneate parts trifid, the ultimate segments linear to oblong, subglabrous, sometimes more or less ciliate, callous-tipped, the whole blade 2–5 cm. wide, somewhat shorter; cauline leaves simpler, shorter-petioled, quite persistent, the uppermost linear, entire; racemes rather lax, 2–10-flowered; bracts linear, 5–12 mm. long; pedicels strigose, 5–25 mm. long, the bracteoles ca. 4.5 mm. long; flowers whitish with a bluish or greenish tinge, or blue; the upper sepal ca. 6–7 mm. long, somewhat strigulose and with an almost straight or slightly curved horizontal strigulose spur 3–4 mm. wide at the base, 12–16 mm. long; lateral sepals oblong, ca. 8 mm. long, strigose along the midrib, the lower pair strigose over the entire outer surface and more pointed; upper petals glabrous, 2-lobed, slightly shorter than the sepals and ca. 7 mm. wide; lower petals ca. 8 mm. long, oblong-oval, sometimes with a cordate base, abruptly narrowed to a narrow claw; stamens somewhat shorter than the sepals, the filaments dilated below, glabrous; carpels 3, pubescent, 8–9 mm. long in fruit; seeds dark, subglobose, ca. 2 mm. in diameter, with rings of scales.

TYPE: near Lambese, North Africa, *Balansa 1853*, as *D. junceum* (photo. BH).

DISTRIBUTION. Calcareous areas below 2500 m., Morocco to Tunis.

ILLUSTRATIONS. MAIRE, Fl. de l'Afrique du Nord **11**: 82. 1964.

REPRESENTATIVE SPECIMENS. **Morocco:** *O. Polunin 2138*; *Gattefossé 220b*;

Font Quer 209; *Jahandiez 742, 858*; *E. K. Balls 3133*. **Algeria:** *Kralik*, June 2, 1858; *Cosson*, July 26, 1854, July 22, 1861; *Faure*, Aug. 3, 1933; *Chevallier 255*.

Material at British Museum has the pale-flowered plants more erect and with stouter stems, the blue-flowered plants more spreading and diffuse, and with slender stems.

3. **Delphinium dasycaulon** Fresen, Mus. Senckenb. **2**: 272. 1837. FIG. 3.

? *D. dasycaulon* var. *minor* Cufodontis, Bot. Inst. Univ. Wien **39**: 103–126. 1958.

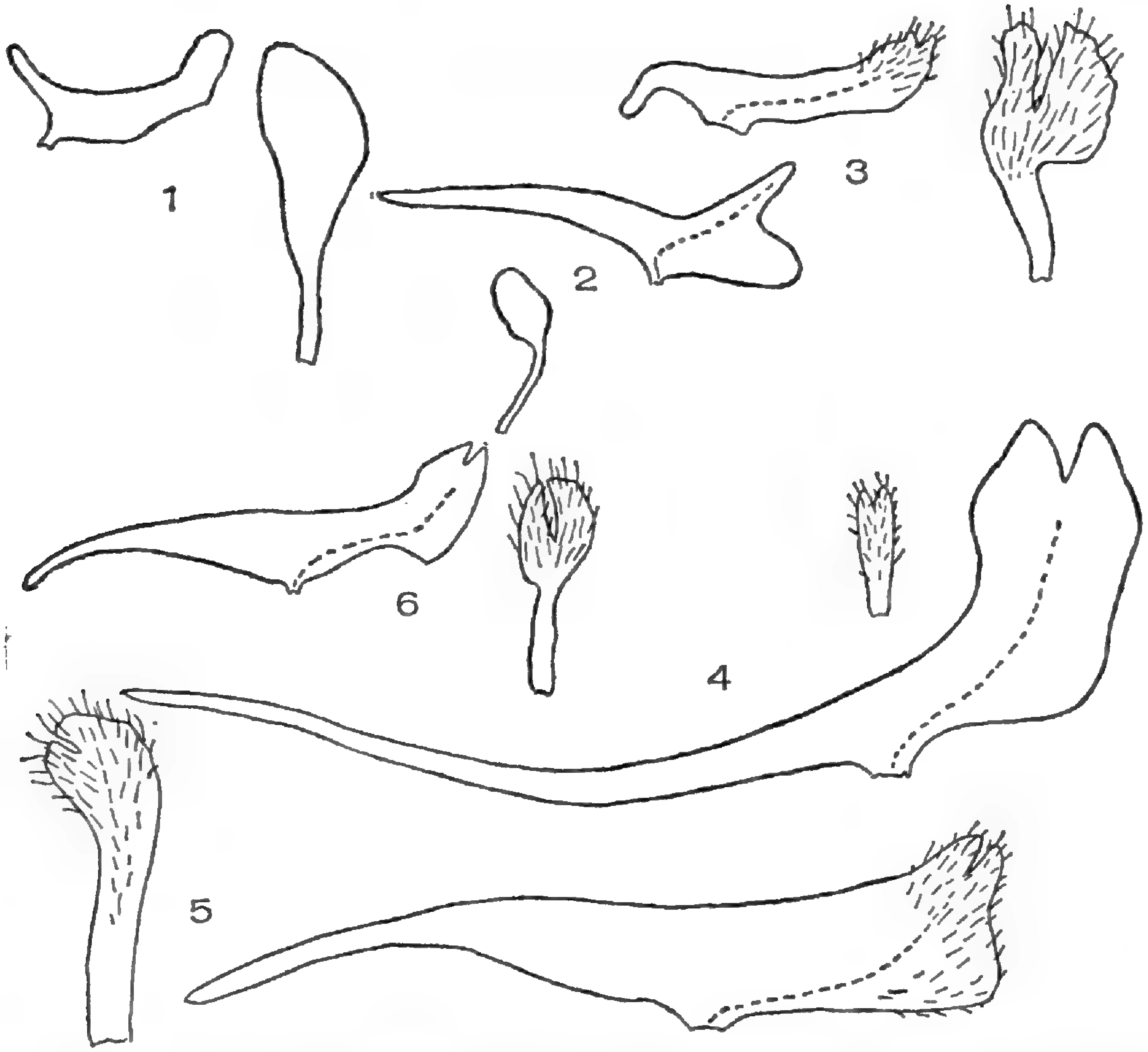
Perennial from a woody elongate root, the stem largely solitary, weakly erect, 5–15 dm. tall, slender, scattered villous, more or less openly branched above; basal and lower cauline leaves 1–1.5 dm. wide, with slender petioles 1–4 dm. long, the blades 3–5-parted into broad incised lobes, the upper leaves remote, reduced, 3-parted into simpler divisions, often ca. 1 cm. wide; inflorescence of few open subnaked branches with remote bracts ca. 1 cm. long; flowers often more or less crowded at ends of branches, bright blue to paler; pedicels 5–20 mm. long, densely pubescent, the 2 bracteoles at the middle or above, entire, linear or nearly so, 5–10 mm. long; sepals oblong to obovate, 1.3–1.8 cm. long, the upper with an outer brownish spot, crisp-pubescent, the spur 5–8 mm. long, ca. 4 mm. wide at the base, pubescent, more or less decurved, lateral sepals strigose along the middle, lower pair strigose along upper half from base to tip; upper petals cream, more or less lanceolate, 8–14 mm. long, 2-toothed at apex, short-pubescent upward, the spur 3–6 mm. long; lower petals blue, 10–14 mm. long, the limb oval, unequally bifid, bearded, narrowed into a claw 5–6 mm. long; stamens 5–8 mm. long, somewhat pubescent, dilated at the base; follicles 3–5, crisp or spreading pubescent, 12–20 mm. long, 3 mm. wide, the beak 2 mm. long; seeds covered with numerous imbricate scales.

TYPE: Simen, Ethiopia, *Rüppell*.

DISTRIBUTION. Open woodland and grassland, 1400–3000 m., Ethiopia, Karara Hills of eastern Sudan, eastern Belgian Congo, Kenya, Tanganyika, Kirk Range of Mozambique and eastern Nigeria.

REPRESENTATIVE SPECIMENS. **Ethiopia:** *Schimper 397, 752*; *Scott 231*; *Curle 140, 380*; *Archer 8657*; *F. G. Meyer 7465*; *Schweinfurth & Riva 1472*; *Pappi 390, 4811*; *Mooney 5820, 6264*; *Bally 7035, 10033*; *Massey 62*. **Northern Rhodesia:** *Burtt 6114, 6214*; *Nash 274*; *Milne-Redhead 444*; *F. White 2742*. **Sudan:** *Robbie 6*. **Kenya:** *Mooney 7528*. **Belgian Congo:** *Dubois 1049*; *Kassner 2748*; *de Witte 343*; *Robyns 2155*. **Tanganyika:** *Chapman 321*; *Brass 16990, 17150*; *Jackson 1860*. **Nigeria:** *Migeod 344*; *Lightbody 26257*; *Tamajong 22210*; *Hepper 2847*; *Unwin 214*. **Mozambique:** *Mendonça & Wild 994*.

Delphinium dasycaulon has a remarkable distribution from Ethiopia to the Congo, Kenya, Mozambique and Nigeria. It is quite distinct from



FIGS. 1–6. Petals in *Delphinium* (length given for upper petal includes spur). FIG. 1. *D. staphisagria.* Left-hand figure, upper petal (16 mm. long) with spur to left; right-hand drawing, of lower petal, 10 mm. high, from *Alleizetti*, May 1, 1953 (MO). FIG. 2. *D. balansae.* Spurred petal 10.5 mm. long, lower petal 7.5 mm. long, from *Chevallier 255* (F). FIG. 3. *D. dasycaulon.* Spurred petal 14 mm. long, lower petal 13 mm., from *Pappi 4811* (MO). FIG. 4. *D. leroyi.* Spurred petal 48 mm. long, from *Greenway 9711* (NY); lower petal 6 mm. high, from *MacInnes 206* (MO). FIG. 5. *D. macrocentron.* Spurred petal 38 mm. long, lower petal 14 mm., from *Piemeisel & Kephart 553* (US). FIG. 6. *D. sylvaticum.* Spurred petal 22 mm. long, lower petal 10 mm., from *St. Lager*, 1909 (NY).

the other similarly distributed species (*D. leroyi* and *D. macrocentron*) in its much smaller flowers, especially in its shorter spurs. It would, therefore, be expected to have quite different pollinators.

In spite of going so far into the tropics, these three species inhabit areas with temperate climates.

4. **Delphinium leroyi** Franch. ex Huth, Bot. Jahrb. **20**: 474, *pl. 6, fig. 5.* 1895. FIG. 4.

D. goetzeanum Engl. Bot. Jahrb. **30**: 308. 1902. Type, from the Ruhudge River, at 1900 m., Ubena, March 25, 1899. At Kew in a type cover is *Goetze 804* from Ubena.

D. wellbyi Hemsl. Kew Bull. **1907:** 360. 1907. Based on a type from between Harrar and Addis Ababa, *Wellby*, 1898 (K!).

D. macrocephalum Engl. Bot. Jahrb. **45:** 267. 1910. Based on *Jaeger 434* from Wanegehochland, between Olmoti and Ossirwa. Not seen.

D. gommingeri Volkens ex Engl. Bot. Jahrb. **45:** 266, 269. 1910. The type, *Gomminger* from Kilimanjaro, not seen.

D. ruspolianum Engl. Bot. Jahrb. **45:** 267. 1910. *Riva* on the Ruspoli Expedition, Dscharibule, Gallahochland. Not seen.

D. candidum Hemsl. Bot. Mag. **133:** *pl. 8170.* 1907. From between Mt. Elgon and Kisumu, Uganda, grown in the garden of Lady Hindslip in 1904 (K!).

Perennial from a woody rhizome, the stem mostly one, erect, with scattered slender hairs below, retrorsely crisp pubescent above, 4–15 (–20) dm. high, slender, branched in the inflorescence; basal and lower leaves with petioles 12–35 cm. long, sparsely pilose; the midcauline petioles shorter, dilated at the base, retrorsely pubescent; upper remote, passing into sessile bracts; blade of lower leaves to ca. 1 dm. wide, more or less reniform-rounded in outline, palmatifid into 5 main cuneate-obovate divisions, these in turn 3-lobed and ending in ultimate broad teeth; main cauline leaves more narrowly parted and sharply toothed; inflorescence paniculate with few-flowered lax racemes; bracts lance-linear, mostly entire, 1–3 cm. long; pedicels suberect, 4–12 cm. long, with 2 bracteoles near middle or in upper half, these largely 5–15 mm. long; flowers fragrant, white, sometimes with a purplish, pinkish or bluish tinge, or deep blue; sepals with a brownish spot outside, oblong to obovate, 2.5–4 cm. long, the lateral subtruncate, the others more or less pointed, all somewhat crisp pubescent without, the spur horizontal, curved upward, 3–4.5 cm. long; upper petals lance-obovate, the blade 2–3 cm. long, 5–9 mm. wide, glabrous, more or less deeply 2-toothed or -lobed at apex, the spur 3–4.5 cm. long; lower petals clawed, the limb lanceolate or lance-obovate, entire to unequally bilobed to 3-lobed, mostly 0.6–1.5 cm. long, 0.5–1 mm. broad; stamens 6–9 mm. long, the filaments dilated below, more or less ciliate, anthers black or dark brown, sparsely pubescent; follicles 3, more or less pubescent, ca. 2–2.5 cm. long, 3–4 mm. thick, the beak 3 mm. long; seeds dark, ca. 1.5 mm. in diameter, covered with numerous small imbricate scales.

TYPE: Kilimanjaro, *Leroy* (P!).

DISTRIBUTION. At about 1800–3000 m., Ethiopia, southern Sudan, Congo, Tanganyika, Kenya, and eastern Northern Rhodesia.

ILLUSTRATIONS. Bot. Mag. **133:** *pl. 8170.* 1907; Gard. Chron. III. **74:** 217. 1923, **88:** 193. 1930.

REPRESENTATIVE SPECIMENS. **Ethiopia:** *Hiller & Lithgoe 516*; *F. G. Meyer 7539*; *Scott 30*; *Archer 8619*; *Mooney 6705, 7012*; *Gillett 14559, 14936.* **Sudan:** *Jackson 405*; *J. G. Myers 11688*; *H. B. Johnston 1531*; *Chipp 70.* **Kenya:** *Greenway & Doughty 8532*; *Rogers 412*; *Anita Curtis 674, 679, 693*; *Snowden 501*; *Chandler 996*; *Maitland 1263*; *Tothill 2608.* **Tanganyika:** *Schlieben 838, 5084*; *Greenway 9711*; *Brass 17172, 17269*; *Duncan 48117.* **Northern Rhodesia:** *F. White 2741.*

Dr. W. A. Archer, formerly of the National Arboretum at Washington, D.C., told me some years ago that the natives in the region of Addis Ababa, Ethiopia, collect large quantities of *Delphinium leroyi* for the cut-flower market, partly because of the size of the flowers and partly for their fragrance. As can be seen from the synonymy, the species varies greatly in flower color, but the floral morphology seems quite consistent, as do foliage and habit.

5. **Delphinium macrocentron** Oliver, Jour. Linn. Soc. Bot. **21**: 397. 1885. FIG. 5.

Perennial from a woody rhizome, mostly one-stemmed, the stem erect, coarse, hollow, 6–20 dm. tall, few-branched near summit only, more or less retrorse-pilose throughout, more densely spreading-pubescent above; lower petioles 0.3–3 dm. long, the blades 3–12 cm. broad, 3–5-parted into rather narrow divisions, these in turn laciniate into lance-linear sharply toothed segments; cauline leaves gradually reduced and simpler upward, the uppermost linear and entire to trifid, 3–4 cm. long; inflorescence openly few-branched, the racemes to ca. 10-flowered, rather dense; bracts lance-linear, commonly 1–2 cm. long; pedicels 2–5 cm. long, stout, erect with recurved apex; bracteoles opposite, 5–12 mm. long, in upper part of pedicel; flowers blue and greenish, especially the latter when dry; upper sepal spreading, round-ovate, 12–15 mm. long, densely pubescent without, the spur straight, erect, 2.2–2.6 cm. long, 5–7 mm. wide at base and almost as wide for its entire length; lateral sepals rounded, 10–12 mm. long, pubescent mostly along median part; lower sepals much the same, but more pointed and more generally pubescent; upper petals pale with greenish tinge, the blades 12–16 mm. long, 2-lobed and pubescent at tip, the spurs 2 or more cm. long; lower petals ca. as long, gradually expanded from the broad claw to a shallowly bilobed pubescent tip; stamens ca. as long as sepals, expanded and somewhat ciliate below, the anthers dark; carpels 3, pubescent, erect or recurved when mature, 2–2.8 cm. long, the beak 7–8 mm. long; seeds dark, rounded, ca. 1.5 mm. in diameter, covered with small imbricate scales.

TYPE: Likipia, Kenya, *J. Thomson* (K!).

DISTRIBUTION. Between 1500 and 3500 m., Kenya.

ILLUSTRATIONS. HOOKER, Ic. **16**: *pl. 1501.* 1886; Bot. Mag. **133**: *pl. 8151.* 1907.

REPRESENTATIVE SPECIMENS. **Kenya:** *G. Taylor 1277, 1367, 1309*; *Anita Curtis 870*; *Greenway 7854; Pole Evans & Erens 1435*; *Greenway & Doughty 8519, 8521*; *C. W. Eliot 1545*; *Bogdan 547*; *Snowden 486, 817*; *Lugard 26*; *Hardy & Bally 10777.*

Delphinium macrocentron Oliver seems amply distinct from its closest relative, *D. leroyi,* as a rather local species of Kenya. The peculiar green shade of the flowers, especially as they dry, the thicker shorter spurs, the pubescence of the upper petals, the mostly much shorter sepals set it quite apart.

6. **Delphinium sylvaticum** Pomel, Nouv. Mat. Fl. Atl. 382. 1875.
FIG. 6.

Perennial from a base covered with fibrous leaf vestiges, the stem usually solitary, erect, 4–8 dm. tall, more or less flexuous, striate, branched above, retrorse-hairy below, more spreading-hairy above; radical leaves gone by time of anthesis, the petioles to ca. 3 dm. long, pubescent, the blades 10–15 cm. wide, pubescent, roundish in outline, 3–5-palmately-parted into obovate-cuneiform segments which are more or less deeply incised into lanceolate pointed ultimate divisions; cauline leaves scattered, gradually reduced up the stem, the upper tripartite with trifid segments and 3–6 cm. long; inflorescence an open panicle of many-flowered lax racemes to 2 dm. long; bracts simple to trifid with linear lobes and commonly 5–15 mm. long; pedicels densely pubescent, more or less glandular, 1–2.5 cm. long, the green linear bractlets above the middle, 3–6 mm. long; flowers a lively blue, ca. 2 cm. in diameter; upper sepal strigose, ovate-oblong, ca. 10 mm. long, the spur ca. 15 mm. long, mostly straight, horizontal or ascending, strigose; other sepals oblong-ovate, 10–12 mm. long, the upper pair strigose along the middle, the lower on the entire outer surface; upper petals almost as long, glabrous, cream, 2-toothed; lower petals bearded, bifid, ca. 10 mm. long, gradually attenuate to the broad claw; stamens subglabrous, 5–6 mm. long, bluish except for the dilated membranous lower half; follicles 3, oblong, 12–15 mm. long, more or less loosely pubescent; seeds blackish, 2–3 mm. long, oblong, subtrigonous, densely covered with elongate scales.

TYPE: Guerouch, Beni-Foughal, Algeria, *Pomel.* Not seen.

DISTRIBUTION. In fairly well watered places, largely in eastern Algeria and in TUNISIA.

ILLUSTRATION. MAIRE, Fl. de l'Afrique du Nord 11: 71. 1964.

REPRESENTATIVE SPECIMEN. **Algeria:** D'Azazga a Takouren, Kabylie, *Saint-Lager,* July 18, 1909.

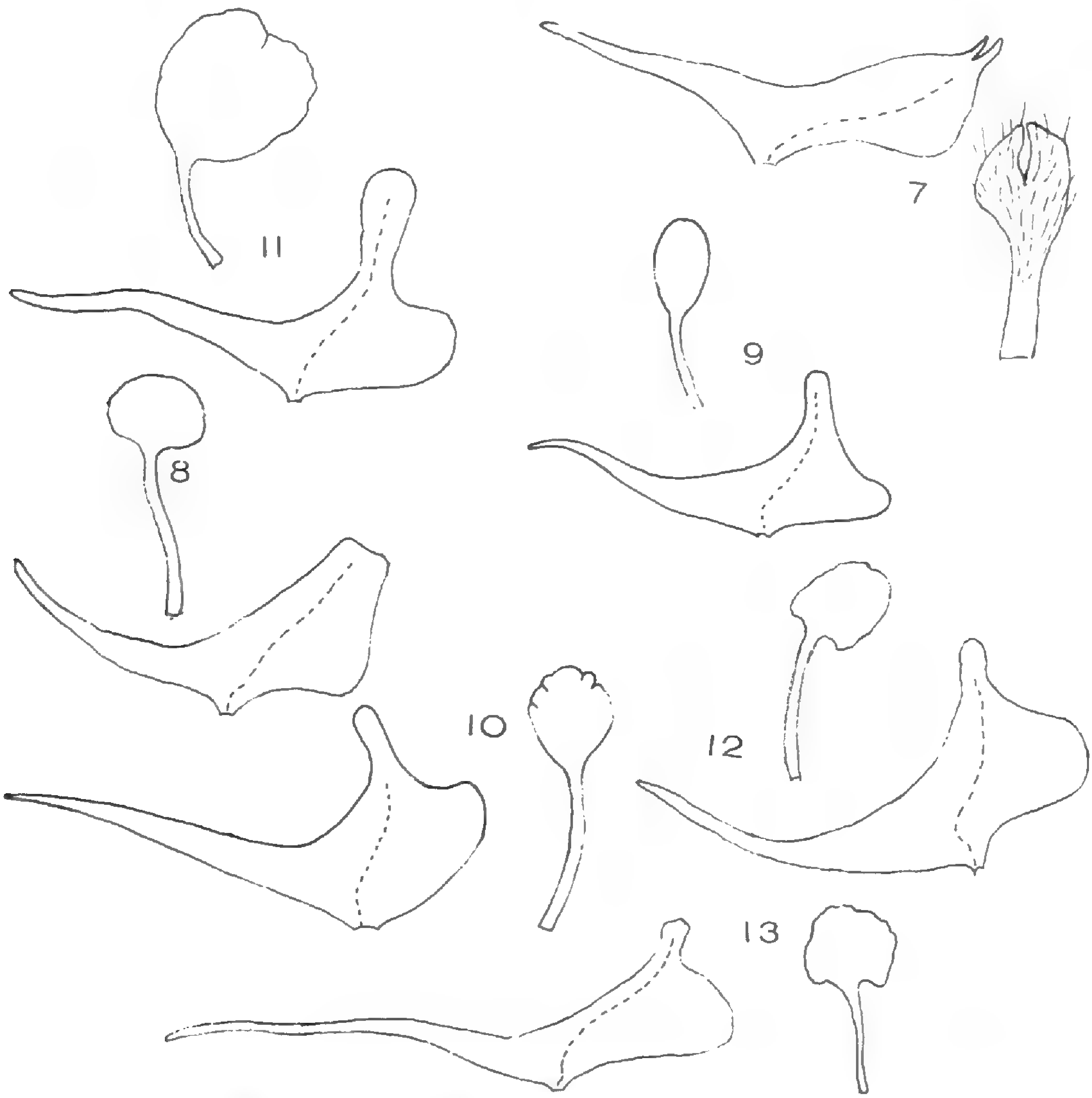
Delphinium sylvaticum Pomel is apparently an endemic of rather local distribution and not well represented in herbaria. Of the perennial African species of the genus it agrees with *D. dasycaulon, D. leroyi* and *D. macrocentron* in its rather large leaves and mostly three carpels, but is more northern in distribution.

7. **Delphinium pentagynum** Lam. Encycl. 2: 264. 1786. FIG. 7.

D. pentagynum vars. *homeotrichum, glabratum, phialotrichum,* and *heterotrichum* Maire, Bull. Soc. Hist. Nat. Afr. Nord **20:** 209–210. 1929. A series based on pubescence, whether the hairs are bulbous at base or not, gland-tipped or not, appressed or not.

D. hybridum Willd. subsp. *fissum* (W. & K.) Huth var. *pentagynum* (Lam.) Huth, Bot. Jahrb. **20**: 341. 1895.

Perennial from a tuberous root, base of plant covered with fibrous remains of old leaves; stems one to few, 2–7 dm. tall, more or less pubescent below with rather long retrorse hairs, glabrous or pubescent above, mostly somewhat branched in the inflorescence; basal leaves in a rosette, often withered at anthesis, long-petioled, the blades rounded to subreniform in outline, 3–7 cm. broad, subglabrous to pubescent, palmately 3–5-parted



FIGS. 7–13. Petals in *Delphinium* (length given for upper petal includes spur). FIG. 7. *D. pentagynum.* Spurred petal 22 mm., lower petal 12 mm. long, from *Faure*, May 31, 1908 (US). FIG. 8. *D. cossonianum.* Spurred petal 10 mm., lower petal 5.5 mm. long, from *Gattefossé*, June 15, 1936 (MO). FIG. 9. *D. peregrinum.* Spurred petal 13 mm., lower petal 9 mm. long, from *Balansa 728* (A) FIG. 10. *D. nanum.* Spurred petal 25 mm., lower petal 13 mm. long, from *Letourneux*, 1877 (MO). FIG. 11. *D. obcordatum.* Spurred petal 22 mm., other 13 mm. long, from *Gattefossé*, June 18, 1936 (MO). FIG. 12. *D. gracile.* Spurred petal 22 mm., other 11 mm. long, from *Reverchon 249* (GH). FIG. 13. *D. halteratum.* Spurred petal 29 mm., other 10 mm. long, from *Faure*, April 8, 1929 (BH).

into cuneiform-obovate segments, these more or less lobed into narrow or rather broad lobes or teeth, acute to mucronate; cauline leaves remote, short-petioled to subsessile, the segments commonly divided into linear lobes; inflorescence open, simple to several-branched, laxly 4–10-flowered on each branch; bracts green, the lowermost sometimes dissected, most are simple, linear, 3–10 mm. long; pedicels pubescent to glabrous, 3–20 mm. long, bibracteolate near the middle or below; flowers pale or dirty violet-blue, 2–2.5 cm. in diameter; upper sepal appressed pubescent without, ovate, 9–12 mm. long, the spur horizontal or ascending, straight or somewhat curved, pubescent, 12–16 mm. long, 3–4 mm. wide at base; lateral and lower sepals more or less oblong, 12–16 mm. long, the upper petals strigose along middle line, the others over the whole outer surface; upper petals glabrous, yellowish usually tinged with blue, 20–22 mm. long including the spur, 2-toothed at tip; lower petals with the limb oval, bearded, blue, bifid, 9–12 mm. long; stamens 7–8 mm. long, glabrous or sometimes ciliate, broadly dilated in lower half; follicles 5 (rarely 3, 4, or 6), usually pubescent, divergent, 12–14 mm. long including styles; seeds obpyramidal, dark, 1.2–1.5 mm. long, with long straight scales.

TYPE: "on trouve cette plante dans le Portugal"; in Lamarck Herbarium, Paris (P-LA).

DISTRIBUTION. In semiarid and wetter regions, below 1500 m., Morocco, Algeria, Iberian Peninsula.

ILLUSTRATIONS. DESFONTAINES, Fl. Atlant. **1**: *pl. 111.* 1798; MAIRE, Fl. de l'Afrique du Nord **11**: 68. 1964.

REPRESENTATIVE SPECIMENS. **Morocco:** *Font Quer 108, 153*; *Faure*, May 17, 1933; *Fairchild 59*. **Algeria:** *Faure*, May 31, 1908, May 19, 1936; *Allard 2739*; *Durando 402*; *Balansa 575*; *Munby 35*; *Jamin 4.*

Among the small-flowered species along the northern fringe of Africa is the *D. pentagynum* group including that species and *D. nevadense* and *D. emarginatum.* They constitute the Series "Pentagyna" of Pawlowski (Fragm. Fl. & Geobot. **9**: 436. 1963), whose key and treatment I am following. They are a western Mediterranean group of southern Europe and northern Africa. They are perennial, rather small-leaved and few-flowered and have from three to five carpels.

8. **Delphinium emarginatum** Presl, Delic. Prag. 6. 1822.

D. emarginatum var. *africanum* Maire, Fl. de l'Afrique du Nord **11**: 66. 1964. No type cited. Maire says he cannot distinguish a noticeable difference from the Sicilian plant.

Near to *D. pentagynum* Lam., the petioles dilated at the base; stem to 8 dm. tall, pubescent throughout or glabrous above; stem-hairs retrorse-appressed, not more than 0.6 mm. long; sepals 10 mm. long, bluish-lilac, glabrous without, not longer than the spur; petals bilobed into attenuate obtusish lobes; filaments glabrous; follicles 3, erect, glabrous.

TYPE: Sicily.

DISTRIBUTION. Occasional in Algeria and northern Tunisia; Sicily.

ILLUSTRATION. MAIRE, Fl. de l'Afrique du Nord **11**: 65. 1964.

REPRESENTATIVE SPECIMENS. **Algeria:** Mustapha near Algiers, *Gandoger 614*; Bone, en Barbarie, Decaisne dedit 1835. **Tunisia:** Hamman-el-Lif, Mt. Dj. Bou-Kournein, *S. Murbeck 2*.

9. **Delphinium nevadense** Kunze, Flora (Regensb.) **29**: 647. 1846.

D. emarginatum Presl var. *nevadense* (Kunze) Maire, Fl. de l'Afrique du Nord **11**: 66. 1964.

Near to *D. emarginatum* Presl, the stems glabrous above, distinctly angled, to 12 dm. tall; stem-hairs retrorse, but not appressed, up to 0.9 mm. long; sepals and spur glabrous; sepals 10–13 mm. long, bright blue, yellow-spotted above, distinctly shorter than the spur; petals simply emarginate; filaments more or less ciliate at summit of dilated part; follicles 3, glabrous.

TYPE: "Sierra Nevada, ad fluvium Monachil, inter frutices, prope San Geronimo," Spain, probably *Boissier*. Not seen.

DISTRIBUTION. Southwestern Spain, northwestern Africa.

REPRESENTATIVE SPECIMENS. **Tunisia:** Djebel Zoghouán, July 2, 1854, *Kralik 22*. **Morocco:** Montes des Kebdana, June 12, 1934, *Sennen & Mauricio*.

10. **Delphinium cossonianum** Batt. Bull. Soc. Hist. Nat. Afr. Nord **8**: 215. 1917. FIG. 8.

D. cossonianum var. *laxiflorum* Gattefossé & Maire in Maire, Bull. Soc. Hist. Nat. Afr. Nord **29**: 404. 1938.

Annual, more or less finely strigulose, or subglabrous below, 2–7 dm. tall, erect, simple or few branched, the stems angled; basal leaves gone by flowering time; cauline leaves short-petioled to subsessile, usually present at anthesis, closely placed, commonly 1.5–4 cm. long, tripartite into segments 2–3 times divided into linear parts, glabrous, subcoriaceous; racemes densely and usually many flowered, up to 4 dm. long; bracts green, exceeding pedicels, 2–3.5 cm. long, strigulose; pedicels strigulose, ridged, 4–10 mm. long, the 2 bracteoles linear, 7–15 mm. long; flowers deep lively blue; upper sepal ca. 1 cm. long, somewhat strigulose, the spur horizontal or ascending, slightly curved, 10–13 mm. long; lateral sepals oblong, 8–10 mm. long, slightly strigulose along the middle; lower sepals similar, but more generally strigulose; upper petals white at base, violet at apex, retuse or emarginate, ca. 8 mm. wide at summit; lower petals ca. 9 mm. long, the rounded violet limb more or less cordate at base and narrowed abruptly into the claw; stamens shorter than the petals, the filaments whitish, glabrous; carpels 5 (3, or 4), usually glabrous, becoming almost 1 cm. long; seeds dark, ca. 1 mm. in diameter, with rings of scales.

Type not designated. Battandier had three specimens collected by Grant near Fez and Meknès in central Morocco. These I have not seen, except for a specimen from Fez, *Abdul Grant*, com. Aug., 1887 (K).

DISTRIBUTION. Argillaceous soils of rather arid plains and hills, particularly in central and eastern Morocco.

ILLUSTRATION. MAIRE, Fl. de l'Afrique du Nord **11**: 74. 1964.

REPRESENTATIVE SPECIMENS. **Morocco:** *Pitard 2925, 2926, 2929*; *Jahandiez 94*; *Gattefossé*, June 15, 1936; *Maire*, June 22, 1936; *C. G. Garnett*, May 7, 1936.

Among the annual species of *Delphinium* in Africa the only one with five carpels is *D. cossonianum*. It is a Moroccan endemic noteworthy because of its rather remarkable dense, many-flowered racemes of deep but lively blue flowers.

11. **Delphinium peregrinum** L. Sp. Pl. **1**: 531. 1753. FIG. 9.

Synonymy to be in a paper on Asian species.

Annual, more or less gray-pubescent on stems with short stiff, often retrorse hairs, 2–7 dm. tall, usually virgately branched from below, the branches stiff, straight or sometimes spreading, ridged; lower leaves 3–5-parted, the parts cut into 3 or more linear-lanceolate lobes, blades 1–3 cm. long, often wider, longer than the petioles, glabrous, coriaceous; basal and middle leaves deciduous by anthesis; upper leaves entire, linear, much reduced, sessile; racemes terminal, often rather dense, many flowered, bracteate, the bracts subulate, 3–6 mm. long; pedicels stiff-pubescent, to almost 1 cm. long; bracteoles 2, to ca. 3 mm. long; flowers violet; upper sepal 7–8 mm. long, pubescent, prolonged into a straight ascending spur 1.5–2 cm. long and 3–5 mm. wide at base; lateral sepals lance-oblong, pubescent without, 5–7 mm. long; lower pair more pointed and with pubescence more median; upper petals bilobed, ca. 7 mm. long, yellowish at base, violet toward apex, the upper lobe linear, erect, the lower broad, rounded; lower petals 8–10 mm. long, the blade longer than wide, gradually narrowed into the slender claw; stamens 5–8 mm. long, with more or less lavender filaments; follicles 3, pubescent to glabrous, 7–8 mm. long, including the style; seeds ca. 1 mm. long, rounded, scaly, the scales united into rows.

TYPE: "Habitat in Italia, Sicilia, Melita"; in Clifford Herbarium (BM).

DISTRIBUTION. Eastern Mediterranean region from Libya, Sicily, Malta and Dalmatia to Egypt, Turkey, Asia Minor and Iran.

ILLUSTRATION. SIBTHORP & SMITH, Fl. Graeca **6**: *pl. 506*. 1827.

REPRESENTATIVE SPECIMENS. **Libya:** Attag, Fueihat, Cyrenaica, *Keith 731*; Zuwetini Terraces, Tripolitania, at 2000′, *B. C. Park 362*.

Of the annual species of North Africa with three carpels, two are eastern Mediterranean and have the laminae of the lower petals cuneate at the base and pass gradually into the claw. Of these, *D. peregrinum* is the better known and ranges from Libya and Sicily into Asia where it is quite polymorphous. I am grateful to Dr. R. K. Brummitt for sending me a mounted dissected flower from a Libyan collection at Kew to verify identification.

12. **Delphinium nanum** DC. Syst. 1: 349. 1817. FIG. 10.

D. peregrinum L. subsp. *nanum* (DC.) Graebner in Asch. & Graebn. Syn. 5. **2:** 701. 1929.

Annual, widely and stiffly branched from base, to subsimple, the branches simple or nearly so, more or less hirtellous or spreading-pubescent throughout, the hairs sometimes grayish, more or less interwoven, plants mostly 3–15 cm. high; lower leaves obovate in outline, broadly 3-lobed, long-cuneate at base, 4–6 mm. long, the lobes broad, undivided; main cauline leaves largely simple, narrowly oblanceolate, 1–2.5 cm. long, narrowed at base into a broad petiole, gradually reduced up the stem, the upper bractlike, sessile, 2–6 mm. long; racemes short, loose, few-flowered; pedicels 1–5 mm. long, bibracteolate, the bracteoles lance-linear, 3–4 mm. long; flowers bluish-purple to brownish-violet, with yellow base; upper sepal 6–7 mm. long, densely pubescent as is the horizontal or ascending spur which is 3–4 mm. wide at base, 15–20 mm. long; lateral sepals subovate, 6–7 mm. long, with median strip of pubescence; lower sepals oblong-lanceolate, 6–7 mm. long, tomentellous-pubescent; petals pale, the upper broadly bilobed, glabrous, 7–8 mm. long, 8–10 mm. wide; lower to ca. 1 cm. long, the blade roundish-oblong, ca. 4 mm. wide, narrowed to a claw 4 mm. long; stamens 5–8 mm. long, the filaments apparently bluish; carpels 3, sparsely pubescent, to ca. 8 mm. long in fruit and 2 mm. wide, the beak 2–2.5 mm. long; seeds ca. 1 mm. long, almost round, dark brown, with very closely appressed overlapping scales.

TYPE: near Alexandria, Egypt, *Delile*; probable isotype (BM!).

DISTRIBUTION. Lower Egypt from Bengasi to Adjedabia, especially in Maramarica.

ILLUSTRATION. TÄCKHOLM, Students' Fl. Egypt, *pl. 57.* 1956.

REPRESENTATIVE SPECIMENS. **Egypt:** *Delile*, 1803; *Parquet 49*; *Letourneux, Gaillardet 121*; *Ehrenberg*, 1820; *Muschler*, Feb. 1903; *Mrs. Palmer*, 1932.

Delphinium nanum is very close to *D. peregrinum*, but is a much more pubescent dwarfish species of the very arid deserts of Egypt. It has rounder shorter laminae in the lower petals and fewer-flowered racemes.

13. **Delphinium obcordatum** DC. Syst. 1: 350. 1817. FIG. 11.

D. halteratum Sibth. & Sm. var. *obcordatum* (DC.) Huth, Bot. Jahrb. **20:** 477. 1895.

D. macropetalum DC. Syst. **1:** 350. 1817.

D. halteratum Sibth. & Sm. var. *macropetalum* (DC.) Ball, Spicil. Fl. Marocc. 310. 1878.

D. peregrinum L. var. macropetalum (DC.) Maire, Fl. de l'Afrique du Nord **11**: 79. 1964.

Annual or biennial, 1–3(–6) dm. tall, with slender stems and many long, divaricate branches, usually strigulose; racemes 2–10(–15)-flowered, usually lax; pedicels and sepals strigulose; sepals deep blue-violet, 8–10 mm. long, the spur ca. twice as long; upper petals with a lamina 1 cm. long, winged from near the base, the spur ca. 15 mm. long; lower petals with the lamina exserted, roundish, more or less obcordate, not or little shorter than the claw, not cordate at base; follicles 7–11 mm. long, ⅓–⅕ as wide, slender, densely strigulose, often divaricate.

TYPE: "in Barbaria", North Africa, *P. Durand.* Type not seen.

DISTRIBUTION. Sandy and fallow or rocky places below 1100 m., Morocco, Algeria; Spain.

ILLUSTRATION. DELESSERT, Ic. **1**: *pl. 57. 1820.*

REPRESENTATIVE SPECIMENS. **Morocco:** *Murdochee*, 1875; *Balansa*, May, 1867; *Hooker*, 1871; *Gattefossé*, June 18, 1936; *Font Quer 201.* **Algeria:** *Marsilly*, 1847; *Reverchon*, May, 1896; *Faure*, June 17, 1934; *Gandoger*, 1906–7.

In the group of annual species with three carpels there seem to be four species along the Mediterranean coast of north Africa very closely related to *Delphinium halteratum* and by Maire (Fl. de l'Afrique du Nord **11**: 76–81. 1964) even included under *D. peregrinum*, but the much more abrupt contraction of the lower petals into the claw seems to me to set them quite apart and I am following Pawlowski (Fragm. Fl. & Geobot. **9**: 438–444. 1963) in his concept of this complex. He proposes a new series *Halterata* as contrasted to the series *Peregrina.* As shown in the key at the beginning of the present paper, the distinction between the constituent species is based largely on the shape of the laminae of the lower petals and is quite technical. One certainly feels that *D. halteratum* is more than subspecifically distinct from *D. peregrinum* as in the Maire treatment. Pawlowski has carefully worked out synonymy and characterized the species and I am happy to follow his treatment for *D. obcordatum*, *D. gracile*, *D. verdunense* and *D. halteratum.*

14. **Delphinium gracile** DC. Syst. 1: 347. 1817. FIG. 12.

D. cardiopetalum DC. var. *gracile* (DC.) Willk. in Willk. & Lange, Prodr. Fl. Hisp. **3**: 970. 1880.

D. halteratum Sibth. & Sm. var. *gracile* (DC.) Huth, Bot. Jahrb. **4**: 477. 1895.

Stems 2–9 dm. tall, with long slender virgate branches, strigulose to subglabrous; upper leaves mostly entire; racemes usually lax, 2–15(–30)-flowered; sepals often pale lilac-violet to whitish, 7–9 mm. long, strigulose-puberulent; spur mostly 2–2½ times as long as sepals; limb of upper petals ca. 12 mm. long, the spur ca. 17 mm. long; lower petals with a limb ca. 5 mm. long, exserted, cordate or subcordate at base, somewhat oblong, 1½–2 times as long as wide, the claw ca. 7 mm. long; follicles 6–11 mm. long, 2½–4 times as long as wide, glabrous or sparsely strigulose.

TYPE: Andalusia, Spain, *Lagasca*. Not seen.

DISTRIBUTION. Occasional in fallow and waste places below 1200 m., Morocco and Algeria; Spain and Portugal.

REPRESENTATIVE SPECIMENS. **Morocco:** *Ibrahim*, June 23, 1888; *Font Quer 200*. **Algeria:** *Reverchon 249*; *Faure*, June 7, 1906; *Garrigues*, 1887; *Le Cesve*, 1923, 1933; *C. G. Abbot*, 1911.

15. **Delphinium verdunense** Balbis, Cat. Stirp. Hort. Bot. Taur. App. **3**: 31. 1813.

D. cardiopetalum DC. Syst. **1**: 347. 1817.
D. halteratum Sibth. & Sm. var. *cardiopetalum* (DC.) Huth, Bot. Jahrb. **20**: 477. 1895.
D. tribracteolatum DC. Syst. **1**: 350. 1817.
D. halteratum Sibth. & Sm. var. *tribracteolatum* (DC.) Huth, Bot. Jahrb. **20**: 477. 1895.

Much like *D. halteratum*; leaves usually all divided into linear-oblong segments; racemes short and dense, mostly 5- to 15-flowered; sepals deep blue-violet, 8–12 mm. long, strigulose; spur 14–19 mm. long; lower petals with the limb up to ¾ as long as the claw, included, strongly cordate at the base; follicles 6–10 mm. long, 2 ½–4½ times as long as wide, almost glabrous.

TYPE: Verdun, southern France.

DISTRIBUTION. Apparently occasional in fallow fields, clearings, etc., Morocco and Algeria; southwestern Europe.

ILLUSTRATION. PAWLOWSKI, Fragm. Fl. & Geobot. **9**: 442. 1963.

REPRESENTATIVE SPECIMENS. **Morocco:** *Gattefossé*, 1933. **Algeria:** *Garrigues*, 1887.

I am following Pawlowski (Fragm. Fl. & Geobot. **9**: 441. 1963) in taking up the name *D. verdunense* for what has generally been called *D. cardiopetalum*. His description and excellent illustration have greatly aided me in interpreting the few North African collections I have seen.

16. **Delphinium halteratum** Sibth. & Sm. Prodr. Fl. Graeca **1**: 371. 1806 and Fl. Graeca **6**: *pl. 507*. 1826. FIG. 13.

D. peregrinum L. ssp. *halteratum* (Sibth. & Sm.) Batt. Fl. Alg. 16. 1888.
D. peregrinum sensu many auth., not L.
D. peregrinum L. var. *confertum* Boiss. Voy. Espagne **2**: 12. 1839–45.
D. halteratum Sibth. & Sm. var. *confertum* Fenzl ex Huth, Bot. Jahrb. **20**: 477. 1895.

D. cardiopetalum DC. var. *oranense* Debeaux, Rev. Bot.. 8: 264. 1890.

Annual, the stems glabrous or mostly retrorsely strigulose, erect, simple or more usually branched, at least above, 1–8 dm. tall; lower leaves 3–5-parted, the parts cuneate, with lance-linear mucronate divisions; blades commonly 1.5–4 cm. wide and long, glabrous to pubescent, on petioles to the same length; upper cauline leaves shorter petioled to subsessile, commonly 3-parted into lance-linear lobes or simple, acuminate, the upper and middle leaves persisting until anthesis; racemes few to many flowered; bracts subulate, 3–10 mm. long; pedicels strigulose to pubescent, to ca. 1 cm. long, with 2 bracteoles; flowers blue-violet; upper sepal 7–9 mm. high, mostly strigulose without, the spur ascending, strigulose, ca. 3–4 mm. wide at base, 15 mm. long; lateral sepals lance-oblong, ca. 7 mm. long, with a median strigulose band; lower sepals more pointed and more generally strigulose; upper petals ca. 1 cm. long, greenish yellow at base, violet in upper half, bilobed, the upper lobe narrow, erect, the lower rounded; lower petals scarcely exserted, the lamina orbicular, truncate or rounded and weakly cordate at base, ca. 3–4.5 mm. in diameter, rather abruptly narrowed into a longer claw; stamens 5–7 mm. long, with somewhat lavender filaments; carpels 3, usually strigose, rarely glabrous, 7–10 mm. long in fruit; seeds subglobose, the scales coalesced in ca. 3 horizontal rows.

TYPE: "In Sicilia, et, ni fallor, in monte Athô, legit Sibthorp" (OXF).

DISTRIBUTION. Sandy and disturbed places, in the western Mediterranean of southern Europe and northern Africa, especially about Oran, Algeria.

ILLUSTRATIONS. SIBTHORP & SMITH, Fl. Graeca 6: *pl. 507.* 1826; PAWLOWSKI, Fragm. Fl. & Geobot. 9: 440, 441. 1963.

REPRESENTATIVE SPECIMENS. **Morocco:** *Font Quer 200, 201, 202*; *Ibrahim*, June 19, 1898; *Mauricio 7759, 9215*; *Pitard 2927, 2928*; *Jahandiez 632.* **Algeria:** *Balansa 650, 651*; *Le Cesve 4363*; *Munby 22*; *Reverchon 249*; *Faure*, 1934; *Duffour 2317.*

2. **Consolida** (DC.) S. F. Gray

Consolida, as a genus, S. F. Gray, Nat. Arr. Brit. Pl. 2: 711. 1821. As a section, DC. Syst. 1: 341. 1817. As a subgenus, Huth, Bot. Jahrb. 20: 337. 1895; Dalla Torre & Harms, Genera Siphonogamarum 165. 1901.

Plants annual. Leaves laciniate. Inflorescence racemose or paniculate, the flowers zygomorphic. Sepals 5, petaloid, the posterior one spurred. "Petal" one, apparently representing the fused superior petals of *Delphinium*, sometimes called "nectary" or "honey-leaf"; subentire to 3–5-lobed, bearing a single nectariferous spur extending into the sepal spur. Stamens in 5 spirally arranged series. Carpel 1, forming a follicle.

Type species, *C. regalis* S. F. Gray (*Delphinium Consolida* L.).

A highly specialized genus ranging from the western Mediterranean to central Asia, but with several species widely cultivated and escaping from gardens in many parts of the world.

KEY TO AFRICAN SPECIES OF CONSOLIDA

a. Follicle 6–15 mm. long, more or less compressed; plants mostly branched from the base and with widespread open habit.
  b. Spur 10–22 mm. long, exceeding the blade of the upper sepal in length.
    c. Sepals 7–8 mm. long, lilac; middle lobe of "petal" scarcely evident, much exceeded by the forward-projecting lateral lobes. Morocco, Algeria. . . . . 1. *C. mauritanica.*
    c. Sepals mostly 10–16 mm. long; middle lobe of "petal" evident, not exceeded by the lateral lobes.
      d. Middle lobe of "petal" not divided at apex. Algeria, Tunisia. . . . . 2. *C. pubescens.*
      d. Middle lobe of "petal" with two small terminal lobes at least 1 mm. long. Occasional garden escape. . . . . 3. *C. regalis.*
  b. Spur 5–7 mm. long, ca. equal to blade of upper sepal. Egypt. . . . . 4. *C. deserti.*
a. Follicle 15–25 mm. long, subterete; main stem forming an axis into the inflorescence; side branches few.
  e. Bracteoles usually below the middle of the pedicel; sepals 12–14 mm. long; spur ca. 15 mm. long. Garden escape. . . . . 5. *C. ambigua.*
  e. Bracteoles near the summit of the pedicel; sepals 10–12 mm. long; spur ca. 10 mm. long. Morocco, Algeria. . . . . 6. *C. orientalis.*

1. **Consolida mauritanica** (Coss.) Munz, comb. nov. FIG. 14.

Delphinium mauritanicum Cosson, Bull. Soc. Bot. Fr. **27:** 68. 1880.
D. Loscosii Costa var. *brevirostratum* Pau, Bull. Soc. Iber. Ciencias Nat. **22:** 91. 1923.

Annual, more or less densely cinereous-pubescent with spreading and retrorsely appressed hairs (many in the upper part stiff and with bulbous base), usually 1-stemmed, 2–5 dm. tall, branched from base and/or above, the branches stiff, more or less divaricate; lower leaves not or scarcely rosulate, mostly withered at anthesis, with petioles 2–3 cm. long, largely tripartite, then again divided into numerous linear lobes, the blades commonly 1–2.5 cm. in diameter; cauline leaves rather crowded on main stem, gradually reduced upward and shorter-petioled, the uppermost sessile, a few mm. long, remote; upper branches with few remote flowers; bracts mostly with few linear lobes and 2–5 mm. long; pedicels 3–10(–20) mm. long, the bractlets near the middle, linear, entire, 2–4 mm. long; flowers lilac, 12–15 mm. in diameter; sepals lance-oblong, obtuse, pubescent without, 7–8 mm. long, each with a greenish median pubescent band; spur slightly curved, horizontal or ascending, ca. 15 mm. long; the "petal" whitish with colored border, almost as long as the sepals, 12–14 mm. wide, with 2 rounded lobes at the outer corners and 2 short median teeth; stamens somewhat shorter than the "petal", ciliolate on the dilated lower part; anthers ca. 0.8 mm. long; follicle oblong, more or less compressed laterally, 10–12 mm. long, strigose, muricate-tubercled near ventral suture; seeds ca. 2 mm. long, obpyramidal, subtetragonous, blackish, covered with horizontal rows of overlapping scales.

TYPE: Lalla-Maghrnia, Oran, Algeria, May 24, 1856, *Bourgeau* (P!; isotype, K).

DISTRIBUTION. Clearing in woodland, rocky places, etc. below 1500 m., Morocco, Algeria.

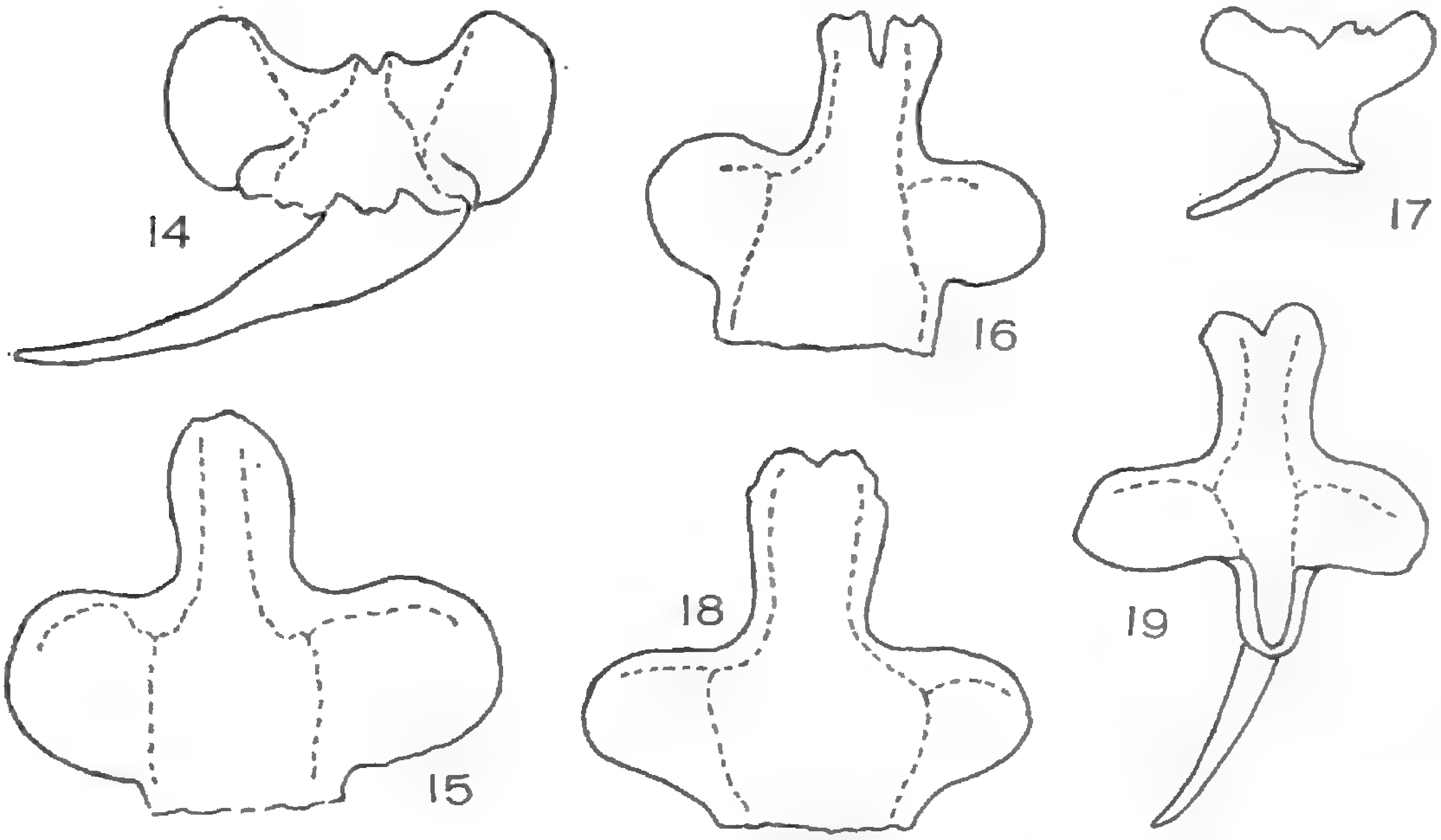
ILLUSTRATIONS. COSSON, Ill. Fl. Atlant. 1: *pl. 3.* 1882; MAIRE, Fl. de l'Afrique du Nord **11**: 60. 1964.

REPRESENTATIVE SPECIMENS. **Morocco:** *Benoist*, July 2, 1918; *Font Quer 202 bis*; *Sennen & Mauricio 7754; Jahandiez 333, 802b.* **Algeria:** *Faure*, June 30, 1933, July 11, 1923; *Lefranc 501*; *Warion 2, 670; Battandier*, May, 1922.

2. **Consolida pubescens** (DC.) Soó, Österr. Bot. Zeitschr. **71**: 241. 1922. FIG. 15.

Delphinium pubescens DC. Fl. France **6**: 641. 1815.
D. pubescens DC. var. *dissitiflorum* Cosson, Compend. **2**: 46. 1887.

Retrorse-strigulose, with some upper hairs bulbous at the base, mostly 1-stemmed, 1–5 dm. tall, more or less branched, especially above, rather



FIGS. 14–19. "Petal" in species of *Consolida* (some shown with spur, some without). FIG. 14. *C. mauritanica.* Blade 13 mm. wide, from *Faure*, June 30, 1933 (GH). FIG. 15. *C. pubescens.* Blade 18 mm. wide, from *Toulouse*, June 19, 1841 (US). FIG. 16. *C. regalis.* Blade 15 mm. wide, from *Taccan*, 1926 (NY). FIG. 17. *C. deserti.* Blade 8 mm. wide, from *Uvarov*, 1932 (BM). FIG. 18. *C. ambigua.* Blade 17 mm. wide, from *Levine 824* (GH). FIG. 19. *C. orientalis.* Blade 13 mm. wide.

leafy in lower half; lower leaves in a basal rosette, petioled, gradually reduced upward and becoming sessile, all multifid into more or less mucronate linear lobes, the blades pubescent, commonly 2–3 cm. in diameter; flowers few to several at end of main stem and branches, lilac, pale blue or rose or whitish, 1–2 cm. in diameter; bracts mostly simple, sometimes palmatifid, commonly 1–2 cm. long; pedicels 1–3 cm. long; bracteoles entire, linear, 3–5 mm. long, opposite or alternate; sepals ovate to ovate-oblong, obtuse, strigose, short-unguiculate, commonly 10–15 mm. long, each with a greenish spot toward the tip; spur straight or nearly so, horizontal, 18–20 mm. long, more or less strigose; "petal" 15–18 mm. wide, glabrous, with 2 large rounded lateral lobes and a median emarginate to slightly divided lobe 3–4 mm. long; stamens 4–6 mm. long, the filaments dilated ⅔ their length and ciliolate; anthers yellow, 1 mm. long; follicle strigose, 10–15 mm. long, the style glabrous; seeds obpyramidal, dark, 1.5–2 mm. long, covered with transverse rows of scales.

TYPE: "in agris et segetibus regionis Gallo-Mediterraneae."

DISTRIBUTION. Stony steppes and open places, high plateaus and Saharan Atlas; Algeria, Tunisia; southern Europe.

ILLUSTRATIONS. COSTE, Fl. France **1**: 50. 1901; MAIRE, Fl. de l'Afrique du Nord **11**: 57. 1964.

REPRESENTATIVE SPECIMENS. **Algeria:** *Chevallier 535b*; *Kralik 23*; *Lefranc 501.* **Tunisia:** *Letourneux*, April 29, 1884; *Pitard 651*; *Murbeck*, May 25, 1896. **Libya:** *K. M. Guichard*, March 4, 1955.

3. **Consolida regalis** S. F. Gray, Nat. Arr. Brit. Pl. **2**: 711. 1821. FIG. 16.

Delphinium consolida L. Sp. Pl. **1**: 530. 1753.

Plant 2–12 dm. tall, more or less divaricately, freely and rather finely branched, subglabrous to retrorse-strigulose; radical leaves petioled, early deciduous, the main cauline leaves trifid, then again partite into ultimate linear mucronate, strigulose lobes 1–5 cm. long; flowers few, in rather open terminal racemes, deep blue, or more seldom, pink to white; bracts mostly simple, linear, 3–15 mm. long; pedicels very slender, 1–5 cm. long; bracteoles linear, alternate to opposite, often well below the flower, 1.5–4 mm. long; sepals 9–16 mm. long, more or less ovate, narrowed at both ends, scarcely- or short-unguiculate, strigose, mostly along the midrib in the lateral pair; spur 17–22 mm. long; "petal" blue to cream, 12–15 mm. wide, the spur 16–17 mm. long, middle lobe of limb 3.5–5 mm. high, shortly 2-lobed at apex, each of these lobules often emarginate; lateral lobes rounded, 4–5 mm. long; stamens 4–7 mm. long, the filaments dilated on lower portion, anthers 0.6–0.7 mm. long, yellow; follicle to 2 cm. long, including the 2–3 mm. style; seeds dark, with transverse rows of subcontiguous scales.

TYPE: "Habitat in agris Europae restibilibus."

Distribution. Europe, Caucasia, Turkey. Occasional escape from gardens in northern Africa.

Illustration. Reichenbach, Ic. Fl. Germ. **4**: *pl. 66*. 1840; Hegi, Fl. Mittel.-Eur. **3**: 487. *pl. 114*. 1909; Marie, Fl. de l'Afrique du Nord **11**: 62. 1964.

4. **Consolida deserti** (Boiss.) Munz, comb. nov. Fig. 17.

Delphinium deserti Boiss. Fl. Orient. **1**: 83. 1867.

Plant 5–30 cm. tall, diffusely branched from below, short viscid-hairy; leaves 5–25 mm. long, short-hairy, palmately parted into oblong-linear segments, these again laciniate in the main leaves, the tips sharp; bracts 5–8 mm. long, oblong-linear; pedicels 1.5–3 cm. long; bracteoles near middle of pedicel, 3–5 mm. long; flowers small, yellow; sepals hairy, oblong, 4–6 mm. long; spur straight, 5–6 mm. long; "petal" obcordate, ca. 6 mm. wide, 4-lobed, the outer lobes longer, semi-ovate, the middle ones smaller, a row of brownish red spots across the base of the lobes; spur horizontal, equalling the blade of the "petal", ca. 5–6 mm. long; filaments sparsely hairy; anthers yellow, rounded, 0.5 mm. long; follicle oblong, viscid-hairy, 6–10 mm. long, 2–2.5 mm. wide, the beak slender, ca. 2 mm. long; seeds oblong, with densely imbricate scales about the cupuliform center.

Isotypes: *Bové 131* from desert between Suez and Gaza, July 1832 (K!; P!).

Distribution. Egypt and Asia Minor, in desert conditions.

Representative specimen. **Egypt**: "Luksor", *R. Muschler*, March 1904.

5. **Consolida ambigua** (L.) Ball & Heywood, Repert. Sp. Nov. **66**: 151. 1962. Fig. 18.

Delphinium ambiguum L. Sp. Pl. ed. 2. 749. 1763.
D. ajacis sensu auth., not L. Sp. Pl. **1**: 531. 1753.
Consolida ajacis sensu auth., not (L.) Schur, Verh. Siebenburg. Ver. Naturf. **4**: 47. 1853.

Subglabrous, especially below, to more or less pubescent, especially above, with short fine appressed or spreading hairs, mostly 1-stemmed, 3–10 dm. tall and with ascending-horizontal branches above; lower leaves long petioled, the blades 2–5 cm. in diameter, multifid into ultimate mucronate linear segments largely 1–1.5 mm. wide; cauline leaves gradually reduced upward, the upper sessile, often 1–2 cm. long; bracts entire to multifid, the lower often at least as long as the pedicels, the uppermost 2–3 mm. long; inflorescence rather lax, each branch ending in a few- to many-flowered raceme; pedicels commonly 1–3 cm. long; bractlets mostly 1.5–4 mm. long, usually below the middle of the pedicel; flowers blue to rose to white, 2–2.5 cm. across; sepals ovate, attenuate at base, obtuse at apex, more or less pubescent, each with a greenish subapical spot, ca. 12–14 mm. long; spur ca. 15 mm. long, straight or slightly curved; "petal" 3-lobed, the central lobe oblong, ca. 6 mm. long, with 2 short rounded lobules, the 2 lateral lobes rounded, ca. as long, the spur 15–16 mm. long; stamens 6–7 mm. long, the filaments abruptly dilated at base, glabrous, anthers yellow; follicle pubescent, cylindric, 16–22 mm. long, the style ca. 2 mm. long; seeds black, ca. 2.5 mm. long, oblong-trigonous, with undulating transverse rows of scales.

TYPE: Mauritania, northwest Africa, the type (LINN) a double garden form.

DISTRIBUTION. Mediterranean region, but African material seems to be garden escapes.

ILLUSTRATIONS. REICHENBACH, Ic. Fl. Germ. **4**: *pl. 67.* 1840; MAIRE, Fl. de l'Afrique du Nord **11**: 54. 1964.

6. **Consolida orientalis** (Gay) Schröd. Abhandl. Zool.-Bot. Ges. Wien **4**(5): 25. 1909. FIG. 19.

Delphinium orientale Gay in Desm. Cat. Dordogne 12. 1840, nomen; Boiss. Fl. Orient. **1**: 79. 1867.

D. hispanicum Willk. Prodr. Fl. Hisp. **3**: 969. 1880. Type not cited.

D. orientale Gay ssp. *hispanicum* (Willk.) Batt. in Batt. & Trab. Fl. Alg. 15. 1888.

D. orientale var. *hispanicum* (Willk.) Huth, Bot. Jahrb. **20**: 376. 1895.

D. ajacis L. var. *orientale* (Gay) Finet & Gagnep. Bull. Soc. Bot. Fr. **51**: 467. 1904.

Mostly 1-stemmed, simple or branched, especially above, erect, 2–6 dm. tall, the lower parts retrorse-strigose, upper with more or less crisped pubescence, some hairs gland-tipped, some swollen at base; leaves mostly subglabrous, the lower petioled and early withered, the principal leaves multifid, crowded on stems, the blades 2–4 cm. long, the segments linear or lance-linear, 1–2.5 mm. wide, more or less ciliolate; uppermost leaves sessile; flowers few to many, in racemes that are rather dense in anthesis, more open in fruit; bracts green, the lower with linear parts, the upper entire, linear, 5–20 mm. long; pedicels 0.5–4 cm. long, bibracteolate near the summit; flowers 1.5–2.5 cm. in diameter, dark purple or violet to rose or white, sepals round-ovate to oval or somewhat narrower, 10–12 mm. long, abruptly contracted into a pubescent basal claw, almost as long as the blade which is rounded to obtuse at the summit, more or less pubescent; spur ca. 1 cm. long; "petal" usually of same color as sepals, 3-lobed, 8–10 mm. long, the median lobe ovate to oblong-ovate, 2-lobed, somewhat longer than the rounded lateral lobes; stamens ca. 6–7 mm. long, the filaments dilated at the base, with some gland-tipped hairs at upper end; anthers yellow, ca. 1.5 mm. long; follicle strigose, 14–22 mm. long, oblong-cylindric, with some hairs gland-tipped, the style 1.5–2 mm. long; seeds brownish black, obpyramidal, angular, 1.5–2 mm. long, with several undulating transverse rows of short scales.

Type: described from cultivated material from the Orient, isotype (K!).

Distribution. Grain fields and disturbed places, Morocco and Algeria; Spain, Hungary to Asia.

Illustrations. Bot. Mag. **169**: (n.s.) *pl. 186.* 1952; Davis, Fl. Turkey **1**: 129, *fig. 2.* 1965.

Representative specimens. **Algeria:** *Dukerley 3805*; *Balansa 1009*; *Maire 4887*; *Reboud 203*; *Choulette 203 bis*; *E. G. Paris 402.*

A number of color forms has been proposed by Maire, Fl. de l'Afrique du Nord **11**: 55–56. 1964.

SYNONYMY OF AFRICAN SPECIES OF CONSOLIDA AND DELPHINIUM

Consolida — genus #2
  C. ajacis = C. ambigua
  C. ambigua = species #5
  C. deserti = species #4
  C. mauritanica = species #1
  C. orientalis = species #6
  C. pubescens = species #2
  C. regalis = species #3
Delphinium — genus #1
  D. ajacis = Consolida ambigua
  D. ajacis var. *orientale* = Consolida orientalis
  D. ambiguum = Consolida ambigua
  D. balansae = species #2
  D. balansae formae *caeruleum* & *pallidum* = D. balansae
  D. candidum = D. leroyi
  D. cardiopetalum = D. verdunense
  D. cardiopetalum var. *gracile* = D. gracile
  D. cardiopetalum var. *oranense* = D. halteratum
  D. consolida = Consolida regalis
  D. cossonianum = species #10
  D. cossonianum forma *laxiflorum* = D. cossonianum
  D. dasycaulon = species #3
  D. dasycaulon var. *minor* = D. dasycaulon
  D. deserti = Consolida deserti
  D. emarginatum = species #8
  D. emarginatum var. *africanum* = D. emarginatum
  D. emarginatum var. *nevadense* = D. nevadense
  D. goetzeanum = D. leroyi
  D. gommingeri = D. leroyi
  D. gracile = species #14
  D. halteratum = species #16
  D. halteratum var. *cardiopetalum* = D. verdunense
  D. halteratum var. *confertum* = D. halteratum
  D. halteratum var. *gracile* = D. gracile
  D. halteratum var. *macropetalum* = D. obcordatum
  D. halteratum var. *obcordatum* = D. obcordatum
  D. halteratum var. *tribracteolatum* = D. verdunense
  D. hispanicum = Consolida orientalis
  D. hybridum ssp. *fissum* var. *pentagynum* = D. pentagynum
  D. leroyi = species #4
  D. loscosii var. *brevirostratum* = Consolida mauritanica
  D. macrocentron = species #5
  D. macrocephalum = D. leroyi
  D. macropetalum = D. obcordatum
  D. mauritanicum = Consolida mauritanica
  D. nanum = species #12
  D. nevadense = species #9
  D. obcordatum = species #13

D. orientale = Consolida orientalis
D. orientale ssp. and var. *hispanicum* = Consolida orientalis
D. pentagynum = species #7
D. pentagynum vars. *glabratum, heterotrichum, homeotrichum, phialotrichum* = D. pentagynum
D. peregrinum = species #11
D. peregrinum var. *confertum* = D. halteratum
D. peregrinum ssp. *halteratum* = D. halteratum
D. peregrinum var. *macropetalum* = D. obcordatum
D. peregrinum ssp. *nanum* = D. nanum
D. pubescens = Consolida pubescens
D. pubescens var. *dissitiflorum* = Consolida pubescens
D. ruspolianum = D. leroyi
D. staphisagria = species #1
D. sylvaticum = species #6
D. tribracteolatum = D. verdunense
D. verdunense = species #15
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Staphisagria macrosperma = D. staphisagria

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Balansa 575, D. pentagynum; *650, 651*, D. halteratum; *1009*, C. orientalis; May, 1867, D. obcordatum
Bally 7035, 10033, D. dasycaulon
Battandier, May, 1922, C. mauritanica
Benoist, July 2, 1918, C. mauritanica
Bogdan 547, D. macrocentron
Bornmüller 2013, D. staphisagria
Bourgeau 428, 1231, D. staphisagria
Brass 16990, 17150, D. dasycaulon; *17172, 17269*, D. leroyi
Burtt 6114, 6214, D. dasycaulon
Cesve, Le, 4363, D. halteratum; 1923, 1933, D. gracile; 1938, D. staphisagria
Chandler 996, D. leroyi
Chapman 321, D. dasycaulon
Chevallier 255, D. balansae; *535b*, C. pubescens
Chipp 70, D. leroyi
Choulette 203 bis, C. orientalis
Cosson, 1854, D. staphisagria; July 26, 1954, July 22, 1961, D. balansae
Curle 140, 380, D. dasycaulon
Curtis, Anita, 674, 679, 693, D. leroyi; *870*, D. macrocentron
Delile, 1803, D. nanum
Dubois 1049, D. dasycaulon
Duffour 2317, D. halteratum
Dukerley 3805, C. orientalis
Duncan 48117, D. leroyi
Durando 402, D. pentagynum; 1855, D. staphisagria
Ehrenberg, 1820, D. nanum
Eliot, C. W., 1545, D. macrocentron
Fairchild 59, D. pentagynum
Faure, July 11, 1923, June 30, 1933, C. mauritanica; Aug. 3, 1933, D. balansae; May 17, 1933, May 19, 1933, May 31, 1933, D. pentagynum; 1934, D. halteratum; June 7, 1906, D. gracile; June 17, 1934, D. obcordatum.
Font Quer 107, 209, D. staphisagria; *108, 153*, D. pentagynum; *201*, D. obcordatum; *200, 202*, D. halteratum; *202 bis*, C. mauritanica
Gaillardet 121, D. nanum
Gandoger 614, D. emarginatum; 1906–7, D. obcordatum
Garnett, C. G., May 7, 1936, D. cossonianum
Garrigues, 1887, D. gracile; 1887, D. verdunense
Gattefossé 220b, D. balansae; 1933, D. verdunense; June 18, 1936, D. obcordatum

Gillett 14559, *14936*, D. leroyi
Greenway 7854, D. macrocentron; *9511*, D. leroyi
Greenway & Doughty, *8519*, *8521*, D. macrocentron; *8532*, D. leroyi
Guichard, March 4, 1955, C. pubescens
Hardy & Bally 10777, D. macrocentron
Hepper 2847, D. dasycaulon
Hiller & Lithgoe 516, D. leroyi
Hooker, 1871, D. obcordatum
Ibrahim, June 22, 1888, D. gracile; June 19, 1898, D. halteratum
Jackson 405, D. leroyi; 1860, D. dasycaulon
Jahandiez 94, June 15, 1936, D. cossonianum; *333*, *802b*, C. mauritanica; *632*, D. halteratum; *742*, *858*, D. balansae
Jamin 4, D. pentagynum
Johnston, H. B., *1531*, D. leroyi
Kabylie, July 18, 1909, D. sylvaticum
Kassner 2748, D. dasycaulon
Keith 731, D. peregrinum
Kralik 22, D. nevadense; *23*, C. pubescens; June 2, 1858, D. balansae
Lefranc 501, C. mauritanica
Letourneux, April 29, 1884, C. pubescens
Lightbody 26257, D. dasycaulon
Lugard 26, D. macrocentron
Maire 4887, C. orientalis; June 22, 1936, D. cossonianum
Maitland 1263, D. leroyi
Marsilly, 1847, D. obcordatum
Massey 62, D. dasycaulon
Mauricio 7759, *9215*, D. halteratum
Mendonça & Wild 994, D. dasycaulon
Meyer, F. G. 7465, D. dasycaulon, *7539*, D. leroyi
Migeod 344, D. dasycaulon
Milne-Redhead 444, D. dasycaulon
Mooney 5820, *6264*, *7528*, D. dasycaulon; *6705*, *7012*, D. leroyi
Munby 22, D. halteratum; *35*, D. pentagynum; 1844, 1850, D. staphisagria
Murbeck 2, D. emarginatum; May 25, 1896, C. pubescens
Murdochee, 1875, D. obcordatum
Muschler, March 1904, C. deserti; Feb., 1903, D. nanum
Myers, J. G. 11688, D. leroyi
Nash 274, D. dasycaulon
Mrs. Palmer, 1932, D. nanum
Pappi 390, *4811*, D. dasycaulon
Paris, E. G. 402, C. orientalis
Park, B. C. 362, D. peregrinum
Parquet 49, D. nanum
Pitard 651, C. pubescens; *2925*, *2926*, *2929*, D. cossonianum; *2927*, *2928*, D. halteratum
Pole Evans & Erens 1435, D. macrocentron
Polunin, O. 2138, D. balansae
Reboud 203, C. orientalis
Reverchon 249, D. gracile; May, 1896, D. obcordatum
Robbie 6, D. dasycaulon
Robyns 2155, D. dasycaulon
Rogers 412, D. leroyi
Schimper 397, *752*, D. dasycaulon
Schlieben 838, *5084*, D. leroyi
Schweinfurth & Riva 1472, D. dasycaulon
Scott 30, D. leroyi; *231*, D. dasycaulon
Sennen & Mauricio 7754, D. mauritanica; June 12, 1934, D. nevadense
Snowden 486, *817*, D. macrocentron; *501*, D. leroyi
Tamajong 22210, D. dasycaulon
Taylor, G. 1277, *1309*, *1367*, D. macrocentron
Tothill 2608, D. leroyi
Unwin 214, D. dasycaulon
Warion 2, C. mauritanica
White, F. 2741, D. leroyi; *2742*, D. dasycaulon
Witte, de, 373, D. dasycaulon

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FLORAL BIOLOGY AND SYSTEMATICS OF EUCNIDE (LOASACEAE)

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THE GENUS *Eucnide* presents a pattern of species differences somewhat unusual among flowering plants. The eleven species are very similar in all respects except floral morphology, in which they differ widely. For example, the corollas in several species are apopetalous while in others they are sympetalous, forming a long tube. Characters such as apopetaly and sympetaly are so well established as criteria for separating major families of flowering plants that it is difficult to determine their taxonomic importance when they occur as differences between otherwise similar species. We shall evaluate the taxonomic significance of floral morphology in *Eucnide* by two approaches. The gross features of floral morphology will be analyzed by determining their anatomical basis so that more refined comparisons between the species can be made. The biological importance of floral structures will be evaluated by considering their role in reproduction of the local populations. The assessment of the taxonomic importance of these characters will be independent of the correlations that they ultimately give in our classification.

Since the publication of *Monographia Loasacearum* (Urban & Gilg, 1900) the species of Loasaceae subfamily Mentzelioideae have been grouped into three genera: *Mentzelia, Eucnide*, and *Sympetaleia*. Although monographs of *Mentzelia* (Darlington, 1934) and *Eucnide* (Waterfall, 1959) have been published, no attention has been given to *Sympetaleia* since the turn of the century. Recent collecting activities in Baja California have greatly increased the material of *Sympetaleia* available for study, and this, along with the collection of the rare *Sympetaleia tenella* nearly 40 years after its discovery, has directed our attention to this group. Our initial examinations of *Sympetaleia* led us to the question of its generic limits and affinity to both *Eucnide* and *Mentzelia*. Consideration of all three genera has indicated the general importance of floral biology in this subfamily and has suggested the necessity for an entirely new evaluation of the specific differences. Our inescapable conclusion is that the differences between *Eucnide* and *Sympetaleia* are no greater than differences within *Eucnide*, and that these differences, when viewed against a background of the entire subfamily, make it clear that one genus with three sections is the most accurate representation of our concept of the affinities within the *Eucnide-Sympetaleia* complex.

Subfamily Mentzelioideae, to which *Eucnide* belongs, is distinguished from other Loasaceae by the numerous stamens not grouped in fascicles. Other Loasaceae either have only five stamens, as in subfamily Gronovioideae, or numerous stamens arranged in discrete fascicles opposite the petals and accompanied by elaborate petaloid staminodia, as in subfamily Loasoideae. Within subfamily Mentzelioideae the genus *Mentzelia* is distinguished by its three parietal placentae (five only in *M. decapetala*) with the ovules inserted in two distinct vertical rows on each placenta and by the seeds, which are variously shaped but always large and not longitudinally grooved. The remaining species of this subfamily, which we consider to comprise the genus *Eucnide*, are characterized by five placentae, each with many rows of minute, longitudinally grooved seeds (Fig. 1). We recognize 11 species in *Eucnide* and arrange them in three sections as follows:

sect. Eucnide	series Eucnide	*E. bartonioides*
		E. grandiflora
		E. lobata
	series Tubiflorae	*E. cordata*
		E. hypomalaca
		E. hirta
		E. xylinea
sect. Mentzeliopsis		*E. urens*
sect. Sympetaleia		*E. aurea*
		E. rupestris
		E. tenella

MATERIALS AND METHODS

Much of our information about *Eucnide* comes from material of 17 populations, representing nine species, that we have been able to study in detail. Table 1 lists these collections and indicates how each was studied. Some have been observed as natural populations and some have been grown in the greenhouse at Los Angeles. All of these collections have been available in great quantity so that detailed morphological and anatomical studies could be made. Material was fixed in formalin-acetic-alcohol and then either cleared in lactic acid or embedded in paraffin, sectioned, and stained. Additional material from herbarium specimens of other species was restored by gentle boiling and cleared or sectioned, so that all species have been studied from both sectioned and cleared material. Meiosis has been examined with the usual method of fixing buds in 1:3 acetic-ethanol, squashing anthers in acetocarmine, and observing with a phase microscope. Meiosis was observed in at least three different individuals from most of the populations studied. Controlled pollinations were made in all populations grown in the greenhouse. The stamens were first removed and then the style and stigma were covered with a segment of plastic soda straw to prevent accidental pollinations. When the stigma became receptive the soda straw was removed momentarily while the desired pollen was applied to the stigma. In addition to our own collections we have studied the specimens in the following herbaria: A, BM, BR, CAS, CU, DS, E, F, GH, K, LA, M, MO, NY, POM, RSA, SMU, SRSC, TEX, UC, US.

TABLE 1. **Collections of Eucnide of particular importance in this investigation.**

	COLLECTOR & LOCALITY	HAPLOID CHROMOSOME NO.	GARDEN CULTURES	FIELD STUDY
Sect. **Eucnide**				
E. bartonioides	*Thompson* & *Ernst 3283*; Big Bend National Park, Texas	21	+	+
E. cordata	*Chambers 1004*; Cataviñá, Baja Calif., México	21	+	–
	Wiggins 15884; Puertecitos, Baja Calif., México	21	–	–
E. grandiflora	*Ernst* & *Delgadillo 2475*; NW of Nacaltepec, Oaxaca, México. Garden voucher, *Thompson 3386*	21	+	+
E. hirta	*McVaugh 15108*; Near Lake Chapala, Jalisco, México	21	+	–
E. lobata	*King 4505*; Ciudad Victoria, Nuevo León, México	21	+	–
	Waterfall 15324; Monterrey, Nuevo León, México	21	+	–
Sect. **Mentzeliopsis**				
E. urens	*Thompson 3184*; Panamint Valley, Inyo Co., Calif.	21	–	+
	Thompson 3182; Death Valley Buttes, Inyo Co., Calif.	21	–	+
	Thompson 3339, *Raven 11784*; Hoover Dam, Clark Co., Nevada	21	+	+
Sect. **Sympetaleia**				
E. aurea	*Carter* & *Sharsmith 4160*; Sierra Giganta, Baja Calif., México	21	+	–
	Carter & *Sharsmith 4260*; Isla Danzante, Baja Calif., México	21	+	–
	Carter & *Ferris 3879*; W of Loreto, Baja Calif., México	21	–	–
	Wiggins & *Ernst 543*; Santo Domingo, Sierra Giganta, Baja Calif., México	21	–	+
E. rupestris	*Raven 14802*; N of San Felipe, Baja Calif., México	21	–	–
	Thompson 3316; S of San Felipe, Baja Calif., México	21	–	+
E. tenella	*Wiggins*, *Carter* & *Ernst 280*; Misión Los Dolores, Baja Calif., México	—	–	+

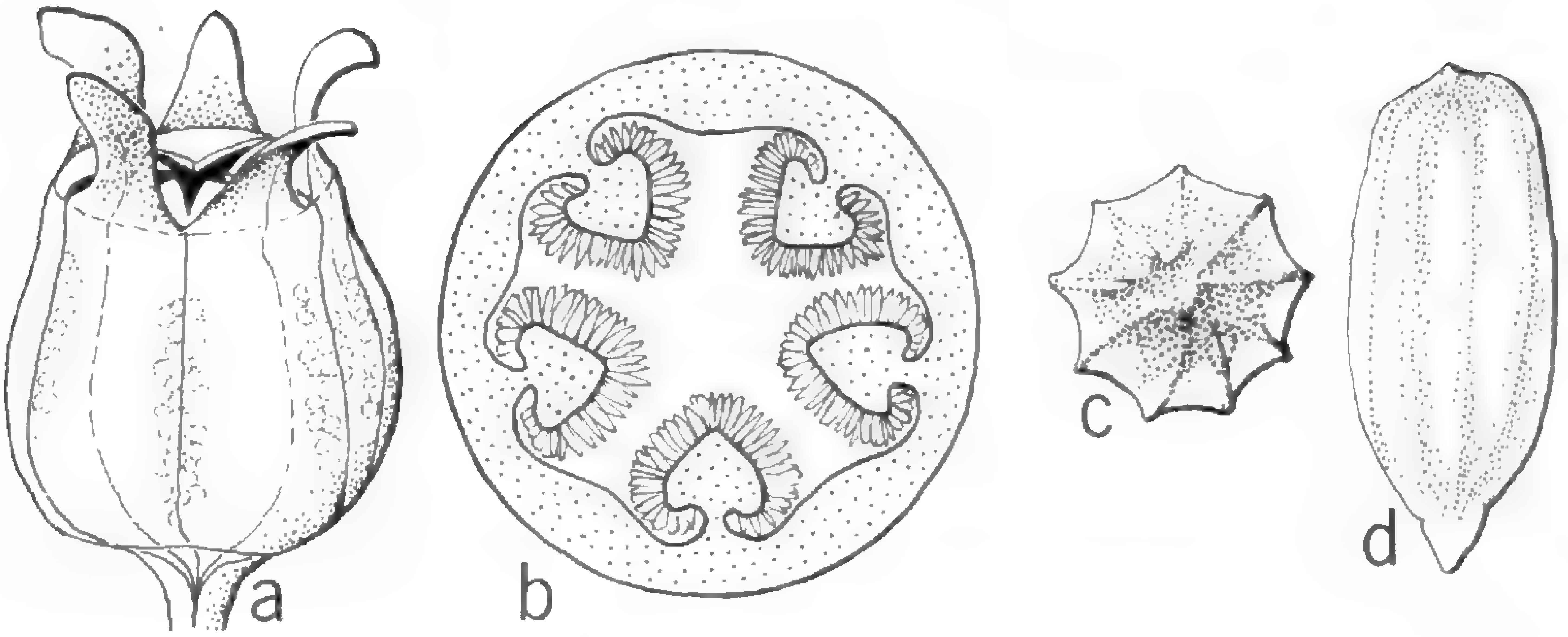

FIG. 1. Characteristic fruit, placentation, and seed in *Eucnide*. a, capsule, *E. tenella*, showing position of ovules, valves, and major veins, × 10; b, ovary, *E. urens*, transverse section showing ovules and cordate placentae, × 4; c, seed apex, *E. aurea*, × 70; d, seed, *E. aurea*, longitudinal view, × 75.

COMPARATIVE MORPHOLOGY

Morphological variation throughout *Eucnide* is somewhat unusual in that particular structures show either striking diversity or great uniformity. We have chosen to emphasize this aspect of the pattern of variation by discussing comparative morphology under two headings, considering first the morphological diversity, which occurs primarily in the flowers, and following this with the morphological similarities that occur throughout the remainder of the plant body.

Morphological diversity. Our three taxonomic sections are founded on morphological innovations in the conformation of the corolla and the spatial relationships of the anthers and stigma. The corollas are apopetalous or sympetalous anatomically, but this difference is bridged and made ambiguous by a peculiar condition of false sympetaly. Within either the apopetalous or sympetalous categories there are species with open, spreading corollas and species with narrow, tubular corollas. Among the species with spreading corollas and those with tubular corollas there are examples with included or exserted anthers and stigma. In our first two taxonomic sections, false sympetaly (i.e., apopetaly) is correlated with anthers that become two-locular at anthesis. In our third section, true sympetaly is correlated with anthers that become unilocular.

In section EUCNIDE, the corollas are white to yellow and are falsely sympetalous at the base. The staminal filaments are more or less filiform above but fused basally into a relatively very short tube (0.5–3 mm. long) to which the petals always are united. It is their union with this tube that holds the petals together when both stamens and petals abscise from the top of the ovary. We consider these corollas anatomically apopetalous but functionally slightly sympetalous by virtue of their union with the staminal tube. Two modifications are evident in this flower type. In either case, the anthers and the stigma are conspicuously exserted from the corolla and the anthers are two-locular at anthesis. On the one hand, series *Eucnide*, with three species, has more or less open flowers in which the petals and the stamens are loosely spreading (FIG. 2a, b). On the other hand, series *Tubiflorae*, with four species, has relatively long, cylindrical flowers in which the petals remain erect and broadly imbricate, even though the falsely sympetalous portion is only 2–3 mm. long (FIG. 2c). In the latter series, the position of the petals compresses the stamens into a tight, narrow, brush-like cluster.

In section MENTZELIOPSIS, with only one species, *Eucnide urens* (FIG. 2d), the corolla is pale yellow to nearly white, and the broad, rigid lobes are narrowly imbricate and spread to form an open funnel. We consider the corolla apopetalous, as in section EUCNIDE. Although the staminal tube to which the petals are united is 5–8 mm. long, it is relatively short, being about a fifth the length of the corolla. The anthers and stigma are distinctly included and only a little more than half as long as the corolla. Above the staminal tube, the stout free filaments are slanted inward forming a kind of chamber around the style. The anthers are two-locular at anthesis. A few of the filaments, the outermost and longest, curve outward at the top, holding their anthers away from the stigma. The proximity of most of the anthers to the style, however, and their inwardly nodding position causes most of the pollen to be shed into the interstices of the filaments and into the chamber the filaments create around the style. The deposition of the pollen into this chamber is peculiar to this species of *Eucnide* but it recalls a very similar situation found in the genus *Mentzelia* section BICUSPIDARIA.

In section SYMPETALEIA, with three species, the corollas clearly are sympetalous anatomically, the stamens are epipetalous, and the anthers (to be discussed shortly) are unique. In *Eucnide tenella* (FIG. 2f), the whitish corolla (ca. 8 mm. long) with spreading narrow lobes, is united for about a third of its length into a narrow tube. The anthers are exposed on long filaments that equal or slightly exceed the stigma and corolla. In *E. aurea* (FIG. 2g), the yellow or brilliant reddish orange corolla (ca. 15–20 mm. long) is distinctly salverform, with broad, sometimes imbricate lobes, and is united for about two-thirds its length into a narrow tube. The nearly sessile anthers are included within the tube, and below them is a ring of upwardly curving hairs. In *E. rupestris* (FIG. 2e), the greenish corolla (to ca. 15 mm. long) with shadings of yellow or brown, is more or less cylindrical, with rigidly erect, valvate lobes, and is united into a tube for about three-fourths of its length. The anthers are included within the tube, the lower ones subsessile and the upper ones on short, stout, erect filaments. In the lower portion of the corolla beneath the stamens, as in *E. aurea*, there is a ring of upwardly curving hairs. The ring of hairs is absent in *E. tenella*. In this section the anthers are unilocular at anthesis.

The interesting differences in the structure of the anthers require explanation. The anthers vary in general external conformation, but more important, the original masses of sporogenous tissue, as well as the final pollen chambers (locules), differ both in shape and in number (FIG.

3a–q). All of the anthers are basifixed, and the microsporangia are lined with a well-defined tapetal-endothecial region. The anthers of section EUCNIDE and section MENTZELIOPSIS are divided medially by the connective, which sometimes projects slightly beyond the microsporangia; otherwise, the anthers are slightly emarginate apically (FIG. 3a, b, f). Transverse and longitudinal sections of these anthers (with the plane of section indicated in FIG. 3a, b, and the sections shown in FIG. 3c, d, e) clearly demonstrate that the sporogenous tissue of each occurs in four separate, straight, vertical masses. The two masses of sporogenous tissue on the same side of an anther are marked externally by a longitudinal groove (FIG. 3b, c) and are separated internally from each other only by the tapetal-endothecial layer. The paired masses of sporogenous tissue on one side of the anther are separated from those on the other side by the tissues of the connective. As the pollen matures, the tapetal-endothecial tissue breaks down joining the adjacent lateral pollen masses in a single locule on either side of the connective so that just before dehiscence, the anther becomes two-locular. The dehiscence is longitudinal at the lateral grooves. In the ovate to elliptical anthers of section EUCNIDE, the wall of the locule frequently becomes reflexed so that after dehiscence, the exposed portion of the anthers is the lining of the locule (FIG. 3f). In the linear-sagittate anthers of section MENTZELIOPSIS the wall of the locule usually does not reflex and the lining is less conspicuously displayed.

In section SYMPETALEIA, the anthers are reniform (FIG. 3g) and the connective never reaches the apex of the anther. Transverse and longitudinal sections (FIG. 3i–l; m–p) show the unusual nature of these microsporangia. In *Eucnide tenella* and *E. aurea* the sporogenous tissue occurs in two horseshoe shaped masses, for, although FIG. 3i shows four masses of sporogenous tissue, these are continuous over the apical portion of the anther (FIG. 3k, l). The nature of the sporogenous tissue in *E. rupestris* is particularly illuminating. In the portion of the anther facing the style (i.e., adaxially) the sporogenous tissue of the two sides of the anther is continuous apically (FIG. 3o) just as in *E. tenella* and *E. aurea.* In the portion of the anther toward the corolla (i.e., abaxially), however, the sporogenous tissue is not continuous, but occurs in two lateral masses separated apically by a thin septum (FIG. 3p).

Thus, in *Eucnide tenella* and *E. aurea* there are two masses of sporogenous tissue, while in *E. rupestris* there are three. When the pollen matures, the tapetal-endothecial tissues break down joining the pollen masses laterally so that in all three species the anthers have a single locule just prior to dehiscence. The anthers dehisce at the lateral groove (FIG. 3h), which, in section SYMPETALEIA, is continuous over the apex of the anther. After dehiscence, the anthers are peltate with the anther wall slightly cupped or opened out flat (FIG. 3q).

Morphological unity. The diversity in morphology and anatomy among the species of *Eucnide,* which permit the recognition of the species groups, is restricted to the flowers, i.e., corolla, stamens, and style. Underlying these striking differences, however, are many similarities in basic

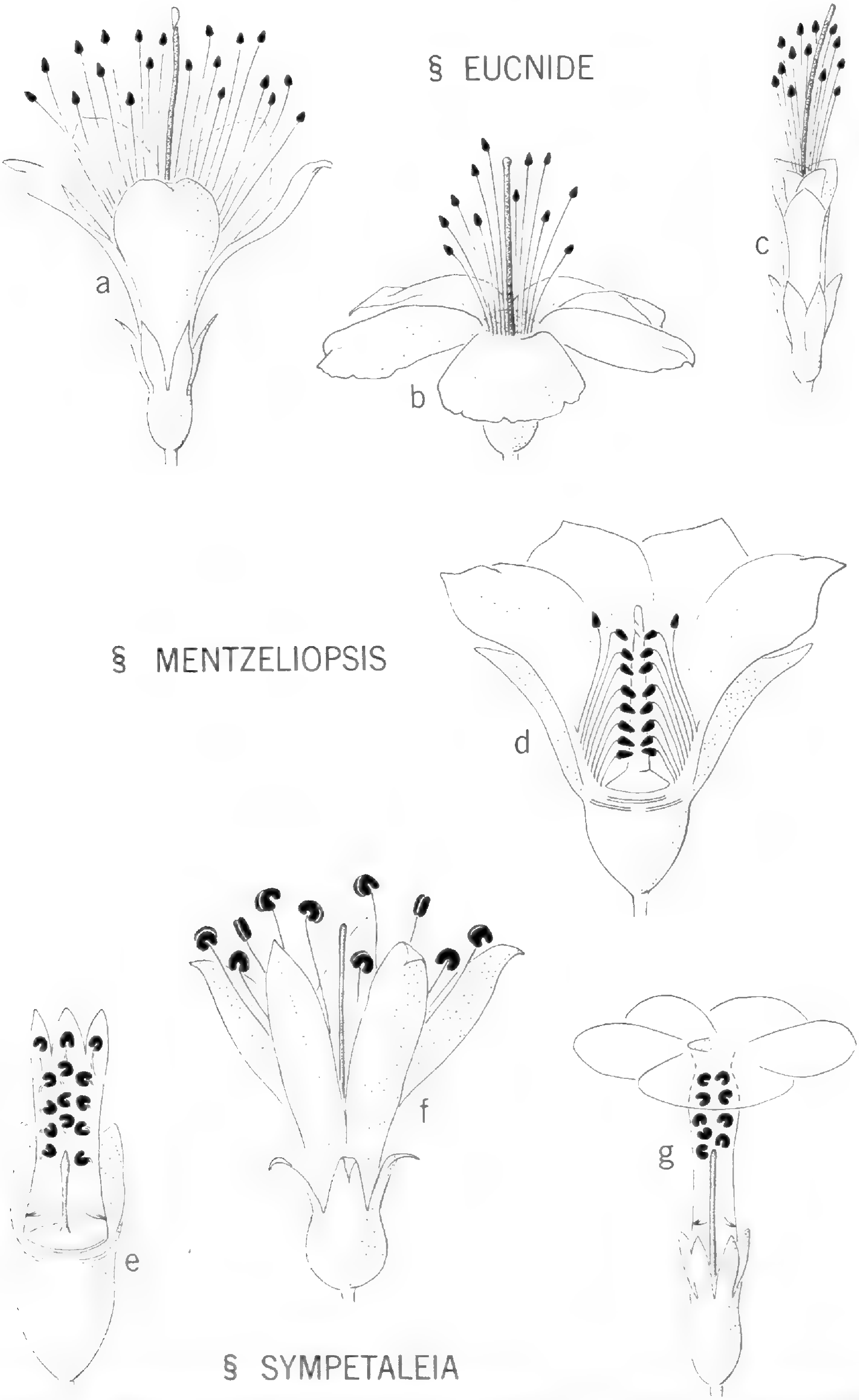

Fig. 2. Flowers of *Eucnide* reduced to nearly the same length, showing shape of corolla and position of stigma and stamens. a, *E. bartonioides*, × 1; b, *E.*

floral and vegetative architecture which are unique to the genus and point out its morphological unity.

The plants are herbaceous, short lived perennials, often with the lower stems stout and appearing woody. Plants of *Eucnide aurea*, *E. bartonioides*, *E. cordata*, *E. hirta*, *E. lobata*, and *E. urens* all flowered about three months after the seeds were sown in a warm greenhouse in Los Angeles and seemed able to persist as perennials. Some species, such as *E. aurea*, *E. bartonioides*, and *E. rupestris*, also may be successful facultative annuals.

The leaves are alternate, simple, and of more or less characteristic appearance throughout the genus. They are petiolate, with the blades mostly cordate, orbicular to ovate with crenate, lobed or incised margins. The venation varies from nearly palmate in some species to quite pinnate in others; however, the general outline and appearance of the leaves remain very similar. In some species the upper surface of the leaves appears to be varnished.

The plants usually are densely pubescent with several kinds of trichomes that are characteristic of the family and often stinging to the touch. The trichomes are unicellular and either smooth or variously reflexly barbed; some are swollen at the base or rest upon multicellular epidermal platforms.

The ovary is inferior and unilocular, with each of the five parietal placentae alternate with the sepals. In transverse section the placentae are cordate in outline, intrude deeply into the locule of the ovary, and are densely covered with minute, horizontally radiating ovules (FIG. 1b).

The dry, dehiscent fruits are globular to obovoid and are surmounted by the persistent sepals (FIG. 1a). In contrast to the usually fragile walls of the fruit, the apex is hard and durable and divides into five valves which are attached opposite and interior to the sepals (i.e., alternate with the placentae). The valves open wide, permitting the sifting out of the seeds. Frequently, the style remains attached to the tips of the valves and is torn as they open.

The numerous seeds (FIG. 1c, d) are pale or straw colored, 0.5–1.25 mm. long, and usually acute at the attached end and rounded at the free end. They are conspicuously ribbed or grooved longitudinally with the parallel crests either straight or spirally twisted, both forms often occurring in the same capsule. In some instances, the seeds are slightly constricted near the middle. At the time of their dispersal, the seeds are filled by the embryo.

The pollen is oblate (shorter on the polar axis), tricolporate (each of the three narrow furrows with a median, round pore), and without prominent surface sculpturing.

The pedicels (or peduncles) in all species curve as the capsules mature

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lobata, sepals removed, × 3; c, *E. cordata*, × 1¼; d, *E. urens*, forward stamens, one petal, and two sepals removed, × 1; e, *E. rupestris*, corolla shown as though transparent, forward two sepals removed, × 2; f, *E. tenella*, × 5½; g, *E. aurea*, corolla shown as though transparent, × 2⅘.

and, in some species, elongate from a few millimeters at anthesis to as much as 33 cm. by the time the seeds are shed. In the plants grown in the greenhouse, the capsules always pointed north; from this we assume that the pedicels are negatively phototropic. Elongating pedicels are developed best towards the base of the plants, and, since these portions often are dry and broken in larger plants, they usually are not preserved on herbarium specimens and may not be noted by collectors.

The chromosome number has been determined for eight species representing all three sections of the genus. In each cytological examination, 21 pairs of chromosomes were observed in the meiosis of the pollen mother cells, and there were no cytological anomalies. The voucher specimens and collection data for these determinations are given in TABLE 1.

Another expression of the basic similarity of the flowers is found in vascular anatomy. In all species (whether apopetalous or sympetalous), the vascular pattern is fundamentally similar, differing only slightly in complexity from species to species and from specimen to specimen. The vascularization of a flower of *Eucnide cordata*, diagrammed in FIG. 4, may be taken as representative of the genus. Ten equally spaced primary traces (a, b) emerge from the pedicel and ramify, sending tracheary threads to the floral organs. Each of the five primary traces that is opposite a calyx lobe is called a sepal trace (a); each of the alternate five primary traces that is opposite a corolla lobe is called a petal trace (b). A sepal trace sends a small branch inward leading to stamens (c) and then becomes the median sepal vein (a′). A petal trace divides several times, first giving off lateral branches leading to stamens (c), then a pair of stouter veins (d) which become the adjacent marginal veins of adjacent sepals; the remaining median branch (b′) becomes the petal vein. A sepal thus receives three veins, each of them originating from a different primary trace; the adjacent marginal veins of two sepals are derivatives of the same primary trace that provides the petal vein. In the complex petal trace, the veins leading to stamens are given off at the same or slightly lower level than the veins leading either to the sepals or petals. About eight stamens are vascularized from each petal trace but only about two stamens are vascularized from each median sepal trace. Inward branches from all ten primary traces toward the top of the ovary form a plexus (e) of tracheary tissue in the disc-like apex (i.e., the valves) of the ovary from which five veins emerge leading to the style (not shown).

The general pattern of flower vascularization is not altered by the degree of sympetaly and fusion of filaments with the corolla tube. The vertical diagrams in FIGURE 5 compare two sepal traces (a) and one petal trace (b) in the falsely sympetalous flower of *Eucnide cordata* and in the truly sympetalous flowers of the three species of section SYMPETALEIA. The vascularization of the most diverse flower types is fundamentally similar. The divergence of the stamen traces (c) from the petal trace (b) occurs at relatively the same level below the articulation of the corolla in all of the flowers regardless of the degree of petal-filament union. The petal trace (b) always is more complicated than the sepal trace (a), and the vascular supplies to the placenta, valves, and style (e) all arise in the same way.

The differences between the sympetalous and apopetalous flowers concern the degree of relatively simple lateral fusion of nonvascular tissue without alteration of the tracheary tissue. It is noteworthy that in fresh material of *Eucnide aurea,* one of the most sympetalous examples in the genus with long salverform corollas with essentially sessile epipetalous anthers, the corolla tube readily can be stripped away leaving behind the anthers supported by the staminal tube. The corolla also can be torn from the staminal tube along a kind of cleavage plane in the apopetalous species with long filiform stamens. The differences, therefore, between the falsely sympetalous corollas (those actually apopetalous) and the truly sympetalous corollas seem to be relatively minor anatomically.

In respect to habit, leaves, hairs, fruits, pedicels, placentae, seeds, pollen, chromosome number, and pattern of floral vascularization, the species of *Eucnide* are remarkably similar. Quite the opposite is shown, however, with the corollas and stamens where there is great diversity in form, the differences being correlated to delimit three species groups, each with its own distinctive flower type.

BREEDING SYSTEM

The self-pollinations made in all of the greenhouse cultures listed in TABLE 1, representing six of the eleven species of *Eucnide,* resulted in full sets of viable seeds, while unpollinated flowers formed neither seeds nor mature capsules. In the absence of any indication of apomixis we take this to indicate that the plants tested were self-compatible. In these plants, therefore, the pollination system determines the inbreeding-outbreeding balance by controlling the amount of self- and cross-pollination. The main factors of the pollination system are the natural pollinators and floral morphology, in particular the position and developmental timing of the anthers and stigma. In *Eucnide* the morphology of the flowers is not only a convenient marker of the reproductively isolated units but is an important element in the operation of the populations, serving to adjust the populations to specific pollinators and to regulate the amount of inbreeding and outbreeding.

Section Eucnide. In all of the species of section EUCNIDE the flowers have yellow to pale yellow or nearly white petals and exserted stamens, and they open in the late afternoon. The species differ, however, in flower size, the degree of spreading of the petals, and in the timing of anther dehiscence so that there are three different floral forms. We have studied flowering in greenhouse cultures of *Eucnide bartonioides, E. cordata, E. grandiflora, E. hirta,* and *E. lobata,* representing all of the three types of flowers (FIG. 2). In *E. bartonioides* the flowers are large, with the yellow petals usually 3 cm. long and spreading away from the exserted stamens. The flowers first open in the late afternoon, at which time the already receptive stigma exceeds the anthers by a few millimeters

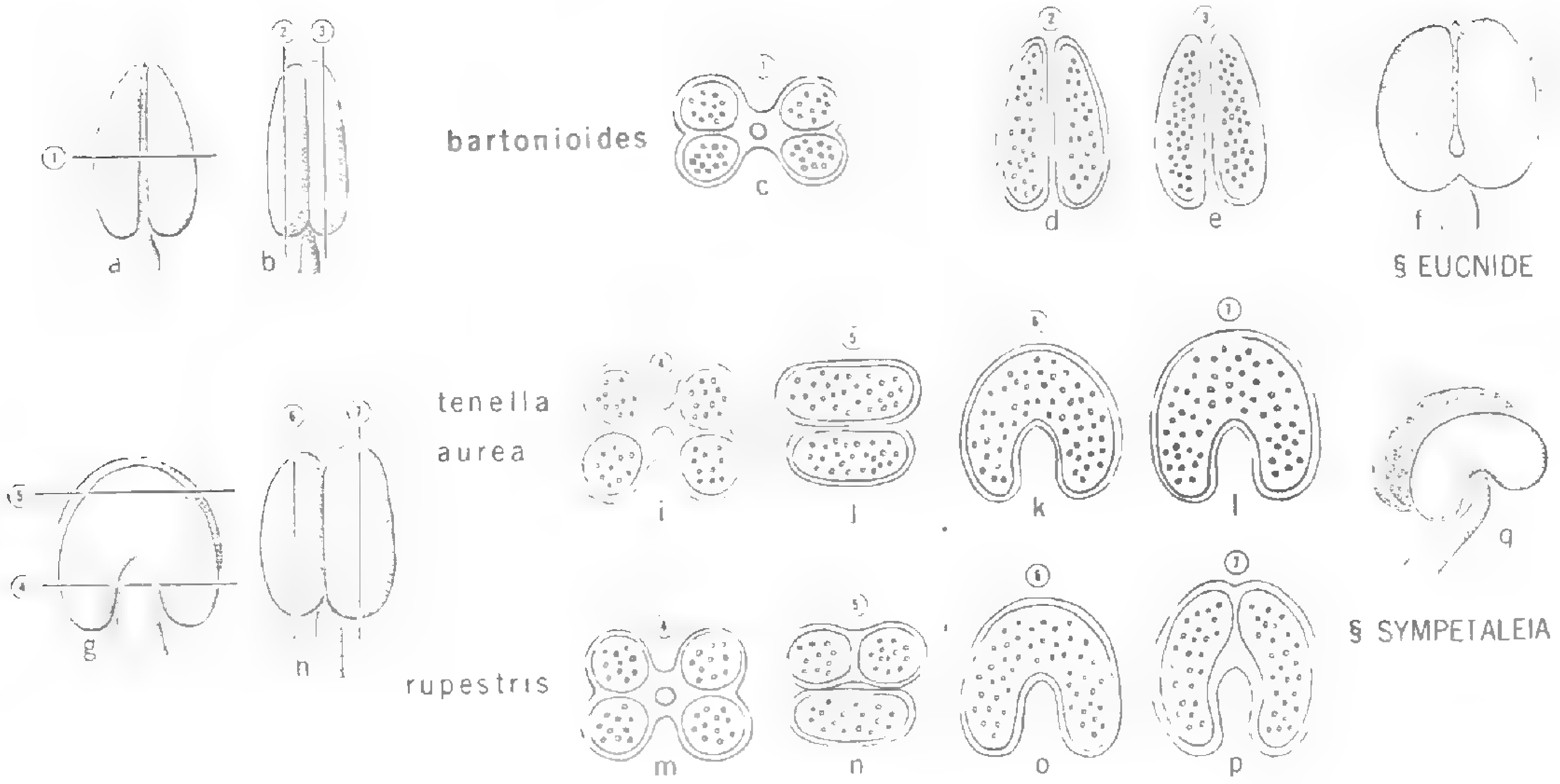

FIG. 3. Morphology of anthers in *Eucnide*. a–f, sect. EUCNIDE: a, adaxial view of anther, × 6; b, same, lateral view; c–e, transverse section and longitudinal sections of "a" and "b" at positions indicated by numerals 1–3; f, lateral view of anther after dehiscence. g–q, sect. SYMPETALEIA: g, adaxial view of anther; h, lateral view; i–l, transverse and longitudinal sections of "g" and "h" at positions marked by numerals 4–7; m–p, same; q, abaxial view after dehiscence. Anthers of sect. EUCNIDE and sect. MENTZELIOPSIS (not shown), have four microsporangia and become two-locular at anthesis. Anthers of sect. SYMPETALEIA are unilocular at anthesis; *E. aurea* and *E. tenella* have two microsporangia, but *E. rupestris* has three. a–f, × 6; g–q, × 19.

(FIG. 2a), so that in completely undisturbed flowers there is no pollination and no seeds are formed. The anthers are sufficiently close to the stigma, however, so that even a slight jarring of a flower at anthesis results in some self-pollination. These observations on plants growing in the greenhouse indicate that in natural populations outcrossing would be encouraged by large insect visitors that would first touch the extended stigma as they approached the flower. The same pollinator would cause selfing by bending the stigma back into the anthers, as well as by visiting different flowers of the same plant. Thus, in natural populations the inbreeding-outbreeding balance must lie well toward the inbreeding extreme. Although we have not observed pollination of *E. bartonioides* in natural populations, we can make a reasonable prediction about its pollinator, since a model is available in the flowers of *Mentzelia laevicaulis* (sect. BARTONIA) which are very similar in general conformation, size, color, and opening time. We know that *M. laevicaulis* is pollinated by hawkmoths (Sphingidae), and the similarity of the flowers suggest that *E. bartonioides* also is hawkmoth pollinated.

In *Eucnide lobata* the flowers are small, with the deep yellow, rotate petals only 1 cm. long (FIG. 2b). The fully developed flowers have the stamens arranged in two distinct tiers: the shorter, outer stamens and the longer, inner stamens. The flower first opens in the late afternoon, at which time the outer stamens are fully expanded and release their pollen. The inner stamens, however, remain convolute around the base of the style. The stigma is receptive at this time, but, because the outer stamens are shorter than the style and held away from it, no pollination can occur unless an insect visits the flower. On the following morning, the inner, longer stamens straighten out and release their pollen more or less directly onto the stigma, so that even completely undisturbed flowers in the greenhouse set a full complement of seeds. Thus the manner in which the flower matures presents an initial opportunity for insect visitors to effect some outcrossing, while automatic self-pollination follows the following morning. Populations of *E. lobata* probably have a somewhat greater range of outbreeding than the populations of its near relative, *E. bartonioides*. If pollinators are abundant, seed production and outbreeding would be very high; however, in the absence or shortage of pollinators seed production would remain high but the population would shift to maximal inbreeding. The breeding system is highly labile, responsive to conditions of the environment, and integrated by the natural pollinators. While the natural pollinators of *E. lobata* are unknown, the flowers of this size, form, and color in *Mentzelia* and other groups usually are bee pollinated.

A third line of flower development occurs in *Eucnide cordata*. The petals are very pale yellow, nearly white, about 2 cm. long, and tightly imbricated about the filaments of the exserted stamens (FIG. 2c). The style elongates first, while the petals are still tightly enclosing the anthers. The filaments then elongate, forcing the anthers out of the corolla, but they remain well below the stigma. The petals never spread, and flowers with stamens in various stages of emergence from the corolla can be seen throughout the day, making it difficult to say when the flowers open; the pollen, however, is released in the late afternoon. The stamens still are held together by the imbricated petals, and the pollen is shed well below the stigma. Some of the flowers in an inflorescence, particularly the first to mature, are held more vertically and in these self-pollination does not occur in undisturbed flowers. Other flowers in an inflorescence, particularly those that develop later, are held more horizontally or even point downward. In these flowers there is opportunity for pollen to fall on the stigma, and some of these flowers, even though undisturbed, form some viable seed. Self-pollination in undisturbed inflorescences is not very effective, since only about 25 per cent of the possible seed production is realized. Although no information about natural pollinators is available for *E. cordata*, the structure of the flower, along with the well exserted stigma, indicates dependence on a pollinator. Flower and inflorescence structure in *E. cordata* function to regulate the amount of inbreeding and outbreeding, the opportunity for inbreeding being more restricted in this species than in either *E. bartonioides* or *E. lobata*.

The flowers in *Eucnide hirta* have the same general structure as those of *E. cordata*, with one important exception. In *E. hirta* the style elongates somewhat less in proportion to the rest of the flower, and the stigma is surrounded by the anthers at the time pollen is shed. Thus, self-pollination always occurs, and every flower in undisturbed greenhouse plants produces a capsule full of seeds. The natural pollinators of *E. hirta* are unknown but even with an active pollinator the populations must be primarily inbreeding.

The species of section EUCNIDE thus show striking differences in gross floral morphology. Without any modification of the basic floral structure, variation in relative lengths of stamens, styles, and corolla and position of the petals are harmoniously recombined to give three flower types the function of which is explicable in terms of the pollination system. All are probably insect pollinated. Within each flower type there are accommodations for flexibility in the amount of self- and cross-pollination, with this feature being most highly developed in *Eucnide lobata*.

Section Mentzeliopsis. In *Eucnide urens*, the only species of this section, the flowers are large, with the pale cream-colored petals about 5 cm. long. The stigma exceeds the anthers but does not extend beyond the petals. The stamens press inward around the style, the sturdy filaments forming a pollen chamber well below the stigma (FIG. 2d). Undisturbed flowers do not set seed, and natural populations must be highly dependent on insect visitors. We have studied pollination in two natural populations of this species, one on either side of the Panamint Mountains, Inyo Co., California. The population near Death Valley Buttes (*Thompson 3182*) was studied on 16 April, 1961, from 8:00 A.M. until 2:00 P.M. The population in Panamint Valley (*Thompson 3184* and *3187*) was studied on 6 May, 1961, from before sunrise until sunset. In addition, several other populations have been spot checked, and these observations confirm those made in more detail at the above localities. The flowers of *E. urens* open in bright sunshine at about 9:00 A.M., and pollen is released immediately into the pollen chamber. The flowers soon are visited by a melittid bee, *Hesperapis laticeps* Crawford, that remains active until early afternoon, when the desert winds usually increase in force. These pollinators alight on the exposed stigma and style and force their way head first into the pollen chamber. On backing out from the pollen chamber, they again touch the stigma. Although other insects occasionally are found in the corolla of *E. urens*, only *Hesperapis laticeps* enters the pollen chamber and affects pollination. The behavior of *Hesperapis laticeps* in the *E. urens* flowers results in both cross- and self-pollination.

This species is the only *Eucnide* with this type of flower and pollination system, but, in spite of its unique gross morphology, the basic architecture of the flower is the same as all of the other species of the genus. Flowers with the same gross morphology and the same pollinators occur in *Mentzelia* sect. BICUSPIDARIA, but in *Mentzelia* this flower type is developed from an entirely different basic flower structure. For example, the seeds, placentae, and floral vasculature in *Mentzelia* are entirely different from those in *Eucnide*.

Section Sympetaleia. The three species of this section show the greatest diversity in the features of gross floral morphology and corolla color that are associated with the pollination system. In all species, however, the flowers have tubular corollas and open in the morning. In

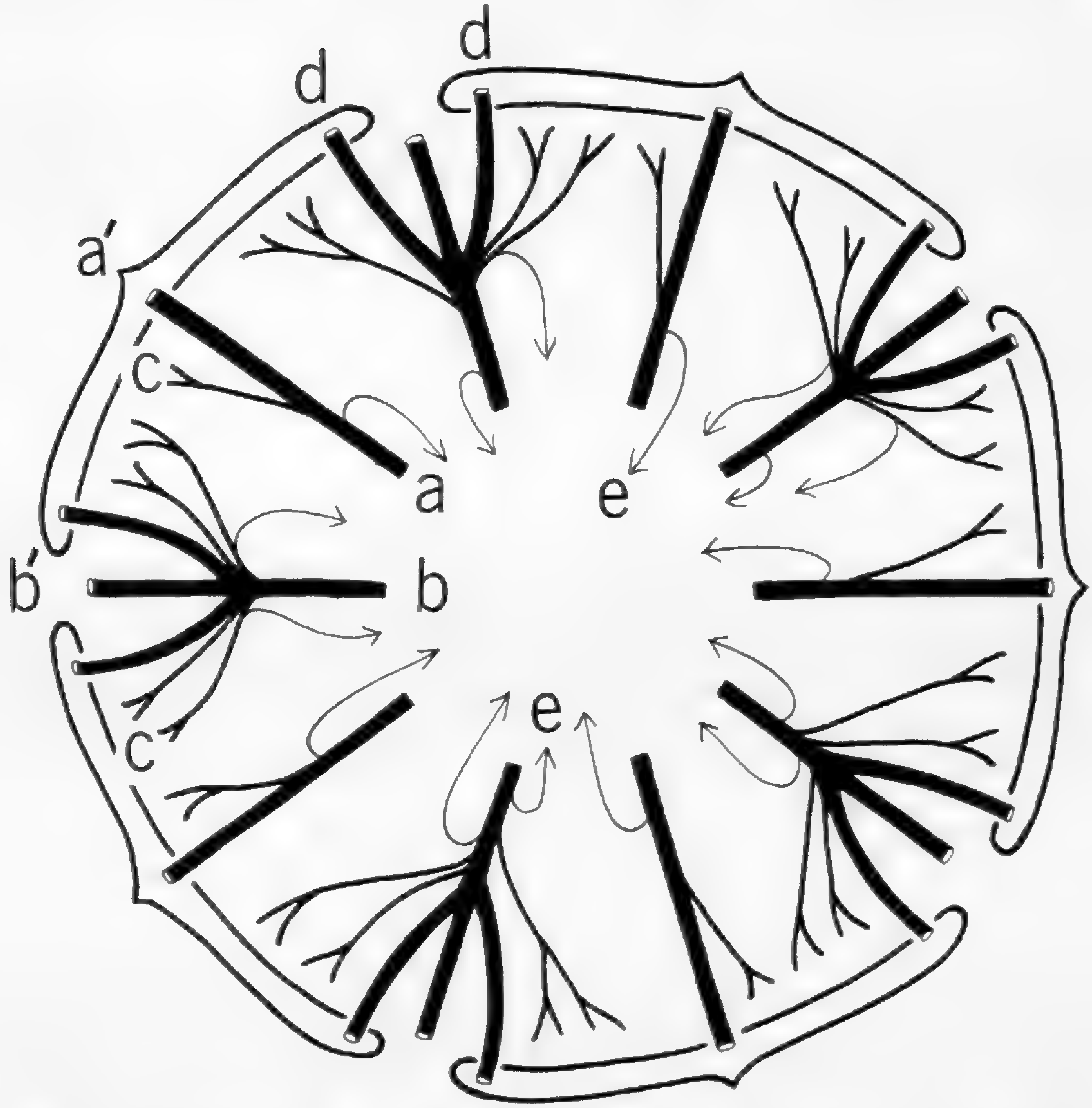

FIG. 4. Diagram of the major vascular traces and veins of the flower, in *Eucnide cordata*, transverse view from above. a, sepal trace; a′, median sepal vein; b, petal trace; b′, petal vein; c, staminal traces; d, lateral sepal vein; e, traces to valves and style.

Eucnide aurea the corolla is salverform and the anthers are sessile on the corolla tube (FIG. 2g), but the two populations represented in our cultures differ in flower color and size. The plants from Danzante Island (*Carter & Sharsmith 4260*) have strong reddish-orange corollas about 20 mm. long. When the anthers release their pollen, the stigma is at or just above the ring of hairs in the lower portion of the corolla tube below the stamens. About two days later, the style elongates until the now-receptive stigma is slightly exserted from the sympetalous corolla. In the plants from the Sierra Giganta (*Carter & Sharsmith 4160*) the flowers are smaller, with yellow corollas about 15 mm. long. Although the style elongates as it does in the Danzante Island plants, the elongation is relatively less, the stigma never being exserted at all and usually not exceeding the middle of the mass of anthers. Both the red and the yellow forms of *E. aurea* are self-compatible, and undisturbed flowers set seed in the greenhouse. It should be pointed out that if pollinator activity is high the pollen of an individual flower might be depleted before the style elongates and the stigma becomes receptive. This would tend to increase outbreeding in environments where pollinators were abundant. Although we have no observations on the natural pollinators of *E. aurea,* the color and form of the flowers suggest that Lepidoptera and humming birds could be effective.

In *Eucnide rupestris,* the flowers are very inconspicuous to the human eye. The corolla is green, somewhat darker than the leaves, and usually a little more than one centimeter long. While others have recorded a metallic luster on the corolla lobes we could not detect such an appearance in the population that we studied on an overcast day. The anthers are more or less sessile in the corolla tube, the stigma is located among the anthers, and the style does not elongate as it does in *E. aurea*; pollen thus falls directly on the receptive stigma (FIG. 2e). No pollinators were seen during a mid-day, three-hour observation period in one population, but it was noted that every capsule on every plant was forming a full complement of seeds. This is evidence that the plants are self-compatible as well as self-pollinating. The information that we have about *E. rupestris* suggests that it is the most autogamous species of *Eucnide,* a feature correlated with its great range and morphological uniformity.

In *Eucnide tenella,* the corolla is white or cream colored and less than one centimeter long, the anthers are exserted, and the stigma is located among the anthers (FIG. 2f). We have not grown plants of this species and have made only very brief observations on one natural population. From the structure of the flowers we can determine that self-pollination occurs readily, and the prevalence of self-compatibility throughout the genus would indicate that *E. tenella* also is self-compatible. We know nothing of the natural pollinators, but the information on flower structure suggests a rather high degree of inbreeding for *E. tenella.*

Enough information is available about the breeding system of the species of *Eucnide* to allow us to outline the general pattern for the genus. The system is based on self-compatibility, with the inbreeding-outbreeding balance determined by the amounts of self- and cross-pollination permitted by the pollination system. The features of floral morphology involved in the pollination system are then important parameters of the entire breeding system. Each of the sections of *Eucnide* has distinctive features of floral morphology that are developed without alteration of the basic structure of the flower. The flowers in section EUCNIDE have yellow, cream or nearly white petals, exserted anthers, and open in the late afternoon. We speculate that this section is largely insect pollinated. In section MENTZELIOPSIS the flowers open in the morning, and the stamens form a pollen chamber that limits effective pollination to bees with a very special behavior. In section SYMPETALEIA the corollas are tubular, but otherwise the flowers are diverse, with corollas varying from inconspicuous green to highly conspicuous vermilion. We speculate that the latter is butterfly or hummingbird pollinated. Throughout the entire genus, and especially in section Sympetaleia, the basic floral structure has permitted morphological adjustments to a wide range of pollinators. It is important to note that species pairs, that is, species that are more similar to each other than to any other species, may differ in their breeding system. Thus *E. hirta* is a self-pollinating version of *E. cordata*. *Eucnide rupestris,* the most autogamous species, is most like the outcrossing *E. aurea*. Even within *E. aurea* there are two flower forms that we have not seen fit to recognize in formal taxonomy but which differ in their floral biology, one being more self-pollinated than the other. It is also important to emphasize that species as dissimilar as *Eucnide urens* and the species of *Mentzelia* (sect. Bicuspidaria) can have nearly identical pollinating systems, although the basic morphology of the two groups is entirely different.

HYBRIDIZATION

Numerous pollinations were made between plants of different sections, but all of these failed to produce viable seeds and no hybrids were obtained. The crosses attempted were: *Eucnide aurea,* of section Sympetaleia, with *E. bartonioides*, *E. cordata*, and *E. lobata,* of section Eucnide, and reciprocals; *E. urens,* of section Mentzeliopsis, with *E. bartonioides* and *E. lobata,* of section Eucnide. Interspecific pollination within section Eucnide usually resulted in capsules full of viable seeds; plants of two hybrid combinations were grown and their fertility determined.

Eucnide lobata (3298–2) ♀ × *E. bartonioides* (3283–6) ♂. The F_1 plants grew vigorously and flowered profusely. The parents differ greatly in floral morphology (see Fig. 2b, a), and the hybrids were recognized by their intermediate flowers. Two of the hybrid individuals were tested for fertility and both produced less than two per cent good pollen. The large number of chromosomes made exact determination of chromosome pairing in most microsporocytes impossible, but 23 cells at metaphase showed 14 to 16 bivalents with the remainder of the chromosomes involved in multivalents or present as univalents. Heteromorphic bivalents were noted and unequal segregations at anaphase I of 20 to 22 and 19 to 23 were common. Although several flowers were self-pollinated, no viable seeds were obtained.

Eucnide cordata (3300–2) × *E. lobata* (3298–2) and reciprocal. The F_1 plants were vigorous and flowered profusely. The morphology of the flowers was intermediate between the very different flowers of the parents (see Fig. 2c, b). Five hybrid individuals were tested for fertility. All had less than five per cent good pollen. Meiosis in all five plants was irregular. Chromosome pairing was analyzed more or less completely in a total of 43 cells from all five of the F_1 plants. Most cells had about 15 bivalents, with the remainder of the chromosomes involved in multivalents or present as univalents. Heteromorphic bivalents were noted, and anaphase I cells with 21–21 segregations were less frequent than those with unequal segregations. Self-pollinations on all five plants failed to produce seeds. There were no differences noted between the reciprocals.

The data from these cross-pollinations indicate a strong incompatibility between plants of different sections of *Eucnide* that operates at the level of crossability. Within section EUCNIDE hybrids are readily obtained between the most morphologically diverse species, but the F_1 plants, although easily obtained, are sterile.

DISTRIBUTION AND ECOLOGY

The genus *Eucnide* is distributed from the southwestern United States, through Mexico to Guatemala. Section MENTZELIOPSIS, with only one species, *E. urens*, occurs in the Death Valley region of California and in the lower Colorado River basin, with an outlying station in Baja California (MAP 1). *Eucnide urens* is the only species of the Mojave Desert area, and its distribution at elevations usually below 4000 feet does not overlap that of any of the other species of *Eucnide*. The three species of section SYMPETALEIA occur in Baja California, with *E. rupestris* extending into California, Arizona, Sonora, and Sinaloa (MAP 2). All are restricted to the Sonoran Desert region and do not occur above 3000 feet elevation. The species of this section apparently are allopatric — at least there are no data available to indicate that they ever occur as adjacent populations. Section EUCNIDE, with seven species, has the widest range of the three sections. *Eucnide cordata* and *E. hypomalaca* occur in the Sonoran Desert area of Baja California and Sonora (MAP 4). The remaining species of this section inhabit southern Texas, eastern and southern Mexico, and Guatemala (MAPS 3, 4). In the northern portions of this range, about latitude 29° north, the populations usually occur below 3000 feet. In southern Mexico, at latitude 18° north and in Guatemala, at latitude 15° north, the populations occur at elevations from 2000 feet to 8000 feet above sea level.

Some interesting relationships between the breeding system and distribution are found in *Eucnide*. The four species with long, narrow flowers, series *Tubiflorae*, replace each other geographically (MAP 4). In series *Eucnide*, the two species with large flowers, *E. bartonioides* and *E. grandiflora*, also are allopatric, but the third species, *E. lobata*, with small, rotate flowers, is at least geographically sympatric with *E. bartonioides* in part of its range (MAP 3). Species with different flower types, hence placed in different sections or series, often are sympatric. For example, *E. cordata*, of section EUCNIDE, is sympatric with each of the three species of section SYMPETALEIA, and, likewise, *E. xylinea*, of series *Tubiflorae*, is sympatric with both *E. lobata* and *E. bartonioides* of series *Eucnide*. Distribution and floral morphology in *Eucnide* are related through the generalization that species with similar flower types, and thus probably with similar pollination systems, are always allopatric; and conversely, sympatric species always have different flower types and presumably different

FIG. 5. Comparison of vasculature in two sepals and one petal in *Eucnide*, showing insertion of stamens and ovules for four species, adaxial view. a, sepal trace; a′, sepal vein; b, petal trace (with ovules); b′, petal vein; c, stamen traces; d, lateral sepal vein; e, traces to valves and style; f, peripheral veins of ovary wall.

pollination systems. *Eucnide rupestris* with its small, greenish flowers is the strictest inbreeder of section SYMPETALEIA. It is also the most widespread and least variable of the three species in the section.

Although the genus *Eucnide* ranges over a large segment of the southern portion of North America, all eleven species occupy the same general habitat. They all occur primarily on cliffs or rocky slopes, although scattered individuals or transient populations occasionally occur in washes and on lower, more stable slopes below the more permanent populations. Cliffs and rocky slopes are themselves a discontinuous phase of the topography of an area, and, as a result of their restriction to these habitats, the populations of *Eucnide* are relatively small and discontinuous. The negatively phototropic and elongating pedicels found in many of the species of *Eucnide* function to maintain the populations on steep cliffs. When the pedicels turn away from the light they assure that the opening of the capsule is directed toward the face of the cliff when the seeds are shed, increasing the chance for lodging of the seeds in a crack in the rocks. In the species with greatly elongating pedicels, such as *E. bartonioides*, the entire capsule may be forced deep into a crevice before the seeds are released.

TAXONOMIC RATIONALE

To any student of variation and evolution in plants the outstanding feature of *Eucnide* is the great diversity in the morphology of corolla and stamens which contrasts so sharply with the uniformity in all other characters. We submit that a systematic interpretation of such a group should reflect a prior interpretation of flower structure derived from a consideration of the floral biology of natural populations. Clearly, pollination is the process that gives meaning to floral morphology. In *Eucnide,* with its breeding system based on self-compatibility, the pollination system, with floral morphology as its important component, is not only an essential feature of reproduction but also regulates the amount of inbreeding. Even slight differences in floral morphology can make some individuals better inbreeders and others more effective outbreeders. Any situation that favors inbreeding will select for the flower forms that promote self-pollination. Thus the catastrophy of the loss of a pollinator might lead to the rapid evolution of the flower type of a highly autogamous form. This might account for the origin of such autogamous species as *E. hirta* and *E. rupestris*. Conversely, a population that is established as highly autogamous with but a minimum of outcrossing by casual insect visitors might provide the stable base for the selection of an outbreeding form with a very specific adjustment of floral morphology and pollinator. We feel that the origin of very distinct floral types and pollination systems in *Eucnide* may be facilitated by autogamy and more readily visualized if an autogamous stage is imposed between the two very specialized forms. For example, the direct origin of a bee-pollinated flower, such as that of *E.*

urens, from the hawk-moth flower of *E. bartonioides* by the occurrence of a "hopeful monster" in an *E. bartonioides* population is less probable than the transition through an autogamous stage. The striking similarity between the flowers and pollination system of *E. urens* and *Mentzelia involucrata* must be the result of evolutionary convergence. It is difficult for us to imagine either a single step or a series of steps, each with a specific pollinator, that could accomplish this convergence without any resort to autogamy. The autogamous species, therefore, may be phylogenetically very important in *Eucnide* and not merely evolutionary "dead ends." We speculate further that the architecture of the *Eucnide* flower with its fusion of petals and numerous filaments provides for a plasticity that allows for modification to different flower types without alteration of the basic anatomical structure and without incurring any modification of seeds, leaves, or fruits. It is important for us to present our speculations on these matters because they are the compelling thoughts we hold as we subjectively consider variation in *Eucnide* and make the taxonomic decisions required for our classification.

Our comparative study of the anatomical details of floral morphology has pointed out the great overall similarities among the species of *Eucnide* which previously have been overshadowed by the gross differences. Furthermore, we give less taxonomic weight than previous authors to these striking differences in morphology of corolla and stamens because we feel that as components of the pollinating system they are evolutionarily labile. We conclude that there are three coordinate groups in *Eucnide* rather than two as proposed by the previous classification which grouped the taxa into two genera, *Eucnide* and *Sympetaleia*. Our conclusion that these three groups are best considered sections rather than genera rests on our evaluation of their degree of affinity viewed against our understanding of generic levels in the remainder of the family. The differences and similarities between the three sections of *Eucnide* that we propose are equivalent to those between the sections of *Mentzelia*, the group of species most similar to *Eucnide*.

TAXONOMY

The revision of *Eucnide* by Waterfall (1959) has greatly simplified our task of presenting a formal taxonomy, for, although he excluded *Sympetaleia*, his treatment of the species that he did place in *Eucnide* basically is the same as ours. Accordingly, our comments on the classification and nomenclature of these species are limited primarily to presentation of additional information or to minor points of differences in opinion. We present the distribution of each species with detailed dot maps and cite only critical specimens. More extensive citations of specimens are given in Waterfall's revision, and we can provide on request a complete list of specimens. Our discussion of the species of section *Sympetaleia* are somewhat more detailed because these have not been monographed previously.

Eucnide Zucc. Del. Sem. Hort. Monac. 4th unnumbered page. 1844.[1]

Microsperma Hook. Icon. Pl. *pl. 234.* 1839; not *Microspermum* Lag. Gen. et Sp. Nov. 25, 1816.
Sympetaleia A. Gray, Proc. Amer. Acad. **12:** 161. 1877.
Loasella Baill. Bull. Soc. Linn. Paris. **1:** 650. 1887.

Plants herbaceous, pubescent, potentially perennial (or annual), sometimes ± woody at base, the stems usually less than 1 m. long. Leaves alternate, exstipulate, petiolate, the blades pinnately to palmately veined, broadly ovate (rarely obovate) to suborbicular, often cordate at base. Hairs smooth, needlelike, or variously reflexly barbed. Inflorescences ± racemose, terminal or axillary, usually bracteate, of 1 to many flowers. Flowers pedicellate (or pedunculate), 5-merous, ± regular, bisexual, epigynous. Sepals 5, free, persistent. Petals 5, yellow, ± white, greenish or reddish orange, apopetalous, but united at base to staminal tube, or corolla sympetalous. Stamens few to many, maturing centripetally; filaments free above and ± filiform but connate basally into a short tube (and united to base of free petals), or filaments epipetalous; anthers basifixed, exserted or included, oblong to ovoid and 2-locular at anthesis, with longitudinal dehiscence, or reniform peltate and 1-locular at anthesis, with apically confluent dehiscence; pollen oblate, 3-colporate. Gynoecium 5-carpellate; stigma exserted or included and equaling or exceeding the anthers, globular to linear and sometimes twisted, of 5 appressed (sometimes spreading) lobes (or stigma a small terminal tuft of hairs); style usually filiform (sometimes thick), usually elongating and somewhat persistent; ovary inferior, ± spherical, obovoid to clavate, 1-locular, with 5 intruded, transversely cordate parietal placentae; ovules numerous on each placenta, anatropous. Fruits globular to narrowly obovoid, often nodding or reflexed on conspicuous pedicels (or peduncles), dehiscent apically by 5 centrifugally opening triangular valves interior to and opposite the persistent sepals. Seeds minute (usually less than 2 mm. long), numerous, ± oblong, grooved or ribbed longitudinally, sometimes spirally twisted, pointed at the micropylar end, ± rounded at chalazal end. Seedling cotyledons subreniform to ovate, short-petiolate. TYPE SPECIES: *E. bartonioides* Zucc. (Name from Greek, *eu*, pretty, and *knide*, nettle, "Schönnessel.")

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[1] The place of publication for this name is "Delectus Seminum in Horto R. Botanico Monacensi Collectorum Anno 1844," a list of seeds offered by the Munich Botanical Garden. The name *Eucnide bartonioides* first appeared on the 2nd page with an asterisk which leads one to the 4th (last) page where both the generic and the specific characters are set forth in Latin. The description closes with "Zuccarini in Act. Monac. Acad. inedit," doubtless a reference to Abhandl. Bayer. Akad. Wiss. 4(2): 5. *pl. 1.* 1845, where the identity of this taxon is established by the plate. In the absence of other type material this plate ought to be accepted as the lectotype for *E. bartonioides*. The final printed line reads "Monachii, 28 Dec. 1844." The only original of this publication known to us is deposited in the library of the Conservatoire et Jardin Botaniques, Genève. We are grateful to C. E. B. Bonner and J. E. Dandy for locating this rare publication and for making a photocopy available to us.

The generic name *Microsperma*, first used in Loasaceae for *M. lobata* Hook. in 1839, is earlier than the generic name *Eucnide* Zuccarini, published at the end of 1844. In Loasaceae, *Microsperma* was used in original descriptions also for *M. rudis* Schauer (1847) and *M. grandiflora* Groenland (1861). Since *Microspermum* had been used in Compositae by Lagasca in 1816 the name *Microsperma* in Loasaceae was rejected as a homonym in 1900 by Urban & Gilg in favor of *Eucnide*. If the view of Urban & Gilg is regarded as contrary to Art. 75 (a subjective decision) then it will be necessary to conserve *Eucnide* or, failing this, to adopt the name *Microsperma* for this genus. We have submitted a proposal for the conservation of the well known name *Eucnide*.

The genus *Eucnide*, including 11 species, is divided into three sections. Two series are distinguished in section EUCNIDE on the basis of the form of the corolla. In series *Eucnide*, primarily of eastern Mexico, *E. bartonioides* and *E. grandiflora* are very similar, differing principally in size, color of the corolla, and in distribution. *Eucnide bartonioides* and *E. lobata* normally are strikingly dissimilar but a few specimens, ironically, almost seem to bridge the morphological gap, and the ranges of the two species overlap. Series *Tubiflorae* is widely distributed in Mexico. Three of the species, *Eucnide cordata*, *E. hirta*, and *E. hypomalaca*, are quite similar, differing mostly in corolla size, inflorescence, pubescence, elongation of the fruiting pedicels, and position of the stigma in relation to the anthers. As in series *Eucnide*, these species are isolated geographically from one another and from the more distinctive *E. xylinea*, also of series *Tubiflorae*.

The section MENTZELIOPSIS of the far southwestern United States, comprised of a single species, *E. urens*, is very different morphologically from all other species of the genus.

Section SYMPETALEIA, almost confined to Baja California, is composed of three species that are strikingly dissimilar from one another in morphology and color of the corolla.

KEY TO THE SPECIES

1. Corolla united for at least ½ its length into a narrow, relatively long tube (8–10 mm.) with a ring of hairs below the ± sessile, included anthers.
   2. Corolla salverform, bright yellow or reddish orange; sepals half the length of the corolla tube or less; fruiting pedicels elongating greatly (to 27 cm.); southern Baja California. .... 9. *E. aurea.*
   2. Corolla ± cylindrical, with erect lobes, dark green with shadings of yellow and/or brown; sepals at least half as long as the corolla tube; fruiting pedicels reflexed, elongating only a few centimeters; Baja California, local in southern California, southwestern Arizona, Sonora, and Sinaloa. .... 10. *E. rupestris.*
1. Corolla united for ¼ or less of its length into a relatively short, ± inconspicuous tube (1–8 mm.); ring of hairs lacking; all anthers on long filaments, exserted or included.
   3. Anthers reniform (sporogenous tissue continuous over the connective).

exposed, 1-locular and peltate at anthesis, the dehiscence confluent apically; corolla white or pale yellowish, to 10 mm. long; stigma among the anthers; fruiting pedicels elongating at least several centimeters; rare and local, eastern Baja California Sur. . . . . 11. *E. tenella.*

3. Anthers ovate to oblong (sporogenous tissue interrupted apically by the connective), 2-locular at anthesis, the dehiscence not confluent; flowers mostly larger.
    4. Stigma and stamens both distinctly included, about ½ to ¾ as long as the open, funnelform, rigid corolla; filaments linear, stout, compressed around the style; fruiting pedicels 1–2 cm., not elongating; desert regions of California, Nevada, Utah, Arizona; local in northeastern Baja California. . . . . 8. *E. urens.*
    4. Stigma and stamens exserted or clearly exposed; Texas, Mexico, Guatemala.
        5. Corolla open and stamens spreading (series *Eucnide*).
            6. Corolla rotate, to about 12 mm. long or 2 cm. wide; outer stamens shorter than stigma, inner stamens slightly exceeding the minute, subcapitate stigma; fruiting pedicels 1–2 cm., not elongating; northeastern Mexico to Puebla. . . . . 3. *E. lobata.*
            6. Corolla open-funnelform and larger.
                7. Stigma ± linear-truncate, to about 6 mm. long, less than 1 mm. broad, sometimes separating into 5 narrow lobes; sepals to about 2.2 cm. long; petals to about 4 cm. long; stamens to 5 cm. long; style to 5.5 cm. long; fruiting pedicels elongating up to 33 cm.; Texas, eastern Mexico south to San Luis Potosí. . . . . 1. *E. bartonioides.*
                7. Stigma obconical, to 2.5 mm. broad, 2–3 mm. long, 5-lobed; sepals 2.5–5 cm. long; petals 5.8–8 cm. long; stamens 8–11 cm. long; style 10–12 cm. long; Oaxaca and Guatemala. . . . . 2. *E. grandiflora.*
        5. Corolla ± cylindrical, the petals broadly imbricate and holding the stamens in a long, narrow cluster (series *Tubiflorae*).
            8. Leaves small, to 15 mm. long, 10 mm. wide, villous-canescent; flowers solitary at ends of heavy branches; corolla to 25 mm. long, fruiting pedicels to 2.5 cm. long; rare, western central Coahuila and southwestern Tamaulipas near Nuevo León boundary. . . . . 7. *E. xylinea.*
            8. Leaves larger, 3–12 cm. long, 2.5–10 cm. wide, pubescent but not villous-canescent; flowers usually clustered; corollas 2–4 cm. long.
                9. Inflorescence many flowered, usually on a distinct peduncle, hence above the leaves; petals 1.5–2.5 cm. long; pedicels not elongating in fruit; Baja California, islands of the Gulf of California, and near Guaymas, Sonora. . . 4. *E. cordata.*
                9. Inflorescence few flowered, not on a distinct peduncle; petals 2–4 cm. long; pedicels sometimes elongating in fruit.
                    10. Pubescence on pedicels with simple hairs conspicuously longer than the reflexly barbed hairs; pedicels greatly elongate in fruit; south-central Mexico and Guatemala. . . . . 5. *E. hirta.*

10. Pubescence on pedicels with reflexly barbed hairs at least as long as the simple hairs; fruiting pedicels unknown; Sonora, southwestern Chihuahua, and northern Sinaloa. .... 6. *E. hypomalaca.*

1. **Eucnide bartonioides** Zucc. Del. Sem. Hort. Monac. 4th unnumbered page. 1844.[1]

Mentzelia gronoviaefolia Fisch. & Mey. in Fisch., Mey. & Ave-Lallemant, Index Sem. Hort. Petrop. **10**: 54. 1845 (not before 3 Feb.).

Microsperma bartonioides Walp. Repert. Bot. **5**: 777. 1845–46 (probably 1846).

Inflorescences of a few flowers, terminal, or the flowers axillary. Corolla 1–4 cm. long, yellow, paler below, the petals spreading. Anthers exserted, slightly exceeded by the linear (to 6 mm. long) stigma. Pedicels to 3–4 cm. long at anthesis, usually elongating to 15 cm. or more in fruit.

Map 1. Distribution of section Mentzeliopsis in the southwestern United States and Baja California, Mexico.

The size of the corolla (and the leaves) is quite variable. The small flowered forms can be confusingly similar to depauperate plants of *Eucnide lobata* even though these two species normally are quite distinct. (See discussion of *E. watsonii* under *E. lobata.*)

DISTRIBUTION. United States: southwestern Texas; and Mexico: northeastern states southward into San Luis Potosí (MAP 3). HOLOTYPE: The descriptions were based on plants grown in the Munich Botanical Garden from seeds probably collected by de Karwinski (perhaps number *285*, gathered in Chihuahua, Mexico, in 1843; not seen by the present authors). Regarding the latter, Urban & Gilg (1900, p. 108) remarked: "Colitur in hortis Europaeis ab anno 1844 e seminibus Karwinskianus." At least 170 specimens have been annotated.

2. **Eucnide grandiflora** (Groenl.) Rose, Contr. U. S. Natl. Herb. **3**: 317. 1895.

Microsperma grandiflora Groenl. Rev. Hort. **1861**: 349. *fig. 84.* 1861.
Eucnide guatemalensis Standl. & Steyerm. Field Mus. Publ. Bot. **23**: 178. 1944.
Eucnide grandiflora var. *guatemalensis* (Standl. & Steyerm.) Waterfall, Rhodora **61**: 242. 1959.

Inflorescences of a few large flowers, terminal, often each flower subtended by a small leaf. Corolla to 8 cm. long, nearly white, the petals spreading. Anthers exserted, the filaments to 11 cm. long. Stigma exceeding the anthers, conspicuously enlarged, 2–3 mm. long, 2–2.5 mm. broad, the stout style to 10–12 cm. long. Pedicels to about 4 cm. long, not elongating in fruit.

The closest affinity is with *Eucnide bartonioides. Eucnide guatemalensis* (holotype, *Steyermark 50818,* Guatemala, F), known only from the type collection, appears to be conspecific with *E. grandiflora*; varietal status seems unnecessary.

This species first became known through the illustrated description of *Microsperma grandiflora* Groenland. The plant described was grown in Bruxelles from seeds obtained from the firm of Vilmorin-Andrieux, France. The original source of material may have been a collection by Roezl made in Mexico before the end of 1861. Rose based his new combination on Groenland's description and plate of *M. grandiflora* on the grounds of the unusually large flowers and the color of the petals. The very distinctive character of the stigma, however, is not shown in Groenland's plate, which otherwise more or less resembles *Eucnide bartonioides*. In the apparent absence of holotype or isotype, the above plate should be taken as lectotype for both Rose's and Groenland's binominals. The material designated by Waterfall as "lectotype" *C. G. Pringle 10077*, US 462126; see Rhodora **61**: 242. 1959) would be a neotype and inappropriate in view of the above plate.

DISTRIBUTION. Mexico: State of Oaxaca; and Guatemala: Huehuetenango (MAP 3). SUGGESTED LECTOTYPE: The *Fig. 84,* p. 350, in Groenland, Rev. Horticole **1861**: 349–351. 1861. At least 17 specimens have been annotated.

3. **Eucnide lobata** (Hook.) A. Gray, Boston Jour. Nat. Hist. **6**: 192. 1857.

Microsperma lobatum Hook. Icon. Pl. **3**: *pl. 234.* 1839, "*Microsperma lobata.*"
Mentzelia lobata (Hook.) Walp. Repert. Bot. **2**: 224. 1843.
Eucnide floribunda S. Wats. Proc. Amer. Acad. **17**: 358. 1882.

Inflorescences of few to many flowers, usually more or less terminal (or flowers sometimes solitary, axillary). Corolla usually 6–12 (or 15) mm. long, rotate, the lobes broad. Anthers and stigma exserted and usually about equal. Stigma capitate (or sometimes about 1 mm. long, oblong). Pedicels short (rarely 2 cm. long) at anthesis, usually reflexed in fruit but not elongating conspicuously.

The stamens developmentally are in two ranks. The inner ones are convolute around the base of the style when the flowers first open and the outer ones are extended but shorter than the stigmas. On the second day the inner stamens elongate past the outer ones and equal the length of the stigma. A very few collections have giant-sized corollas. *Eucnide floribunda* (holotype, *E. Palmer 832*, Coahuila, GH) was based upon somewhat distinctive specimens with strict, elongated, more or less secund inflorescences. We have not seen the holotype of *Microsperma rudis* S. Schauer, Linnaea **20**: 721. 1847 (presumably based upon *Aschenborn 233*, collected in Mexico); it was the opinion of Gray (1857), Urban & Gilg (1900), and Waterfall (1959) that this binomial belonged in synonymy under *E. lobata*. The northeast margin of distribution of *E. lobata* overlaps the range of *E. bartonioides*, and there would be the possibility of some hybridization. Although these species normally are strikingly distinct, some depauperate specimens are difficult to determine and, in some instances, could be annotated as extreme variants of either species.

Eucnide watsonii Urban & Gilg, Nova Acta Akad. Leop.-Carol. **7**: 105. 1900. was based upon plants with few and rather small flowers (petals about 10 mm. long; stamens about equalling the petals) on relatively long pedicels (2–5 cm. long). The holotype, *E. Palmer 1067* (K), was collected between Tampico and San Luis Potosí, Mexico. An isotype at the Gray Herbarium also agrees with the above description and confirms, more or less, the placement by the original authors of this material between *E. lobata* and *E. bartonioides*. Waterfall (1959) treated the binomial as a synonym of *E. lobata*. During our study we have placed it alternately in synonymy under both *E. lobata* and *E. bartonioides*. Several other herbarium collections can be matched more or less with the holotype and isotype of *E. watsonii* but we remain in doubt regarding the biological status of this material.

DISTRIBUTION. Mexico: eastern states from Coahuila to Puebla (MAP 3). HOLOTYPE: *Berlandier*, Santa Catarina, near Monterrey, Nuevo León, Mexico (K). This sheet has on it pencil sketches for the plate that appeared with the original description in *Icones Plantarum*. At least 142 specimens have been annotated.

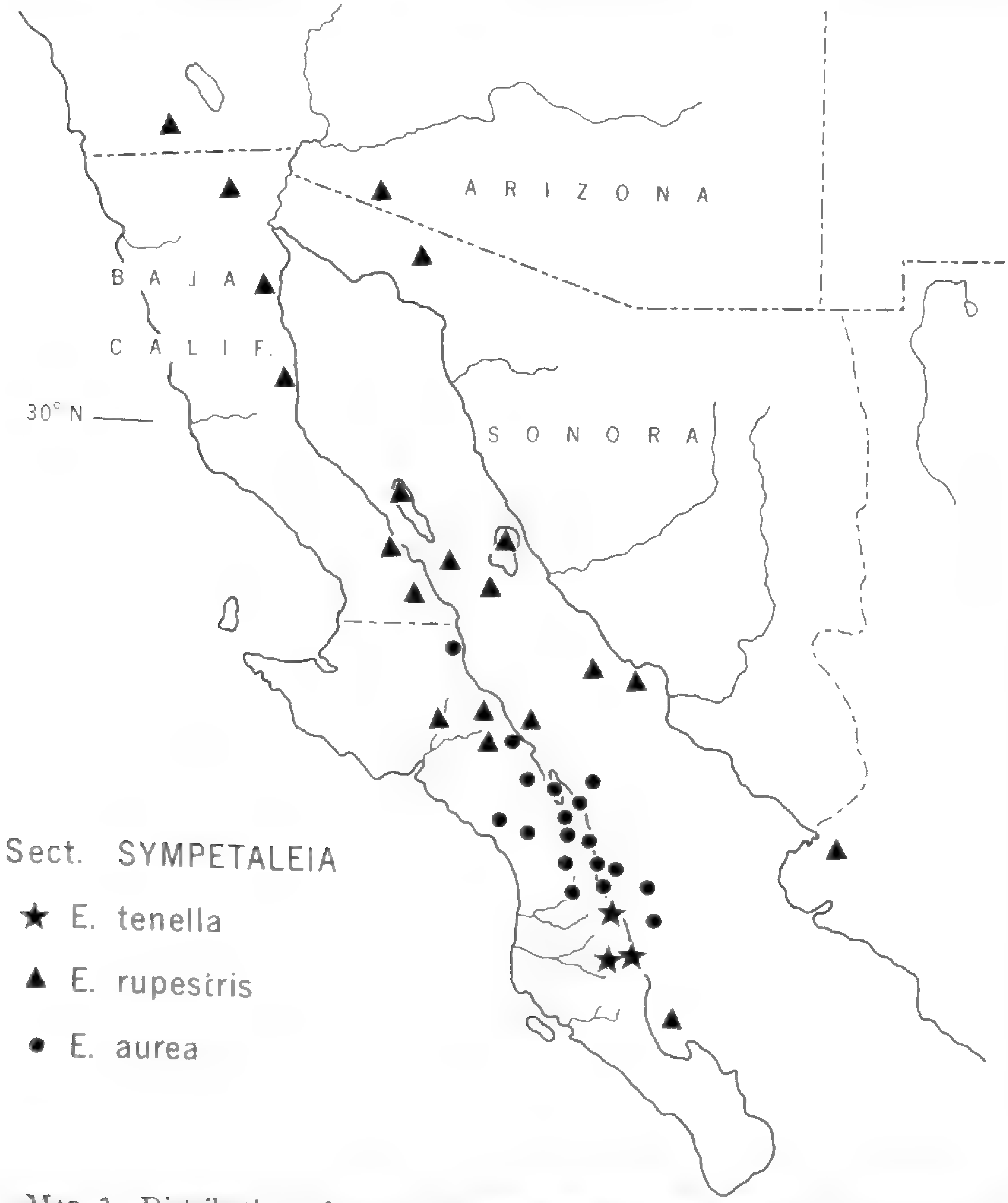
Series **Tubiflorae** Thompson & Ernst, ser. nov.

Series in sect. Eucnide, sed differt: corolla longe cylindrica, petala late imbricata, quasi tubus angustus, stamina in fasce angusto. Circa 4 species inclusae. TYPUS: *E. cordata* (Kell.) Kell. ex Curran.

4. **Eucnide cordata** (Kell.) Kell. ex Curran, Bull. Calif. Acad. 1: 137. 1885.

Mentzelia cordata Kell. Proc. Calif. Acad. 2: 33. 1860.

Inflorescences of many flowers, crowded, terminal, and much branched (sometimes elongating in fruit). Corolla about 1.5–2.5 cm. long, white



MAP 2. Distribution of section SYMPETALEIA in the region of the Gulf of California, Mexico.

(or yellowish), narrowly cylindrical, holding the stamens in a narrow cluster. Anthers exserted, well exceeded by the small, more or less clavate stigma. Pedicels short (rarely to 2.5 cm. long), not appreciably elongating in fruit.

This species most closely resembles *E. hirta*, of south-central continental Mexico, but is distinguished by its almost white corolla, very long exserted style, and pedicels which do not elongate.

DISTRIBUTION. Mexico: Baja California Norte and Sur (including Cedros Island and some islands in the Gulf of California) and near Guaymas, Sonora. (MAP 4). HOLOTYPE: *Dr. J. A. Veatch*, "Cerros Island." The species has been recollected on Cedros Island, its only insular station on the Pacific side of Baja California, by several botanists including Greene, Palmer, Anthony, and Mason. None of the original material seems to have survived at the California Academy of Sciences. An apparent isotype is preserved at the Gray Herbarium and probably this should be taken as the lectotype. At least 190 specimens have been examined.

5. **Eucnide hirta** (G. Don) Thompson & Ernst, comb. nov.

Mentzelia hirta G. Don, Gen. Syst. Gard. Bot. **3**: 66. 1834.
Eucnide sinuata S. Wats. Proc. Amer. Acad. **17**: 358. 1882.
Eucnide nelsonii Rose, Contr. U.S. Natl. Herb. **12**: 286. 1909.
Eucnide pringlei Rose, Contr. U.S. Natl. Herb. **12**: 287. 1909.

Inflorescences of few to several flowers, more or less terminal or axillary. Corolla about 2.5 (4) cm. long, yellow, narrowly cylindrical, holding the stamens in a narrow cluster. Anthers exserted. Stigma linear (or narrowly oblong), to 2 mm. long, more or less equalling the anthers (or sometimes exceeding them). Pedicels well developed, often 2 cm. long at anthesis, elongating in fruit to as much as 8 cm.

The holotypes of *Eucnide sinuata* (*Botteri 266*, GH) and of *E. nelsonii* (*E. W. Nelson 6926*, Michoacán, US 399295) are conspecific with *E. hirta*. *Eucnide pringlei* var. *pringlei* (holotype, *C. G. Pringle 10077*, Guerrero, US 462195; *H. E. Moore, Jr., 2122*, Hidalgo, GH), known only from two collections, seems to be a robust form of *E. hirta* with larger flowers. *Eucnide hirta*, distinguished by its yellow corolla, shorter style, and elongating pedicels, appears to be a continental counterpart of *E. cordata*. (See also *E. hypomalaca*).

DISTRIBUTION. Mexico: south-central states, from San Luis Potosí to Guerrero; and discontinuously in Guatemala: Jalapa (MAP 4). HOLOTYPE: *Sessé & Mociño*, Mexico (BM). At least 57 specimens have been annotated, many of them as *E. sinuata*, but we now know that the correct name is *E. hirta*.

6. **Eucnide hypomalaca** Standl. Field Mus. Publ. Bot. **22**: 41. 1940.

Eucnide pringlei var. *hypomalaca* (Standl.) Waterfall, Rhodora **61**: 239. 1959.

Inflorescences of few flowers, terminal (or flowers axillary). Corolla large, to about 4 cm. long, white, narrow, holding the stamens in a narrow cluster. Anthers and stigma exserted.

It is not known whether the pedicels elongate in fruit. The flowers suggest a giant-sized form of *Eucnide cordata*, perhaps with the petals slightly spreading. The species is known from only five localities. We find this material distinct from *E. hirta* (and also from *E. pringlei* var. *pringlei* which we consider an unusually large form of *E. hirta*). The species is distinguished by its distribution, the large, rather coarse flowers, the whitish, heavily veined corolla, and the prominent barbed hairs of the pedicels.

DISTRIBUTION. Mexico: northern and (discontinuously) southern Sonora and near the boundaries of adjacent northern Sinaloa and southwestern Chihuahua (MAP 4). HOLOTYPE: *H. S. Gentry 1315*, Sonora (F). OTHER SPECIMENS: Chihuahua: *Hartman 1016* (GH, UC); *Hewitt 272* (GH). Sinaloa: *Breedlove 1507* (LA); *Mason & Brewer 1855* (UC). Sonora: *Gentry 3021* (GH, MO); *Gentry 14445* (US); *Kaiser s.n.*, April 17, 1951 (CAS).

7. **Eucnide xylinea** C. H. Muller, Amer. Midl. Nat. **27**: 487. 1942.

Flowers solitary, terminal on short leafy shoots. Corolla to 2.5 cm. long, yellow, narrowly cylindrical, holding the stamens in a narrow cluster. Anthers and stigma exserted. Pedicels 2–3 cm. long, not elongating in fruit.

This very distinctive species is distinguished by its solitary flowers, especially matted habit, and villous-canescent small leaves (to about 1.5 cm. long). It is known only from three stations.

DISTRIBUTION. Mexico: western central Coahuila and discontinuously in southwestern Tamaulipas near the southern Nuevo León boundary (MAP 4). HOLOTYPE: *C. H. Muller 3311*, Coahuila (US 2109944). OTHER SPECIMENS: Coahuila: *Johnston 9003* (GH); *Muller 3311* (GH, UC); *Stewart 1075* (GH). Tamaulipas: *Stanford, Lauber, & Taylor 2449* (DS, RSA).

Section **Mentzeliopsis** Thompson & Ernst, sect. nov.

Flores apopetali, sed petalis basi cum tubo filamentarum breviter coalitis. Antherae in anthesi biloculares. A sectione Eucnide differt: stigma antheraeque in corolla inclusae, staminum filamenta crassa interne obliqua, receptaculum pollinare circumstylare formantia. Species unica. TYPUS: *E. urens* Parry.

8. **Eucnide urens** Parry, Amer. Nat. **9**: 144. 1875.

Mentzelia urens Parry ex Gray, Proc. Amer. Acad. **10**: 71. 1874 (non Vell. Fl. Flum. **5**: 97. 1825).

Eucnide synandra A. Nelson, Bot. Gaz. **47**: 428. 1909.

Eucnide parryi House, Bull. N.Y. State Mus. **234**: 67. 1922 (a substitute name for *E. urens*).

Inflorescences of several flowers, terminal (the flowers sometimes subtended by small leaves). Corollas about 5 cm. long, pale yellowish white, the petals rigid, spreading. Stamens included, the filaments somewhat thick, slanted inward around the stout style. Stigma included, slightly exceeding the anthers. Pedicels short, to about 1.5 cm. long, neither reflexed nor elongated in fruit.

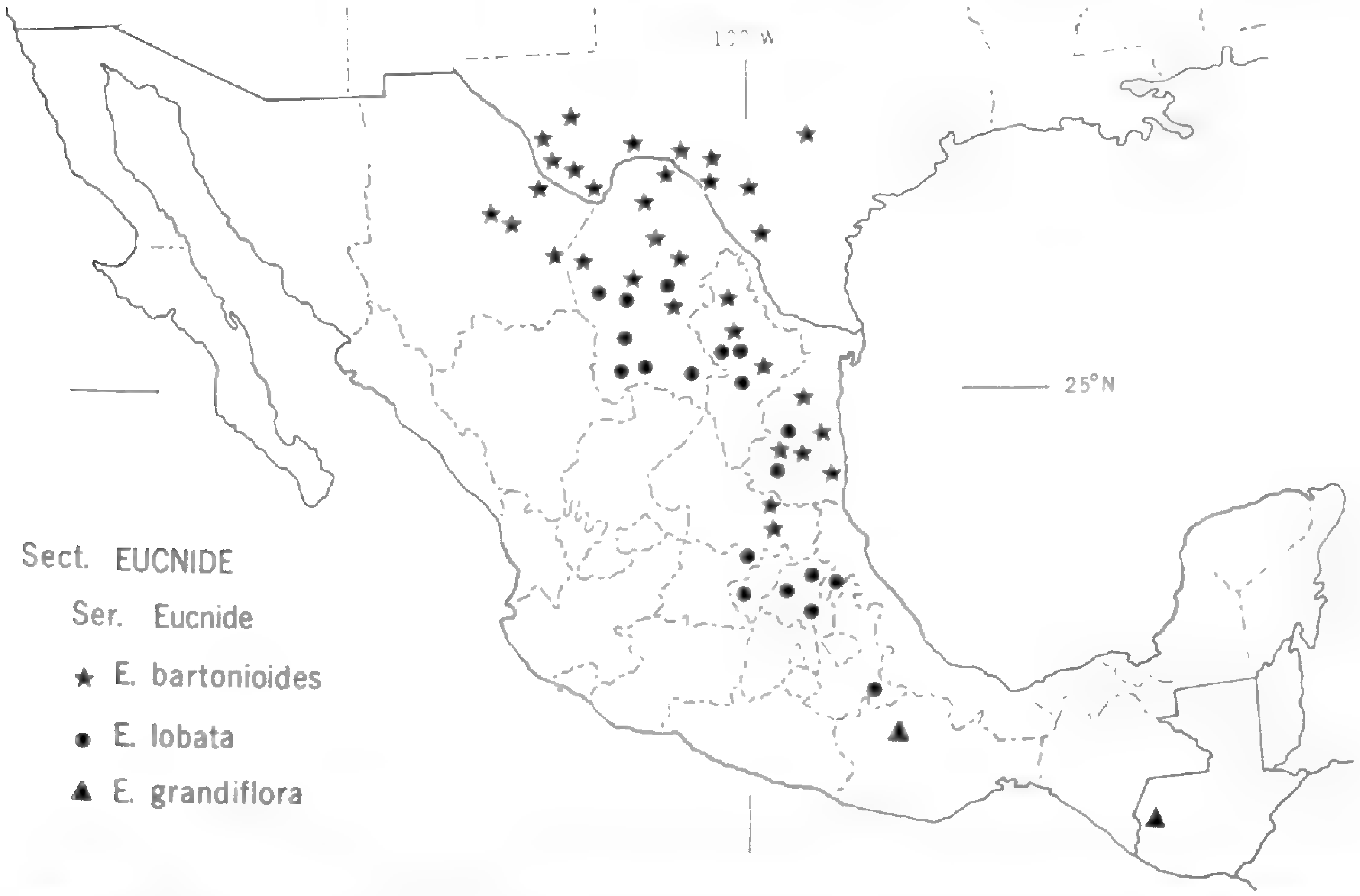
DISTRIBUTION. United States: eastern California, southern Nevada, southwestern Utah, western Arizona, and discontinuously in Mexico: eastern Baja California Norte (MAP 1). LECTOTYPE: *C. C. Parry 79*, Utah (GH); see U. T. Waterfall, Rhodora **61**: 236. 1959. At least 196 specimens have been annotated.

Section **Sympetaleia** (A. Gray), Thompson & Ernst, stat. nov. Basionym: *Sympetaleia* A. Gray, Proc. Amer. Acad. **12**: 161. 1877.

Classes 2 morphologici: corollae tubus quam lobi longior, antherae inclusae, filamenta brevia (typo incluso); vel corollae tubus quam lobi brevior, antherae plus minusve exsertae, filamenta longa. Differt: corolla vere sympetala, antherae anthesin uniloculares, stamina quasi epipetala. Species 3 inclusae. TYPUS: *Sympetaleia aurea* A. Gray = *Eucnide aurea.*

9. **Eucnide aurea** (A. Gray) Thompson & Ernst, comb. nov.
Sympetaleia aurea A. Gray, Proc. Amer. Acad. **12**: 161. 1877.

Inflorescences usually of many crowded flowers, terminal, sometimes



MAP 3. Distribution of section EUCNIDE, series *Eucnide*, in Texas, Mexico, and Guatemala.

elongating appreciably in fruit (or flowers sometimes solitary, axillary). Corolla 1–2 cm. long, bright yellow or strong reddish orange, salverform, the lobes broad and rounded. Stamens epipetalous, included, the anthers more or less sessile; a ring of upwardly curved hairs below the stamens. Style filiform, the stigma minute, situated among the anthers (or sometimes barely exposed in the mouth of the corolla tube). Pedicels usually short at anthesis but elongating conspicuously, sometimes to 27–33 cm. in fruit.

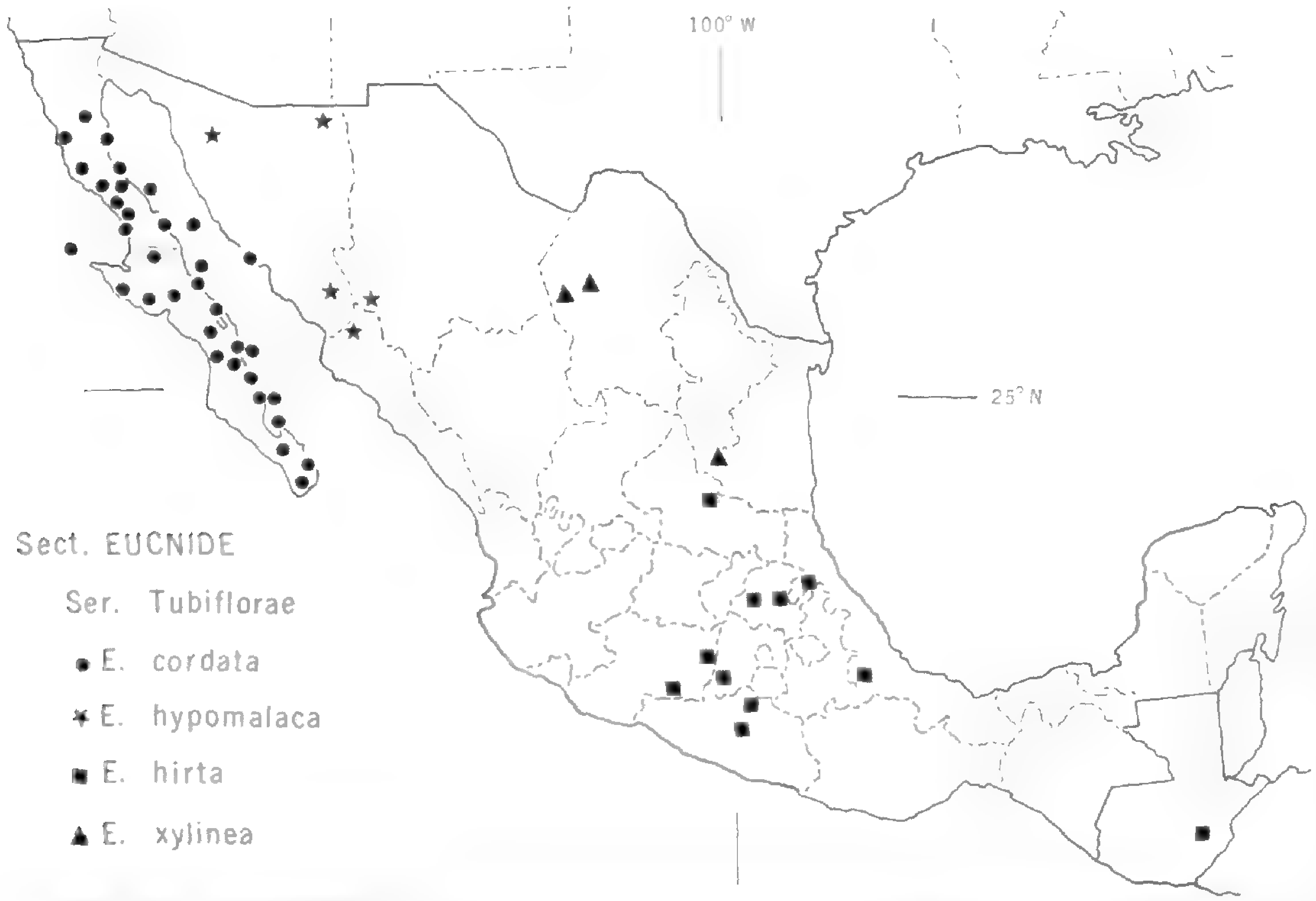
This species probably includes two taxa: one has smaller yellow corollas with stigma included; the other larger reddish orange corollas with stigma becoming slightly exposed.

DISTRIBUTION. Mexico: Baja California Sur, including some islands in the Gulf of California (MAP 2). HOLOTYPE: *Dr. Thomas H. Streets*, Pulpito Point (GH). At least 70 specimens have been annotated.

10. **Eucnide rupestris** (Baill.) Thompson & Ernst, comb. nov.

Loasella rupestris Baill. Bull. Soc. Linn. Paris **1**: 650. 1887.
Sympetaleia rupestris (Baill.) S. Wats. Proc. Amer. Acad. **24**: 50. 1889.

Inflorescences usually of many crowded flowers, terminal, sometimes elongating appreciably in fruit (or flowers sometimes solitary, axillary). Corolla 1–1.5 cm. long, mostly greenish with shadings of brown and/or yellow, narrowly cylindrical and inconspicuous on the plants, the lobes to 5 mm. long, rigid and erect. Stamens epipetalous, included, the anthers subsessile or on short, stout filaments, with a ring of upwardly curved



MAP. 4. Distribution of section EUCNIDE, series *Tubiflorae*, in Mexico and Guatemala.

hairs below the stamens. Style short and thick, the stigma not exceeding the lower anthers. Pedicels usually short at anthesis, sometimes reflexed in fruit and elongating up to 2 cm.

DISTRIBUTION. United States: Southern California and southwestern Arizona; and Mexico: Baja California Norte and Sur including some islands in the Gulf of California, also northwestern Sonora and discontinuously in northwestern Sinaloa (MAP 2). HOLOTYPE: *Thièbault 1099* (P); photograph (A) examined, courtesy of R. A. Howard. At least 55 specimens have been annotated.

11. **Eucnide tenella** (I. M. Johnst.) Thompson & Ernst, comb. nov.

Sympetaleia tenella I. M. Johnst. Proc. Calif. Acad. IV. **12:** 1106. 1924.

Flowers few, small, mostly axillary. Corolla about 8 mm. long, white (? or yellowish), the tube inconspicuous, the lobes narrow and loosely spreading. Anthers exserted on filiform filaments, spreading. Stigma minute, terminal on the filiform style and equalling the staminal filaments in length; ring of hairs below the stamens lacking. Pedicels filiform, about 1.5 cm. long at anthesis, elongating in fruit to 8–10 cm. The corolla while distinctly sympetalous and short tubular, very closely approaches in form the corollas of sect. EUCNIDE, series *Eucnide,* thus differing conspicuously in form from the corollas of the other two species of sect. SYMPETALEIA. The species has been collected only three times.

DISTRIBUTION. Mexico: eastern Baja California Sur (MAP 2). HOLOTYPE: *I. M. Johnston 3091,* Agua Verde Bay (CAS 1239). Other specimens: *Wiggins 15546* (DS); *Wiggins, Carter & Ernst 280* (DS, LA, OKLA).

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THE GENUS DUABANGA

Don M. A. Jayaweera

The genus *Duabanga* was first suggested by Buchanan-Hamilton as a new genus with characters connecting the Lagerstroemias and the Sonneratias. Probably the name is derived from "Duyabangga" a vernacular name for the tree in Tripura. Roxburgh (1832) had collected and described as *Lagerstroemia grandiflora* a plant which was the same as that collected by Hamilton and sent to Sir Joseph Banks in 1798 and described by him as *Duabanga sonneratioides* in 1835. Roxburgh's *L. grandiflora* was later transferred to the genus *Duabanga* by Walpers. *Duabanga* and *Sonneratia* compose the family Sonneratiaceae.

The two genera have been placed under various other families by different authors. Lindley (1836) placed *Sonneratia* in the tribe Myrteae (Myrtaceae) and *Duabanga* in Lagerstroemieae (Lythraceae) while Miquel (1855) placed *Sonneratia* in the tribe Sonneratieae (Myrtaceae) and *Duabanga* in Lythreae (Lythraceae). Bentham and Hooker (1867) included both genera in the Lythreae (Lythraceae) and this was adopted by Koorders and Valeton (1894), while Koehne excluded both genera from his monograph on the Lythraceae. Niedenzu (1892) placed *Duabanga* in the family Blattiaceae along with *Sonneratia* as a synonym to *Blatti*. Engler (1897) formed the family Sonneratiaceae to include the two genera.

The family is distinguished from the Lythraceae by flower, pollen, and anatomical characteristics. In Sonneratiaceae the ovary is partially fused to the receptacle, forming a distinctive half-inferior fruit. The smooth pollen has two or three regularly placed germ pores, and fiber bundles are distributed in the pith.

The small genus *Duabanga* consists of three species, *D. moluccana* Bl., *D. grandiflora* (Roxb. ex DC.) Walp. and *D. taylorii* sp. nov., all large trees growing in the rain forest extending from the southeastern Himalaya to New Guinea and on the islands in between. A new species, *Duabanga taylorii*, described here, is named for Sir George Taylor, Director of the Royal Botanic Gardens, Kew. The seed of this species was received, probably from Java, in 1853, and four trees planted in the Royal Botanic Gardens, Peradeniya, have now reached an average height of over 128 feet, 26 feet in girth at breast height, and a spread of 79 feet (Fig. 6).

Key to the Species

Stamens uniseriate.
  Stamens 12; trunk columnar; flowers 4-merous; ovary dome-shaped; fruit 1–3.7 cm. long. .... *D. moluccana.*

Stamens 24–45; trunk branched 1.8–6 m. from ground; flowers 4- or 5-merous; ovary ovate; fruit 1.5–2.5 cm. long. . . . . *D. taylorii.*
Stamens biseriate; trunk straight and columnar; flowers 6-merous; stamens indefinite; ovary conical; fruit 3–4.2 cm. long. . . . . *D. grandiflora.*

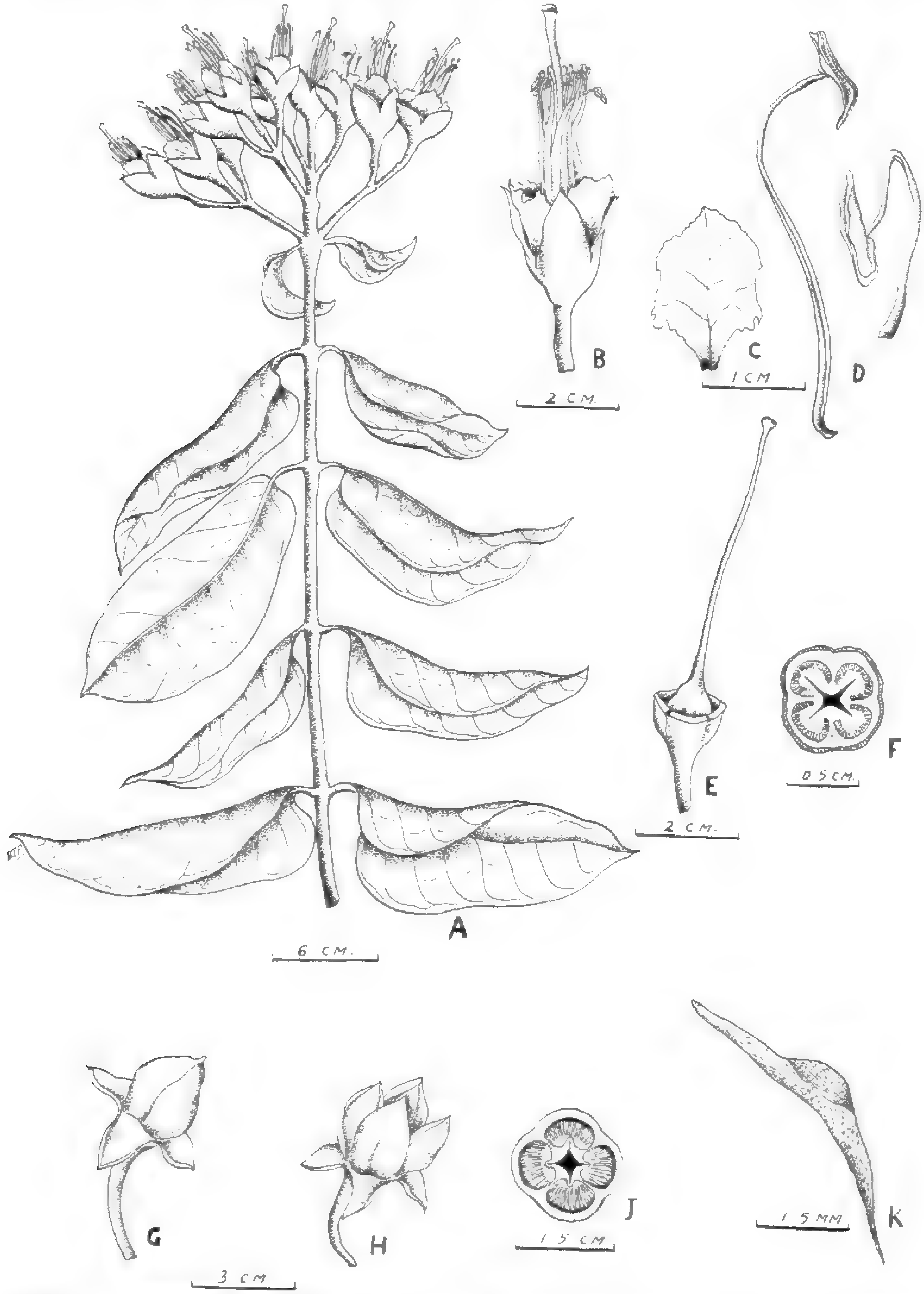


FIG. 1. *Duabanga moluccana.* A, branch with inflorescence; B, flower, lateral view; C, petal; D, stamens; E, pistil of the flower with the calyx removed; F, transverse section of the ovary; G, fruit, lateral view; H, dehiscing fruit; J, transverse section of a fruit before dehiscence; K, seed.

Duabanga moluccana Blume, Mus. Bot. Lugd.-Bat. **1**: 109. 1849. (FIG. 1)

Duabanga borneensis R. Knuth, Repert. Sp. Nov. **38**: 121. 1935.

Large or medium-sized trees, 8–42.4 m. tall, trunk more or less columnar, branching at 23 m. from ground, unbuttressed or faintly buttressed, young branchlets quadrangular, winged, becoming terete when mature, with 9–15 pairs of leaves; young leaves and stems covered with short adpressed hair but becoming glabrescent, internodes 2–9.5 cm. long, with 2 pairs of projections corresponding to bases of wings at base, branches brittle; leaves simple, opposite, oblong, oval, ovate, lanceolate or ovate-oblong, 4–32.6 cm. long, 2.1–12.5 cm. broad, more or less cordate with rounded lobes or rounded at base, acuminate, acute, coriaceous, glabrous, entire, costa prominent below with 5–28 pairs of widely patent, arcuate, lateral veins merging into an intramarginal vein, petiole 0.3–1.2 cm. long; flowers regular, bisexual, perigynous in simple or compound, dichasial, terminal, minutely pubescent corymbs, buds ovoid-oval, pubescent, 0.4–2 cm. long, 0.3–1.5 cm. broad, bracts lanceolate or spathulate, caducous, 0.65–1.1 cm. long, hairy, pedicels 0.2–2 cm. long, strongly quadrangular, ridges extending to fused margins of sepals; calyx funnel-shaped, 1–2.3 cm. in diameter, segments 4, oblong-ovate, 0.5–1.6 cm. long, 0.4–1 cm. broad, short acuminate, acute, thick, fleshy, green, persistent in the fruit; petals 4, greenish cream-white, with center pink, 1.6–1.8 cm. long, 0.8–1.1 cm. broad, short clawed, valvate, overlapping in bud, caducous; stamens 12, uniseriate on a narrow circular rim round the ovary, filaments greenish white, broad and flat at the base, filiform, recurved, caducous, about 3 cm. long, anthers brownish white; ovary half-inferior, dome-shaped, broader than tall, 0.5 cm. long, 4-locular, with numerous ovules on cushion-shaped placentae, style 2.5–4 cm. long, greenish yellow, stigma faintly 4-lobed, dark green with a brown center; fruit oblong-ovoid, loculicidally dehiscent, capsule 4-valved, 1–3.7 cm. long, 0.8–2 cm. broad, slightly narrowed at base on a stout quadrangular pedicel with persistent calyx segments; seeds numerous, testa drawn out on either side, 5 mm. long from end to end.

ILLUSTRATIONS. VIDAL, Synopsis de Familias. Atlas *pl. 52, fig. F, 1–5.* 1883; KOORDERS & VALETON, Atlas der Baumarten von Java **4**: *fig. 784.* 1918; JAYAWEERA & HOWARD, Baileya **10**: *fig. 5.* 1962.

DISTRIBUTION. The tree flourishes along streams and slopes in primary forests of Java, Borneo, Celebes, Moluccas, New Guinea, Talaud, Lesser Sunda and Philippine Islands at altitudes between 10 m. and 1250 m., attaining a height of 8–42.4 m. and a girth of 1.12–2.3 m.

Borneo. SARAWAK: *Haviland & Hose 3622 M*; Gaat, Upper Rajan River, *Clemens 21548.* BRITISH NORTH BORNEO: Paitan, *Maidin 2669*; Pinta-san, *Clemens 34202*; Sandakan, *Elmer 20262*; *Sapilok & Kabili s.n.*; without locality, *Wood s.n.; Kadir A531, A561.* NETHERLANDS BORNEO: Berau, *NIFS b.b. 18890, b.b. 19237, b.b. 18872, b.b. 18811*; Sangkulirang, *Aet* (exp. E. Walsh) *695*; Sambodja, *de Voogd 1610*; Klumpeng, *NIFS b.b. 17272.* **Celebes.** Poso, Kalaena,

FIG. 2. *Duabanga taylorii*, a drooping branchlet and a mature leaf in outline.

NIFS b.b. 28740; Malini, *NIFS Cel/III-90*; Manado, *NIFS b.b. 28231*. **Halmahera.** MOLUCCAN TERNATE: Batjan Is., *NIFS b.b. 16441*; *Weda Is., NIFS b.b. 24926*. **Philippine Islands.** LUZON: Bulacan Prov., *Ramos 21746*; Angat, *Llanos 233*; Rizal Prov., *Vidal 2883*; Bosoboso, *Ramos 4577*; *Ahern's collector 3246*; *Ramos 1341*; Sorsogon Prov., Irosin (Mt. Bulusan), *Elmer 15326*; Tabayas Prov., Guinayangan, *Hagger 254*; Laguna Prov., Los Banos (Mt. Maquiling), *Elmer 18275*; Mount Prov., Tanit, *Lizardo 29386;* Albay Prov., *Vidal 261*; without locality, *Ahern US 446105*; *Garcia 1110*; *Loher 2149*; *Whitford 814*; *Merritt 11409*; *Ahern 158, 106*; *Ahern's collector 2003*. NEGROS: Santa Cruz, *William's collector 2885*. MINDANAO: Davao Prov., *de Mesa 27477*; Pagpawan Sitio, *Edano 11601*; Cotabato, *Ferraris 23045*; without locality, *Ahern, US 445972*, *Miranda 20521*, *Quadras 336*. **New Guinea.** NETHERLANDS NEW GUINEA: Idenburgh River, Bernhard Camp, *Brass & Versteegh 13514, 14015*; Palmer River, *Brass 7289*; Madang Dist., *Hoogland 5224*. BRITISH NEW GUINEA: Papua, Djamu, *Schlechter 17582*.

The leaves of collections from Borneo, *Elmer 20262*, *NIFS b.b. 18811, 18872*, and *19237*, are rounded at base, while those from Celebes, *NIFS Cel/III–90*, *b.b. 28740* and *Ramos 4577* from Luzon are faintly cordate, and those from elsewhere are quite cordate at the base. The fruits of *Brass & Versteegh 14015* from New Guinea are fusiform and, along with those from Sarawak, *Clemens 7287*, are much larger than those from collections elsewhere.

The tree growing at the Royal Botanic Gardens, Peradeniya, Ceylon, is 42.4 m. tall, 2.3 m. girth at breast height, with a columnar trunk branching at 23 m. from ground level. It flowers throughout the year.

This species is distinguished from the others by its columnar trunk and smaller, 4-merous flowers with 12, uniseriate stamens.

Duabanga taylorii sp. nov. (FIGS. 2, 3)

Arbor ingens, late patens, ramunculis pendentibus; folia magna, opposita, oblonga, integra, glabra, apice acuminata, basi cordata cum lobis inaequaliter orbiculatis, 5–25 paribus arcuatarum costarum infra conspicuarum cum vena intramarginali. Flores flavidi-albi, 5 cm. diam., in cymis simplice vel dichotomice terminalibus compositi; sepali 4 aut 5 aut plus, triangularia, valvati, carnosi, in gemma uniti; petali 4 aut 5 aut plus, liberi, flavidi-albi, ungulati, caduci; stamina 24–45, 1-seriata, filamentis longis, antheris introrsus versatilibus; ovarium semi-inferum, carpellis 4 aut 5 aut plus, compositum, 4- aut 5- aut plus locularibus, placenta axillari; capsula loculicidalis cum sepalis persistentibus; semina plurima, minima, filiformia, testa obvia.

Large trees, 33–44.5 m. tall with a spread of 22.6–25.6 m., trunk 7.3–8.8 m. in circumference branching at 1.8–6 m. from ground level, buttressed, young branchlets 1.2–5.2 m. long, quadrangular, soon becoming terete when mature, drooping, brown and lenticelled, internodes 5–12.5 cm. long, 13–44 pairs to a branchlet; leaves opposite, oblong, 2.7–43.5 cm. long, 1.4–17.2 cm. broad, cordate at base, lobes unequal, rounded, abruptly acuminate,

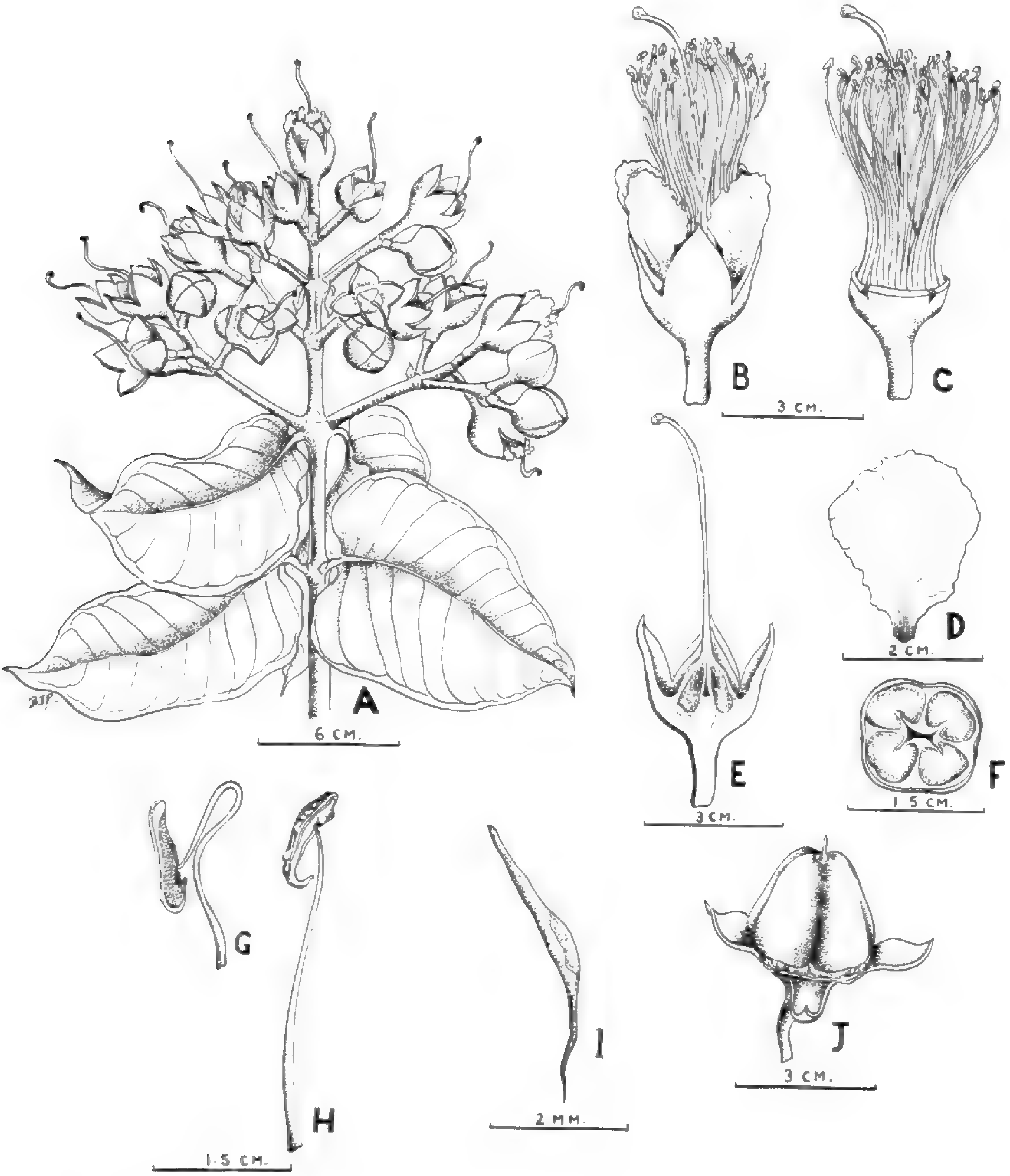


FIG. 3. *Duabanga taylorii.* A, branch with inflorescence; B, flower, lateral view; C, flower with the sepals and petals removed to show the stamens; D, petal, spread out; E, longitudinal section of the half-inferior ovary, petals and stamens removed; F, transverse section of an ovary; G, stamen at an early stage showing the recurved filament; H, stamen showing the hardened resinous globules at the back of the anther; I, seed; J, fruit with persistent calyx and base of style.

acute, entire, glabrous, veins 5–25 pairs, arcuate, prominent on the under surface with an intramarginal vein, petiole 0.5–0.6 cm. long, young leaves reddish brown in color; flowers regular, bisexual, perigynous, 5 cm. diameter, yellowish white, in simple or dichasial terminal cymes, buds ovate, 2.2 cm. long and as broad, puberulent, later becoming glabrous, pedicel 1.1 cm. long, articulate, quadrangular or terete; sepals 4 or 5,

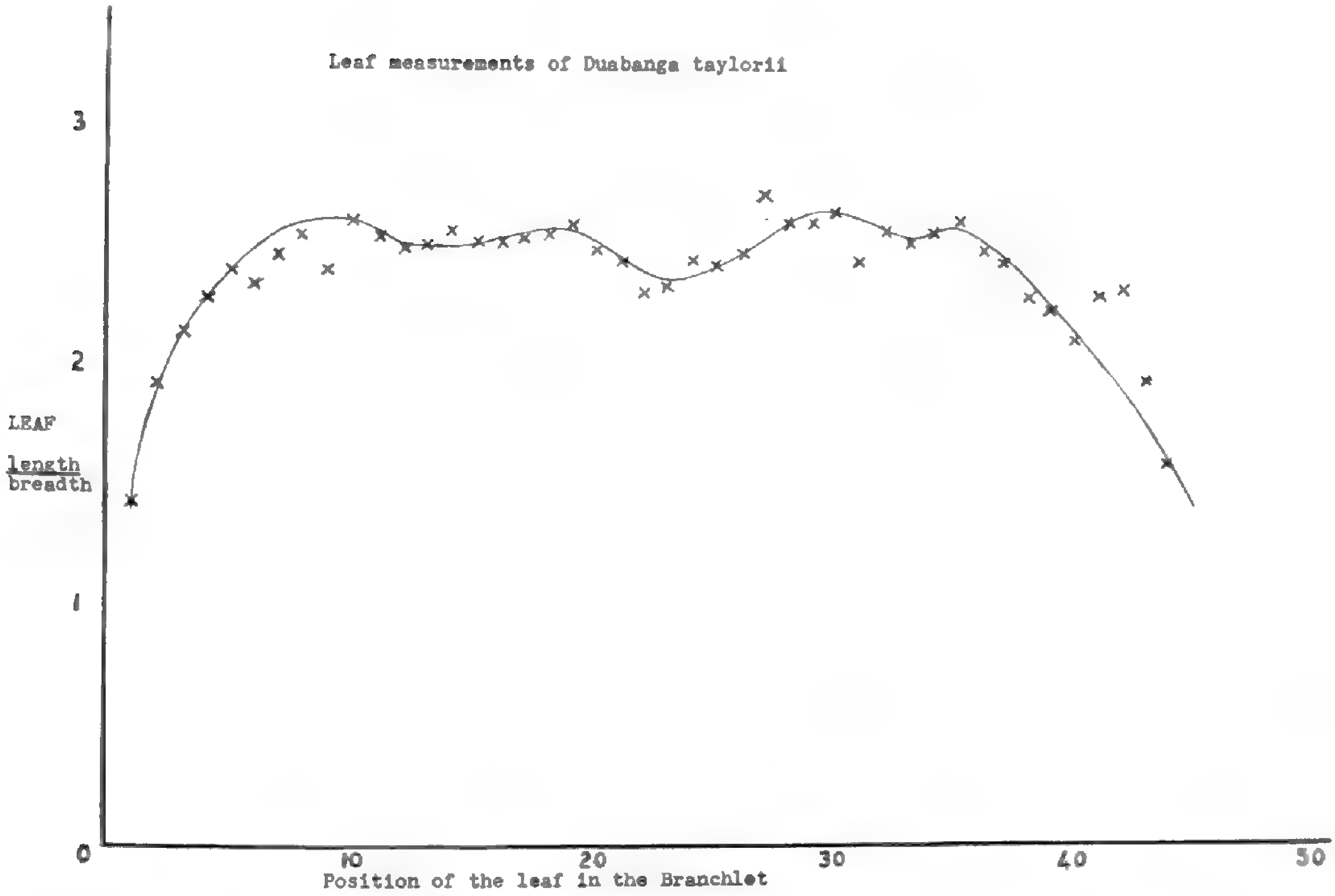


FIG. 4. *Duabanga taylorii*, showing the variation of leaf size in relation to position of leaves on the branchlets.

rarely 6 or more, valvate, triangular, fleshy, green, 1.8–2 cm. long, 1.2–1.8 cm. broad, fused in the bud; petals 4 or 5, rarely 6 or more, free, valvate, 2.5–2.7 cm. long, 2–2.1 cm. broad, obovate, short clawed, yellowish white, crinkled and plicate at the margin; stamens 24–45, uniseriate on a narrow circular rim round the ovary, filaments 4–4.7 cm. long, broad and flat at the base, recurved in bud, anther 1 cm. long, splitting longitudinally, versatile, introrse, glandular at the back, exuding a secretion which on drying hardens to resinous globules with pollen grains embedded within; ovary half-inferior, ovate, half-buried in the receptacle, upper portion dome shaped, 4–7-locular with axile placentation, style 5 cm. long, yellowish green, stigma capitate and dark green; fruit a broadly ovate, loculicidally dehiscent capsule, 1.5–2.5 cm. long, 1.7–2.5 cm. broad with persistent calyx segments; seeds numerous, very small, filiform, testa attenuate, 5.5 mm. long from end to end.

DISTRIBUTION. This is probably a native of Java; seed was introduced into the Royal Botanic Gardens, Peradeniya, Ceylon, in about 1853. It flourishes along river banks in the moist mid-country at an elevation of 457 m. above sea level.

Ceylon. PERADENIYA: Royal Botanic Gardens, *Jayaweera 2498*, July 8, 1964, holotype (PDA) and 4 isotypes; *Jayaweera 2496, 2497*.

There are four large trees of this species about 112 years old, growing at the Royal Botanic Gardens, Peradeniya, most probably the original introduction. The drooping branchlets bear 13–44 pairs of leaves. The first pair and the last pair of leaves just before the production of the inflorescence are very small, while the intermediate ones are larger, the largest being in positions 16–18, 27 and 28, and 32–39 all over 30 cm. long. The largest leaf measured was the 34th which was 34.8 cm. long and 13.7 cm. broad (FIG. 4).

Floral counts of over 500 flowers were made (TABLE 1), and they were predominantly 4- or 5-merous. Some 17.6 per cent of the flowers had 30 stamens each, 13.4–15 per cent had 27–29 stamens and 13 per cent had 31 stamens each.

This species, *Duabanga taylorii*, differs from the others in the lower branching habit of the main trunk, the number of calyx and corolla segments, and the number of stamens which are uniseriate. It is, however, related to *D. moluccana* by its 4-merous flowers but differs in the number of stamens.

TABLE 1. **Variation in Numbers of Floral Parts in Duabanga taylorii.**

STAMEN NUMBER	24	25	26	27	28	29	30	31	32	33	34	35	36	45	
NUMBER OF SEPALS, PETALS, AND CARPELS															TOTAL FLOWERS
4, 4, 4	1	15	30	57	48	41	21	12	1	1	—	—	—	—	227
4, 4, 5	—	1	3	3	10	7	19	12	4	2	—	—	—	—	60
4, 4, 6	—	1	—	4	7	8	12	7	7	3	3	1	—	—	53
4, 4, 7	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
5, 4, 5	—	—	—	—	—	1	—	—	—	—	—	—	—	—	1
5, 5, 4	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1
5, 5, 5	—	—	1	3	8	15	30	31	19	12	4	2	—	—	125
5, 5, 6	—	—	—	—	—	1	2	1	1	—	—	—	—	—	5
6, 5, 5	—	—	—	—	—	—	1	1	—	1	—	—	—	—	3
6, 6, 4	—	—	—	—	—	—	—	—	—	2	—	—	—	—	2
6, 6, 5	—	—	—	—	—	1	1	1	—	3	—	2	—	—	8
6, 6, 6	—	—	—	—	—	1	1	—	2	2	4	—	—	—	10
7, 6, 4	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
7, 7, 6	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
8, 8, 6	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
TOTAL INDIVIDUALS	1	17	34	67	73	75	88	65	34	26	12	6	1	1	500

Duabanga grandiflora (Roxb. ex DC.) Walp. Repert. **2**: 114. 1843. (FIG. 5)

Lagerstroemia grandiflora Roxb. (Hort. Bengal. 39. 1814) ex DC. Mem. Soc. Hist. Nat. Genève **32**: 84. 1826.

Duabanga sonneratioides Buch.-Ham. Trans. Linn. Soc. **17**: 177–178. 1835.

Leptospartion grandiflorum Griff. Ic. Pl. As. **4**: 591. 1854.

Medium or tall tree, 6–40 m. tall, all parts glabrous, trunk straight, erect, with a smooth ash-colored, wrinkled and fissured bark; branches spiral or whorled on the trunk, drooping; branchlets quadrangular be-

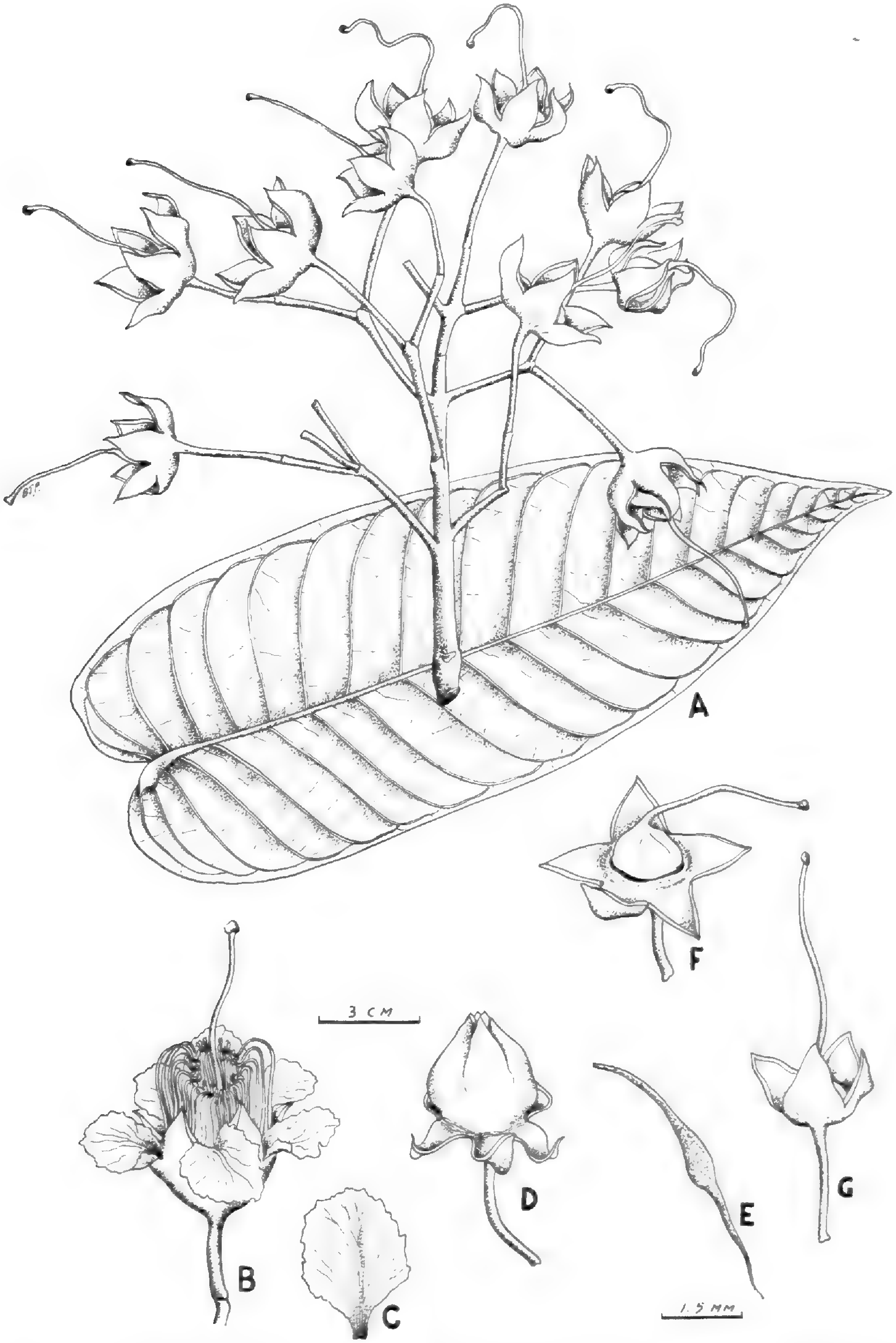
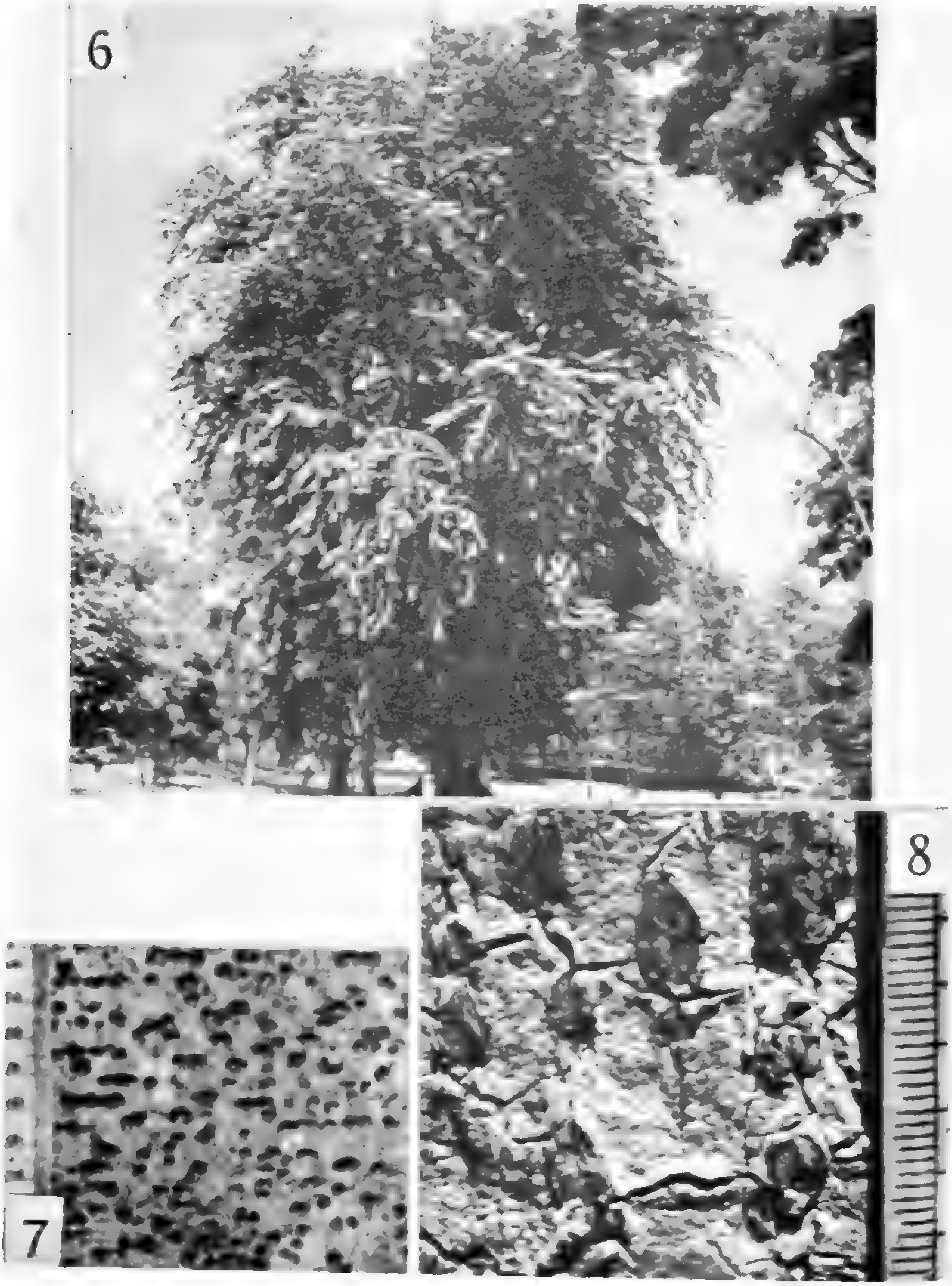


FIG. 5. *Duabanga grandiflora*, drawn from herbarium specimen *Howard & Wagenknecht 15058*, January 19, 1960; stamens and petals have fallen from the flowers. A, inflorescence and a leaf; B, reconstructed flower; C, petal; D, dehiscing fruit, lateral view; E, seed; F and G, abnormal forms with 5-merous and 4-merous perianths, respectively.

coming terete when mature; leaves opposite, large, distichously arranged, 6.5–30 cm. long, 4–11.8 cm. broad, oval, oblong, or ovate-oblong, cordate at base, lobes rounded, short-acuminate, entire, chartaceous, glabrous above, glaucous beneath, with 12–28 pairs of lateral veins, widely patent, prominent below, arcuate into an intramarginal vein, petiole short, stout, 0.4–1.2 cm. long; flowers large, regular, bisexual, perigynous 2.2–3.3 cm. across or more, many in lax, drooping, dichasial corymbs at the ends of branches, pedicels articulate, 1.5–4 cm. long; flower buds conical, 6-ridged, 1.8–2.5 cm. long, 1.8–2.2 cm. broad; sepals 6, sometimes 5 and very



FIGS. 6–8. *Duabanga taylorii.* 6, A full-grown tree in the Botanic Gardens, Peradeniya. 7, 8, Magnifications of the lenticelled bark of the trunk.

rarely 4, 1.2–2.5 cm. long, 0.8–1.3 cm. broad, ovate, acute, valvate, fused at the base with the receptacle into a wide cup-shaped calyx tube, 1.7–2 cm. across; petals 6, free, valvate, clawed, ± 4.4 cm. long, ± 2.7 cm. broad, obovate, plicate along the margin; stamens numerous, perigynous, biseriate, filaments long, filiform, 4.7–5.7 cm. long, broad at base, anthers versatile and curved; ovary half-inferior, conical, 1–1.4 cm. long, 1.2 cm. broad, 6-locular with numerous ovules on axile placentae, style 3.2–6 cm. long, stigma slightly lobed; fruit an ovoid-globose, pendulous, glabrous capsule, 3 cm. long, 3.2–3.5 cm. broad with persistent calyx segments, dehiscing loculicidally into 6–9 valves from apex downwards, seeds numerous, minute, filiform, 4 mm. long from end to end of the attenuate testa.

ILLUSTRATIONS. HOOKER f., Ill. Himal. Plants, *pl. 11.* 1855; JAYAWEERA & HOWARD, Baileya **10**: *pl. 4.* 1962.

DISTRIBUTION. This species grows along banks of streams and in ravines from sea level up to 2280 m. elevation in Assam (India), Andaman Islands, Burma, Thailand, Cambodia, Malay Peninsula, Indo-China, and in Yunnan on the mainland of China. It is deciduous and flowers from January to April, bearing fruit from April to June.

India. SIKKIM: without locality, *Hook. f. & Thomson s.n.*; Darjeeling, *Kowan 24480.* ASSAM: Duars, *Biswas 1943*; Lakhimpur, *Rock 960*; S. Lushai Hills near Fort Lunglek, *Gage 72*; without locality, *King's collector 252*; Calcutta Bot. Gard., *Biswas 9400*, cultivated. **Andaman Islands.** Long Island, *Kirat Ram 3666*; S. Andamans, *Prain's collector 19.* **Burma.** CHIN HILLS: Kaupetlet, *Dickason 8616*; Rangoon, Myout Chaw, *Dickason 6942.* **Thailand.** Khwae Noi River Expedition 1946, *Bloembergen 21*; Ban Khai, *den Hode & Kostermans 473*; Doi Luang, *Rock 1802*; without locality, *Rock 665, 992*; *Mrs. Collins 953, 1141.* **Malaya.** PAHANG: Cameron's Highlands, *Henderson 23662.* **Cambodia.** Without locality, *Pierre 536.* **Indo-China.** TONGKING: Hoo Bink, *Petelot 6371.* **China.** YUNNAN: Lang-tsang Hsien, *Wang 76628*; Tsang-Yuang, *Wang 73303*; Cheli Hsien, *Wang 79292.* **U.S.A.** FLORIDA: Homestead Subtropical Exp. Station, *Howard & Wagenknecht 15058*, cultivated.

This species of *Duabanga* is distinguished from the others by its straight trunk, large 6-merous flowers, and numerous biseriate stamens.

USES. The wood is used for building purposes; it is close grained and coarsely fibrous and takes on a mottled grayish polish.

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ROYAL BOTANIC GARDENS,
PERADENIYA, CEYLON

STUDIES IN SWIETENIA (MELIACEAE): OBSERVATIONS ON THE SEXUALITY OF THE FLOWERS

HSUEH-YUNG LEE

THE FLOWERS OF MELIACEAE have usually been described as perfect, or rarely unisexual and polygamo-dioecious. Of all the references consulted, only C. S. Sargent, in his *Silva of North America*, discussed the sexuality of the flowers of *Swietenia*, which he described as perfect. After three years of observation and pollination tests I have come to the conclusion that the flowers of *Swietenia* are, rather, unisexual, and that the trees, which bear both staminate and pistillate flowers, are monoecious.

These studies were conducted on sixteen-year-old trees of both *Swietenia mahagoni* Jacquin and *S. macrophylla* King at the plantation of Chungpu Branch Station of the Forest Experiment Station of Taiwan. Some trees 30 to 40 years old were also examined. The factors considered in the observations were the distribution of staminate and pistillate flowers on the inflorescence; the structure of the flowers; the sex of fallen flowers; and the results obtained from selfing of staminate flowers by bagging, selfing pistillate flowers by bagging, and by controlled pollination. The flowering period of *Swietenia* in Taiwan is from about 20th to the 30th of May, with the flowers of *S. macrophylla* always opening about one week earlier than those of *S. mahagoni*. The work was carried on and repeated during the years 1963 to 1965.

Of about 700 flowers of the two species of *Swietenia* examined no perfect flower was found. Although the appearance of the flowers is similar, the structure of the staminate and pistillate flowers is quite distinct.

STAMINATE FLOWERS. The ovary of the staminate flower is conical, with a long style and discoid stigma. The ovary, which is about 2 mm. in diameter, bears many reduced ovules. The anthers are sessile and inserted on the inner side of the staminal tube slightly lower than the clefts. The stigma is borne above the anthers so the shedding pollen adheres to the style instead of the stigma (FIGS. 1 and 2).

PISTILLATE FLOWERS. The ovary of the pistillate flower is globular and about 3 mm. in diameter. The style is very short, and the discoid stigma is thickened. The stigma is borne slightly below the clefts of the staminal tube and is encircled by the reduced anthers. The anthers become black when the flower opens and shed no pollen. In each of the five locules of the ovary are 12–14 well developed ovules (FIGS. 1 and 2).

INFLORESCENCE. The axillary paniculate inflorescence is composed of many small 3-flowered cymes in which the central flower opens first. These determinate cymes are borne in turn on an indeterminate panicle. The inflorescence should, therefore, properly be called a thyrse (FIGS. 7 and 8).

The inflorescence of *Swietenia mahagoni* is about 10 cm. long and is

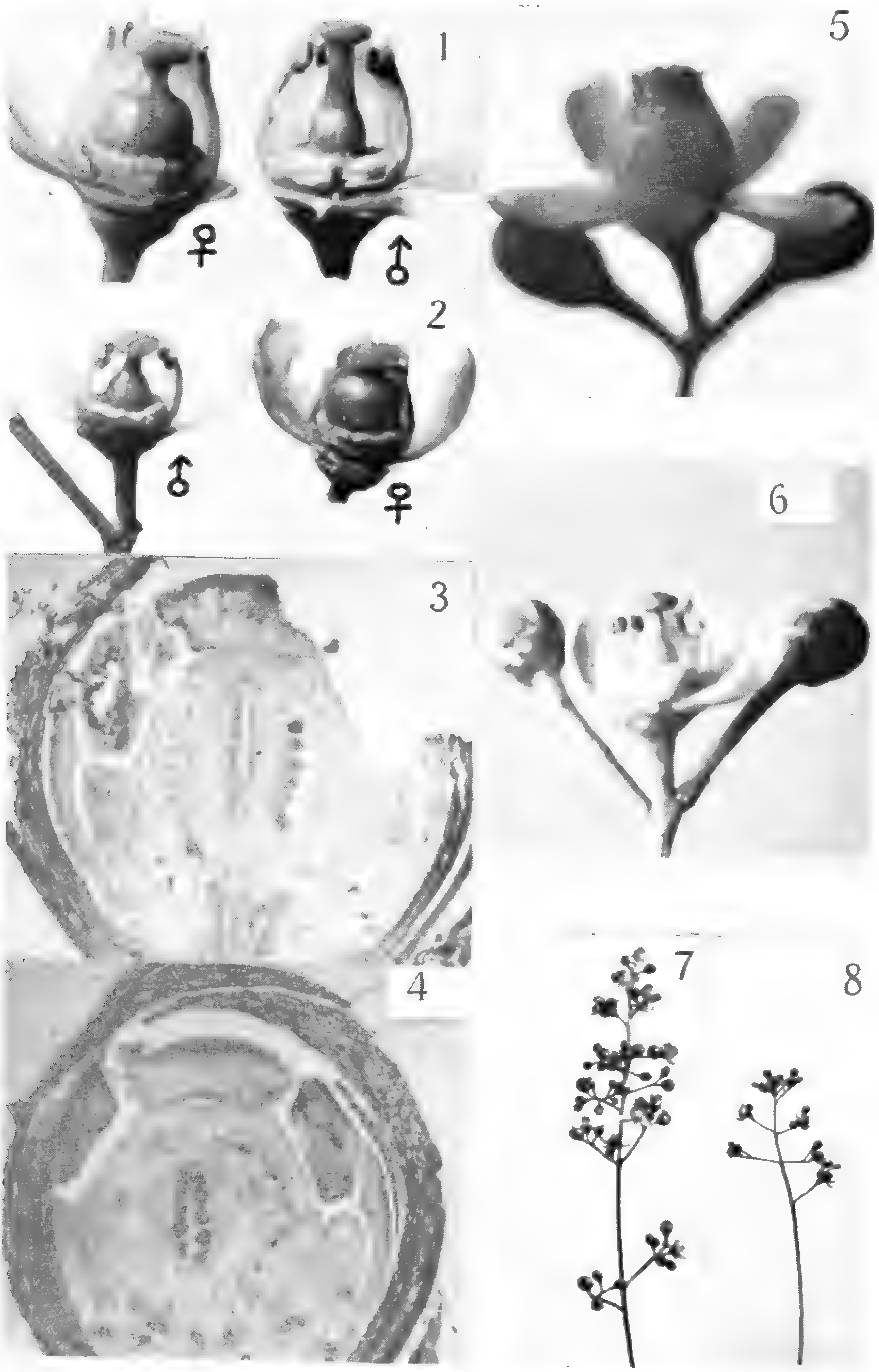

FIG. 1. flowers of *Swietenia macrophylla*, some petals and portion of staminal tube removed, × ca. 36; FIG. 2. flowers of *S. mahagoni*, some petals and portion of staminal tube removed, × ca. 36; FIG. 3. longitudinal section of staminate

much shorter and more slender than that of *S. macrophylla*, which reaches 20 cm. or more and is stouter. Most of the inflorescences in both species bear only staminate flowers; a few bear only pistillate flowers, and some inflorescences on the tops of trees bear both staminate and pistillate flowers. The number of flowers in each inflorescence varies in the two species. In *S. mahagoni* the number of flowers in a single thyrse is from 10 to 50, while in *S. macrophylla* it varies from 40 to 100. On a small branch of *S. mahagoni* examined there were 360 pistillate flowers and 204 staminate flowers on 8 inflorescences. From our observations it seems that the number of flowers and the proportion of pistillate flowers to staminate will vary with the nutritional state of each tree. One tree under observation (no. L_1) bore many pistillate flowers in 1963 and 1964 but only a few in 1965. On a whole tree, according to our observations, the number of staminate flowers is about ten times more than the pistillate ones.

EXAMINATION OF FALLEN FLOWERS. Hundreds of flowers which had fallen at flowering time were examined. None of these flowers was pistillate. The flowers seem to have fallen naturally after the shedding of pollen. The few pistillate flowers which were occasionally found on the ground consisted only of the receptacle and swollen ovary; the fallen staminate flowers, on the other hand, were complete. It seems reasonable to conclude, therefore, that the fall of the pistillate flowers was due to nutritional deficiency, not to incomplete fertilization. The small inflorescence branch apparently can not supply enough nutriment for all the developing ovaries. This condition seems to make quite clear that the staminate and pistillate flowers of *Swietenia* are distinctly separate.

In an effort to show that the pistillate flowers bear no functional anthers they were bagged before the opening of the corollas. All the bagged pistillate flowers faded in three days because no pollen grains were produced. The staminodia of these pistillate flowers proved to be functionless.

In the same way staminate flowers were also bagged before the opening of the flowers. The same result was observed. The reduced ovary of the staminate flowers did not develop, although the pollen was viable.

CONTROLLED POLLINATION. The pollen shed from anthers of staminate flowers always forms masses with sticky fluid. Some of the pollen masses from newly opened staminate flowers was transferred with a brush to stigmas of bagged pistillate flowers. In all the flowers so treated the ovaries developed and formed rounded young fruits, many of which fell because of growth competition. Usually only one fruit on each inflorescence developed to maturity.

Since the establishment of the genus *Swietenia* by Jacquin in 1760 the

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flower bud of *S. mahagoni* showing pollen grains in anther, × ca. 100; FIG. 4, longitudinal section of pistillate flower bud of *S. mahagoni*, showing empty anthers, × ca. 100; FIG. 5, cymule of *S. macrophylla*, × ca. 36; FIG. 6, cymule of *S. mahagoni*, × ca. 36; FIG. 7, inflorescence of *S. macrophylla*, × ca. ¼; FIG. 8, inflorescence of *S. mahagoni*, × ca. ¼.

flowers have always been described as perfect (hermaphroditic). Taxonomists based their conclusions on the morphological structure of the flowers neglecting to consider whether the organs were functional or not. From the relative position of anthers and stigma it is easy to determine the sex of the flower. In the references cited, Sargent's illustration shows a staminate flower; Rendle's illustration of *Swietenia mahagoni* a pistillate flower; King's figure of *S. macrophylla* a pistillate flower; and Liu's monograph a staminate flower of *S. mahagoni.*

As a result of these investigations and pollination tests I conclude that the flowers of *Swietenia* are unisexual and trees of this genus are monoecious.

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SOME PROBLEMS OF TROPICAL PLANT ECOLOGY

ARTURO GÓMEZ-POMPA[1]

DURING THE LAST SEVEN YEARS there has been in progress a series of phytoecological studies on the warm-humid zones of the lowlands of the Gulf of Mexico. This work has contributed a large quantity of data and many collections of herbarium specimens as a consequence of a systematic sampling carried on in various regions in the lowlands. A detailed presentation of these studies may be found in Gómez-Pompa *et al.* (1964a).

One of the most important points of the methodology is the selection of areas which are arbitrarily limited and are named for some important locality, so that we have the regions of Misantla, of the Tuxtlas, of Córdoba, etc. Once such a region is delimited, a survey is made taking into account and sampling its floristic and environmental variations.

Before explaining the outstanding characteristics and problems of these studies, I wish to discuss some general considerations about certain diverging tendencies which concern ecological studies in tropical zones.

CONSIDERATIONS OF SOME TENDENCIES IN PHYTOECOLOGICAL STUDIES OF TROPICAL ZONES

The basis of the problems and controversies in tropical ecological studies is related to the origin and initial development of plant ecology which occurred in northern extratropical countries and from which we inherited not only a confusing terminology but also a rather dogmatic approach to ecological research. The confusion reached an extreme in usage of terms completely inadequate for the tropical region. An example is the case of the name *tropical rain forest*. This term has no real meaning because there are forests in very rainy areas of the tropics similar to those in temperate areas, such as coniferous forests and deciduous forests which, floristically

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[1] I am glad to acknowledge the help and interest of Dr. Jean Langenheim, University of California, Santa Cruz; Dr. Herbert L. Mason, University of California, Berkeley; and Dr. L. C. Bliss, University of Illinois, Urbana, who all read the manuscript with great care and made important comments and suggestions. I am much indebted to Dr. B. G. Schubert, Arnold Arboretum, Harvard University, who did much of the translation from my Spanish text.

and ecologically are very different from the real "selvas." The selvas are composed of many dominant species of trees and include also lianas, epiphytes and one to several understories of trees. So, the term tropical rain forest causes confusion and when it is translated into Spanish the problem becomes worse. On the other hand, we have the more precise term *selva* which has real meaning but has not been widely accepted in the ecological literature in English.

Since ecological studies began in Europe where the vegetation is mostly altered and the portion conserved in original form is very small, the detailed phytosociological studies of the school of Zurich-Montpellier came into being (Becking, 1957). On the other hand, in the United States with great extensions of vegetation practically unaltered at that time, the school of Clements (1936) with its climax method arose. A very detailed analysis of the origin, development, and method of approach, as well as other aspects of these two lines of ecological thought was presented by Whittaker (1962).

The various methodologies developed in different areas have led to results which at first seem opposed but which, in fact, should not even be compared because of the different emphasis of each. For example, the *monoclimax* of Clements, so severely attacked, does not differ much from the hypothesis of the *polyclimax* of other authors. In relation to this Cain (1947) says: "One is led to wonder to what extent the problem is really one of semantics and only an academic exercise." In fact, much of the discrepancy is due to false interpretation made in good or bad faith by supporters or detractors of the method. Examples are the complex diagrams of the dynamism of the *seres* which some followers of Clements carry out and which Clements himself avoided. The development of the complexity of such problems reaches a point where verification of contrary ideas must be made in the field and not by theoretical discussions, which instead of clarifying each question only bring more confusion to the little which is common among them. For this reason critics of the Zurich-Montpellier school in the United States are unable to establish a basis for their arguments for, as Cain has said (1947) "No American plant association, I believe, has yet been studied thoroughly and throughout its range in the manner of the plant sociologists."

This fact becomes even more serious when we realize that the great majority of the studies on vegetation are made in such a form that their verification is very difficult. This has permitted persons without preparation for this type of work or after only superficial observations to propose "theories" (hypotheses) very difficult to demonstrate.

All these problems have been inherited also in studies of tropical vegetation, but with certain peculiarities which make them even more obvious. Among the problems are: a) the existence of environmental conditions very distinct from those of the extratropical zones; b) a very rich flora in large part unknown; and c) a lack of ecologists, so that, as a result, a large majority of the studies are pursued by botanists of extratropical countries usually on short visits.

From the great quantity of works written concerning the vegetation of the tropics we are able to extract two principal tendencies derived from a fundamental problem in ecology, the concept of the unit in studies of vegetation, or perhaps better, the *association.*

One tendency is that followed by many ecologists who accept definable plant associations, and, although not following the original meaning of Clements (1936) use some of his ideas and terminology. To explain this trend I quote a paragraph from Beard (1955) in his work on the types of vegetation of tropical America, "The basic unit is the plant association which is a floristic grouping, being the largest possible group with consistent dominants either of the same or closely allied species. Associations may be divided into minor floristic groups, to which it was proposed to apply the Clementsian terminology."

The most important of the several schools of ecological thought may be aligned with this tendency. Among them two are outstanding for their influence on studies of tropical vegetation. These are the school of Clements which has been followed in various works on tropical vegetation (Chatterjee 1958; Rosayro 1958; Phillips 1934–1935) and has influenced many others. The second, the school of Zurich-Montpellier, which has had a relatively broad acceptance in many works on various tropical zones (Bharucha 1958; Cuatrecasas 1934; Dilmy & Kostermans 1958; Heyligers 1963; Mangenot 1950–1958).

Although, in fact, the two schools differ so notably they have one point in common which is the recognition of some organization of plant communities.

Within this same tendency we ourselves are able to find a place. that is, we accept artificial units of vegetation as a means and not an end in our studies of vegetation: "The concept of association must be more or less artificial, having the objective of establishing units which permit us to study the whole by means of its parts or having an obvious utility for facilitating our studies." (Gómez-Pompa *et al.* 1964a.)

The second tendency refuses the idea of the organization of these units (Raup 1942). To explain this tendency I quote from Gleason (1939) who has been considered its postulant. "Since every community varies in structure and since no two communities are precisely alike, or have genetic or dynamic connection, a precisely logical classification of communities is not possible. The individualistic concept denies that all vegetation is thus segregated into communities." He considers plant communities as "coincidences" of the individual distribution of the species.

The Gleasonian approach has had a very important effect on vegetation studies in general, but unfortunately this is not so for the tropics. Probably the reason is the inherent difficulty of tropical vegetation. It is interesting to note that Gleason has been badly misinterpreted by many; as he does not deny the existence of associations, one often thinks that his inclusion of them is contradictory. In the work on Puerto Rico. Gleason and Cook (1927) say "In summary it may be repeated that plant associations are the basic units of vegetation, that they are the results of immigration and environmental selection, and their duration is short or long, depending on the rate of environmental change. . . . The duty of an ecological survey is to describe these associations, to correlate them with their environment and to discuss their past history and probable future so far as clear evidence exists on which such discussion may be based."

In reality I think that a contradiction does not exist and the fundamental difference is the broad or narrow meaning which different authors have given to the "association"; some have gone very far in the extension of their possible associations and also in their concept, presenting an indefensible point of view. This is, in a way, the case of many followers of Clements and also, in a somewhat different sense that of some phytosociologists. On the other hand, the attitude of denying the existence of associations as some followers of Gleason have done, is rather extreme and denies a fact which, as mentioned earlier, Gleason himself accepts.

My position in regard to this has been that it is difficult to theorize in regard to such problems and that the first thing which must be done, at least in tropical countries, is to study the vegetation and obtain facts and data from which it will be possible to derive ideas and to base some definite position. In other words, it is very difficult to classify without having previously studied the object to be classified. One cannot make a decision without having the data on which to base the decision. In the case of tropical vegetation, in fact, the problem is that very few serious studies have been pursued in an extensive methodical form in the field.

We may wonder why this had happened. I believe that the reason is related to the complex mixture of species in the lowland tropics, added to the fact that the identification of them is extremely difficult because of the poor knowledge of these floras and the very few botanists who can recognize species in the field. The solution to this problem has been made following two main trends, one is related to the study of large samples of a stand using squares of different sizes, this type of work has given very valuable information about floristic composition of rain forests, number of trees per area using local names of species, etc., and the other trend is to present studies of very large areas or countries using just a few species to illustrate some of the groupings.

From the studies carried out by us in the warm humid regions of Mexico, it has been possible, I believe, to extract some data which will give an idea of the path to follow in this line of investigation.

PHYTOECOLOGICAL STUDIES IN THE WARM HUMID ZONES OF MEXICO

I do not intend in this paper to make an analysis of the studies carried on up to now in these zones, but only to present a series of facts derived from them, which seem to have a basic importance for the understanding of plant communities in the lowland tropics.

1. It is important to acknowledge that in each region or subregion studied there exist groups of species which have "preferences" and include

PROFILE 1 (ABOVE). This profile includes the most important primary plant communities in the area. The rainfall is about 3000 mm. per year and the average of monthly temperatures is 24.8° C. (Redrawn from Gómez-Pompa, Hernández P. & Sousa, 1964b.)

PROFILE 2 (BELOW). This profile includes the most important primary plant communities in the area. The rainfall is about 2300 mm. per year and the average of monthly temperatures is about 25° C. (Redrawn from Gómez-Pompa, Hernández P. & Sousa, 1964b.)

in some cases, strict affinities for certain ecological conditions. For example, in the region of Papaloapan (Gómez-Pompa *et al.*, 1964b) we find a marked contrast in the floristic composition of the limestone hills with the rest of the region occupied mainly by lateritic soils of various types. Even in the lateritic soils we find marked contrasts in the floristic composition according to the topographic variations, internal drainage, and hydromorphism. These contrasts may be drastic or gradual, based on the relationship to the same changes in the local edaphic conditions. A synthetic and diagrammatic profile of a subregion (Tuxtepec-Jacatepec) has been reproduced from the study mentioned above as PROFILE 1.

In the *Brosimum alicastrum* selvas of the limestone hills many species are found which grow only in this type of soil in this area, among them: *Mirandaceltis monoica, Mastichodendron capiri* var. *tempisque*, *Protium copal*, *Astronium graveolens*, *Croton* aff. *reflexifolius*, *Sickingia rhodoclada* and many more. This fact is confirmed by other observations, made in many parts of the world, on the importance of calcium as an element in the soil which restricts the entrance of calcifugous species and permits the success of calciphilous species (Jefferies & Willis 1964), although the explanation is obscure especially for warm humid tropical zones.

In the case of the topographic variations within the lateritic soils, however, it should be noted that the floristic differences are less evident among them. Nevertheless, there also exist groups of species with similar patterns of distribution in relation to these edaphic variations.

2. These kinds of affinities or preferences are found not only among "primary" species but also in secondary species (Sousa 1964). This is of great importance inasmuch as in these species there may be found elements of great importance for experimentation on the problems of "preferences."

3. Another fact of interest is that these local patterns of special distribution occur in shrubby and arboreal species in a way perhaps more notable than in other biological forms (vines, herbs, etc.). It is possible that this fact may have become a little distorted because the major emphasis of our studies has been on shrubby and tree species. The most surprising observation is that in a great number of cases the most restricted of such species in certain soil conditions are the most abundant, frequent, and in some cases dominant ones in the environmental condition in which they are found. This fact has an enormous usefulness since it has permitted the use of such species as indicators for cartographic work on a small scale.

It is also notable that if a different region, not very remote, is studied, the whole panorama discussed in the preceding paragraphs may change. It is something of a problem to state exactly why it changes so much because the differences depend upon the area, and vary from region to region. The floristic composition of two regions may be very similar, the ecologically important species may continue to be important but they may "behave" either in a very distinct or in a similar manner. A typical example of this may be seen in the profile of the subregion of Los Naranjos-

Temascal (Profile 2), where, in comparison with that of Tuxtepec-Jacatepec, we meet the same important species, as for example *Terminalia amazonia*, found in acid soils on the slopes of the limestone hills, as well as on the margins of arroyos, etc. On the other hand, *Brosimum alicastrum* continues to occupy an important place in limestone soils, so that we may continue analyzing successively the "behavior" of species in the two sub-regions and shall see the whole gamut of change. For example, *Curatella americana*, a species with affinities for the soils of oak woods of Tuxtepec, Oaxaca, is one of the most important arboreal species of the savannas of Los Naranjos, Veracruz, on very different soils.

If the comparison is extended to a more distant region and other species are used the method is similar. For example, in Jacatepec, *Robinsonella mirandae* is typical in calcareous soils and is one of the dominants, but in the region of the Tuxtlas, Veracruz, it is also one of the dominants, here in soils derived from volcanic ash. *Crescentia cujete*, which in the profile of Temazcal-Los Naranjos is typical of argillaceous savanna soils (Fig. 1), is found in British Honduras forming an important and typical part of the forests of *Pinus caribaea* on sandy soils (Fig. 2). On the other hand, in this same country *Brosimum alicastrum* is also found on calcareous soils as in our two profiles.

With a basis in these facts, presented in condensed form, we are able

Fig. 1. Savanna with *Crescentia cujete* in Veracruz (see profile 2). Other arboreal species in these savannas are: *Curatella americana*, *Byrsonima crassifolia*, *Coccoloba barbadensis*. *Bromelia karatas* is shown growing at the base of *Crescentia*. These savannas are found in clay soils in flatland areas used mainly for cattle.

FIG. 2. Between Orange Walk and Belize (British Honduras). *Crescentia cujete* can be seen at the edge of the savanna, growing adjacent to the *Pinus caribaea* forest. The palm is *Paurotis wrightii*. These savannas grow in white sandy soils.

to follow the two tendencies explained above, and the decision to follow one or the other will be related to the information used.

1. If considerations are based on the study of only one region or a subregion it is probable that the presence of more or less well defined *patterns of distribution which fall within the strictest limits of the definitions of "association"* can be proven.

2. If several regions are considered and compared, the species studied may present very marked differences in their responses to the diverse ecological situations throughout their range of distribution and may, on this basis, *refute all the definitions of "association."* The independent behavior of each species to the different ecological conditions to which it is submitted in the range of its distribution will make the name, for example, "selva de *Terminalia amazonia*" have no significance.

A difference in basic information seems, therefore, to be the cause of the majority of the discussions on this much debated subject. In relation to this problem I have adopted a position which may, perhaps, conciliate the extremes. This position involves an analysis of the facts in the light of the present botanical knowledge and an effort to explain the apparent discrepancies by taking as a base the species as a fundamental unit and point of departure, as Gleason has done in his individualistic concept.

AN HYPOTHESIS TO EXPLAIN THE FACTS

I believe that in the study of tropical vegetation it is necessary to have more hypotheses to work with, because accumulations of facts as such, have a limited importance if we do not have some links between them to form some generalized ideas for a better understanding of tropical environments.

When a species is cited from a region as, for example, *Terminalia amazonia* in Chontalpa, Tabasco (FIG. 3), we are dealing, in fact, with a small fragment of the total population of this species, or rather we are dealing with a small fraction of one of the many populations which comprise the species whose total range of distribution covers an area from Brazil to Mexico. This local population is very small considering not only its total distribution, but also the fact that it is a tree species. The gene pool of this population may be very different from that of another population in Panama or in Brazil. The differences between these populations are due to many factors which basically have the effect of discontinuities within the total population of the species.

This phenomenon is very well known and has had a strong influence on taxonomic studies although some taxonomists ignore the concept of the polytypism of species populations. In modern concepts of the species the existence of various populations within one species is taken into account. Mayr (1963) defines the species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." In consideration of this idea and others having a

FIG. 3. *Terminalia amazonia* selva with its typical stratified treetops, in the state of Tabasco. This selva grows on plains or small hills, on deep, well drained, lateritic soils.

similar focus (Dobzhanski 1941, Huxley 1940), authors tend to call it a biological species concept, and all agree that the species is commonly composed of systems of populations, a theory which is of much interest to us.

Of the possible explanations of discontinuities those of most interest to me are the ones which enable me to establish an explanation for the ecological restriction of certain species to local regions. The most important of those which I have considered may be explained by one example. On many occasions I have had the opportunity to see isolated individuals of tree species which have survived the effects of disturbance in different regions. In the majority of cases these individuals have been undisturbed because of existing shade or because they do not infringe on agricultural or grazing activity (FIG. 4), one of the principal causes of the destruction of the original vegetation. In other situations there are survivors of fires and other disturbances, both artificial and natural (FIG. 5). If such a disturbed zone is abandoned and left to recuperate its vegetation through a secondary succession, it will be noticed that the majority of the plantules of trees which develop will surely come from the mature tree which has persisted. If, in the model we are considering, one (or few) of the trees left belong to the species *Terminalia amazonia*, the future small local population will come from a single tree (in the case of a self-compatible species) or from a few individuals (in the case of self-incompatible species). As a result there is a genetic change which may or may not be morphologically evident depending on the genotype of the parent tree. This phe-

FIG. 4 (LEFT). Isolated tree of *Terminalia amazonia* in a valley near Cordoba, Veracruz. This tree has survived in spite of human disturbance. At the bottom can be seen some selvas growing on limestone. This species is not found in such areas as it grows chiefly on acid soils.

FIG. 5 (RIGHT). Isolated tree of *Terminalia amazonia* near Macal river in British Honduras. This tree has survived a cyclone that threw down most of the trees in the area.

nomenon may be included in some of the distinct types of "genetic drift." This change may be very abrupt depending on the genetic constitution of the parent tree from which a local gene complex will be derived. It may or may not permit the initial population to have characteristics enabling it to compete successfully. An example of this mechanism may possibly be seen in the oak scrub of *Quercus oleoides* (FIG. 6) in the Llanos de Alvarado, Veracruz, a population with an aspect very distinct from the *encinares* of *Q. oleoides* of the neighboring regions (Gómez-Pompa, 1965). These populations resemble the "founder populations" of Mayr (1963) of which he says, "this term (Founder Principle) designates the establishment of a new population by a few original founders which carry only a small fraction of the total genetic variation of the parental population. The descendant population contains only the relatively few genes that the founders have brought with them until replenished by subsequent mutation or by immigration," to which I might add (in the case of plants) that these populations may continue a certain level of gene flow with other populations of the same species, adjacent or distant.

We do not know with certainty that this has happened in the past or that it is happening now; but we know that the majority of so-called virgin forests show evidence of human activity in the past, or at least evidence of fires, inundations, hurricanes, and other catastrophic events which, we may assume, have left some individuals as the basis of future regeneration of the vegetation. Clausen (1962), in reference to such a situation says, "Each local population of a species has probably been started by a limited number of individuals, and it may be effectively isolated from other colonies by spatial isolation."

FIG. 6. Oak scrub of *Quercus oleoides* near Alvarado, Veracruz. This population grows on flat, clay soils, near the coast of the Gulf of Mexico.

Another possible explanation of a similar phenomenon (with a different origin, however) is in the consideration of an area denuded by a catastrophe of nature such as volcanic activity. The material with which the vegetation is reconstructed will be provided in large part by the margins of surrounding species populations. Of all the propagules only those will survive which can compete in and are adapted to the new environment. This could result in a possible change in the new populations. This genetic drift will be more obvious if the surrounding zone presents different edaphic characteristics such as limestone soils, or even different climatic ones. This type of situation may be imagined to have occurred in many zones of the lowlands of the Gulf of Mexico.

As the basis for such a mechanism a quotation from Grant (1963, p. 286) seems pertinent: "In other cases the natural population may be large but has descended from a few migrant individuals. This is often the case in organisms which colonize new areas. A volcano may destroy all traces of pre-existing life on a mountain . . . ; a fire may sweep through a forest; or a tree may simply die of old age, exposing a spot of bare ground. The new ground becomes colonized by migrant plants and animals from surrounding areas. It is not likely that colonizing individuals can bring with them a complete sample of the genetic diversity in the old ancestral population. If the founders of the new population are few in number they could, by chance, represent only one or a few of the genetic variants in the ancestral population from which they came."

These ideas may well explain in part the pronounced response of some shrubby and tree species to certain regional ecological conditions. This is so especially for tropical zones in which the following characteristics are present: (1) that low winter temperature is not the most important limiting ecological factor with which the species has to contend and adapt, as is the case in extra-tropical regions; (2) that natural selection works in these local regions fundamentally in relation to edaphic differences, or rather that the soil plays a very important part in the selection of such individuals in these regions. This fact has been mentioned for different regions in the tropics (Van Steenis 1956). In relation to the soil factor Mason (1946), from his experience in California, says "Of the various categories of environmental factors, the condition of any factor or combination of factors may serve to restrict the range of some species of plants. Of those factors however, the edaphic factor is most apt to occur in sharply defined patterns and often in small areas."

With this hypothesis as a basis, the problem of the distinct behavior of some species from region to region may then be explained.

As noted previously, the possible origin of populations may be different if the parent sources have different genetic constitution. This is more outstanding if we note also that no two areas have the same environmental conditions. We may find environments which are very similar, but into which new factors have entered to produce very strong variation.

The "environment" concept is very complex; nevertheless, in relation to the behavior of plant species in the Mexican tropics, we can make the following artificial classification.

1. **Highly selective environmental factors.** These factors are relatively independent, such as soils derived from limestone, with different texture and structure; or, poorly drained savanna soils. Several species follow these soils in areas with differing climates and topography. Such is the case of: *Brosimum alicastrum*, *Protium copal*, *Mirandaceltis monoica*, *Mastichodendron capiri* var. *tempisque*, *Trophis racemosa*, *Manilkara zapotilla*, etc., for the limestone areas in many regions of the lowland tropics in Mexico; and of *Curatella americana*, *Crescentia cujete*, *Byrsonima crassifolia* of many savannas of tropical America. Finally, the most extreme type of selective environment is probably the mangrove swamp with a typical floristic composition in many different areas.

2. **Poorly selective environmental factors.** These factors do not imply a great selectivity of species from region to region. The behavior of the species is very variable and seems to depend on variation of independent local factors, such is the case of many different deep, well drained, acid soils. In these soils the following selvas will serve as an example: selvas of *Terminalia amazonia*, *Dialium guianense*, *Pseudolmedia oxyphyllaria*, *Vatairea lundellii*, *Bernoullia flammea*.

Since these are not very selective, the floristic composition and the relative abundance of a single species may vary remarkably from one region to another in relation to still other factors, the most interesting probably being the historical factor. The historical factor may provide the explanation of the origin of the local flora in time and space. Some of these acid soils bear forest which is commonly known as "mixed" rain forest and which seems to have no fixed pattern of species composition, but rather a random dispersal of species. The nutrient mosaics in some of these local areas must play a very important role in such "random" dispersal of species but unfortunately, little is known about these mosaics in the tropics of the New World.

3. **Intermediate factors.** In this category are factors which may be highly selective locally but which are not "followed" by species from region to region, for example, recent alluvial soils. In such soils, characteristic species may be found, but they may differ depending on the region. In this category also two other factors may be included, topography and slope exposure which provoke responses from the species which can be explained only locally. In some cases the variation is very gradual and the responses of the species are equally gradual forming a continuum.

On the basis of this hypothesis we may cite an enormous number of problems needing study which will allow us to open new lines of investigation for the development of plant ecology in the tropics. Among them are:

a). The problem of the experimental initiation of the secondary successions, which will permit us to know something of the modern historical factors and of the behavior of the individuals in these stages. Work of this type has already begun in Mexico (Sarukhán, 1964).

b). The detailed study of the behavior of specific local populations.

c). Work on transplants between populations of the same species coming from different regions, and the initiation of studies of ecotypic differentiation, as well as transplant experiments of species to different environmental conditions from those under which they live. These studies should provide fundamental information for the proposed hypothesis. Also, this type of study could provide the key for resolving the problem of tropical silviculture.

d). The study of breeding systems of the ecologically important species from which may be obtained information about some of the most interesting species. These studies must be complemented, however, with cytogenetical studies permitting extraction of information basic to fundamental problems in ecology and in tropical forest genetics.

Such an approach to the study of tropical plant ecology will remove it from the isolation to which it has been subjected by other sciences, since its problems are related to similar problems in other fields as evolution, taxonomy, population genetics, and so forth. As Mayr (1947) noted "At first sight the concept of geographically and ecologically variable species seems full of contradictions. We see that in one locality a species is restricted to a very definite habitat niche, while in another locality it occurs in a different, sometimes very different niche. We know that through selection in each of these populations a definite gene complex has developed, which permits the population to survive and thrive in spite of competition, predation and all sorts of other adversities."

All the information obtained by the development of genecology, supported by the work of Turesson (1923, 1936), Clausen, Keck, and Hiesey (1940), and more recently by McMillan (1964), Kruckeberg (1951), and Critchfield (1957), is related to such an approach and the impact of the results becomes increasingly stronger because of the same basis of the study, which in the revision of this field by Bennett (1964) is defined as ". . . the study of the genetic mechanisms which operate, within organisms, and between organisms and their environment, at the level both of the individual and of the population, viewed as a process, which at the population level produce those changes known collectively as micro-evolution."

I think that these studies have to be initiated for tropical plants if we want to get to the basis of the problems.

Surprisingly, the definition of genecology seems to be closely related to the one we proposed for autecology, in which it is limited to "the study and definition of those environmental factors affecting the survival, adaptation, and fertility of the individuals of one species." Since the factors can be defined in broad zones only with difficulty, and since they vary from region to region, we might say that autecology deals with the study of those factors in the macro and microenvironment (as well as the plants) affecting the survival, adaptation and the dynamics of reproduction, of those individuals belonging to one or several regional specific populations. I think it is important to make the comparison between the field of autecology and genecology because at certain levels there is no great difference, only perhaps a difference of emphasis, as long as both are studied in detail.

All the studies related to these fields are the true basis of synecology. Since in tropical areas such studies scarcely exist, any serious, purely theoretical controversy on tropical vegetation is without basis and must, therefore, await the collection, organization and study of facts and data.

There is a tremendous task in front of us because of our lack of knowledge of tropical plants. We need more and better taxonomic studies of tropical plants, we need also more biological information of them. It is my belief that ecological studies can make a very important contribution to taxonomy if vouchers are mentioned and widely distributed to herbaria. There is great potentiality in the combination of the taxonomy and ecology of tropical plants; there is much to be learned about speciation problems in the tropics and it is my hope that botanists of tropical countries can contribute significantly in this respect.

SUMMARY

1. Most of the studies in tropical plant ecology have been carried on using methods and ideas developed in temperate regions.

2. Controversies have arisen because of very poor field work in the tropics, and because of lack of extensive surveys to prove or disprove some of the ideas.

3. The two apparently opposite ideas, of the existence or absence of clear cut associations in the warm humid tropics, are used to illustrate the confusion existing in tropical plant ecology.

4. An hypothesis to conciliate the two positions in accordance with the facts obtained in studies done in the Mexican tropical lowlands is presented, based on the following factors: a) the edaphic mosaics as a basis of natural selection of local species populations; and b) on the fact that there are not two areas with identical environments; c) on the characteristics of the origin and "behavior" of plant populations in local environments; d) on the natural selection of species populations in local environments as an explanation of the striking patterns of species in these local areas.

5. It is suggested that new methods are much needed in the study of tropical plant ecology and that the evolutionary genecological approach will make a significant contribution to the understanding of the phenomena responsible for what we are finding in vegetation studies in the tropics.

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ANATOMY OF THE PALM RHAPIS EXCELSA, IV. VASCULAR DEVELOPMENT IN APEX OF VEGETATIVE AËRIAL AXIS AND RHIZOME[1]

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PREVIOUS ARTICLES IN THIS SERIES have analyzed quantitatively the course of vascular bundles in the vegetative aërial stem and in the rhizome of *Rhapis excelsa* (Zimmermann & Tomlinson, 1965; Tomlinson & Zimmermann, 1966a). The present article extends our descriptive analysis of *Rhapis* to the apex of both aërial and underground axes, tracing vascular strands, in their earliest recognizable condition as procambial strands.[2] From this we can make certain deductions about the way in which the vascular system develops. No attempt is made to describe the development of phloem and xylem tissues within the procambial strands, this important aspect being reserved for a future article.

As Esau (1965, p. 33) has pointed out, information on leaf trace relationships in monocotyledons, especially the perennial types, is incomplete; the apparent complexity of these plants has inhibited their investigation. Nevertheless our analysis of *Rhapis* has shown that the basic plan is quite simple, only the overall large number of bundles obscures this.

Despite the rather artificial attempts by earlier anatomists to classify monocotyledonous vascular systems (e.g., by Falkenberg, 1876), only two main groups need be considered (Priestley & Scott, 1937), namely those with a nodal plexus of vascular tissue, exemplified by the grasses, and those without nodal plexi, exemplified by the palms. The former have been studied quite extensively (Kumazawa, 1961; Scott and Priestley, 1925; Sharman, 1942). However, in the non-nodal type of monocotyledons the only study which continuously relates development of the vascular strands to their distribution in the mature stem is that by Priestley *et al.* (1935) in *Alstroemeria*, an analysis which is worthy of wide attention. A notable observation of these workers is that vascular bundles are recognizable as acropetally growing strands in the developing stem long before the leaf which they ultimately supply is produced. *Alstroemeria* is, however, a relatively diminutive monocotyledon and its vascular system is much less elaborate than that of even the smallest palm.

Because of the greater bulk and complexity of palms, workers have been content to describe development in general terms. The earliest literature

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[1] A further contribution towards a continuing study of the anatomy of the palm stem by one of us (P.B.T.) supported by N.S.F. Grant GB 2991.

[2] The terminology used in this paper, as well as in the others of this series, is a purely descriptive anatomical one (see the statement in Zimmermann & Tomlinson, 1965, p. 167 top).

discusses mostly the hypothetical "endogenous" growth of vascular bundles and is now largely of historical significance. Branner (1884) summarizes this history in his introductory pages. Branner's own factual contribution is noteworthy because he grasped the principle governing the distribution of vascular bundles in the mature palm stem, but he obscured it in a developmental discussion which seems not to be based on observation. Falkenberg's (1876) developmental account is also theoretical. His illustration of the palm is at best incomplete and, as we have shown, has been more a source of error than information for later writers (Tomlinson & Zimmermann, 1966b). Baranetzky's (1897) account of vascular bundle development in monocotyledons describes simply a centrifugal or centripetal, sometimes mixed centrifugal and centripetal, direction of development but adds nothing to our knowledge of the longitudinal course of differentiation. More recently Ball (1941) has verified the "centrifugal" development of vascular bundles recorded by Baranetzky in palms. Ball and other writers on the shoot apex of palms (Chouard, 1936; Eckardt, 1941; Helm, 1936) have simply described and illustrated the general topography of the meristematic regions in palms, showing that thickening growth of the stem is not a direct result of the shoot apical meristem proper but is associated with a primary thickening meristem developed below the expanding leaf primordia.[3] Otherwise no attempt seems to have been made to follow the distribution of leaf traces in the meristematic crown, although it is clear that an understanding of development is impossible without knowledge of the course of vascular bundles.

In *Rhapis*, as in other small palms, activity of the primary thickening meristem is such that the overall outline of the meristematic crown is a shallow cone rather than a bowl. This is fortunate, because analysis is facilitated when vascular bundles can be followed continuously in one direction through serial sections. The crown is also of a size suitable for handling by orthodox microtechniques. In addition, our previous quantitative analysis of the mature *Rhapis* stem has provided the information about vascular organization which, as Esau (1965) emphasizes, is an essential prerequisite for developmental understanding. For convenience this vascular organization in mature stems is very briefly outlined below, although the reader is referred to the first two papers of this series for details (Zimmermann & Tomlinson, 1965; Tomlinson & Zimmermann, 1966a). Familiarity with the facts in these two articles will greatly facilitate the understanding of the present paper.

In *Rhapis* all bundles of the central cylinder behave essentially alike. Each axially running vascular bundle is linked, at regular intervals, to leaves via a branch, the leaf trace. We have called the distance between leaf contacts of a given bundle the "leaf-contact distance" or "leaf-contact interval." This distance can be measured in number of internodes (cf. Zimmermann & Tomlinson, 1965, p. 169, *Fig. 3*). The departing leaf trace

[3] Distinction must be made between the shoot apex proper, which in palms produces only leaf primordia, and the meristematic region of the whole apex. Subsequently, the former will be referred to as "apex", the latter as the "crown."

shows the familiar outward curve originally recognized by von Mohl (1824) as characteristic for all palms. Each leaf is supplied by relatively few major bundles, but by a larger number of intermediate and minor bundles. Major leaf traces originate from the more central bundles so their outward curvature is most pronounced. Major bundles also give off leaf traces at the longest intervals (about 15 internodes). Intermediate and minor bundles are progressively more restricted to the periphery of the central cylinder and consequently the outward curvature of their leaf trace branches is less pronounced. In addition the leaf-contact distance is progressively shorter for bundles farther towards the periphery. Each continuing bundle (vertical bundle) above the level of departure of the leaf trace initially follows the outward curve of the leaf trace to the crowded periphery of the central cylinder, whereupon it turns erect and then gradually approaches the stem center again to give off a further leaf trace at some higher level (cf. Zimmermann & Tomlinson, 1965, p. 169, *Fig. 3*). During this gradual inward movement the bundle describes a shallow helix in the direction of the phyllotactic spiral. In the rhizome bundles deviate less from the axial direction and the helical path is scarcely evident (cf. Tomlinson & Zimmermann, 1966a, p. 254, *Fig. 4* below). In addition, there is greater irregularity of leaf-contact distance and bundle continuity.

In both axes lateral continuity between different bundles is achieved by short bridges between outgoing leaf traces and nearby vertical bundles. Cortical bundles occur in both types of axes as anastomosing strands continuous from the leaves, independent of the vascular system in the central cylinder, and ultimately ending blindly below.

PREPARATION OF MATERIAL

Vegetative stem and rhizome apices of *Rhapis excelsa*, together with enveloping leaf bases, were isolated from plants cultivated at Fairchild Tropical Garden and fixed in FAA. During dissection a record was kept of the state of development of the youngest exposed leaves in such a way that the corresponding leaves could be identified in serial sections. Stem apices and surrounding leaves thus prepared were cylindrical blocks of the order of 1–1½ × 2–3 cm. Blocks were desilicified in hydrofluoric acid, dehydrated and embedded in paraffin wax by routine procedures and sectioned serially at thicknesses from 8 to 15 μ. Shrinkage of material was inevitable but did not interfere with subsequent analysis. Sections were stained either in safranin and Delafield's haematoxylin on the one hand, or in erythrosin and toluidin blue on the other. Most observations were made on serial transverse sections but longitudinal series were also used for comparison. The bottom slides of the series of sections show all the anatomical features of the mature axis except that tissues are immature, e.g., metaxylem elements and fibers have not yet developed secondary walls.

GENERAL TOPOGRAPHY OF THE CROWN

For the sake of clarity we shall now introduce the reader to the general topography of the crown. This actually represents part of the results of the present study; but by giving this short initial description it will be easier for the reader to understand the next chapter of the paper describing the method of serial-section analysis wherein we break newer ground.

Aërial stem (FIGS. 1, 2, 6, and 7). We have not investigated the shoot apical meristem proper. Reference may be made to Ball's (1941) work on this subject in those species he examined. In palms this apical meristem functions largely as a "leaf-initiating" meristem. In *Rhapis* it includes no procambial tissue, i.e., no vascular strands can be discerned above the youngest primordium. The overall outline of the crown of *Rhapis* is a shallow cone, without the bowl-shaped depression of larger palms. This difference between smaller and larger palms is related to the activity of the primary thickening meristem and is not a fundamental one.

Leaves in *Rhapis* are arranged in a 2/5 phyllotactic spiral (FIG. 1). Each leaf has a closed tubular base tightly enclosing younger primordia, but somewhat thickened on the dorsal side. This dorsiventral difference in thickening is more pronounced distally in each leaf and is most easily seen in successively younger leaves cut at the same level, as towards the center of FIG. 1. FIG. 1 is drawn from a section cut too high to show the circular attachment of primordia 2–5. This leaf-base topography is the result of leaf growth by a pronounced basal meristem after the establishment of an encircling attachment. Development of this encircling attachment in the young primordia must be rapid because in the sections examined it is only incomplete in the youngest primordium (P1).

Procambial strands are evident even in the youngest primordium included in FIG. 1, their further rapid increase is indicated in the counts for total numbers of strands in successively older leaves plotted in FIG. 4. Immediately below the apical meristem proper, and continuous with it, is a dome-shaped or umbrella-like mass of meristematic cells. This undifferentiated meristematic "cap" (subsequently referred to simply as the cap) is pierced by leaf traces entering the youngest primordia. The cap is more or less easily visible on single sections of the rhizome crown, but it is much less easily recognizable in the crown of the aërial stem, except if one runs rapidly through transverse section series with the motion-picture analyzer.

Towards the lower border of the cap individual procambial strands are distinguishable from vacuolating cells. These strands are the distal extremities of the vertical bundles which, when traced upwards from below, end blindly in the cap. This cap-like meristem therefore is continuous with the crowded periphery of the central cylinder of the mature stem. The more central stem tissue, immediately below the shoot apex and enclosed by the cap, contains procambial strands already linked to leaves via the leaf traces which penetrate the cap.

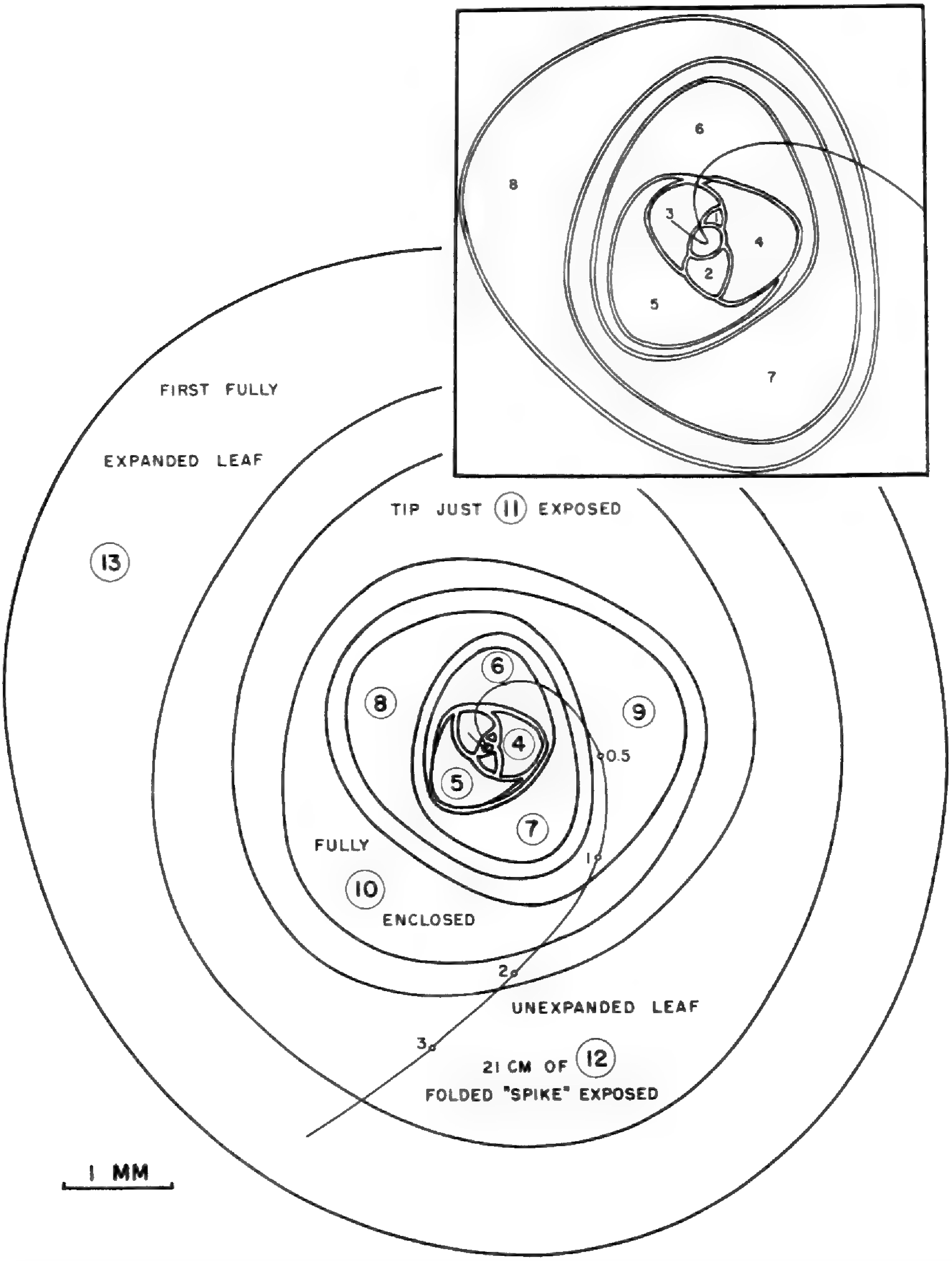


FIG. 1. *Rhapis excelsa.* Transverse section through the crown of the vegetative aërial axis. Leaf primordia are numbered from within, number 1 (P1) is the youngest that can be discerned. P14 is omitted. P1 is the only primordium which does not completely encircle the stem at its attachment, P2–P5 are cut above their encircling bases. This crown is the same as the one shown in the diagrammatic longitudinal section on FIG. 2. The spiral indicates the path of a dorsal major leaf trace from P3 (note the sharp turn below the apex). The numbers along the spiral indicate millimeters below the apex. INSET: central portion of section at higher magnification.

It must be emphasized at this point that the cap is *not* identical with the primary thickening meristem. The primary thickening meristem must be located *under* (i.e. inside) the cap. In neither of the crowns can the primary thickening meristem be structurally recognized in single sections because cell divisions are not uniform in any one direction. Towards the base of the crown, however, at the level of insertion of recently expanded leaves, ground meristem cells divide in a predominantly transverse plane, producing the vertical files of cells which indicate uniform elongation of the axis without distinction between nodal and internodal regions (Fig. 7).

Procambial strands in longitudinal section are strikingly distinct from the surrounding ground tissue as fascicles of cells with coincident end walls. The nuclei of each tier of cells at the same level produces a "tiger-tail" effect in longitudinal view. This indicates the origin of procambial strands from undifferentiated meristem by numerous longitudinal divisions in series of meristematic cells, the common end wall of each tier indicating the limits of each parent meristematic cell. This coincidence of end walls persists in the vascular tissues of mature vascular bundles (Tomlinson, 1961. p. 58). In transverse section procambial strands are less conspicuous, except where the sections include the nuclei. Otherwise they are distinguished by their narrow cells with somewhat densely staining cytoplasm. Limits of procambial strands are not sharp in the more meristematic regions where they become progressively more difficult to recognize.

Rhizome (Figs. 3, 8, and 9). The apical region of the rhizome (Fig. 8) is similar to that of the aërial stem in all essential details, except for being smaller (cf. Figs. 2 and 3). The 2/5 phyllotactic spiral is less obvious because the dorsiventral asymmetry of the leaves is less marked. The meristematic cap at the lower edge of which the vertical bundles terminate is more clearly visible in the rhizome than in the aërial stem (Fig. 9).

Helical path of bundles. The helical path of the procambial strands in the uncrowded center of the crown is not evident in any single section. Only a short length of any one bundle is included in single sections because of the conical shape of the crown. However, the spiral path can be demonstrated by plots of bundles. As an example, a major trace of P3 is given in Fig. 1. The trace is projected vertically into a transverse plane, the numbers along its path representing the vertical distance below the apex in millimeters.

In flat or bowl-shaped crowns of larger palms the overall spiral path of a number of bundles can be included within a single section. This is shown, for example, in *Chrysalidocarpus lutescens* (Fig. 5). This demonstration of the helix as an inherent feature of the crown in palms is historically significant because it finally settles an old controversy. Meneghini (1836) suggested that the helix is a mechanical consequence of torsions set up in the palm stem as it develops. This suggestion was debated at some length by early authors such as von Mohl (1849) but without examination of developing palm stems. Clearly the initiation of vascular bundles along a spiral pathway requires a physiological explanation, not a mechanical one.

METHOD OF SERIAL-SECTION ANALYSIS

This chapter describes how the serial transverse sections were analyzed. and how FIGS. 2 and 3 were constructed. These two figures contain most of the information obtained during the present study; they form the basis for subsequent discussion of development.

Two aërial and one rhizome crown were analyzed in full quantitative detail. Both aërial crowns showed an almost identical course of vascular strands, they will therefore not be discussed separately.

Initially the sections were surveyed so that the general topography of the crown could be established. Diameter measurements of the axis at each leaf insertion (in its dorsiventral plane) were plotted against section number. The resulting diagram shows a radial longitudinal section of the apex, *but with all the leaves in the same plane* (FIGS. 2 and 3). The vertical scale of these figures indicates the axial dimensions (i.e., the thickness of the sections when stacked up) and the horizontal scale is the radial distance of the plotted strands from the stem center. Measurements of peripheral strands were made from the strand to the stem periphery, more central strands were measured from the strand to the stem center, which was established by eye and marked with a spot of India ink on the cover glass. This visual determination of the center is of ample accuracy because the transverse sections are far from exactly circular. It did mean that plotted positions do not fall precisely on the smooth curves drawn in FIGS. 2 and 3; to this extent these plots are made diagrammatic. Of course, bundles do run along a more or less smooth path; if plotted curves come out a little irregular it is because there is no fixed point of reference in the axis.

As a given vascular strand was followed, its distance from the stem center was measured about once every 300 μ and its position was then plotted on the diagram. The way in which continuous recognition of the same strand was achieved is described below. The largest major bundle from each leaf was followed in turn, from the leaf insertion to the base of the crown (the lowest section in the series). Plotting started with the oldest available leaf (P14) and continued with each progressively younger leaf. Each bundle having been followed in the downward direction as a leaf trace, plotting was then continued in the reverse direction but now along its diverging vertical bundle, as far towards the shoot apex as the strand could be discerned. For successively younger leaves this operation became increasingly difficult because their traces are correspondingly less well differentiated.

FIGS. 2 and 3 show, therefore (as solid lines), the course of the largest major leaf trace which enters the axis from the dorsal side of the leaf. A minor and a cortical bundle from P11 are also indicated in FIG. 2. It must be emphasized again that these figures are not drawings of actual longitudinal sections because all dorsal sides of the leaves have been rotated into a single radial plane. Furthermore, the spiral path of the strands is entirely ignored. This spiral path is shown for a major bundle from P3 in FIG. 1.

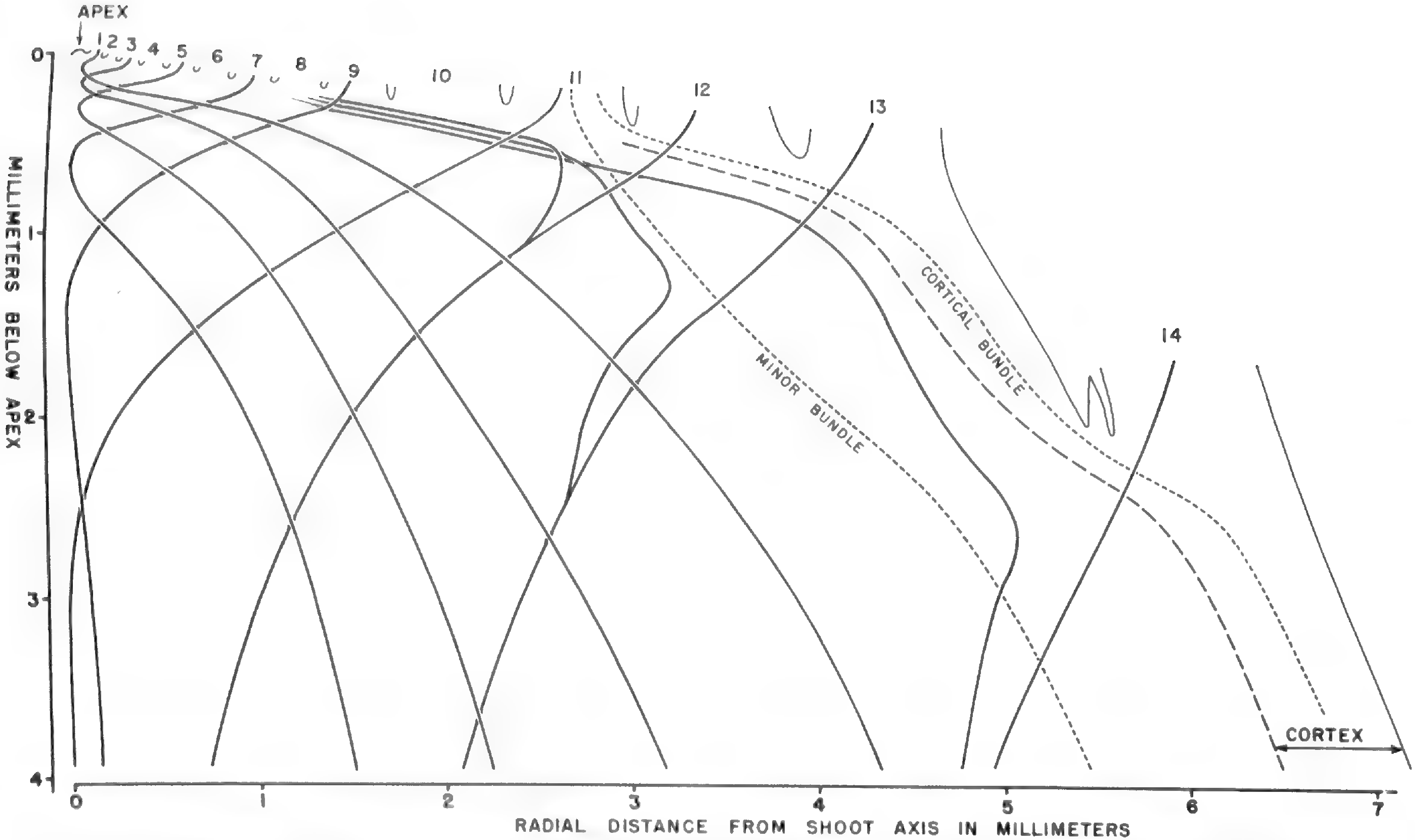


FIG. 2. *Rhapis excelsa.* Diagrammatic radial longitudinal section through the crown of the aërial vegetative axis based on measurements as described in the text. This is not a drawing of a single longitudinal section. All dorsal sides of leaf insertions are rotated into a single radial plane so that major leaf traces can be compared. The spiral path of the bundles is ignored. Leaf numbering as in FIG. 1. All solid lines are major bundles. A minor and a cortical (fibrous) bundle of P11 are included for comparison (dotted lines). Broken line separates cortex from central cylinder. Traces to P2, P4, P6, P8, and P10 are omitted for the sake of clarity.

projected vertically onto a tranverse plane. The same trace is shown in FIG. 2.

The reliability of these plots depends on the certainty with which a single bundle can be followed. Anyone who carefully looks at the photomicrographs in this article will realize that it is not easy to follow an individual bundle throughout a series of sections, especially if he considers that the stem contains about a thousand central vascular, and another two thousand five hundred cortical bundles. Therefore, during the plotting a motion picture was prepared with the drawing method outlined earlier (Zimmermann & Tomlinson, 1965). This procedure provided the physical discipline needed to ensure that continuity of a vascular strand was not lost. The problem of loss of continuity became increasingly severe in the vascular strands associated with the youngest primordia. Here the procambial strands are narrow, poorly differentiated and make sharp turns near the center of the stem. However, it was found that in critical areas (the top half millimeter), by making two superimposed drawings in contrasting colors at two magnifications for each section, the procambial strands could be followed with certainty. The drawing at low magnification served for quick orientation, the one at high magnification for identification of the strand under observation.

The most important data thus obtained are the resulting plots (FIGS. 2 and 3). Nevertheless, the motion pictures were quite useful to verify continuity and to allow study of incidental anatomical features. Moreover, it demonstrates in a few minutes the discoveries resulting from several weeks of hard work. In the motion picture of the rhizome crown, for example, the cap can be seen as a closing diaphragm which "sweeps away" all vertical bundles; a dynamic demonstration of the way vertical bundles "fuse" into the cap.

COURSE OF VASCULAR BUNDLES IN THE CROWNS

FIGURES 2 and 3 show the course of vascular traces in the top 3 to 4 millimeters of the crown of the aërial axis and the rhizome respectively. They are all dorsal major traces except those clearly labelled in the figure. These two figures show a very complex three-dimensional system reduced to a single radial plane, as described in the previous chapter. In order to reconstruct the three-dimensional system, the reader has to go through the following mental exercise. All points of entry of dorsal major bundles from leaf base to stem have to be rotated around the stem axis back to their five respective radial plans so that the 2/5 phyllotactic requirement is fullfilled (i.e., P1, P6, P11, etc. belong to the same orthostichy). Then, looking along the stem axis, one has to twist the five radial planes into the spiral shape shown for the trace to P3 in FIG. 1.

A comparison of FIGS. 2 and 3 with the diagrams of the adult axes, shown in previous papers (cf. Tomlinson & Zimmermann, 1966a, *Fig. 4*, below) shows clearly that the vascular pattern of the adult axes is laid down in the crown *before primary thickening growth occurs*. In the crown, leaf traces run axially and vertical bundles run radially. Subsequent

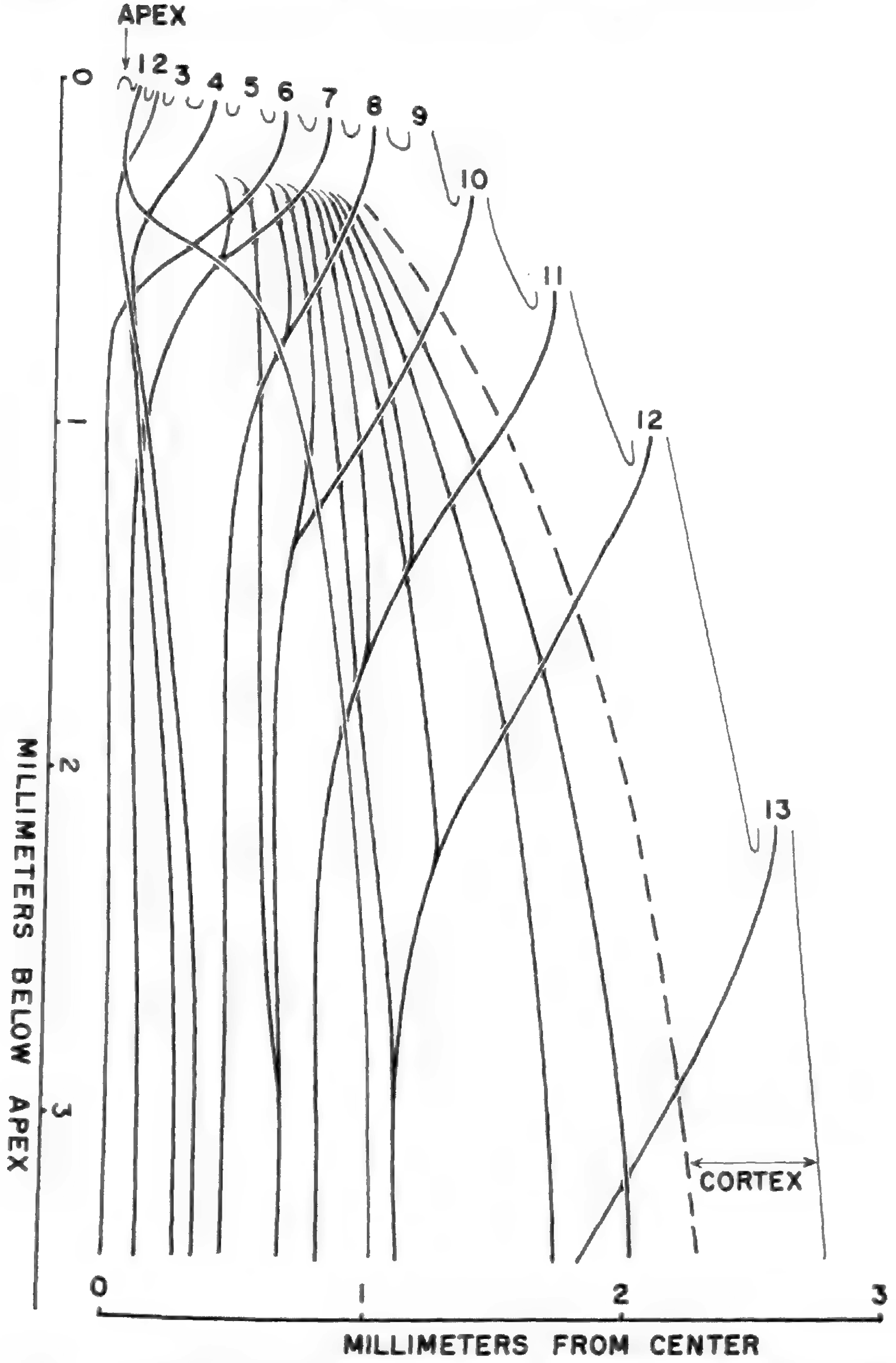


FIG. 3. *Rhapis excelsa.* Diagrammatic radial section through the crown of the rhizome based on measurements as described in the text. Like FIG. 2, this is not a drawing of an actual longitudinal section; all dorsal sides of leaf insertions are rotated to a single radial plane so that successive stages of development of major leaf traces can be compared. All solid lines are major bundles. Broken line separates cortex from central cylinder. Traces to P3, P5, and P9 are omitted for the sake of clarity.

primary thickening growth reorientates the system through 90°, with the result that in the mature stem leaf traces run more or less radially, vertical bundles more or less axially.

Let us now look a little more closely at the aërial stem and examine the major trace system of each successively younger leaf (FIG. 2). Vertical bundles diverging from the major leaf traces to P14 are released somewhat below the bottom of the section series, but are still readily identified because they initially follow the leaf trace closely in its centrifugal path. The major traces to P13 and P12 are complete, but located proportionately higher. No vertical bundle could be recognized diverging from the traces to P11 or any younger primordium. Corresponding to the overall outline of the crown, all vertical bundles of the crowded peripheral region are approximately horizontal at the insertion of P13. In this region they are conspicuous as radially running procambial strands ("tiger tails") in a single transverse section (FIG. 6). About 1/4 millimeter below the apex, approximately at the level of insertion of P8 they all fuse into an undifferentiated meristematic cap (but the cap is not uniform, it is penetrated axially by procambial leaf traces). The cap is, therefore, the meristematic region out of which the congested peripheral vertical bundles differentiate.

Leaf traces, even those which supply the youngest primordium, are all continuous; below they consist of the vertical bundle, above of the leaf trace. The ultimate basal continuity cannot, of course, be demonstrated directly in the short length of axis examined, but since the basal region is fully developed (though not fully differentiated), extrapolation into the mature stem is obvious. With a leaf-contact distance of about 15 internodes for major bundles P1 would connect with P16, P2 with P17, etc.

The curvature of the trace is established by reorientation of central bundles, immediately below the apical meristem, through a right angle; the method of reorientation is described below. These distal leaf traces are more or less perpendicular to the crowded vertical bundles and they pierce the meristematic cap. This development of two procambial systems more or less at right angles to each other is the fundamental feature which accounts for the final configuration of bundles in the mature stem.

The vascular anatomy of the rhizome crown (FIG. 3) is similar to that of the aërial stem, with quantitative differences which reflect distinguishing features of the mature rhizome. Inward and outward curvature of bundles is less pronounced. The meristematic cap is larger and more easily recognizable in single sections (FIGS. 8 and 9). The youngest leaf trace with attached vertical bundle is that supplying P7. The greater plasticity (i.e., irregularity in construction) of the mature rhizome trace system is further verified in the crown where leaf traces may give off more than one vertical bundle (as the traces to P11 and P12, FIG. 3) or none.

DEVELOPMENTAL INFERENCES

From the information in the diagrams, FIGS. 1–4, the essential features of vascular development in the crown of *Rhapis* become clear. By counting

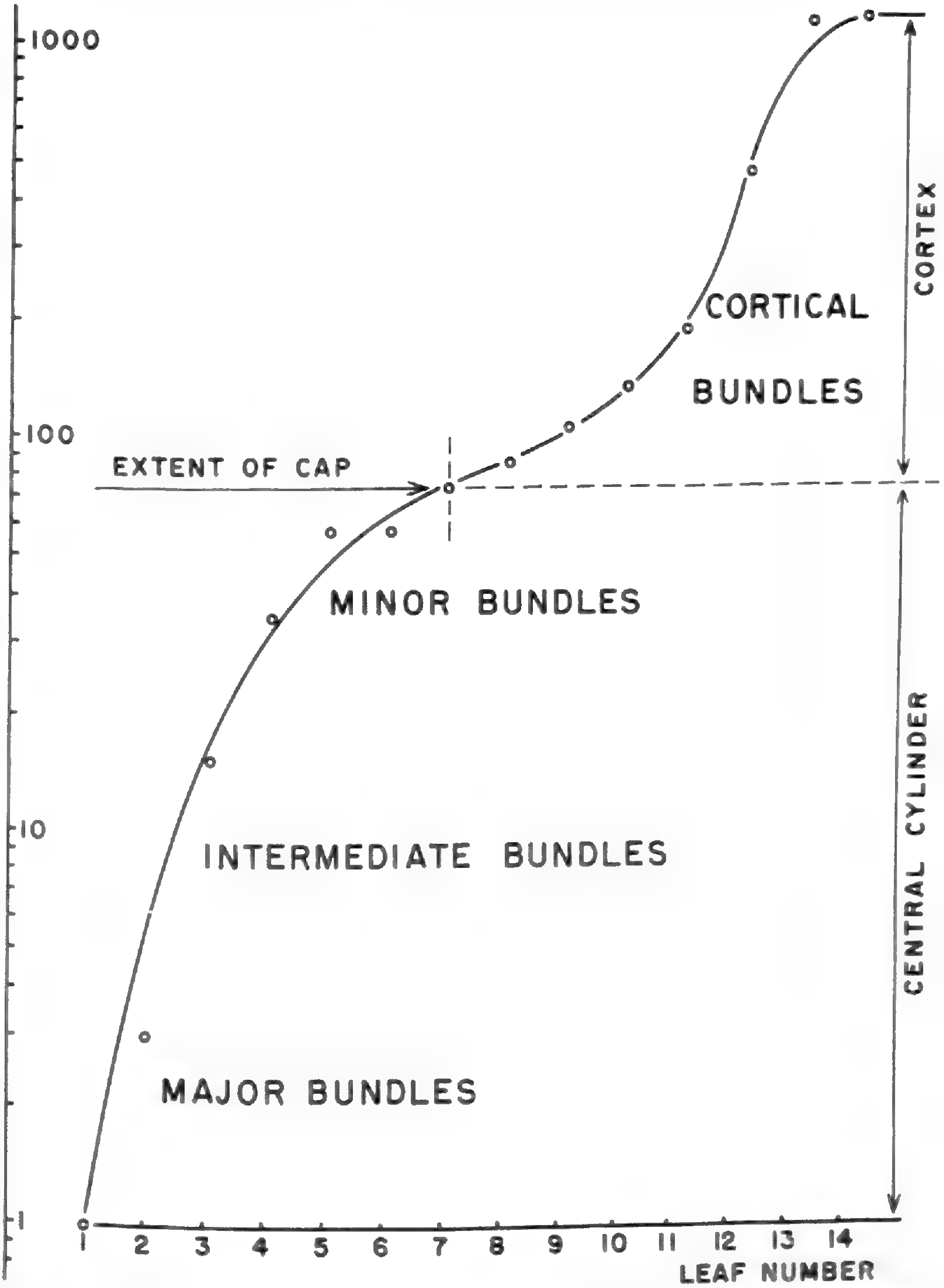


FIG. 4. *Rhapis excelsa.* Logarithmic plot of total number of vascular bundles in the base of each successively older leaf, counted in transverse sections, against leaf number. The apparent double peak of frequency of leaf trace initiation (i.e., the differential of the number of bundles) may be an artifact resulting from the difficulty of recognizing fibrous bundles in their early stage of development (see the discussion of this in the text).

the total number of recognizable bundles at the leaf insertion at each developmental stage an idea can be gained of the period over which leaf trace development continues. FIG. 4 is a plot on a logarithmic scale of such a count. It shows that each leaf produces new traces continuously for about 13 plastochrones. In P14 the total number of bundles is established. Quite obviously major bundles are produced first, intermediate ones later, minor ones still later, and cortical ones last. Of the total number of traces in each leaf (a little over 1,000) less than 100 in the stem are bundles of the central cylinder, the remainder are cortical bundles.

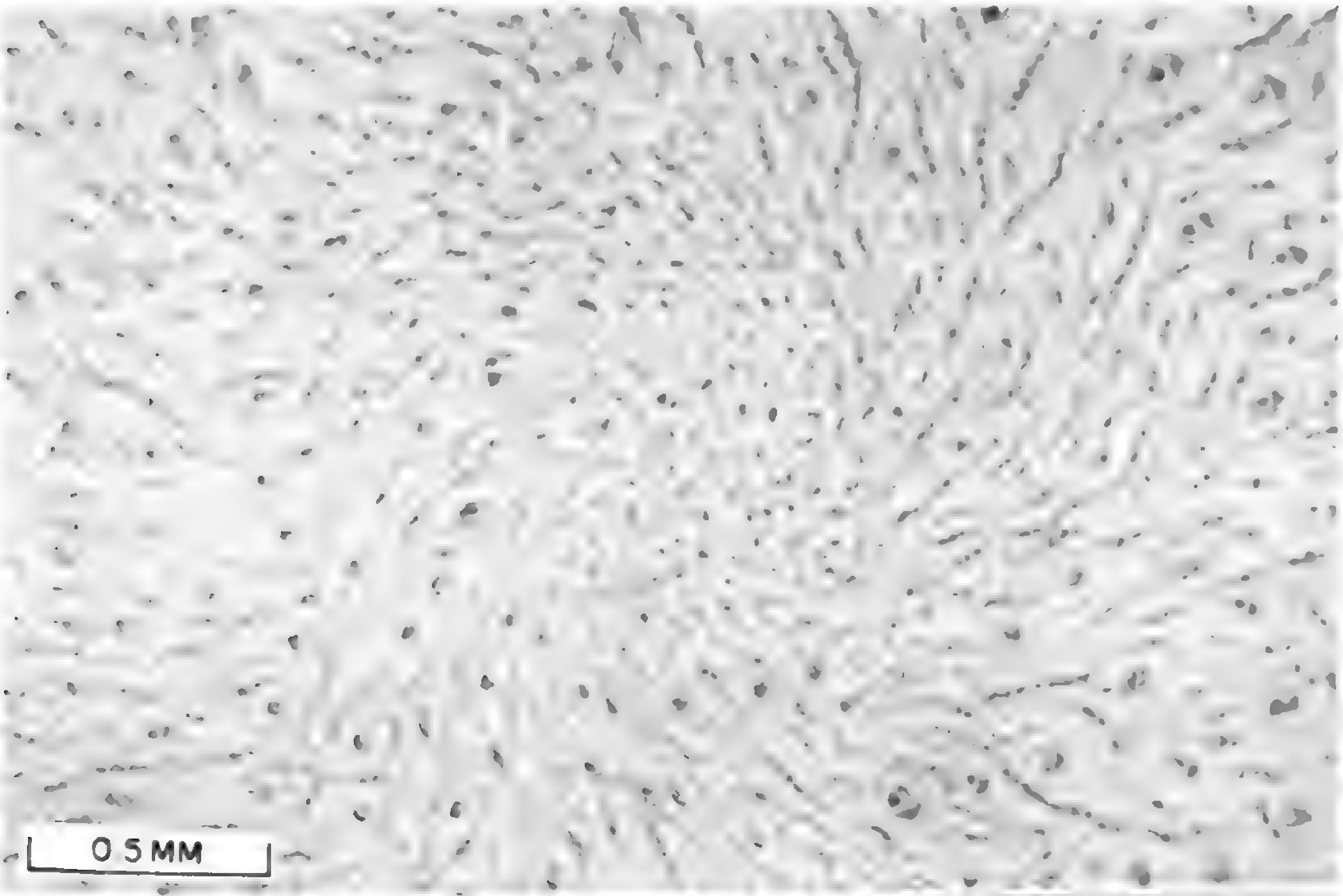
Renewal of the meristematic cap in relation to the origin of different bundle categories. A consideration of successively younger leaf traces in FIG. 2 shows that vertical bundles are differentiated basipetally from the cap, or expressed more correctly, the cap grows distally from the differentiating bundles. The cap must therefore be renewed from above by tissue (below about P1–P8) which at a later stage of development differentiates as vertical-bundle branches of the leaf traces (below about P11).

As a leaf is initiated on the apical meristem its first leaf traces each make contact with the distal extremity of a vertical bundle within the cap. Because early contacts with the leaf are made in the center of the stem the upper portion of the bundle will, after differentiation, still be located in the center. As the leaf grows older newly initiated leaf traces establish vascular contact with more and more centrifugal parts of the cap. These later vascular strands are intermediate and then minor ones, they reach less far into the stem center and their leaf-contact distances are shorter. Shorter leaf-contact distances for later vascular strands are simply the result of fewer plastochrones during which the vertical bundle differentiates as a distally unconnected strand.

The rhizome crown is similar with an apparent exception that the vertical bundles in the cap keep growing even after leaf contact has been made. It must be remembered that nutrition of the rhizome crown takes place continuously from proximal regions, since scale leaves do not assimilate. In the aërial crown newly matured leaves can supply assimilates to the meristematic region (note in FIG. 1, that leaves of the developmental stage P11 and older, are green and exposed to light). Only future experimental work on the translocation of nutrients in developing regions will allow a clearer understanding of these differences.

Further mention may be made here of the relative irregularity of bundle development in the rhizome (Tomlinson & Zimmermann, 1966a). Vertical bundles occasionally (though rarely) split; vertical bundles commonly fuse to form the "long bridges" described in our earlier account. The number of vertical bundles diverging from a leaf trace is more variable than in the aërial axis and vertical bundles also seem able to continue unlimited growth in the cap without making contact distally with a leaf trace. In the mature rhizome we have followed numerous vertical bundles which had no leaf contact over distances in excess of 15 internodes. With further understanding of developmental processes in *Rhapis* it is likely that these "mistakes" can be seen to belong to the developmental norm.

Leaf trace — vertical bundle linkage and the origin of the cortex. The way in which vertical bundles maintain a constant rate of differentiation in relation to the shoot apex and the meristematic cap is



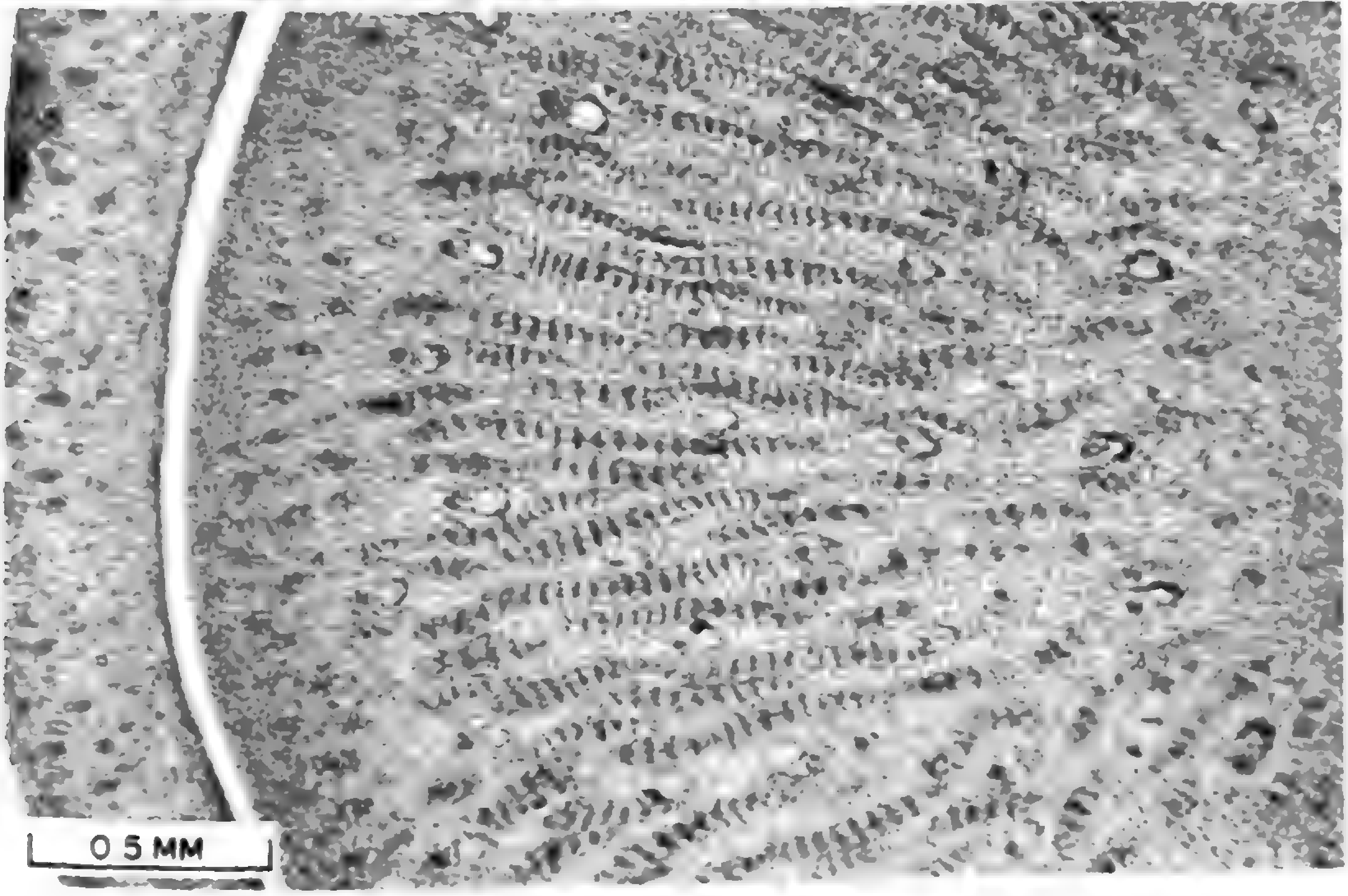


FIG. 5 (ABOVE). *Chrysalidocarpus lutescens*. Transverse section through the (bowl-shaped) crown of the stem 0.5 millimeter below the lowest leaf-primordium insertion. The spiral path of the major leaf traces (their future helical path in the mature stem) can be seen clearly.

FIG. 6 (BELOW). *Rhapis excelsa*. Transverse section through the crown of the aerial vegetative axis 0.5 millimeter below the shoot apex proper. Leaf traces here run axially and are seen in transverse section. Vertical bundles are seen as radially-running procambial strands ("tiger tails"). These represent the peripheral crowded region of the central cylinder in which the bundles do not follow a spiral path.

evident from FIG. 2. Leaf traces are "sent out" by leaves for a period of about 13 plastochrones. The first leaf traces make contact with the central portions of the cap, subsequently initiated leaf traces contact more centrifugal parts of the cap. Still later traces "sent out" by a leaf when it is more than 7 plastochrones old appear outside the cap, i.e., outside the region of blind-ending vertical bundles. These traces must be located outside the central cylinder, that is, in the area of the stem which we recognize later as the cortex. Having failed to make contact with vertical bundles these leaf traces must end blindly below, although they may anastomose among themselves as if still "seeking" vascular contact. This blind-ending cortical system is readily observed in the cortex of both axes; it is particularly well developed in the rhizome. If we compare FIGS. 2 and 4 we can see that the cap extends radially over approximately 7 leaf insertions. Thus over a period of about 7 plastochrones vascular contact between leaf and central cylinder is possible; subsequently all leaf traces are confined to the future cortex of the mature stem.

FIGURE 4 suggests that frequency of leaf-trace initiation occurs in two peaks. This, somehow, seems to be unlikely. It could be a reflection of a

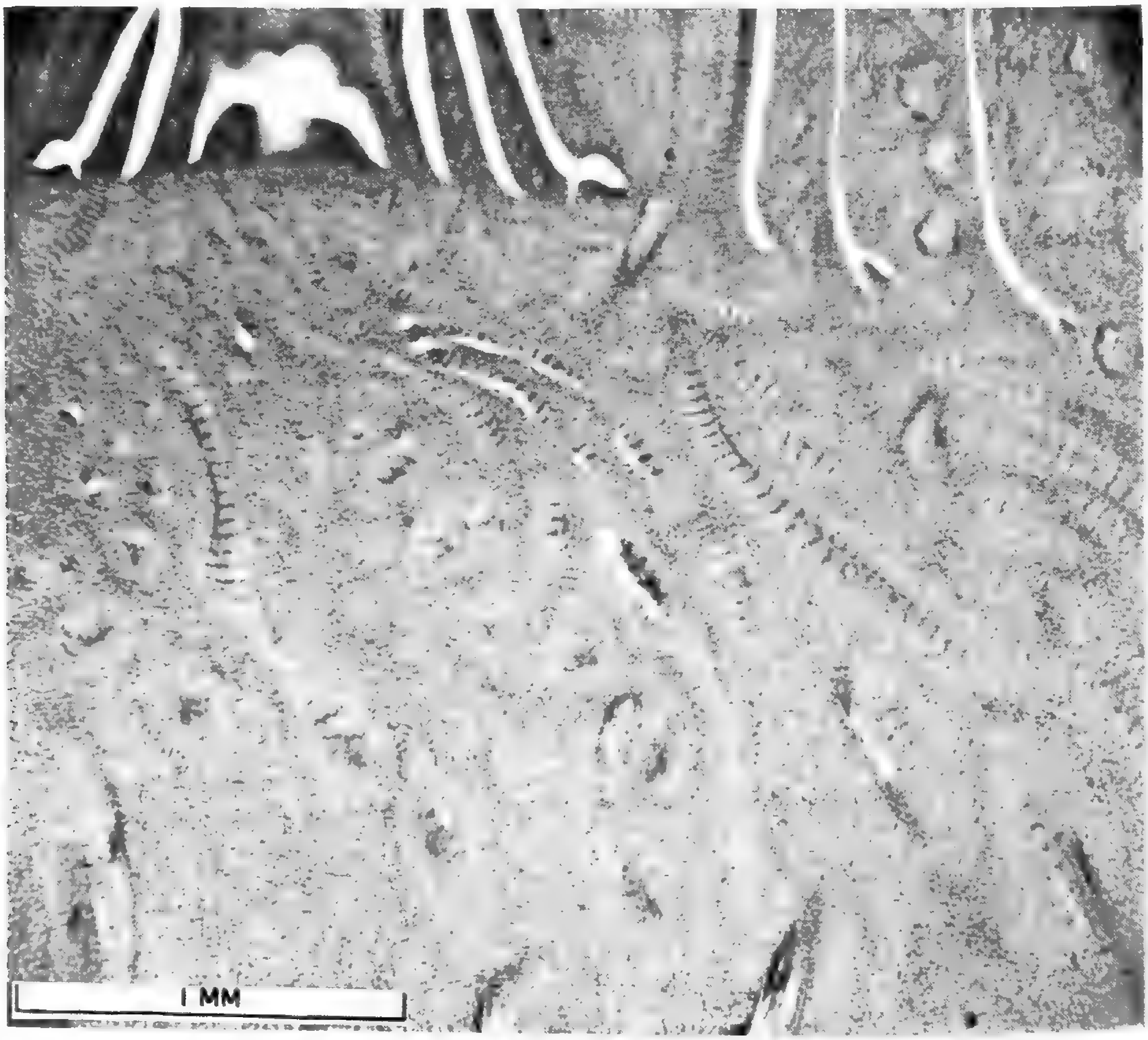


FIG. 7. *Rhapis excelsa.* Approximately median longitudinal section through the crown of the vegetative aërial axis. Because of their spiral path only short lengths of bundles can be seen. Comparison of this photograph with the diagrammatic FIG. 2 indicates major features.

subjective phenomenon resulting from our inability to recognize early stages in differentiation of cortical compared with central bundles. In addition, the leaf base produces branching from existing leaf traces (vertical bundles, satellites, bridges) somewhat before stage 11; these are not included in the count and would "fill out" the curve. At any rate, it is reasonable to assume that only one peak of initiation frequency is involved. FIG. 4 should probably follow a simple sigmoid curve.

Thus a developmental difference between early and late differentiating bundles manifests itself in mature parts as a clear morphological boundary between central cylinder and cortex. Cortex and central cylinder both remain essentially descriptive terms; both regions are axial parts and there is no need to enter into the futile philosophical discussion as to whether cortex may or may not be regarded as a "fundamental part of the stem" or merely as a downward continuation of the leaf base, a discussion to which earlier morphologists were prone (cf. for example, Baranetzky, 1897).

Origin of vertical bundles, bridges and satellites. The question now arises as to where in development the vertical bundle diverges from the leaf trace. This can only be estimated. It is quite evident that these branches must arise in continuity with the leaf trace but directed towards the cap because no vertical bundles ending blindly below have ever been observed in the central cylinder. FIGS. 2 and 3 suggest that branching occurs when a leaf is about 11 plastochrones old in the aërial axis, 6 in the rhizome, since P11 and P6 respectively are the oldest primordia without an identifiable vertical bundle. We easily may have overlooked this vertical bundle but the configuration in FIG. 3 strongly suggests that the vertical bundle arises in continuity with the meristematic cap as soon as the leaf trace has been displaced to a position near the lower margin of the cap.

Further consideration of FIGS. 2 and 3 reveals that only the directly associated leaf can initiate development of vertical bundles, not the much higher one into which the vertical bundle ultimately proceeds. We know from our analysis of both types of axis that leaf-contact distances are of the order of a least 15 internodes for major traces. FIGS. 2 and 3 further support this as they include 14 and 13 leaves respectively but no complete leaf contact. In FIG. 3, assuming that the vertical bundle branch originates when a leaf is 6 plastochrones removed from the apex (it has already appeared in P7), then with a presumed leaf-contact distance of 15 internodes, the upper contact of this new vertical bundle would be to leaf I9,[4] a leaf which does not appear for a further 9 plastochrones. Clearly it would be absurd to assume that I9 initiates the vertical bundle in P6. Even if we were to go to the extreme of assuming that this primordium existed at the apex in an unidentifiable state, a simple computation by extrapolation from the number of cells visible in cross sections of the base of successively younger leaves gives a value for I9 of only a small fraction of a cell. It is

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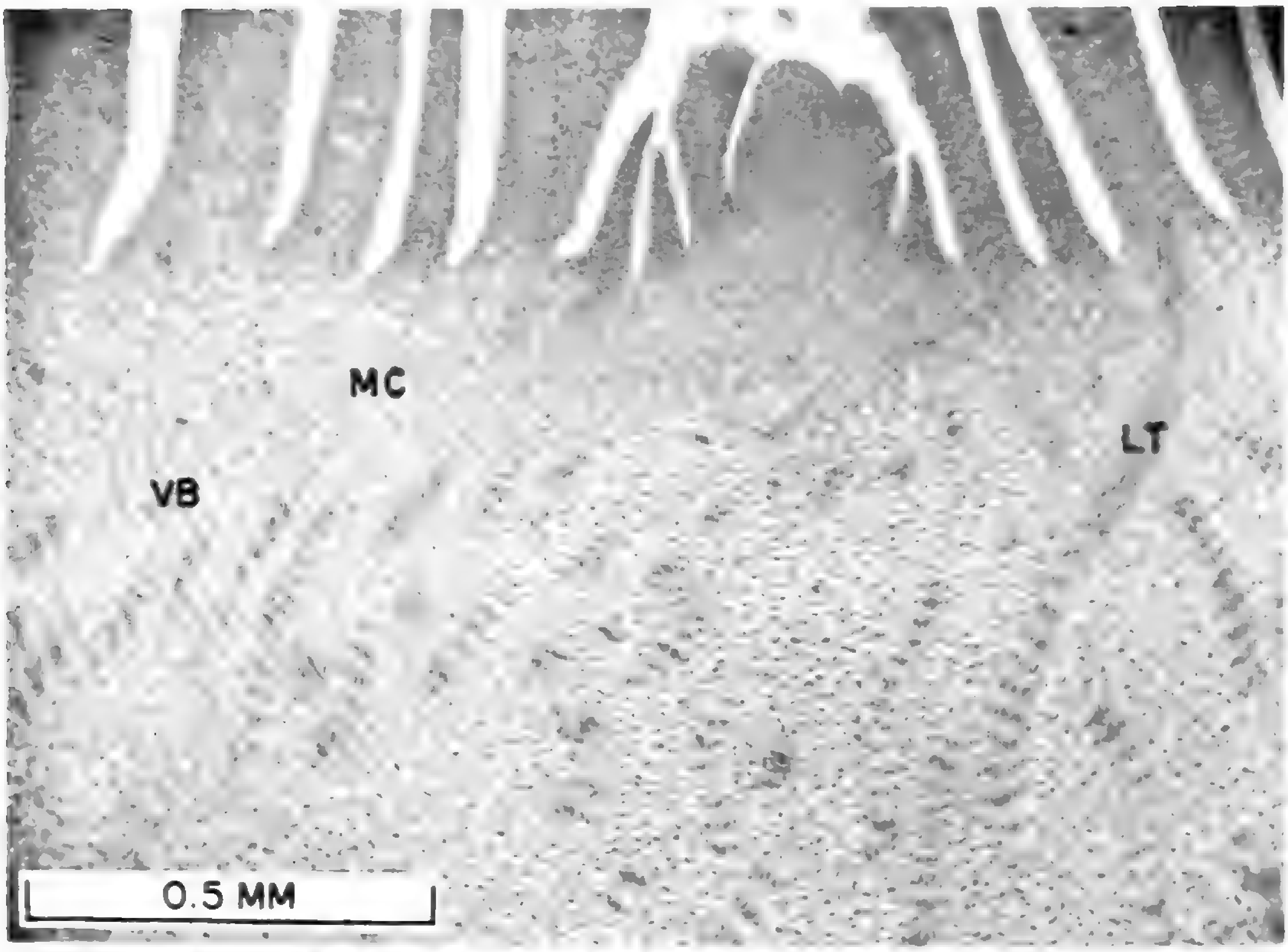
[4] Leaf primordia are numbered P1 (the youngest), P2, P3, etc. Non-existing ones are numbered I1 (to appear next), I2, I3, etc.



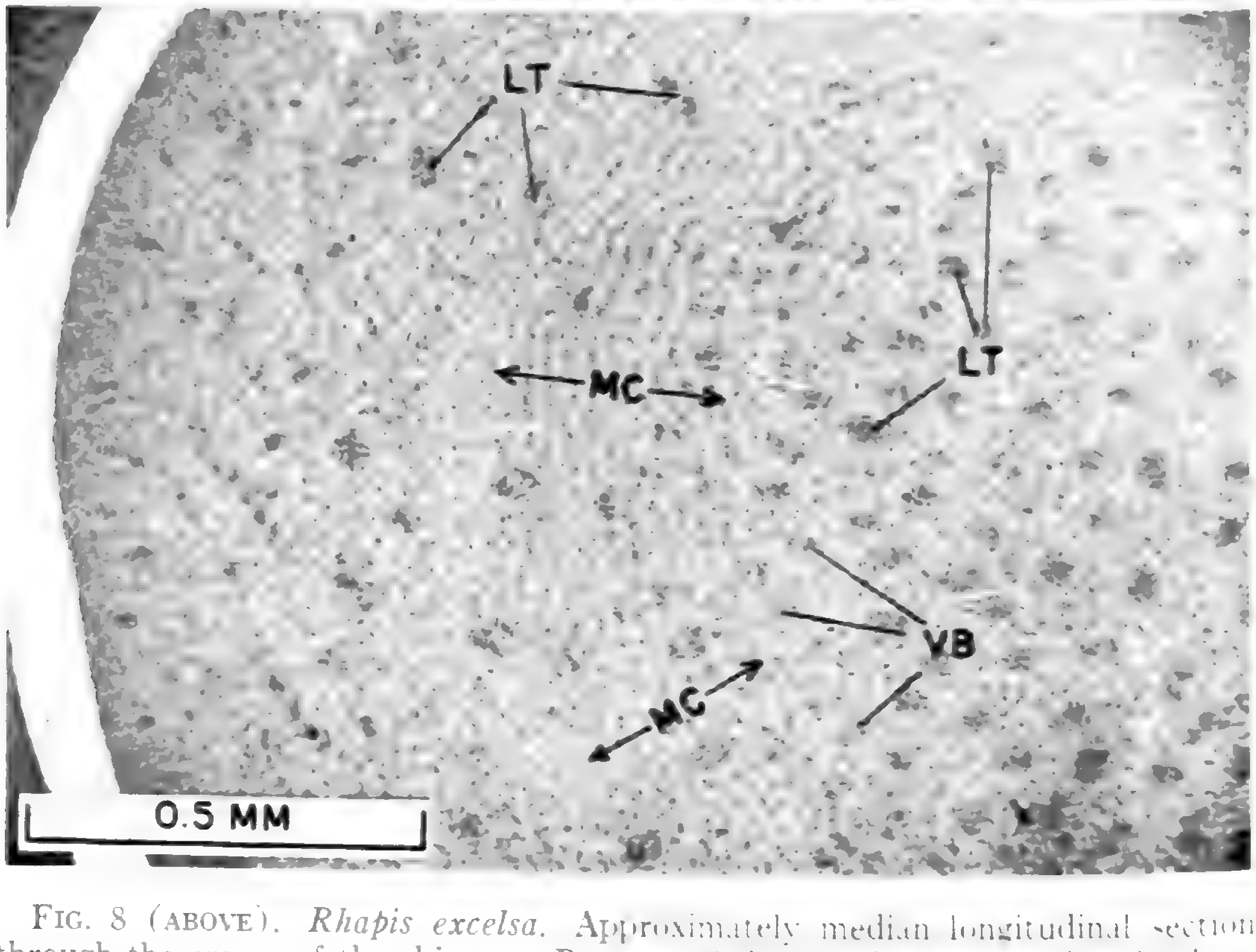


FIG. 8 (ABOVE). *Rhapis excelsa.* Approximately median longitudinal section through the crown of the rhizome. Because of their slight spiral path only short lengths of bundles can be seen. Comparison of this photograph with the diagrammatic FIG. 3 indicates major features. Procambial strands of the vertical bundles (VB) extend distally into an undifferentiated meristematic cap (MC). Leaf traces (LT).

FIG. 9 (BELOW). *Rhapis excelsa.* Transverse section through the crown of the rhizome 0.3 millimeter below the shoot apex. The undifferentiated meristematic therefore quite impossible for vertical bundles to be initiated by nonexistent leaves. This is precisely the conclusion of Priestley and his coworkers (1935) for *Alstroemeria.*

The presence of numerous bridges and satellites (Zimmermann & Tomlinson, 1965) also lends support to the idea that vertical bundles are directed apically in their development. Bridges are usually short and always attached to neighboring vertical bundles in an upward direction. We regard bridges as "frustrated" vertical bundles, i.e., both are microscopically identical and seem to be branches sent out by the leaf trace. Both can now be regarded as developmentally identical, but positional (and probably also temporal) differences determine different fates. It can be envisaged that space for continued upward development of bridges is limited (they almost invariably diverge from leaf traces more distally than vertical bundles); as a result they fuse with other, nearby existing vertical bundles. Satellites may originate in the same manner and grow towards developing inflorescences (which may later abort). The inflorescence primordium, regardless of whether it aborts later or not, may be physiologically equivalent to a shoot apex in that it "attracts" some of the branches which diverge from the leaf trace.

Concluding remarks. We may now summarize our interpretation of vascular bundle development, argued in the previous paragraphs, and the way in which we account for the overall course of bundles in *Rhapis.* First a leaf trace develops in association with a primordium into the meristematic cap. There it meets an oncoming vertical bundle. Vascular continuity thus established, bundle differentiation continues in such a way that it is displaced downward out of the cap (i.e., the cap grows upward away from it). Since the developing leaf is displaced centrifugally, i.e., in the reverse direction to which the vertical bundle had been differentiated there results a sharp bend in the bundle as a whole. This bend, the most centrally located part of the bundle, marks the point of initial contact of leaf trace with cap. Later, at a developmental stage in major traces corresponding to P10 for the aërial axis and P6 for the rhizome, branches develop away from the leaf trace towards apex and inflorescence. Of these the first formed is included in the meristematic cap as the continuing vertical bundle, later ones make bridges to existing vertical bundles while the last ones are inflorescence traces. The final configuration of leaf trace and associated branch bundles as seen in mature axes gives little indication of the direction in which these branches initially diverged, because the point of branching is displaced downward during primary thickening growth as the traces to P12, 13, and 14 suggest in FIG. 2. The sharp angles at which vertical bundles and bridges branch off the leaf trace in the mature stem is

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cap (MC) is seen as a ring penetrated by axially running leaf traces (LT). In the center of the stem (to the right of the cap in the figure and structurally proximal to the cap) are both leaf traces (LT) and vertical bundles (VB), in the periphery of the stem (to the left of the cap in the figure and morphologically distal to the cap) are only leaf traces.

incidental, for they are caused by displacement during primary thickening growth.

RHAPIS COMPARED WITH ALSTROEMERIA

Only in the work of Priestley, Scott and Gillet (1935) on *Alstroemeria* are we afforded a means of directly comparing our observations on *Rhapis* with those on another monocotyledon, although *Alstroemeria* is a great deal simpler than *Rhapis*. Nevertheless, these workers adopted an approach to a study of the developing vascular system in this non-nodal monocotyledon, similar to ours. It is noteworthy that Priestley and his associates also were forced to conclude that leaf traces in *Alstroemeria* developed acropetally long before the leaves they served became evident. On the other hand, *Alstroemeria* differs from *Rhapis* in that (1) there is no cortical system, (2) there are only 3 traces to each leaf, and (3) the leaf insertion occupies only a narrow sector of the stem circumference. This means that bundle linkage is dependent on leaf arrangement. In *Rhapis*, however, leaves encircle the stem completely at their insertion and phyllotaxis is incidental to bundle linkage. Nevertheless, a comparison of the diagrams illustrating the vascular system of *Alstroemeria* with ours for *Rhapis* suggests basic similarities in developmental terms.

SUMMARY

Vascular strands of the aërial axis and rhizome of *Rhapis excelsa* were followed in the meristematic crown with the microcinematographic method of analysis, and their course was plotted. From resulting plots vascular development is inferred. Vascular bundles of the crowded peripheral part of the central cylinder are continuous distally with a meristematic cap on the top center of which is the apical meristem proper. As each leaf develops it initiates leaf traces continuously during 14 plastochrones after inception. Leaf traces are oriented perpendicular to the vertical bundle and link with the blind ends of vertical bundles in the cap. Major vascular bundles are leaf traces initiated very early at a time when the leaf primordium is still located near the stem center. Leaf traces initiated later become intermediate and then minor bundles successively nearer the stem periphery, corresponding to the position of the leaf at the time of their initiation. The last traces, initiated outside the cap, end blindly below and differentiate into the cortical fibrous traces. The cortex, a structurally distinct region of the palm stem, is thus clearly defined by development. Determination of vascular bundles is a property of the meristematic cap effected in such a way that vascular bundles, as soon as they are continuous from a leaf primordium above to a leaf below, are displaced proximally (later centripetally) and so lost from the cap. The cap must be renewed from above by tissue which at a later stage of development differentiates as vertical-bundle branches of the leaf traces.

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We wish to express our further appreciation of the serial sectioning carried out by Miss Lesley Jackson and Miss Veronika Oswald (now Mrs. G. S. Walton) as a preliminary to this investigation.

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TWO NEW AMERICAN PALMS

Harold E. Moore, Jr.

I. A SECOND SPECIES OF ARISTEYERA

Shortly after the publication of the new genus and species *Aristeyera spicata* in this journal (**46**: 5. 1966), Dr. Julian A. Steyermark sent specimens for study which proved to represent a second species, here described as *Aristeyera ramosa*. Since there are major differences between the new *A. ramosa* and *A. spicata*, as listed below, an emendation of the generic circumscription is provided. The branched inflorescence is subtended by three bracts, a most unusual feature in a tribe where only two principal bracts have normally been known heretofore. These characteristics of the inflorescence suggest a less specialized species than *A. spicata*. The smaller number of stamens in the staminate flower and of staminodes in the pistillate flower suggests the possibility that more than six stamens may be a derived rather than a primitive state in the Geonomeae, a possibility requiring further anatomical study before any conclusion can be drawn.

Aristeyera H. E. Moore, char. amplif.

Solitary, slender, unarmed, monoecious protandrous palms sometimes producing short lateral vegetative branches with small leaves and adventitious roots at upper nodes. Leaves normally undivided except for the bifid apex, pinnately nerved; sheath short, rupturing opposite the petiole. Inflorescences interfoliar, erect, subtended by 2 or 3 closely sheathing bracts inserted at or near the base of the peduncle, the lower bract ancipitous, the upper 1 or 2 longer, with rounded margins, opening obliquely at the apex; peduncle elongate, terminating in one or in several subfasciculate spike-like flowering axes, the flowers borne in triads of 2 lateral staminate and a central pistillate (which sometimes aborts in apical triads) sunken in pits, these covered with a bract in bud and arranged in 6–8 vertical series. Flowers about $\frac{1}{3}$ exserted at anthesis: staminate flowers with 3 glumaceous sepals, these distinct and more or less keeled above a short attachment to the receptacle, imbricate at least basally in bud; petals 3, adnate basally to the receptacle, connate above (sometimes unequally so) for $\frac{1}{3}$–$\frac{3}{4}$ their length in a soft tube, the free, slightly asymmetric lobes deltoid, glumaceous, valvate above briefly imbricate bases; stamens (11–) 12–24, exserted at anthesis, the filaments adnate basally to the receptacle, then expanded and connate in a tube surrounding a fleshy, shallowly and acutely, often irregularly 3-lobed pistillode, the free portions of the filaments only slightly longer than the connate portions, erect, anthers inflexed in bud, thecae separate, longitudinally dehiscent, terminal on arms of a bifid connective, arms of the connective and thecae becoming erect or nearly so at anthesis: pistillate flowers with 3 glumaceous distinct sepals imbricate in bud; petals 3, connate basally in a soft fleshy tube with deltoid glumaceous lobes shortly imbricate basally, valvate above in bud, exserted and spreading at anthesis; staminodes (5–6–)7–18, fleshy, connate basally and adnate to the corolla-tube, then free and subulate or linear, exserted and spreading at anthesis; pistil trilocular, triovulate, the ovary with 3 rounded lobes; styles terminal, elongate, loosely united, exserted and more or less thickened above the throat of the staminodial tube at anthesis; stigmas 3, recurved, at anthesis; ovule hemitropous, axile, pendulous, attached near the top of the locule, only one normally maturing. Fruit ellipsoid-ovoid, slightly compressed laterally and slightly keeled apically when dry, the residual stigmas and abortive carpels basal; exocarp smooth; mesocarp rather dry, with longitudinal fibers closely placed around the endocarp, this thin, crustaceous, shining, not adherent to the seed; seed ellipsoid to obovoid and slightly compressed laterally; hilum small, excentrically basal; raphe encircling the seed from hilum to excentrically basal embryo, somewhat impressed and unbranched to furcate or with a few parallel branches; endosperm homogeneous.

Aristeyera ramosa H. E. Moore, sp. nov. FIGS. 1 and 2

Ab *Aristeyera spicata* inflorescentia ramosa bracteis 3 subtenta, rachillis 4–6 subfasciculatis glabris alveolas floriferas in seriebus 6–8 verticalibus gerentibus, florum masculorum staminibus (11–)12, florum femineorum staminodiis (5–6–)7–9 subulatis differt.

Stems solitary, to 3 m. high, 3–8 cm. in diam., often producing short lateral vegetative branches with small leaves and adventitious roots at nodes above. Leaves rigid, subcoriaceous, paler green below (Steyermark); sheath short, ca. 11–17 cm. long at margin of petiole, 6–17 cm. long and frayed into irregular lobes opposite petiole, fibrous, densely brown-tomentose inside and outside; petiole 33–43 cm. long, brown-tomentose below, at least when young, becoming glabrous; blade cuneate in outline, undivided except at bifid apex, 58.5–66.5 cm. long along the rachis, 21–27 cm. wide at apex of rachis, 31 cm. or more long along inner margin of terminal lobes, the rachis glabrous above, more or less brown-tomentose below, primary nerves 34–38 on each side, with scurfy small brown or rusty appressed scales on these and the secondary and tertiary nerves below. Inflorescence erect in flower, becoming pendulous in fruit, subtended by 3 bracts, the lowermost short, 15–20 cm. long, ancipitous, brown-tomentose, becoming glabrous, the middle one inserted close to the lowest or to ca. 8.5 cm. above it, 25–49 cm. long, opening obliquely at apex, densely brown-tomentose, the uppermost similar to the middle bract and exceeding it by 11–18 cm.; peduncle densely brown- or rusty-tomentose, 46–178 cm. long; rachis very short, 1.3–2.5 cm. long; rachillae 4–6, subfasciculate, glabrous, 18–20 cm. long, 6–8 mm. in diam., with flower pits in 6–8 vertical series, becoming maroon-rose or wine-colored in fruit. Staminate flowers at anthesis ca. 6–6.5 mm. long; sepals 5 mm. long; corolla-tube ca. 3 mm.

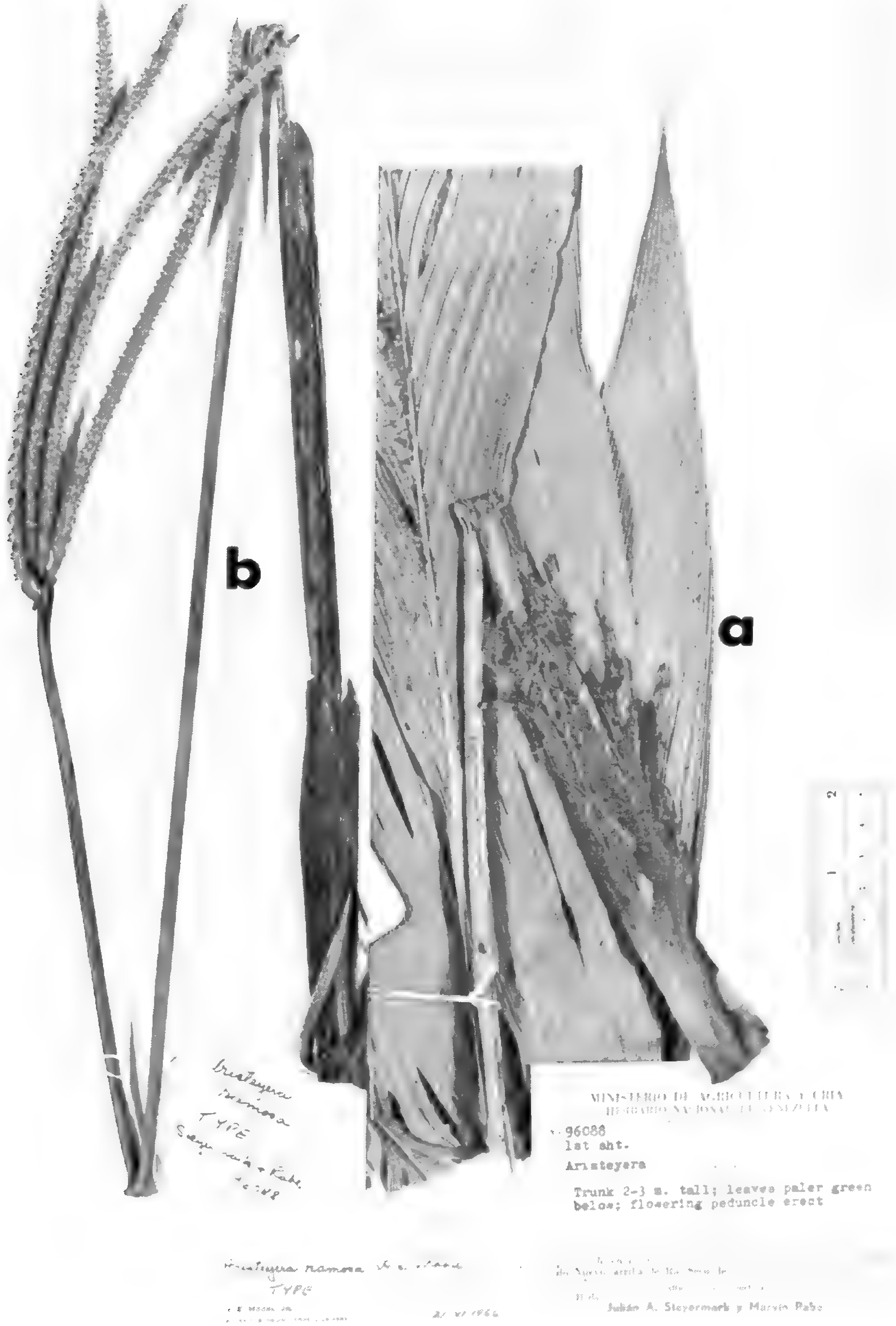

FIG. 1. *Aristeyera ramosa.* a, leaf; b, inflorescence.

long, corolla-lobes ca. 3.4 mm. long; stamens (11–)12; pistillate flowers at anthesis (from preserved material) ca. 7 mm. long; sepals 5 mm. long; corolla-tube ca. 4 mm. long, corolla-lobes 2.6 mm. long, acute; staminodes (5–6–)7–9, connate in a fleshy tube 4 mm. long and adnate to the corolla-

FIG. 2. *Aristeyera ramosa.* c, habit, from kodachrome by J. A. Steyermark; d, portion of inflorescence with pistillate flowers at anthesis, from kodachrome by J. A. Steyermark.

tube, then free, ca. 3.6 mm. long, fleshy, subulate, spreading at anthesis; style exserted and expanded above throat of staminodial tube; stigmas recurved. Fruit (not fully mature) ellipsoid, 15–16 mm. long, ca. 5 mm. in diam., dark purple-red.

VERNACULAR NAME: *anare*

Venezuela. ESTADO SUCRE: Peninsula de Paria, Cerro de humo, laderas pendientes de bosque nublado virgen que miran al norte, a lo largo de las cabeceras de uno de los afluentes del Río Santa Isabel, arriba de Sipara, oeste de Santa Isabel, alrededor de 14 kms. al norte del pueblo de Río Grande Arriba, arriba de Boca de Cumana y Punto Siparo, noroeste de Irapa, alt. 1060 m., 1 Mar. 1966, *Julian A. Steyermark 94803* (BH); Cerro Espejo, selva siempre verde en la cumbre, entre Manacal y Pauji, arriba de Mundo Nuevo, arriba de Río Seco de Irapa, alt. 750–850 m., 6 Aug. 1966, *Julian A. Steyermark & Marvin Rabe 96088* (BH, holotype).

The epithet for this second species of *Aristeyera* is used with reference to both the branched inflorescence and the unusual short lateral branches often produced along the upper portion of the stem. It is perhaps worth noting that in the two collections available, the flower pits are arranged in six vertical series in the three inflorescences of the type while in the single fruiting inflorescence of *Steyermark 94803* they are in eight vertical series on one axis, in six on the remaining five axes.

It may be useful to tabulate the diverging characteristics of the two species in the following way:

Stems not producing lateral branches	Stems often producing short lateral vegetative branches along the upper portion
Bracts subtending the inflorescence 2	Bracts subtending the inflorescence 3
Flowering axis simple, spike-like, densely ferrugineous-tomentose, with flower pits in 8 vertical series	Flowering axes 4–6, subfasciculate, glabrous, with flower pits in 6–8 vertical series
Staminate flowers with 21–24 stamens	Staminate flowers with (11–)12 stamens
Pistillate flowers with 15–18 staminodes, these linear, angled, and sometimes thickened apically	Pistillate flowers with (5–6–)7–9 staminodes, these subulate
Fruit 12–14 mm. long at maturity	Fruit 15–16 mm. long when still immature

II. A NEW SPECIES OF PHOLIDOSTACHYS FROM COLOMBIA

Several years ago, a description of a supposedly new palm was prepared and put aside pending the resolution of some generic problems in the tribe Geonomeae of the subfamily Arecoideae. At the time, not understanding distinctions among those genera with six stamens and sagittate anthers, I had thought this to be a new *Calyptronoma*. In the interim, Mr. R. W. Read has provided preserved material of *Calyptronoma occidentalis* collected in Jamaica, calling my attention to the peculiar cap formed by the petals, and I have been able to study old pistillate flowers of *Pholidostachys pulchra*. On re-studying specimens of the new palm to make them available to the current monographer of the tribe, it is clear that the species does not belong in *Calyptronoma* but is referable to *Pholidostachys*.

At present, only two species, *P. pulchra* from Costa Rica and *P. Kalbreyeri* from Colombia, are assigned to the genus *Pholidostachys*. Each has the inflorescence composed of a single spike-like flowering axis terminating the peduncle and the two are probably to be regarded as synonymous. In the light of generic differences noted below, two other South American species now in *Calyptronoma* will be assigned to *Pholidostachys* (J. G. Wessels Boer, in correspondence). *Pholidostachys dactyloides* differs from *P. pulchra* and *P. Kalbreyeri* in having an inflorescence with several flowering axes. It differs from the other species assignable to the genus, each of which has a ramified inflorescence with an elongate rachis, in the few, subfasciculate rachillae borne on an extremely short rachis. It is these clustered, finger-like rachillae that suggest the epithet used.

An inexplicable error describing the staminodes of *Calyptronoma* as united in a solid receptacle, in a published key (Journal of the Arnold Arboretum **46**: 3. 1966), also calls for rectification. I would, today, separate *Calyptronoma*, *Calyptrogyne*, and *Pholidostachys*, all of which have very similar staminate flowers, as follows:

1. Petals of the pistillate corolla very briefly connate in a tube about as high

as the ovary, the lobes distinct, glumaceous, persistent, not forming a circumscissile cap; staminodial tube gradually widened apically to 6 prominent fleshy lobes as long as or longer than the tube and spreading at anthesis; styles scarcely united except at the base, distinct and stout for most of their length, the stigmatic tips somewhat recurved. Costa Rica to Peru. .... *Pholidostachys.*

1. Petals of the pistillate corolla connate basally in a thin membranous tube for more than half their length, the lobes valvate and thicker, not separating but forming a circumscissile conic cap caducous at anthesis; staminodes connate in a slender tube and adnate to the corolla-tube basally, the upper portion exserted at anthesis, inflated, urceolate, with 6 very short and narrow essentially erect lobes, caducous; styles loosely united for most of their length, sometimes thickened toward the apex, becoming long-exserted after the terminal portion of the staminodial tube has fallen; stigmas recurved.
    2. Upper bract of inflorescence inserted at or near the base of the peduncle, persistent or at length marcescent; inflorescence large, paniculately twice-branched; stems moderately stout, to 20 meters high or more. Greater Antilles. .... *Calyptronoma.*
    2. Upper bract of inflorescence inserted at base of and enclosing the spike-like flowering axis in bud, caducous at anthesis or soon marcescent, leaving a ruff-like scar; stems short, seldom developed above ground. Mexico to Colombia. .... *Calyptrogyne.*

Pholidostachys dactyloides H. E. Moore, sp. nov. FIGS. 3 and 4

Palma mediocris caudice solitario ad 10 m. alto, 8 cm. in diam., pinnis 4–9-nervatis, inflorescentiae rachidi brevissima, rachillis 5–6 tomentosis erectis subfasciculatis alveolas floriferas in seriebus 10 verticalibus gerentibus, fructu obovoideo 14–15 mm. longo, 10–12 mm. in diam., semine late ellipsoideo 9 mm. alto, 8 mm. in diam.

Stems solitary, to 10 m. high, 6.5–8 cm. in diam., grayish-brown. Leaves in a dense crown; sheath short, closed and swollen at the base, with red fibers; petiole 40–50 cm. long, narrow, shining, glabrous and slightly channelled above, rounded and densely ferrugineous-tomentose becoming glabrous below; blade 1.2–1.4 m. long, the pinnae 10–11 on each side of the rachis, this rounded and deciduous-ferrugineous-tomentose below, narrowly convex, elevated centrally with prominent flattish wing-like margins and glabrous above, at least basally; pinnae subopposite to alternate, inserted on the winged margin, all 4–6–9-nerved, with prominently and acutely keeled nerves above, glabrous except for deciduous red-brown elongate scurfy scales along the predominant elevated and truncate nerves below, these alternating with red-purple-margined impressed nerves corresponding to elevated nerves above, the surface densely and minutely pale-puncticulate, lowermost pinnae ca. 50 cm. long, 4.5 cm. wide, pinnae from mid-leaf ca. 70–75 cm. long, 7–9–13 cm. wide, falcate-acuminate, apical pinnae ca. 45 cm. long, 7 cm. wide, 16 cm. along the rachis. Inflorescence interfoliar, subtended by two bracts, the lower ca. 33 cm. long, ancipitous, densely ferrugineous-tomentose, upper bract inserted 4–5.5 cm. above the lower, stouter, ferrugineous-tomentose, coarsely fibrous and

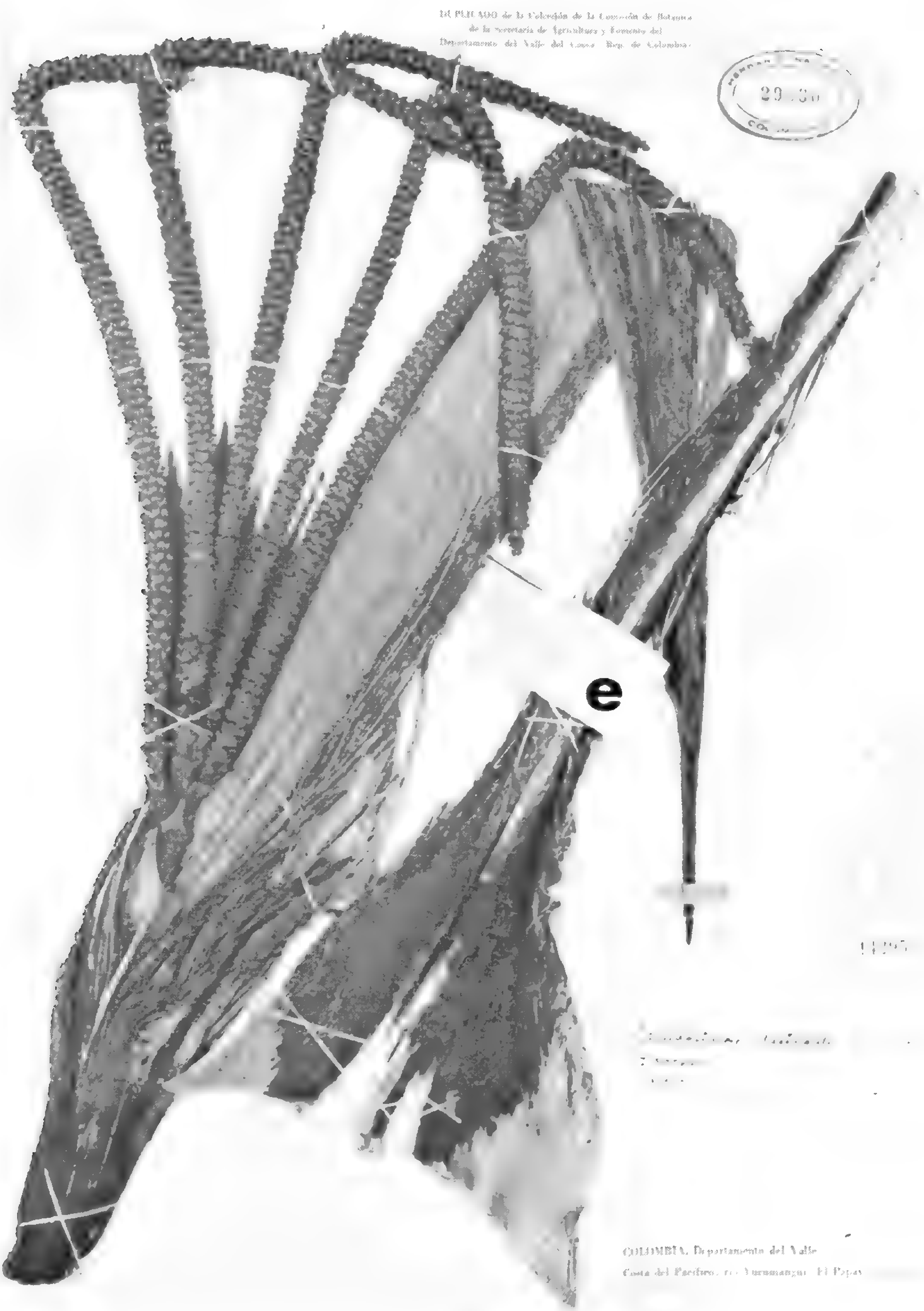

FIG. 3. *Pholidostachys dactyloides.* e, isotype (COL).

fraying in age, not ancipitous, 54–63 cm. long, splitting abaxially and then 4.5–6 cm. wide, attenuate at apex; peduncle 15–22 cm. long, dorso-ventrally compressed and elliptic in section, densely ferrugineous-tomentose, with several acute triangular bractlets to 2 cm. long toward the apex, terminating in a very short rachis and 5–6 erect subfasciculate similarly tomentose rachillae 26.5–33 (–40 in fruit) cm. long, ca. 1 cm. in diam., the pits in

10 vertical series, the lips entire, about as broad as long. Staminate flowers ca. 5.5 mm. long; sepals distinct, 4.5 mm. long, slightly keeled, rounded to subcucullate apically; petals very briefly connate and united with the connate stamen-filaments basally but distinct and valvate above; stamen-

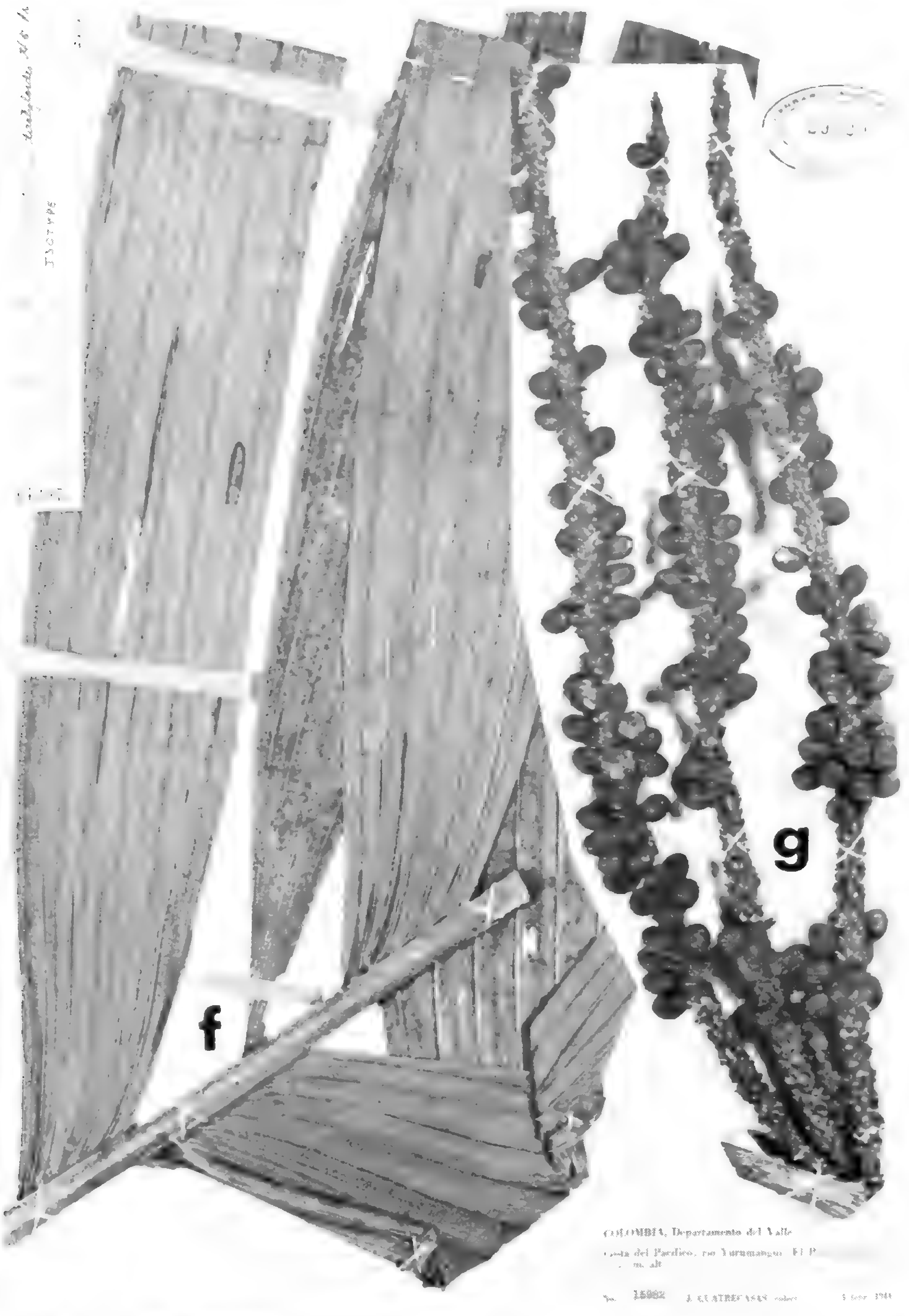

FIG. 4. *Pholidostachys dactyloides.* f. portion of leaf from isotype (COL); g. portion of infructescence from isotype (COL).

filaments united in a 3-angled solid fleshy obconic stipe, then distinct as 6 prominent narrowly triangular fleshy lobes ca. 1 mm. long tapered to very thin inflexed apices and sagittate anthers, these versatile and probably spreading at anthesis; pistillode short, subulate; pistillate flowers with distinct acutish keeled sepals ca. 4.5 mm. long; petals similar to the staminate but united basally with the staminodial tube for about 1.5 mm.; staminodes connate in a soft fleshy obconic tube with 6 fleshy lobes, these spreading at anthesis; pistil trilocular, triovulate, very deeply 3-lobed, the ovaries discrete except on the inner face; styles very briefly united basally, distinct and elongate above, with subclavate spreading exserted stigmas. Fruit black at maturity (*17257*), 14–15 mm. long, 10–12 mm. in diam., obovoid, the fibers of the mesocarp not prominent in dry mature fruit but very conspicuous in the dry immature fruit (*15982*); mesocarp with thick curved anastamosing fibers and an inner layer of slender fibers; endocarp thin, not adherent to the seed: seed broadly ellipsoid, ca. 9 mm. high, 8 mm. in diam., with raphe and chalaza forming a narrow continuous band from the subbasal point of attachment to the basal embryo; endosperm homogeneous.

Colombia. DEPARTAMENTO DEL VALLE: Costa del Pacifico, río Yurumanguí, El Papayo, bosques, 10–20 m. alt., Feb. 5, 1944, *J. Cuatrecasas 15982* (BH, type; COL, F, isotypes); río Cajambre, Barco, 5–80 m. alt., Apr. 21–30, 1944, *J. Cuatrecasas 17257* (COL, F).

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NOMENCLATURAL NOTES ON GOSSYPIUM (MALVACEAE)[1]

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IN THE COURSE OF SURVEYING the genera of Malvaceae in the southeastern United States, I encountered in the genus *Gossypium* several nomenclatural problems which require further comments. These include the type species of *Gossypium*; the nomenclatural status of *G. barbadense* L.; and the sectional names in Hutchinson's classification of *Gossypium* (1947). These problems are dealt with separately below.

THE TYPE SPECIES OF GOSSYPIUM

In 1920, Britton & Brown (Bahama Fl. 273. 1920) designated *Gossypium arboreum* L. as the lectotype species of *Gossypium* L. This choice of lectotype, apparently the earliest for this genus, was also adopted by Britton and Wilson in their *Botany of Porto Rico and the Virgin Islands* (Sci. Surv. Porto Rico Virgin Is. **5**(4): 566. 1924). In 1929, however, Hitchcock and Green (Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 173. 1929), apparently overlooking Britton & Millspaugh's typification, proposed *G. herbaceum* L. as the type of *Gossypium*. This typification has been adopted by at least Prokhanov (Bot. Zhur. SSSR **32**: 66. 1947), Phillips (Genera S. Afr. Flower. Pl. ed. 2. 501. 1951), and Hu (Malvaceae. Fl. China, Fam. 153. 61. 1955). Since Britton & Millspaugh's choice of the lectotype species of *Gossypium* L. appears to be the earliest, antedates that of Hitchcock and Green, and does not contradict the *International Code of Botanical Nomenclature*, it must be followed (see ICBN. p. 20. Art. 8 & p. 64. point 4f. 1961).

THE NOMENCLATURAL STATUS OF GOSSYPIUM BARBADENSE L.

It took botanists about a century and a half to form a notion of *Gossypium barbadense* L. and a further half-century to learn that their concept has been wrong and that the species so called must bear the name *G. peruvianum* Cav. (correctly, *G. vitifolium* Lam.), while *G. barbadense* L. has to be reduced to the synonymy of *G. arboreum* L. Since some taxonomists have accepted the proposed change, while others have not, this economically important species is at present variously called *G. barbadense* L., *G. peruvianum* Cav., and *G. vitifolium* Lam., with consequent nomenclatural and taxonomic confusion. Since rejection of a well-established

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[1] Continuing a series of miscellaneous notes and papers on the flora of the southeastern United States made possible through the interest and support of George R. Cooley and grants from the National Science Foundation.

and generally used scientific name of an economically important plant usually is undesirable and regrettable, any proposal of such a change should be thoroughly discussed, and eventually the necessity of renaming should be reinvestigated. For this reason a review of the nomenclatural status of *G. barbadense* L. would seem to be useful.

The protologue for *Gossypium barbadense* Linnaeus (Sp. Pl. 2: 693. 1753) consists of the following parts: 1) the Linnaean diagnosis, taken from his *Hortus Upsaliensis* (p. 204. 1748), "Gossypium foliis trilobis integerrimis"; 2) Plukenet's phrase-name (Almagest. Bot. 172. 1696), "Gossypium frutescens annuum, folio trilobo [trilobato], barbadense," and a reference to Plukenet's illustration "[Phytogr.] *t. 188. f. 1*"; and 3) the habitat and growth form of the species, "*Habitat in* Barbados," followed by the symbols for "biennial" and "shrub."

The Linnaean *nomen specificum legitimum* (phrase name or diagnosis) seems to refer to the plant grown in the Botanical Garden in Uppsala, because besides the diagnosis the following note and a brief description of this plant are given by Linnaeus in *Hortus Upsaliensis* (*loc. cit.*), "Hospitantur in *Caldario*, biennis, altero anno fructificans. *Desc.* Folia *cordata, triloba, integerrima, hinc diversa, licet fruticosa videatur*, a Gossypio caule erecto. *Hort. cliff. 350.*" On the other hand, the circumstance that Linnaeus applied to his species the epithet *barbadense* taken from Plukenet's diagnostic name, seems to indicate that he based his species on that of Plukenet, which he knew only from the phrase-name and illustration. He apparently believed the plant grown in the botanical garden in Uppsala to be conspecific with that of Plukenet. Thus, *G. barbadense* L. was a mixture of two elements, the plant grown at Uppsala and the species established by Plukenet. Although the vast majority of post-Linnaean botanists considered both elements to be conspecific, Todaro (Osservaz. Talun. Spec. Cotone 90. 1863) regarded *G. barbadense* as based only on the plant cultivated in the botanical garden in Uppsala and described by Linnaeus for the first time in *Hortus Upsaliensis.* "The *G. barbadense* is to us a plant fairly uncertain; it was for the first time described from the Garden in Uppsala. . . The *G. barbadense* is not, as we have believed, a plant described from the illustration of Plukenet, but certainly from the living plant cultivated in the Botanical Garden in Uppsala." (Translation supplied.) Consequently, Todaro removed Plukenet's phrase-name and the reference to his illustration from the synonymy of *G. barbadense* L., but in his later work (Relaz. Cult. Cotoni 234. 1877) he returned both. However, he then believed this species to be different from his *G. maritimum*, the Sea Island cotton, and to occur spontaneously on Barbados (*loc. cit.* 236).

Contrary to Todaro, Watt (Wild Cultiv. Cotton 268, 269. 1907) typified *Gossypium barbadense* by Plukenet's plant, saying: "There can, however, be little doubt as to the botanical type of the species. It was founded by Linnaeus on the description and plate given by Plukenet. . . In the second edition of the 'Species Plantarum' Linnaeus added the information that the leaves below had three glands, but it seems doubtful whether this supplementary feature is a constant characteristic or may not rather be an acquired one through hybridization or adaptation to insect visitors. Plukenet's specimen is in the Sloane Herbarium of the British Museum (vol. 100, f. 105 and Ray 1064–1), and is therefore the absolute type of the species as originally conceived. It is reproduced here (see Plate 46 A). It was fairly accurately represented by Plukenet's figure, also for convenience reproduced by me (Plate 46 B), except that the fruit shown is not present on the specimen." Taking into consideration the confusion (which goes back even to Plukenet himself) surrounding Plukenet's species, Watt further stated that "while accepting his [Plukenet's] t. 188, f. 1 (Plate 46 B) as the type of the species (as Linnaeus did), we must exclude all the synonyms cited by Plukenet." Watt seems to be the first to identify the plant in the Linnaean Herbarium, which bears on the sheet a mark "HU" [*Hortus Upsaliensis*] and an inscription in Linnaeus's handwriting "barbadense ?", as *Gossypium obtusifolium* Roxb., which is now included in *G. arboreum* L. This presumably was the plant grown in Uppsala and described by Linnaeus in *Hortus Upsaliensis* as "*Gossypium foliis trilobis integerrimis*," e.g., the type of *G. barbadense*, in Todaro's opinion.

Todaro's (1863) typification was supported and adopted by Prokhanov (Bot. Zhur. SSSR **32**: 67. 1947) who reviewed in detail (in Taxon **8**: 41–46. 1959) the nomenclatural status of *Gossypium barbadense* L. and came to the following conclusions: "(1) *Gossypium barbadense*, in the original sense of Linnaeus, is merely a broad-leaved variety of *G. arboreum* L. It must bear the name *G. arboreum* L. var. *nadam* (Watt) Prokh. [*G. obtusifolium* Roxb. s. str.], thus the name *G. barbadense* L. becomes a synonym of *G. arboreum* L., and in practice has to be eliminated. (2) The specific epithet *barbadense* is due here to its arbitrary transference by Linnaeus from former collective species of Plukenet. No cotton of the South American group was ever described by Linnaeus. (3) The species of *Gossypium*, up till now erroneously named *G. barbadense* and representing the South American group, must bear as its proper name, *Gossypium peruvianum* Cav. [correctly, the earlier *G. vitifolium* Lam.]." Prokhanov's proposal, although adopted by several Eurasian and American botanists, has not met with general recognition, most authors following Watt's typification, which I shall review later on.

Although Todaro's and Prokhanov's assumption that *Gossypium barbadense* L. was based only on the living plant grown in the Botanical Garden in Uppsala and described by Linnaeus in *Hortus Upsaliensis* does not appear to be quite correct, Todaro and Prokhanov were fully justified in typifying this species by that element. Nevertheless, this typification may be objected to because of the fact that Prokhanov's identification of the above-mentioned plant (made solely on the basis of the Linnaean diagnosis, note, and a very incomplete description) as a broad-leaved variety of *Gossypium arboreum* seems to be fairly unreliable and unconvincing, being an educated guess rather than a determination. Certainly, the specimen from the Linnaean Herbarium, bearing a mark "HU" [*Hortus Upsaliensis*] and Linnaeus's inscription "barbadense ?" must be the basis for identification of the type of *G. barbadense* L. in the sense of Todaro (1863) and Prokhanov (1959). This specimen, then, presumably representing the plant grown in Uppsala and determined by Prokhanov as *Gossypium arboreum* L. var. *nadam* (Watt) Prokh., should be chosen as the lectotype of *G. barbadense* L. in the sense of Todaro and Prokhanov. However, "in choosing a lectotype, any indication of intent by the author of a name should be given preference unless such indication is contrary to the protologue. Such indications are manuscript notes, annotations on herbarium sheets," etc. (ICBN. 65. 1961). The specimen of the Linnaean Herbarium (874.5), identified by Watt as *G. obtusifolium* Roxb. and by Prokhanov as *G. arboreum* L. var. *nadam* (Watt) Prokh., was annotated by Linnaeus himself as "barbadense ?". Designation of this specimen, only questionably referred by Linnaeus to *G. barbadense*, as the lectotype of this species can hardly be justifiable from the standpoint of the *Code*. Consequently, Prokhanov's typification of *G. barbadense* L. with the plant grown in the botanical garden in Uppsala and allegedly represented in the Herbarium Linnaeanum by the specimen of *G. arboreum* L. var. *nadam* (Watt) Prokh. can not be accepted.

As mentioned before, Watt (*loc. cit.*) typified *G. barbadense* L. by Plukenet's plate [Phytogr.] *tab. 188, fig. 1*, clearly saying that *G. barbadense* L. "was founded by Linnaeus on the description and plate given by Plukenet" and that "accepting his [Plukenet's] t. 188, f. 1 (Plate 46 B) as the type of the species (as Linnaeus did), we must exclude all the synonyms cited by Plukenet." Despite the clarity of Watt's typification, his further statement that Plukenet's specimen in the Sloane Herbarium is "the absolute type of the species as originally conceived [by Plukenet, not Linnaeus]," was misunderstood as Watt's choice of Plukenet's specimen as the lectotype of *G. barbadense* (e.g., Hutchinson in Hutchinson, Silow & Stephens, Evol. Gossypium 48. 1947). Recently, however, Wouters (Bull. Jard. Bot. Bruxelles 33: 516. 1963) really assumed Plukenet's specimen to be the type of *G. barbadense*. "Il est donc normal de considérer le spécimen *Plukenet vol. 100. folio 105* comme le modèle de la planche t. 188 fig. 1 de Plukenet, et par conséquent comme le type nomenclatural de *G. barbadense* L. 1753. Il représente indiscutablement *G. barbadense* sensu stricto." Wouters's assumption, however tempting, may be objected to on the following grounds. 1) The specimen *Plukenet vol. 100. folio 105* was not that from which Plukenet's illustration was drawn: this herbarium specimen, lacking any inscription by Plukenet, was arbitrarily designated by Watt (*loc. cit.*) as "the absolute type of the species as originally conceived," only on the basis of similarity of the leaf-shape of the specimen to that of the illustration. Regarding the true model for Plukenet's illustration Watt (*loc. cit.* 269) says the following: "In vol. 132, f. 18 (Duchess of Beaufort's set of plants) there is a specimen, said to represent Plukenet's 'Phyt.' t. 188, f. 1, but which is nearer to the leaves in his herbarium just mentioned [i.e., those of *G. vitifolium* Lam., which was regarded as a distinct species by Watt]." 2) Since the Plukenet specimen in the Sloane Herbarium was not the model for Plukenet's illustration, there is no reason at all for choosing it as the lectotype of *G. barbadense*, because "A lectotype must be chosen from among elements that were definitely studied by the author up to the time the name of the taxon was published and included in the catalogue" (ICBN. 64. 1961).

On the contrary, Watt's choice of Plukenet's illustration (Phytogr. *tab. 188, fig. 1*) as the lectotype of *G. barbadense* would be quite reasonable and admissable if there were no other objections from the standpoint of the Code. However, Todaro had already (Osservaz. Talun. Spec. Cotone 90. 1863, & Relaz. Cult. Cotoni 228. 1877) noticed that the plant illustrated by Plukenet had three-lobed leaves similar to the upper leaves of Sea Island cotton (*G. maritimum* Tod.), but a fruit resembling that of some East Indian species of cotton in its obtuse, almost entire-margined, reflexed bracteoles. Prokhanov (Taxon **8**: 42. 1959) corroborated Todaro's observations and identified the capsule of Plukenet's drawing as that of *G. herbaceum*. Thus, Plukenet's drawing does not seem to portray a real plant, but rather presents a more or less imaginary composite plant with leaves approximately those of Sea Island cotton and capsule approximately that of *G. herbaceum*, thus a plant expressing Plukenet's concept of his collective species (which included the species of the New and Old Worlds) rather than a real plant. Plukenet's drawing presents heterogeneous material consisting of two discordant elements. Since the type material of *G. barbadense* L. is composed of two inseparable discordant elements, this Linnaean binomial must be rejected in compliance with Article 70 of the *International Code of Botanical Nomenclature* (1961). Wouters's proposal to regard the reflexion of the bracteoles of the involucel on the fruit of Plukenet's figure as the result of an interpretation can not be accepted, because in their shape and margin characters (not solely in their reflexed position) the bracteoles of involucel on Plukenet's figure certainly represent the cultivated Old World species. Thus, while disagreeing with Prokhanov in argument, I concur with his proposal that the binomial *Gossypium barbadense* L. must be replaced by *G. vitifolium* Lam. (*G. peruvianum* Cav.) as the correct name for the Sea Island cotton.

Having reviewed the situation concerning the typification of *Gossypium barbadense* L., I have come to the following conclusions:

1. *Gossypium barbadense* L. is a heterogeneous taxon consisting of two main elements, a plant grown in the botanical garden in Uppsala and a species established by Plukenet (Almagest. Bot. 172. 1696, & Phytogr. *tab. 188, fig. 1.* 1691).
2. Todaro's (1863) and Prokhanov's (1959) typifications of *Gossypium barbadense* by the plant grown in the botanical garden in Uppsala can not be accepted since the specimen in the Herbarium Linnaeanum (874.5), allegedly representing this plant and identified by Prokhanov as *G. arboreum* var. *nadam* (Watt) Prokh., was only questionably referred by Linnaeus to *G. barbadense* and therefore can not be chosen as the lectotype.
3. Watt seems to be correct in his assumption that *Gossypium barbadense* L. was based on Plukenet's diagnostic name and figure in Phytogr. *tab. 188, fig. 1*, which is the type of this species. However, the Plukenet

figure, in turn, is heterogeneous, presenting a composite, apparently more or less imaginary, plant with leaves resembling some of those in the Sea Island cotton and the capsule apparently that of *G. herbaceum* L. Therefore, the choice of Plukenet's figure as the lectotype of *G. barbadense* L. is not admissable under the *Code* (ICBN 1961. Art. 70).

4. Typification of *Gossypium barbadense* by the specimen *Plukenet vol. 100, folio 105* (the Sloane Herbarium of the British Museum) is not justifiable in the light of the *Code*, because Linnaeus did not see this specimen or at least did not mention it with the original description.

5. Since *Gossypium barbadense* L. can not be typified, the name must be rejected as a ***nomen ambiguum*** and must be replaced by *G. vitifolium* Lam., the earliest correct name.

THE SECTIONAL NAMES IN HUTCHINSON'S CLASSIFICATION (1947) OF GOSSYPIUM

In 1947, Hutchinson established a classification of *Gossypium* (in Hutchinson, Silow & Stephens, The Evolution of *Gossypium*, pp. 1–53), in which the genus was subdivided into eight sections. The sections, well-delimited morphologically and geographically, represented six main evolutionary, cytogenetically distinct groups, one of which was for convenience divided into three subsidiary groups also designated as sections. Apparently the simplicity, clarity, and easy use of this system led to its general adoption by geneticists and cytotaxonomists. Unfortunately, descriptions of the sections in this classification were given only in English, and the names therefore are not validly published. In order to make Hutchinson's classification nomenclaturally legitimate, I am listing below his sections, along with their correct names and the type species of each.

Section I STURTIANA Hutchinson in Hutchinson, Silow, & Stephens, Evolution of *Gossypium* 16. 1947, *nom. illeg.* = Section **Sturtia** (R. Br.) Todaro, Relaz. Cult. Cotoni 117. 1877. TYPE SPECIES: *G. Sturtianum* J. H. Willis (*G. Sturtii* F. Muell., *nom. illeg.*).

Section II ERIOXYLA Hutchinson, *loc. cit.* 18. 1947, *nom. illeg.* = Section **Erioxylum** (Rose & Standl.) Prokhanov, Bot. Zhur. SSSR **32**: 71. 1947. TYPE SPECIES: *G. aridum* (Rose & Standl.) Skovst.

Section III KLOTZSCHIANA Hutchinson, *loc. cit.* 22. 1947, *nom. illeg.* = Section **Integrifolia** Todaro, Osservaz. Talun. Spec. Cotone 19. 1863. TYPE SPECIES: *G. Klotzschianum* Anderss.

Section IV THURBERANA Hutchinson, *loc. cit.* 24. 1947, *nom. illeg.* = Section **Thurberia** (A. Gray) Prokhanov, Bot. Zhur. SSSR **32**: 71. 1947. TYPE SPECIES: *Thurberia thespesioides* A. Gray (= *G. Thurberi* Tod.).

Section V ANOMALA Hutchinson, *loc. cit.* 27. 1947, *nom. illeg.* = Section **Anomopambak** Prokhanov, *loc. cit.* 66. 1947. TYPE SPECIES: *G. anomalum* Wawra & Peyr.

Section VI STOCKSIANA Hutchinson, *loc. cit.* 30. 1947, *nom. illeg.* = Section **Pseudopambak** Prokhanov, *loc. cit.* 65. 1947. TYPE SPECIES: *G. Stocksii* Mast.

Section VII HERBACEA Hutchinson, *loc. cit.* 32. 1947, *nom. illeg.* = Section **Gossypium.** LECTOTYPE SPECIES: *G. arboreum* L.

Section VIII HIRSUTA Hutchinson, *loc. cit.* 36. 1947, *nom. illeg.* = Section **Magnibracteolata** Todaro, Osservaz. Talun. Spec. Cotone 64. 1863. LECTOTYPE SPECIES: *G. mexicanum* Tod. = *G. hirsutum* L., fide Hutchinson, 1947; see Prokhanov, Bot. Zhur. SSSR **32:** 72. 1947.

The union of the sections *Erioxylum*, *Integrifolia*, and *Thurberia* into a single section including all the American diploid species with the genome D, with consequent reduction of the sections to the rank of subsections, as was done by Mauer (1950), seems to me to be an improvement of Hutchinson's classification of *Gossypium*. These changes introduced by Mauer are given below.

Section **Integrifolia** Todaro, Osservaz. Talun. Spec. Cotone 19. 1863, amplif. Mauer, Acta Univ. Asiae Mediae II. **18**(Biol. 7): 20. 1950. TYPE SPECIES: *G. Klotzschianum* Anderss.

Subsection **Integrifolia** Todaro, Relaz. Cult. Cotoni 188. 1877. (Sect. *Klotzschiana* Hutchinson, *loc. cit.*, *nom. illeg.*)

Subsection **Ingenhousia** (Moc. & Sessé ex DC.) Mauer, *loc. cit.*, excl. **Erioxylum** Rose & Standl. Contr. U. S. Natl. Herb. **13:** 307. 1911. (Sect. *Ingenhousia* (Moc. & Sessé ex DC.) Prokhanov, *loc. cit.* 72, in part, and sect. *Thurberia* (A. Gray) Prokhanov, *loc. cit.* 71. 1947. Sect. *Thurberana* Hutchinson, *loc. cit.* 24. 1947, *nom. illeg.*). TYPE SPECIES: *G. trilobum* (Moc. & Sessé ex DC.) Kearney (*Ingenhousia triloba* Moc. & Sessé ex DC.).

Subsection **Caducibracteolata** Mauer, *loc. cit.*, emend. Brizicky (Sect. *Erioxylum* (Rose & Standl.) Prokhanov, *loc. cit.* 71, and sect. *Ingenhousia* (Moc. & Sessé ex DC.) Prokhanov, *loc. cit.* 72, in part. Sect. *Erioxyla* Hutchinson, *loc. cit.* 18. 1947, *nom. illeg.*). LECTOTYPE SPECIES: *G. armourianum* Kearney.

Delimitation of the subsections *Ingenhousia* and *Caducibracteolata* has been slightly changed in order to bring their limits as close as possible to those of Hutchinson's corresponding sections.

A SYNOPSIS OF THE ASIAN SPECIES OF CONSOLIDA (RANUNCULACEAE)

PHILIP A. MUNZ

AS USED IN THE TITLE of this paper, "Asian" refers to the mainland only and does not include the islands in the Aegean Sea and in the eastern Mediterranean, the plants of which are already treated in Tutin et al., *Flora Europaea*, vol. 1. 1964, and in Davis, *Flora of Turkey*, vol. 1. 1965.

Material of Asian species has been studied as it exists in the principal herbaria of the United States. Considerable work was done in the library of the Arnold Arboretum and Gray Herbarium of Harvard University. Some months were spent in London working at the British Museum (Natural History) and at the Royal Botanic Gardens, Kew, in both of which institutions, as at Harvard, very great courtesy and help were given me. The British Museum secured for my use large loans of herbarium sheets from the Royal Botanic Garden, Edinburgh, and the Komarov Institute, Leningrad. I spent some time also in the Muséum National d'Histoire Naturelle, Paris, where again every courtesy was extended. Smaller loans, largely for individual species, have been obtained from various places and acknowledgment is made in discussion of the species concerned. To all the curators and keepers and to the librarians to whom I am indebted, I express my very great appreciation.

In citing herbarium material I employ the symbols given in *Index Herbariorum* (Lanjouw and Stafleu, Reg. Veg. 31. 1964) as follows:

A	Arnold Arboretum of Harvard University, Cambridge, Massachusetts, U. S. A.
BH	Bailey Hortorium, Cornell University, Ithaca, New York, U. S. A.
BM	British Museum (Natural History), London, Great Britain
CAS	California Academy of Sciences, San Francisco, California, U. S. A.
E	Royal Botanic Garden, Edinburgh, Great Britain
F	Field Museum of Natural History, Chicago, Illinois, U. S. A.
GH	Gray Herbarium of Harvard University, Cambridge, Massachusetts, U. S. A.
K	The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, Great Britain
LE	Herbarium of the Komarov Botanical Institute of the Academy of Sciences of the U. S. S. R., Leningrad, U. S. S. R.
MICH	University Herbarium, University of Michigan, Ann Arbor, Michigan, U. S. A.
MO	Missouri Botanical Garden, St. Louis, Missouri, U. S. A.
NA	United States National Arboretum, Washington, D. C., U. S. A.
NY	The New York Botanical Garden, New York, U. S. A.
P	Muséum National d'Histoire Naturelle, Paris, France
PH	Academy of Natural Sciences, Philadelphia, Pennsylvania, U. S. A.

UC Herbarium of the University of California, Berkeley, California, U. S. A.
US Department of Botany, United States National Museum, Smithsonian Institution, Washington, D. C., U. S. A.

Because of space limitations the large number of herbarium sheets examined is not cited, but an appendix is given with names of collectors, collection numbers, and the taxa to which referred. It should be emphasized that the present treatment is not revisional in nature, but rather synoptic. It is concerned with keying out and describing the Asian species, so that identification can be made of plants collected. Therefore, there is no attempt to set up sections within the genus, a thing which should be done only when the African and European species are also considered.

It is a pleasure to acknowledge obligations to the National Science Foundation for grant number GB–2716, which has been of very great assistance in assembling the data herewith presented.

THE GENUS CONSOLIDA

Lindley (Jour. Hort. Soc. London **6**: 57. 1851), in writing about *Consolida aconiti*, said "Forskahl regarded this curious plant, it is said, as an Aconitum; Linnaeus considered it a Delphinium. In reality it is neither the one nor the other. Its united petals and long sepaline spur, are at variance with the distinct hammerheaded petals and convex back sepal of Aconite. Its petals being reduced to two, and those completely combined into one, equally remove it from Delphinium. That the petaline body is really composed of 2 parts only seems to be proved by its origin, which looks as if opposite the back sepal in consequence of the union of the two contiguous edges of the lateral petals. But it is completely separated from the front sepals, with which it does not in any degree alternate. These considerations lead to the conclusion that the old genus Consolida should be re-established, and by no means confounded with Delphinium proper."

This statement from Lindley seems to me to be about as clear as any that can be made, even now. One wonders why it has taken so many years to recognize *Consolida* as a genus, but it may well be due to the fact (P. H. Davis, Notes Bot. Gard. Edinburgh **26**: 172. 1965) that there was a "widespread belief that *Delphinium* should be typified by *D. consolida* L. *Delphinium* should, in fact, be typified by *D. peregrinum* L. and *Consolida* by *D. consolida* (i.e. *Consolida regalis* S. F. Gray)." At any rate, some of the most recent floras dealing with Eurasian plants, as Tutin et al., *Flora Europaea* **1**: 216–217. 1964, and Davis, *Flora of Turkey* **1**: 119–134. 1965, give generic status to *Consolida* and I am following their procedure.

DESCRIPTION OF THE GENUS CONSOLIDA (DC.) S. F. GRAY [1]

Consolida, as a genus, S. F. Gray, Nat. Arr. Brit. Pl. **2**: 711. 1821. As a section of *Delphinium*, DC. Syst. **1**: 341. 1817. As a subgenus of

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[1] **Pubescence.** Pubescence is a conspicuous and often useful means of characterizing the various species of *Consolida*. The hairs may be white or yellow. White hairs may

Delphinium, Huth, Bot. Jahrb. 20: 337. 1895; Dalla Torre & Harms, Genera Siphonogamarum 165. 1901.

Plants annual. Leaves palmately laciniate. Inflorescence racemose or paniculate, the pedicels subtended by bracts and each usually bearing 2 bracteoles. Flowers zygomorphic. Sepals 5, petaloid, the posterior one spurred, the lateral pair and lower pair not. "Petal" one, apparently representing the fused superior petals of *Delphinium*, sometimes called "honey-leaf" or "nectary," subentire to 3–5-lobed, bearing a single nectariferous spur extending into the sepal spur. The lower petals of *Delphinium* aborted and not represented. Stamens in 5 spirally arranged series, the filaments more or less broadened, the anthers short. Carpel 1, forming a follicle.

Type species, *C. regalis* S. F. Gray (*Delphinium consolida* L.).

A highly specialized genus of over 40 species, ranging from the western Mediterranean to central Asia in arid and semiarid regions. Several species are cultivated and escape from gardens in many other parts of the world.

Key to the Species of Consolida

1. Spur and "petal" lacking. . . . . 29. *C. rugulosa*.
1. Spur and "petal" present.
    2. "Petal" mostly 5-lobed (usually with 1 generally bifid upper lobe, 2 intermediate and 2 lower lateral lobes); spur more or less coiled or circinate at apex; main stem a continued axis through the whole plant with numerous, rather short, very slender lateral branches.
        3. Flowers ca. 23 mm. long, including the spur; sepals blue; pubescence of stems retrorse-appressed; plant to 5 dm. tall; pedicels 2–8 cm. long. Iran. . . . . 1. *C. teheranica*.
        3. Flowers 10–16 (–20) mm. long, including the spur.
            4. Spur uncinate-saccate to almost straight; intermediate lobes of "petal" sharply triangular.
                5. Follicles 14–17 mm. long; spur uncinate, 4–5 mm. long. Mardin. Turkey. . . . . 8. *C. saccata*.
                5. Follicles 5–10 mm. long; spur almost straight, 8 mm. long. Turkestan. . . . . 9. *C. barbata*.
            4. Spur circinately involute at the tip; intermediate lobes of the "petal" not sharply triangular, except in *C. anthoroidea*.
                6. Intermediate lobes of "petal" protruding and longer than the shortly bifid upper lobe; follicle 8–10 mm. long, 3–4 mm. wide. E. Turkey to Iran, Jordan. . . . . 7. *C. anthoroidea*.

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be appressed (usually retrorsely so) or spreading, and in the latter case, may be gland-tipped or not. But the yellow hairs are quite different from those I have met in most groups of plants. Ordinarily they are not gland-tipped, but are strongly enlarged toward the base and apparently are glandular in nature, since good collection labels sometimes state that plants bearing such hairs are viscid. So far as I can see, then, a glandular condition may arise when the slender white spreading hairs are gland-tipped or when there occur the yellow hairs which tend to be strongly enlarged toward the base.

6. Intermediate lobes of "petal" shorter than or subequal to the upper lobe.
    7. The intermediate lobes of the "petal" acute.
        8. Lower lobes of "petal" more or less approximate to the intermediate lobes, ovate; intermediate lobes broadly triangular; follicle semiovate, 6–9 mm. long, 2–3 mm. wide. Anatolia to Lebanon. .... 2. *C. scleroclada.*
        8. Lower lobes of "petal" separated from the intermediate lobes by a broad sinus; intermediate lobes narrowly triangular, sharply acute; follicle linear to linear-oblong.
            9. Follicle linear-oblong with rounded abruptly rostrate apex, 10–13 mm. long; stem appressed-canescent. Central Anatolia. .... 5. *C. stenocarpa.*
            9. Follicle linear, with gradually rostrate apex, 15–22 mm. long; stem with whitish spreading hairs. Dardanelles. .... 6. *D. aconiti.*
    7. The intermediate lobes of the "petal" obtuse.
        10. Stem velvety with whitish spreading hairs mixed with glandular ones; sinus between lateral and intermediate lobes of "petal" ca. ¼ as wide as deep. Thrace to Galatia. .... 3. *C. thirkeana.*
        10. Stem strigulose; sinus between lateral and intermediate lobes of "petal" ca. ½ as wide as deep. Transcaucasia, Armenia, Iran. .... 4. *C. hohenackeri.*

2. "Petal" almost entire to 3-lobed (with 1 often bifid upper lobe and 2 lateral lobes); habit not as above, the stem either branched below or not diffuse above; "petal"-spur not circinate at apex.
    11. Pedicels shorter than sepals at anthesis, sometimes elongating in fruit; bracteoles minute, often looking like additional lobes to the subtending bract; stem leafy, the flowers often from most axils; follicle nearly straight, subterete.
        12. The lateral lobes of the "petal" at right angles to the terminal lobe, longer than wide; spur 5–9 mm. long; flowers deep violet to blue or rose.
            13. The lateral lobes ca. 1.5 mm. long, the terminal lobe ca. 4 mm. long; sepals 13–18 mm. long. Turkey (Caria and Lycia through Phrygia and Cappadocia to Paphlagonia). .... 10. *C. raveyi.*
            13. The lateral lobes of the "petal" 4–5 mm. long, about equal to the terminal lobe; sepals 10–13 mm. long.
                14. "Petal" more or less cruciate, the lateral lobes abruptly narrowed to the base. Turkey (Cilicia). .... 11. *C. cruciata.*
                14. "Petal" more kite-shaped, more or less triangular, since the lateral lobes gradually narrow to the base. Southeastern Anatolia to Syria.
                    15. Bracteoles multifid; sepals 10–13 mm. long; blade of "petal" 12 mm. wide. Turkey to Syria. .... 12. *C. axilliflora.*
                    15. Bracteoles entire; sepals 6–8 mm. long; blade of "petal" 10 mm. wide. Syria. .... 13. *C. gombaultii.*

12. The lateral lobes of the "petal" directed somewhat forward toward the apex of the "petal"; spur 16–25 mm. long; flowers whitish to pinkish.

16. Expanded "petal" 15–20 mm. wide.

17. Sepals 9–11 mm. long; follicle 17–25 mm. long; main cauline leaves entire. Turkestan and northern Iran. . . . . 23. *C. leptocarpa.*

17. Sepals 6–8 mm. long; main cauline leaves divided. Iran, Iraq, Turkestan. . . . . 24. *C. persica.*

16. Expanded "petal" 8–11 mm. wide.

18. The expanded "petal" wider near the base, somewhat narrowed toward the tip. Iran. . . . . . 28. *C. halophila.*

18. The expanded "petal" widened upward.

19. Lateral lobes of "petal" broadly rounded, not at all triangular; expanded "petal" 11 mm. wide. Turkestan to Iran. . . . . 14. *C. stocksiana.*

19. Lateral lobes of "petal" more or less triangular; expanded "petal" 8 mm. wide. Transcaucasia to Afghanistan. . . . . 27. *C. rugulosa.*

11. Pedicels usually longer than sepals.

20. Bracteoles high on the pedicel, hence extending above the base of the flower; leaf-lobes usually very narrow, ca. 0.5 mm. wide; stems widely and few-branched; lateral lobes of the "petal" more convex on upper edge than on lower.

21. "Petal" entire and subcircular; flowers 15–20 in a raceme. Turkish Armenia. 40. *C. olopetala.*

21. "Petal" more or less lobed; flowers fewer, mostly 3–6 in a raceme.

22. Flowers sulphur-colored; terminal lobe of "petal" 3-toothed. Turkey. . . . . 39. *C. sulphurea.*

22. Flowers violet to blue or rose.

23. Spur shorter than blade of sepal, or if equal to it, plant with spreading hairs.

24. Follicle pendent on a recurved pedicel; plant strigose. Eastern Turkey, Iraq. . . . . 35. *C. oligantha.*

24. Follicle erect; plant with spreading pubescence.

25. Flowers rose; spur straight, 5–6 mm. long. Lebanon and Syria to Jordan. . . . . 33. *C. pusilla.*

25. Flowers violet.

26. Spur almost straight, 6–7 mm. long; "petal" with terminal lobe 3 mm. long. Kashmir. . . . . 31. *C. schlagintweitii.*

26. Spur more or less curved, 4 mm. long; "petal" with 3 minute equal lobes. Iran. . . . . 30. *C. linarioides.*

23. Spur equal to or longer than the blade of the sepal, if shorter, the plant with appressed hairs.

27. Pubescence spreading; spur ca. twice as long as upper sepal. Iran. . . 29. *C. trigonelloides.*
27. Pubescence appressed.
    28. Spur 8–10 mm. long; sepals with a basal claw 3–4 mm. long. Lebanon, Jordan. 36. *C. tomentosa.*
    28. Spur 12–24 mm. long; sepals sessile or with a claw ca. 1 mm. long.
        29. "Petal" abruptly narrowed at tip into a beaklike upper lobe; rest of "petal" dome-shaped when spread open; spur 18–24 mm. long. . . . . 38. *C. armeniaca.*
        29. "Petal" either gradually narrowed toward the apex or the upper lobe subequal to the lateral lobes; spur 12–16 mm. long. . . . . 37. *C. hellespontica.*

20. Bracteoles usually lower on the pedicel and not extending above the base of the flower.
    30. Lateral lobes of "petal" more convex on upper edge than on lower and with the subtriangular terminal lobe making a somewhat dome-shaped structure when spread open; central stem the main axis, with few or no short ascending lateral branches; follicle compressed, somewhat curved, ca. 1 cm. long, the style 4 mm. long; spur much longer than sepals. . . . . 34. *C. camptocarpa.*
    30. Lateral lobes of "petal" perpendicular to the terminal lobe or pointing somewhat toward the tip of the "petal" when spread out; style 1–3 mm. long.
        31. Follicle mostly at least 15–25 mm. long, oblong-cylindric; style scarcely 1 mm. long; main stem forming an axis into the inflorescence with few side branches; leaf segments very narrow, ca. 0.5 mm. wide.
            32. Bracteoles usually below the middle of the pedicel; sepals 12–14 mm. long; spur ca. 15 mm. long. . . . . 15. *C. ambigua.*
            32. Bracteoles above the middle of the pedicel; sepals 6–12 mm. long.
                33. Spur ca. 18 mm. long. . 25. *C. deserti-syriaci.*
                33. Spur 6–10 mm. long.
                    34. The spur 6–7 mm. long; follicle 10 mm. long. Kashmir. . . 31. *C. schlagintweitii.*
                    34. The spur 9–10 mm. long; follicle 15 mm. or more long.
                        35. Median lobe of "petal" longer than wide, the 2 apical lobules rounded; sepals 10–12 mm. long. . . . . 16. *C. orientalis.*
                        35. Median lobe of "petal" about equally long and wide, the 2 apical lobules

pointed; sepals 6–9 mm. long. . . . . 32. *C. phrygia.*

31. Follicles 6–15 mm. long; style longer; plants mostly branched from the base with widespread open habit.

36. Spur 10 mm. or more long, exceeding the sepals.

37. Lateral lobes of "petal" at right angles to the middle lobe, not directed toward the tip of the "petal"; stems strigulose; lower bracts entire. . . . . 17. *C. regalis.*

37. Lateral lobes of "petal" directed forward somewhat toward the tip of the "petal"; stems with some spreading hairs in upper parts.

38. The lateral lobes of the "petal" somewhat pointed and semilunate; spur 10–13 mm. long. Armenia. . . 26. *C. cornuta.*

38. The lateral lobes of the "petal" rounded; spur mostly longer.

39. Sepals 10–14 mm. long, narrowed into a claw-like base; bracts laciniate; pedicels glabrous except at the summit. Iraq. . . . . 20. *C. oliveriana.*

39. Sepals 9–10 mm. long, scarcely narrowed at the base; bracts entire; pedicels glandular-pubescent. Armenia. . . . . 19. *C. glandulosa.*

36. Spur 5–7 mm. long, about as long as the sepals.

40. Flowers blue or violet to rose; sepals 5–8 mm. long; lateral lobes of "petal" rounded, not projecting beyond the middle lobe; filaments glabrous. Asia Minor. . . . . 18. *C. incana.*

40. Flowers yellow, especially the "petal"; sepals 4–5 mm. long; lateral lobes of the "petal" semiovate, as long as the median lobe; filaments hairy.

41. Stems strigose, at least below, little or not at all glandular. . . . . . . 21. *C. flava.*

41. Stem with more or less spreading and glandular hairs. . . . . 22. *C. deserti.*

1. **Consolida teheranica** (Boiss.) Rech. f. Ann. Naturh. Mus. Wien **51**: 376. 1941. FIG. 1, A.

Delphinium teheranicum Boiss. Fl. Orient. **1**: 85. 1867.

? *Delphinium intricatum* Pau, Trab. Mus. Ci. Nat. Bot. Madrid **14**: 12. 1918.

Annual, to 5 dm. tall, openly and widely branched, retrorse-strigulose throughout, the branches slender, subdivaricate; leaves largely gone by anthesis, multifid into acute linear segments; inflorescence open with scattered flowers, strigulose and with some glandular spreading hairs with basal yellow pustules; lower bracts largely tripartite, to ca. 1 cm. long; the upper subulate, to ca. 5 mm. long; pedicels slender, 2–8 cm. long;

bracteoles 2 or more, subulate, scattered, well below the flower, ca. 2 mm. long; calyx blue, pubescent without, 8–10 mm. long, not unguiculate, the upper sepal lance-ovate, with a circinate-involute pubescent spur ca. 13–16 mm. long and 4–5 mm. wide at the base; lateral sepals oblong-ovate, blue-membranous except on the narrow central pubescent strip, obtuse; lower sepals narrow-ovate, obtuse, more pubescent; "petal" ca. 23 mm. long, including the spur, the terminal lobe subentire, broad, subcrenulate, longer than the intermediate triangular lobes (scarcely 1 mm. long), the membranous lower lobes grown to the intermediate lobes to near the rounded summit; stamens subequal, the filaments ca. 6 mm. long, dilated below, pubescent above; anthers dark, almost 1 mm. long; follicle subcompressed, somewhat reticulate-veiny, rather straight, 12–15 mm. long, 3–3.5 mm. wide, the style an additional 2 mm.; seeds dark, asymmetrically subcylindrical, almost 2 mm. long, with several continuous transverse rows of short scales.

TYPE: "prope Teheran Persiae ad pagum Gulkak", *Kotschy 884* (W). Not seen.

DISTRIBUTION. Stony places at 1200 to 1300 m., Elburz Mts., n. Iran.

REPRESENTATIVE SPECIMENS: *Rechinger 2015* (K, US); *Furse 2907* (K).

2. **Consolida scleroclada** (Boiss.) Schröd. Ann. K. K. Naturh. Hofmus. Wien **27**: 44. 1913.

Delphinium sclerocladum Boiss. Diagn. I. **8**: 8. 1849.

Delphinium anthoroideum Boiss. var. *sclerocladum* (Boiss.) Boiss. Fl. Orient. **1**: 85. 1867.

One to 5 dm. tall, variously branched and pubescent, the ultimate branchlets very slender; leaves multifid into linear lobes, largely gone by anthesis, roundish in outline; bracts multifid, 2–4 mm. long; pedicels to ca. 1 cm. long; bracteoles lance-linear, 2 or more, largely remote from the flowers, to ca. 2 mm. long; sepals yellowish-white to lilac, 7–8 mm. long, not unguiculate, narrow-oblong, ca. 1.5 mm. wide, hyaline on margins, pubescent on median strip; sepal spur circinate-involute at apex, ca. 7 mm. long, 3.5 mm. wide at base; "petal" 5-lobed, 6–7 mm. long, exclusive of the spur, the terminal lobe ca. 2.5 mm. long, broad, entire; intermediate lobes triangular, acute, slightly shorter; lower lobes membranous, more or less approximate to the intermediate lobes, ovate, ca. 3.5 mm. long; filaments 6–8 mm. long, inflated in lower part, more or less pubescent; anthers yellow, ca. 0.6 mm. long; follicle semiovate, compressed, glabrous, reticulate-veined, 6–9 mm. long, 2–3 mm. wide, the style an additional 2.5–3 mm.

Pedicels puberulous with interspersed spreading glandular hairs; plant more or less pyramidal, rigid up to the ultimate racemose branching. Turkey to Syria. . . . . Var. *scleroclada*.

Pedicels strigulose, without glandular hairs, sometimes glabrescent.

  Branches ascending, the ultimate ones rigid or slender. Turkey, Syria. . . . . Var. *rigida*.

  Branches, especially the basal ones, widely divergent, the ultimate branchlets slender. Syria, Lebanon. . . . . Var. *pumila*.

Consolida scleroclada (Boiss.) Schröd. var. **scleroclada** FIG. 1, B.

Stem puberulous, with spreading glandular hairs among the others; branching racemose, the contour more or less pyramidal, rigid to the ultimate branches.

TYPE: "in montibus demissioribus Syriae borealis inter *Latakieh* et *Aleppum*," *Boissier* in July (G); not seen.

DISTRIBUTION. Dry slopes below 1700 m., northern Syria, southern Turkey (Cilicia).

SPECIMENS SEEN. **Turkey:** *Balansa 730.* **Syria:** *Pinard*, 1846; *Boissier*, June 1866; *Sintenis 1416.*

Consolida scleroclada (Boiss.) Schröd. var. **rigida** (Freyn & Sint.) Davis, Fl. Turkey **1**: 123. 1965.

Delphinium anthoroideum Boiss. var. *rigidum* Freyn & Sint. Öst. Bot. Zeitschr. **41**: 363. 1891.

Consolida euphratica Schröd. Ann. K. K. Naturh. Hofmus. Wien **27**: 43. 1913.

Delphinium sclerocladum Boiss. var. *pseudo-anthoroideum* Davis & Hossain, Notes Bot. Gard. Edinb. **22**: 415. 1958. Type, *Davis 10030* (E) seen.

Strigulose; branches ascending, the ultimate slender or rigid.

TYPE: Armenia Turcica, Chama ad Euphratem, Ichtik prope Tuzla, *Sintenis 2969* (W); not seen.

DISTRIBUTION. Dry slopes and steppes, 900–1700 m., southern Turkey to western Syria and the Syrian desert.

SPECIMENS EXAMINED. **Turkey:** *Post*, 1884; *Siehe 387*; *Davis 30973, 31688, 31592, 35878*; *Bornmüller 3221.* **Syria:** *Davis 6477, 10030, 9992.*

Consolida scleroclada (Boiss.) Schröd. var. **pumila** (Huth) Munz, comb. nov.

Delphinium anthoroideum Boiss. var. *pumilum* Huth, Bot. Jahrb. **20**: 366. 1895.

Delphinium sclerocladum Boiss. var. *pumilum* Hossain & Davis, Notes Bot. Gard. Edinb. **22**: 414. 1958.

Branches, especially the basal, widely divergent; stem 4–20 cm. high; lower leaves rather persistent.

LECTOTYPE: Syria, Zebdaine near Damascus, at 5500 ft., June 6, 1858, *Kotschy 103* (BM); other sheets (K, US).

DISTRIBUTION. At 1200 to 1800 m., western Syria, Lebanon.

SPECIMENS SEEN. *Kotschy 103*; *Bornmüller 32*; *MacDaniels*, 1944; *Bornmüller 11324.*

3. **Consolida thirkeana** (Boiss.) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 1, C.

Delphinium thirkeanum Boiss., Fl. Orient. **1**: 84. 1867.

Two to 3 dm. tall, with rather rigid lateral branches, white spreading pubescence interspersed with yellow glandular hairs with pustular bases;

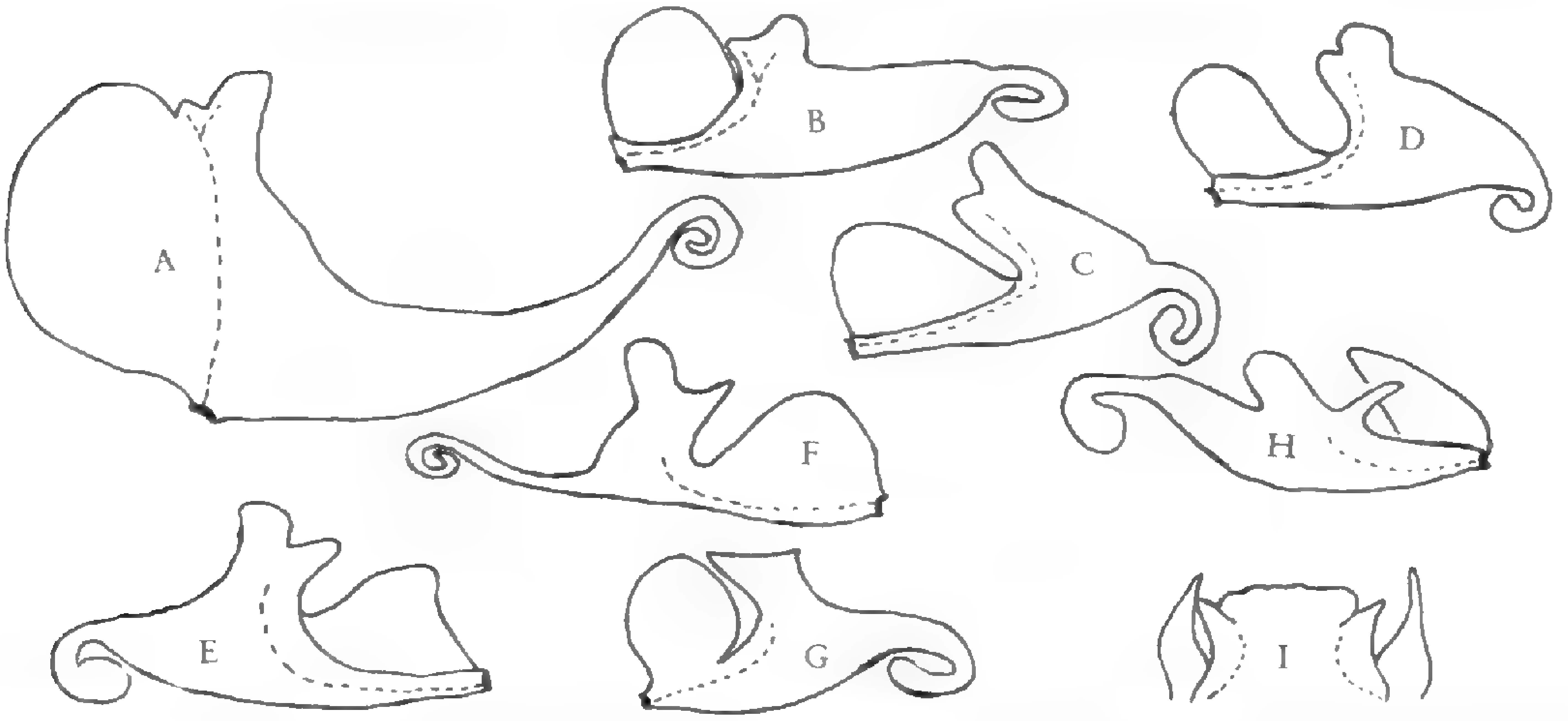

FIGURE 1. **Consolida** species with "petal" of the 5-lobed type, as seen from the side, the lamina base at the bottom of the dotted line (main vein) and of spur. A. *C. teheranica*, the whole (lamina and spur) 23 mm. long; lamina with terminal lobe at its upper right, intermediate lobe small, rounded lower lobe to left; drawn from *Rechinger 2015* (US). B. *C. scleroclada*, the lamina and spur 13 mm. long; drawn from *Balansa 730* (GH). C. *C. thirkeana*, lamina and spur combined 13 mm. long; from *Wiedemann* (GH). D. *C. hohenackeri*, lamina plus spur 11 mm.; from *Bourgeau 7* (UC). E. *C. stenocarpa*, lamina and spur 14 mm.: from *Balansa 857* (UC). F. *C. aconiti*, lamina and spur 20 mm.; from *Sintenis 678* (BM). G. *C. anthoroidea*, lamina and spur 11 mm.; from *Koelz 18498* (MICH). H. *C. saccata*, lamina and spur 14 mm.; from *Sintenis 1186* (PH). I. *C. barbata*, lamina only, front view with broad terminal lobe, sharp narrow intermediate and basal lobes; from *Gontscharow & Grigoriev 871* (NY).

leaves sessile, small, largely gone by anthesis, laciniate with slender crowded lobes; flowers few, scattered; sepals pale blue, 6–7 mm. long, not unguiculate, the lateral lance-oblong, ca. 2 mm. wide, membranous except for the narrow central strip; lower sepals much the same, asymmetrical; upper sepal, including the spur, ca. 13 mm. long, pubescent, the spur circinate-involute, ca. 6 mm. long, 4 mm. wide at base; "petal" 5-lobed, pale with violet tip, ca. 13 mm. long, including the spur, the terminal lobe shortly bifid with rounded parts; intermediate lobes shorter, obtuse; lower lobes membranous, rounded at tip, asymmetrical, ca. 3.5 mm. broad, separated from the intermediate by a very narrow sinus; stamens to ca. 6 mm. long, the filaments dilated below, more or less pubescent above; anthers ca. 0.6 mm. long; follicle semiovate, more or less compressed, glabrous, somewhat reticulate, the rigid style 2 mm. long; seeds with short scales in continuous bands.

SYNTYPES: "in Bithynia (Thirke!)" and "c. Amasya et Tokat, Wiedeman." Both the collections are at Geneva, but I have been unable to see them. I have seen the *Wiedeman* specimens (GH, K).

DISTRIBUTION. Turkey, from Thrace to Galatia, growing at 500 to 1000 m.

ILLUSTRATION of "petal". DAVIS, Fl. Turkey **1**: 127. 1965.

COLLECTIONS SEEN. **Turkey:** *J. Ball*, Oct. 13, 1867; *Sintenis 4882*; *Uvarov 97*; *Bornmüller 13696*.

4. **Consolida hohenackeri** (Boiss.) Grossheim, Fl. Kavkaza **2**: 101. 1930. FIG. 1, D.

Delphinium hohenackeri Boiss., Fl. Orient. **1**: 85. 1867.
Aconitopsis hohenackeri (Boiss.) Kemularia-Nathadze, Trudy Inst. Bot. Tbilisi **7**: 125. 1940.

One to 6 dm. tall, freely branched more or less throughout, retrorse-strigulose except that the upper parts may be subglabrous or with a few hairs with glandular yellow base; ultimate branchlets slender; basal leaves largely gone by anthesis; cauline leaves mostly on lower stems only, laciniate into linear strigulose lobes, subsessile, the leaf-blades largely 1–2 cm. long; bracts mostly entire, subulate, 3–10 mm. long; pedicels 1–3 cm. long, mostly with 2 subulate bracteoles below the flower; inflorescence very open; flowers purple to violet or pale mauve, ca. 1.5 cm. across; sepals lanceolate, ca. 7 mm. long, the spur with a circinate-involute tip and ca. 7 mm. long and 3.5–4 mm. wide at the base, pubescent; lateral sepals lance-elliptic, 3.5–4 mm. wide, mostly membranous except for the strigulose median strip; lower sepals narrower, much like the lateral; "petal" 5-lobed, ca. 11 mm. long, including the spur, the terminal lobes subentire, broad, ca. 1.5 mm. long; the intermediate lobes obtuse, ca. 1 mm. long, the lower separated from the intermediate by a broad sinus, membranous, rounded-oblong and ca. 4 mm. long; filaments 4–5 mm. long, dilated only below, more or less pubescent above; anthers yellowish, ca. 0.7 mm. long; follicle glabrous, semiovate, reticulate-veiny, 6–7 mm. long, 3–4 mm. wide, the beak an additional 3 mm. long; seeds with longish separate scales.

LECTOTYPE: **Turkey**: Prov. Gümüsane, near Baibout in Armenia, July 12, 1862, *Bourgeau 7* (K); this number seen also (E, P, UC).

DISTRIBUTION. Dry places at 900–1800 m., Turkish Armenia, Transcaucasia, Iran.

ILLUSTRATION. "petal", HOSSAIN & DAVIS, Notes Bot. Gard. Edinb. **22**: 416. *fig. E.* 1958; Davis, Fl. Turkey **1**: 127. *fig. 1.* 1965.

REPRESENTATIVE SPECIMENS. **Transcaucasia:** *Wittman 93*; *Radde 307*. **Turkey:** *Sintenis 1336, 7110*; *E. K. Balls 1441A*; *Davis 30825, 32613, 30076*; *Holmberg 2408*. **Iran:** *Haussknecht*, 1868; *Stapf 2771*.

5. **Consolida stenocarpa** (Hossain & Davis) Davis, Notes Bot. Gard. Edinb. **26**: 173. 1965. FIG. 1, E.

Delphinium stenocarpum Hossain & Davis, Notes Bot. Gard. Edinb. **22**: 413. 1958.

Slender-stemmed, divaricately branched throughout, 2.5–4 dm. tall, densely retrorse-strigose below and with some spreading hairs with swollen yellow base, sparsely pubescent above; leaves laciniate into linear lobes, strigulose, the lower with petioles ca. 1 cm. long and blades 1–1.5 cm. long, the lower cauline subsessile, rapidly reduced up the stem; bracts sessile, entire to lobed, 3–7 mm. long; pedicels strigulose, 4–6 (–15) mm. long; bracteoles subulate, 1.5–2 mm. long, alternate to subopposite; flowers widely scattered, bluish lilac to pale dirty mauve; sepals 6–7 mm. long, elliptic, not unguiculate, ca. 3 mm. wide, acute, pubescent and greenish on midrib in the lateral sepals, more generally pubescent on the lower pair; sepal spur pubescent, 6–7 mm. long, 3.5 mm. wide, curved-oblong, circinately involute at the tip; "petal" 5-lobed, 7–8 mm. long, the spur an additional 5–6 mm. long, upper lobe 1.5–1.75 mm. long, bluish, bifid half way into rounded lobes; intermediate lobes narrowly lance-deltoid, 1 mm. long; lower lobes membranous, rounded-oblong, ca. 2.5 mm. long; filaments sparsely pubescent on the inflated lower part; follicle glabrous, linear-oblong, 10–13 by 1.5–2 mm., the style an additional 3–3.5 mm.; seed with short scales.

TYPE: Turkey: Prov. Konya (Lycaonia), between Agabeyli and Korkuyu, *Davis 16638* (E), isotype (K); seen.

DISTRIBUTION. Fallow fields and plains, 900–1300 m., central Anatolia.

ILLUSTRATIONS. "petal"; HOSSAIN & DAVIS, Notes Bot. Gard. Edinb. **22**: 416, *fig. B, C*. 1958; DAVIS, Fl. Turkey **1**: 127. *fig. 1*. 1965.

SPECIMENS SEEN. **Turkey:** *Balansa 857*; *Godfrey & Taysi SH–25*; *Davis 32810, 16643*.

6. **Consolida aconiti** (L.) Lindl. Jour. Roy. Hort. Soc. **6**: 55. 1851. FIG. 1, F.

Delphinium aconiti L. Mantissa **1**: 77. 1767.
Aconitum monogynum Forsk. Fl. Aegypt-Arab., p. xxvii. 1775.

Stiffly much branched, 2–5 dm. tall, with soft, white, spreading pubescence, subglabrate above; cauline leaves short-petioled, roundish in outline, to 2 or 3 cm. long, with many ultimate linear pubescent lobes; lower bracts leaflike, smaller, 3–5-partite, the upper reduced; pedicels very slender, to 3 or 4 cm. long; bracteoles linear, remote from flower, alternate, 3–4 mm. long; flowers few on open branches; sepals ca. 5 mm. long, pale violet with darker median, more or less greenish stripe pubescent without; spur 14–15 mm. long, circinately involute at the apex; "petal" 8–9 mm. long, pale yellow with violet tip, the upper lobe exceeding the acute, narrowly triangular intermediate lobes, the lower lobes separated from the intermediate by a broad sinus; stamens purplish, 5–6 mm. long; anthers dark, oblong, ca. 0.6 mm. long; follicle linear with gradually rostrate apex, 15–22 mm. long, 1.5–2 mm. wide, glabrous, veined-reticulate; seeds few, pyramidal, with elongate scales.

TYPE: "Habitat in Dardanella, *Forskål*; photograph of specimen in the Linnaean Herbarium seen.

DISTRIBUTION. Below 1100 m., region of the Dardanelles, Turkey.

ILLUSTRATIONS. VAHL, Symb. 1: *t. 13*. 1790; DAVIS, Fl. Turkey **1**: 217. 1965.

SPECIMENS. **Turkey:** *Aucher 66*; *Sintenis 678*; *Guichard*, July 29, 1962.

7. **Consolida anthoroidea** (Boiss.) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 1, G.

Delphinium anthoroideum Boiss. Ann. Sci. Nat. II. **16**: 369. 1841.

Delphinium acutilobum Turrill, Kew Bull. **1929:** 223. 1929. Based on *Gilliat-Smith 2086* (K) from near Yam, Tabriz district, Iran; not seen.

Erect, rigidly divaricate, to 8 dm. tall, subglabrous to strigulose below, short spreading-pubescent above and with many yellow-based hairs; leaves 3- to many-parted, the ultimate lobes linear to oblance-linear, the main cauline blades subsessile, ca. 3 cm. long and 5 cm. wide, strigulose; bracts mostly 3-lobed, 7–15 mm. long; pedicels very slender, 1.5–6 cm. long; bracteoles 2–3 mm. long, lance-linear, often more than 2; inflorescence very open, the flowers remote; sepals violet to pale lilac, with greenish tinge toward the apex, pubescent, 6–7 mm. long, not clawed; lateral sepals oblong, rounded apically, 2–3 mm. wide, pubescent along midrib, the 2 lower slightly wider; sepal spur circinately involute at apex, erect, pubescent, ca. 1 cm. long, 5 mm. wide at base; "petal" 5-lobed, more or less rose, the blade 6 mm. long, the upper lobe short, retuse, shorter than the elongate, triangular, divaricate intermediate lobes, the lower lobes membranous, elongate-rounded, almost 4 mm. long; filaments dilated below, slightly pubescent; anthers yellow to orange; follicle glabrous, subcompressed, oblong-obovoid, 8–10 mm. long, 3–4 mm. wide, abruptly narrowed into a style an additional 1 mm. long; seed pyramidal, densely squamate.

TYPE (lectotype by Davis): Syria, *Aucher 65* (G), not seen, but isolectotypes seen at K, P.

DISTRIBUTION. Fallow fields and stony slopes, 600–2000 m., Kurdistan in Turkey, Iraq, Iran, to Syria, Lebanon.

ILLUSTRATIONS. HOOKER, Icon. Pl. V. **2**: *pl. 3151*. 1932; DAVIS, Fl. Turkey **1**: 127. 1965.

REPRESENTATIVE SPECIMENS. **Turkey:** *Aucher 4032*; *Krause 3828*; *Balansa 857*; *Davis 23802*. **Iran:** *Gilliat-Smith 2365, 2388*; *Koelz 18498*; *Furse 3282, 3283, 3254*. **Lebanon:** *Berton 217*. **Syria:** *Gaillardot 389*; *Dinsmore 13024*.

8. **Consolida saccata** (Huth) Davis, Notes Bot. Gard. Edinb. **26**: 173. 1965. FIG. 1, H.

Delphinium saccatum Huth, Bull. Herb. Boiss. **1**: 325. 1893.

Rigid, much branched, several dm. tall, the branches divaricate, slender, largely retrorse-strigulose, but with more or less spreading, short, glandular hairs near the tips; leaves of stem palmately multipartite, to ca. 3 or 4 cm. long, subsessile, the segments linear, strigulose, rather few; inflorescence open, with widely scattered, pale yellowish to blue or white flowers; bracts largely 3–5-parted, to ca. 5 mm. long; pedicels very slender, 0.5–3 cm. long; bracteoles entire, several, scattered, to ca. 2.5 mm. long; sepals ca. 10 mm. long, lance-oblong, ca. 3 mm. wide, with broad white hyaline margin, the lateral pair pubescent along the median strip, lower sepals less hyaline and more pubescent, the upper sepal and spur pubescent, the latter 4–5 mm. long, 2.5 mm. wide at base, hooked-saccate, not coiled, at apex; "petal" pale with bluish tip, 5-lobed, ca. 15 mm. long, including spur, the terminal lobe ca. 3 mm. long, divided half its length, intermediate lobes 1.5–2 mm. long, sharply triangular, outer lateral lobes membranous, 4–5 mm. long, triangular, acute; filaments dilated at base; follicle compressed, glabrous, reticulate-veined, 12–15 mm. long, 3–4 mm. wide, the style an additional 3–4 mm. long.

TYPE: Turkey, Mardin, rocky fields near Rischemil, *Sintenis 1186* (B); the holotype now probably destroyed; isotypes seen at K, MO, P, PH.

DISTRIBUTION. Stony fields, Turkey (E. Mesopotamia, Mardin); northern Iraq.

ILLUSTRATIONS. HUTH, Bull. Herb. Boiss. **1**: *pl. 16, fig. 3.* 1893; DAVIS, Fl. Turkey **1**: 127. 1965.

REPRESENTATIVE SPECIMENS. **Iraq:** *Haines W 1218*; *Agnew*, Sept. 1, 1961.

9. **Consolida barbata** (Bunge) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 16, 62. 1909. FIG. 1, I.

Delphinium barbatum Bunge, Arbeit. Nat. Ver. Riga **1**: 126. 1847.

Delphinium barbatum Bunge var. *hirsutum* Huth, Bot. Jahrb. **20**: 391. 1895. Apparently based on a collection at 800 m., Mt. Karatag, *Regel* in 1882, Turkestan Herb. (LE), which I have not seen.

Two to 8 dm. tall, retrorse-strigulose, erect, the main stem with many short, slender, ascending, side branches throughout its length; leaves numerous along main stem, dissected into linear segments 0.3–0.4 mm. wide, the principal cauline leaves sessile, 1–2 cm. long; bracts divided into linear segments or the uppermost entire, 2–6 mm. long; pedicels 4–15(–30) mm. long, very slender, subglabrous to glandular-pubescent with some hairs yellow and enlarged at the base; bracteoles several, lanceolate, 1–2 mm. long; sepals bearded without, blue, 6–8 mm. long, narrow-ovate, acute, ciliate-bearded at distal margin, the spur ca. 8 mm. long, blue, strigulose or glandular-pubescent, ca. 2.5 mm. wide at base; "petal" whitish with bluish tip, 5-lobed, ca. 8–9 mm. wide, the middle lobe broadly rounded, ca. 4.5 mm. wide, the 2 lateral lobes lance-deltoid, slightly shorter than the median lobe, the outer lobes more membranous, lanceolate, acuminate, ca. 5 mm. long; filaments pale blue, 5–6 mm. long, glabrous; anthers blue, ca. 0.4 mm. long; follicle glabrous, oblong, 5–10 mm. long, reticulate-veined, the style an additional 2.5–3 mm.; seed ca. 1.5 mm. long, narrowly obpyramidal, with transverse rows of scales.

TYPE: Karatau Mts. in upper Sarafschan near Samarkand, Turkestan, Oct., 1841, *Bunge*. The *Bunge* collection at LE is probably the type and has "*Lehmann 38*" on it, as does a specimen at P. I take it this means from the Lehmann herbarium. The LE specimen has a single flower and no leaves; the sepals are ciliate and hide the "petal"; the pedicels are glandular-pubescent.

DISTRIBUTION. Dry places at 700–2000 m., Turkestan.

REPRESENTATIVE SPECIMENS. *Capus 54*; *Regel 52*, 1881; *Komarov*, Aug. 18, 1893; *Gontscharow & Grigoriev 871*.

10. **Consolida raveyi** (Boiss.) Schröd. Abh. Zool.-Bot. Ges. Wien 4(5): 62. 1909. FIG. 2, A.

Delphinium raveyi Boiss. Diagn. I. **1:** 66. 1843.

Erect, simple or more often with few upwardly curved branches from the base, 1–4 dm. tall, strigulose and with short spreading white hairs and many yellow pustular-based hairs, leafy throughout; basal leaves short-petioled, ternate, then further divided into linear pubescent segments; lower petioles to 2 or 3 cm. long, the upper ones gradually shorter; lower blades 1–3.5 cm. wide, upper smaller, passing into trifid leafy bracts ca. 1 cm. long or the uppermost linear, entire, green; flowers solitary in most leaf-axils, erect, sessile, each with 2 linear bracteoles at base so that there is a resemblance to a trifid bract; sepals deep violet, ca. 13–18 mm. long, without the spur; upper sepal linear, ca. 2 mm. wide, pubescent on most of outer surface, the pointed spur to ca. 5 mm. long; lateral sepals pubescent on the midrib and narrow claw, the limb ca. 4 mm. wide; lower sepals with broader claw, the limb 3 mm. wide; "petal" 3-lobed, 12–14 mm. long, 3–4 mm. wide, the terminal lobe divided into 2 small lobules 1 mm. long, the lateral lobes ca. 1.5 mm. long; stamens 5–7 mm. long, the filaments oblong-dilated below, narrow above, more or less pubescent; anthers yellow, ca. 0.8 mm. long; follicle reticulate-veiny, soft hairy, 10–12 mm. long, the beak an additional 1.5–2 mm., the body 3 mm. wide, subcompressed, few seeded; seeds triquetrous, scaly.

TYPE: "in cultis Cariae prope Aphrodisias" [Geyre]. *Boissier*, June 1842 (G not seen); isotypes (K, NY, P) seen.

DISTRIBUTION. Steppes, fields, etc., 700–800 m., Turkey from Caria and Lycia through Phrygia and Cappadocia to Paphlagonia.

REPRESENTATIVE COLLECTIONS. **Turkey:** *Pichler 22*; *Bourgeau 8*; *Balansa 599, 719, 856*; *Bornmüller 1719, 4027, 13690*; *Siehe 175*; *Sintenis 4293*; *Davis 13010, 36622.*

11. **Consolida cruciata** (Hossain & Davis) Davis, Notes Bot. Gard. Edinb. **26:** 174. 1965. FIG. 2, B.

Delphinium cruciatum Hossain & Davis, Notes Bot. Gard. Edinb. **22:** 422. 1958.

Erect, 1.5–4 dm. tall, simple or with few upwardly curved branches from base, strigulose; cauline leaves with petioles 0.5–1.5 cm. long, the blades ca. as long or longer, ternately laciniate into strigulose linear segments; flowers subsessile in most axils, lilac to pink, drying whitish, 10–15 mm. long; pedicels very short, thick; bracts foliaceous, partite, gradually reduced up the stem; bracteoles 2, trisect, equaling flowers; sepals pubescent, the upper 10–12 mm. long, oblong-spatulate, narrowed into a broad basal claw; the 2 lateral ca. 2.5 mm. wide, the 2 lower rhombic-spatulate, obtuse, clawed; spur pubescent, 5–7 mm. long, ca. 2 mm. wide at base, slightly curved, pointed; "petal" 3-lobed, cruciate, 11.5–12.5 by 9.6–11 mm., purple-nerved, more or less abruptly attenuate at base; terminal lobe oblong, 3–5 mm. long, with 2 small rounded lobes at tip; lateral lobes rounded-oblong, flaring; stamens unequal, filaments oblong-dilated below, linear and pubescent above; anthers purplish brown, ca. 1 mm. long; follicle erect, 12–17 by 2–3 mm., terete, strigulose, more or less furrowed longitudinally when mature, the style an additional 1.5–3 mm.

TYPE: Turkey, Prov. Adana (Cilicia), Bozanti at 750 m., *Siehe 362* (E); isotypes (GH, K, P) seen.

DISTRIBUTION. Cilicia, Mersin, Turkey.

ILLUSTRATIONS. HOSSAIN & DAVIS, Notes Bot. Gard. Edinb. **22**: 422. *fig. 4, C & D.* 1958; DAVIS, Fl. Turkey **1**: 127. 1965.

12. **Consolida axilliflora** (DC.) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 2, C.

Delphinium axilliflorum DC. Syst. **1**: 341. 1817.

Delphinium axilliflorum DC. var. *violaceum* Boiss. Fl. Orient. **1**: 75. 1867. With violet flowers; several collections cited; some seen by me.

Delphinium axilliflorum DC. var. *coerulescens* Boiss. *loc. cit.* Flowers pale gray-blue. Two collections cited; one seen by me.

Delphinium axilliflorum DC. var. *minus* Huth. Bot. Jahrb. **20**: 369. 1895. No collections cited.

One to 6 dm. high, strigulose or glabrescent, the stem erect, mostly subsimple, more or less equally leafy throughout; leaves twice trifid, the lower petioled, the upper subsessile, the ultimate segments linear, mostly 1–1.5 mm. wide, strigulose, acute; leaf blades largely 1–2 cm. long; flowers solitary in axils, often from near the base of the plant; pedicels very short; bracteoles subopposite, at base of flower; sepals blue, violet or rose, oblong, obtuse, the lateral and lower pairs 10–13 by 5–6 mm., unguiculate, the lateral with pubescence confined to the median strip; upper sepal narrower, pubescent, the spur slightly curved, pointed, 6–9 mm. long, ca. 2 mm. wide at base; "petal" 3-lobed, kite-shaped, almost 2 cm. long including the spur, the oblong terminal lobe ca. 5 mm. long, with 2 short rounded terminal lobules, the lateral lobes broadly triangular, obtuse, ca. 5 mm. long and wide; stamens unequal, the filaments oblong below, narrowed and more or less pubescent above; anthers brownish, ca. 1 mm. long; follicle more or less glabrescent in maturity, erect and appressed to the stem, ca. 16–20 by 3 mm., longitudinally furrowed when mature, the beak an additional 3 mm.; seeds triquetrous, the broad scales more or less distinct.

TYPE: In Oriente, *Labillardière*; not seen.

DISTRIBUTION. Fields, grassy places, etc., below 1800 m., Turkey (Cilicia to Mesopotamia) to Syria.

ILLUSTRATIONS. DELESSERT, Icon. Pl. 1: *t. 50.* 1820; HOSSAIN & DAVIS, Notes Bot. Gard. Edinb. **22**: 423. 1958; DAVIS, Fl. Turkey **1**: 127. 1965.

REPRESENTATIVE COLLECTIONS. **Turkey:** *Hennipman et al. 1393*; *Balansa 729*; *E. K. Balls 2243*; *Post 213*; *Davis 28753, 28680, 22135.* **Syria:** *Post 218*; *Kotschy*, March 13, 1841; *Letourneux 327*; *Dinsmore 20367*; *Haradjian 2266.*

13. **Consolida gombaultii** (Thiebaut) Munz, comb. nov. FIG. 2, D.

Delphinium gombaultii Thiebaut, Bull. Soc. Bot. France **81**: 114. 1934.

Near to *C. axilliflora*, but glandular-pubescent throughout and also with very short non-glandular hairs; stem erect, simple or slightly branched, 3–5 dm. tall; leafy and flowering from the base; lower leaves 3–4 cm. long, multifid into linear subobtuse segments 1 cm. or so long, ca. 1.5 mm. wide and with very short stubby pubescence; median and upper leaves linear-lanceolate, entire, becoming bracts above, 1–3 cm. long and exceeding the pedicels; pedicels 2–3 mm. long; bracteoles subulate, 2–3 mm. long; flowers small, 8–12 mm. long, arranged in a long slender spike; sepals glandular-pubescent, intensely blue, 6–8 mm. long, oblanceolate, unguiculate; spur ca. 6 mm. long, slightly curved; "petal" pale blue, 3-lobed, the upper lobe bifid, the lateral broader, widespread, pointing slightly forward, the whole "petal" ca. 1 cm. long and broad, its spur almost straight, somewhat shorter than the blade; follicle erect, 10–12 mm. long, 3 mm. wide, short-beaked; seeds gray, squamate.

TYPE: Syria, Djebel Druze, *Gombault 1717*, May 21, 1932 (P); seen.

This species is near *C. axilliflora*, but with shorter pedicels, entire bracts, smaller flowers, shorter follicle, and a more general glandulosity. I have seen no collections other than the type.

14. **Consolida stocksiana** (Boiss.) Nevski in Komarov, Fl. U.S.S.R. 7: 111. 1937. FIG. 2, E, F.

Delphinium stocksianum Boiss. Diagn. II. **1**: 12. 1853.
Delphinium stocksianum Boiss. var. *glabrescens* Boiss. *loc. cit.* 1853. Type, *Griffiths 1376* (K); seen.
Consolida stocksiana var. *glabrescens* (Boiss.) Tamura in Kitamura, Fl. Afghan. 124. 1960.
Delphinium kabulianum Akhtar, Kew Bull. **1938**: 86. 1938. Based on *S. A. Akhtar* from near Kabul, Afghanistan (K); seen.
Consolida stocksiana (Boiss.) Nevski var. *kabuliana* (Akhtar) Tamura in Kitamura, Fl. Afghan. 124. 1960.

Plant 2–5 (–7) dm. tall, branched below, cinereous-strigulose and leafy throughout or with more spreading hairs above; lower leaves long-petioled, tripartite into narrowly lobed segments, the lobes oblong-linear, subobtuse; intermediate leaves with shorter petioles or sessile, the segments entire, linear-spatulate, canaliculate, 1.5–4 mm. wide, with mucronate recurved tips; leaves pretty much shed by anthesis; flowers creamy white, in a long lax spike; pedicels to 6 mm. long, minutely bibracteolate at the base; sepals 7–11 mm. long, with violet median stripes, the lateral sepals pubescent on midrib only; spur vertical, 1.6–2.6 cm. long, 4 mm. wide at base, gradually attenuate, somewhat curved; "petal" 3-lobed, ca. 8 mm. high, 11 mm. wide, the middle lobe 2–2.2 mm. long, with 2 rounded terminal lobules; lateral lobes spreading, rounded, slightly turned upward, 2.5–3 mm. long, the spur 16–18 mm. long; stamens 4–8 mm. long; anthers yellow, 0.7–1 mm. long; follicle cinereous, strigose, erect, short, cylindrical, subarcuate, the slender style one-third as long as the body which is 8–10 mm. by 2.7 mm.; seeds brown, subtriangular, regularly rugulose.

TYPE: Fields in Baluchistan, *Dr. Stocks 979* (K !, isotype; G, holotype, not seen).

DISTRIBUTION. Fields and open places, largely between 1000 and 2000 m., Central Asia: Pamiro-Alai, Turkmannia, Iran, Afghanistan.

REPRESENTATIVE COLLECTIONS. **Afghanistan:** *Furse 6469, 5942, 5943*; *Herb. Griffith 42*; *Kay Beach 5029*; *Hay 210.* **Turkestan:** *Regel*, May 1882, and Sept. 21, 1884.

This species is confused with *Consolida rugulosa* and *C. persica*. From the former it should be separable by the more triangular and not rounded lateral lobes of the "petal". From the latter by the narrower "petal", which is 8–11 mm. wide when expanded, not 15–20 mm. It varies in pubescence and flower size. So far as I can see, the plants described as *C. kabuliana* are small and with smaller flowers than in many populations and those called var. *glabrescens* may have a somewhat more glabrescent follicle in maturity.

15. **Consolida ambigua** (L.) Ball & Heywood, Feddes Repert. **66**: 151. 1962. FIG. 2, G.

Delphinium ambiguum L. Sp. Pl. ed. 2. 749. 1763.
Delphinium ajacis auct. non L. Sp. Pl. **1**: 531. 1753.
Consolida ajacis auct. non (L.) Schur, Verh. Siebenburg. Ver. Naturf. **4**: 47. 1853.
Ceratosanthus ajacis Schur, *op. cit.* 46.

Plant subglabrous, especially below, to more or less pubescent, especially above, with short fine appressed or spreading hairs, mostly one-stemmed, 3–10 dm. tall, generally branched above with ascending-horizontal branches; lower leaves long-petioled, the blades commonly 2–5 cm. in diameter, multifid into ultimate more or less linear mucronate segments largely 1–1.5 mm. wide; cauline leaves gradually reduced upward, the upper sessile, often 1–2 cm. long; bracts multifid to entire, the lower often at least as long as the pedicels, the uppermost 2–3 mm. long; inflorescence more or less lax, each branch ending in a few- to many-flowered raceme; pedicels commonly 1–3 cm. long, often about equal to the diameter of the flower; bractlets mostly 1.5–4 mm. long, usually below the middle of the pedicel; flowers blue to rose or white, 2–2.5 cm. across; sepals ovate, attenuate at base, more or less narrowed into an obtuse apex, 12–14 mm. long, more or less pubescent, each with a greenish subapical spot; spur ca. 15 mm. long, straight or slightly curved; "petal" 3-lobed, the central lobe oblong, with 2 short rounded lobules and about 6 mm. long, the 2 lateral lobes rounded, about as long, spur 15–16 mm. long; stamens 6–7 mm. long, the filaments abruptly dilated at the base, glabrous; anthers yellow; follicle pubescent, cylindric, 16–22 mm. long, the style ca. 2 mm. long; seeds black, ca. 2.5 mm. long, oblong-trigonous, with undulating transverse rows of scales.

TYPE from Mauretania, northwest Africa, a double form in the Linnaean Herbarium 694/4; photograph seen.

DISTRIBUTION. Mediterranean region, but much cultivated and widely escaped as various horticultural forms.

ILLUSTRATIONS. REICHENBACH, Icon. Fl. Germ. **4**: *pl. 67*. 1840; MAIRE, Fl. de l'Afrique du Nord **13**: 54. *fig. 24*. 1964.

REPRESENTATIVE COLLECTIONS. **Transcaucasia:** *Hohenacker 1838*; *F. N. Meyer 541*. **Iraq:** *Rawi 10738*; *Guest 247*. **India:** *Giles*, 1885; *Wight 10, 18*; *Falconer 59*; *H. J. Walton*, Aug. 14, 1904; *G. Watt*, March 1878. **Honan Island:** *Levine 952, 824, 823*.

The question of the application of the name *ambigua* has not been entirely agreed upon. I am following Ball & Heywood (Feddes Repert. **66**: 151. 1962), Chater (Tutin et al., Fl. Europaea **1**: 217. 1964), and Davis (Fl. Turkey **1**: 126. 1965) in using it, but E. Janchen (Feddes Repert. **72**: 34. 1966) disagrees and believes the Linnaean epithet *ajacis* applies to this taxon.

16. **Consolida orientalis** (Gay) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): *25*. 1909. FIG. 2, H.

Delphinium orientale Gay in Desmoul. Cat. Dordogne 12. 1840.

Delphinium ajacis L. var. *orientale* (Gay) Finet & Gagnep. Bull. Soc. Bot. France **51**: 467. 1904.

Delphinium hispanicum Willk. Prodr. Fl. Hisp. **3**: 969. 1880.

Delphinium orientale ssp. *hispanicum* (Willk.) Batt. in Batt. & Trab. Fl. Alg. 15. 1888.

Delphinium orientale var. *brevicalcaratum* Huth, Bot. Jahrb. **20**: 376. 1895. Not typified, but several collections cited seem to belong here, such as *Aitchison, Falconer, Griffith*.

Delphinium bithynicum Griseb. Spic. Fl. Rumel. **1**: 320. 1843. Type from near Bolu, Bithynia, Turkey; not seen by me. Referred to *D. orientale* by Boiss., Fl. Orient. **1**: 79. 1867.

Mostly 1-stemmed, simple or branched, especially above, erect, 2–6 dm. tall, the lower parts retrorse-strigose, upper with more or less crisped pubescence, some gland-tipped hairs and some swollen at the base; leaves mostly subglabrous, the lower petioled and early withered, the upper sessile; principal leaves multifid, crowded on the stems, the blades 2–4 cm. long, the segments linear or lance-linear, 1–2.5 mm. wide, more or less ciliolate; flowers few to many, in racemes that are rather dense at anthesis, more open in fruit; bracts green, the lower with linear parts, the upper linear, entire, 5–20 mm. long; pedicels 0.5–4 cm. long, bibracteolate near the summit; flowers 1.5–2.5 cm. in diameter, dark purple to rose or white; the sepals round-ovate to oval or somewhat narrower, ca. 10–12 mm. long, abruptly contracted into a pubescent basal claw almost as long as the blade which is obtuse or rounded at the summit and more or less pubescent; spur ca. 1 cm. long; "petal" usually of same color as sepals, 3-lobed, 8–10 mm. long, the median lobe ovate to oblong-ovate, 2-lobed, somewhat longer than the rounded lateral lobes; stamens 6–7 mm. long, the filaments dilated at base, with some gland-tipped hairs at upper end; anthers yellow, ca. 1.5 mm. long; follicle strigose, 14–22 mm. long, oblong-cylindric, with some gland-tipped hairs, the style 1.5–2 mm. long; seeds brownish black, obpyramidal, angular, 1.5–2 mm. long, with several undulating transverse rows of short scales.

TYPE: Described from cultivated material originating from the Orient, apparently represented at K; seen.

DISTRIBUTION. Grain fields and fallow places below 1500 m., Mediterranean region to Turkey, Caucasus, Iran, India, Tibet, central Siberia.

ILLUSTRATIONS. CURTIS, Bot. Mag. **169**: *pl. 186*. 1952–3; DAVIS, Fl. Turkey **1**: 129. *fig.* 2. 1965.

REPRESENTATIVE COLLECTIONS. **Caucasus:** *Brotherus 32*; *F. N. Meyer 541*. **Transcaucasia:** *Shevljakov*, June 25, 1935; *Gurvitsch*, July 17, 1936. **Turkestan:** *F. N. Meyer 572*; *Michelson 217*–1911. **Turkey:** *Sintenis 4137, 420*; *Bornmüller 13692*; *Bourgeau 6*; *Balansa 1133*; *Krause 3397, 3723*; *Davis 30598, 28945, 30079, 31992*. **Iran:** *Bunge*, 1858–9; *Furse 2459, 1920*; *Lindsay 1151*; *Rechinger 4173, 5220, 383*. **Afghanistan:** *Herb. Griffith 47*; *Aitchison 444*; *Hay 239*.

Parsa in his *Flore de l'Iran* **1**: 431. 1951, proposes *Delphinium orientale* Sims var. *major*, the description of which makes application of the name very uncertain. The terms sepals and petals are baffling.

17. **Consolida regalis** S. F. Gray, Nat. Arr. Brit. Pl. **2**: 711. 1821.

Delphinium consolida L. Sp. Pl. **1**: 530. 1753.

Plant 2–12 dm. tall, mostly divaricately and rather finely branched, subglabrous to retrorse-strigulose; radical leaves petioled, early deciduous, the main cauline ones trifid, then again parted into ultimate, linear, mucronate, strigulose lobes 1–5 cm. long; flowers few, in rather open terminal racemes, deep blue or more seldom pink or white; bracts mostly simple, linear, 3–15 mm. long; pedicels very slender, 1–5 cm. long; bracteoles linear, alternate to opposite, often well below the flower, 1.5–4 mm. long; flowers (excluding the spur) 9–16 mm. long; sepals more or less ovate, narrowed at both ends, scarcely or short-unguiculate, strigose mostly along the midrib in the lateral pair; spur 17–22 mm. long; "petal" blue to cream, 3-lobed, 12–15 mm. wide, the spur 16–17 mm. long, middle lobe of limb 3.5–5 mm. high, shortly 2-lobed at apex, each of these lobules often emarginate; lateral lobes rounded, 4–5 mm. long; stamens 4–7 mm. long; filaments dilated on lower portion; anthers 0.6–0.7 mm. long, yellow; follicle to 2 cm. long including the 2–3 mm. long style; seeds dark, with subcontiguous scales in transverse rows.

Sepals 12–16 mm. long, usually light violet-blue; stems often relatively simple; follicle usually twice as long as broad. Central and northwestern Europe to Turkey. . . . . Subsp. *regalis*.
Sepals 9–11 mm. long, usually dark violet-blue; stem usually repeatedly branched; follicle usually 3 times as long as wide.
  Follicle glabrous. Turkey to southeastern Europe. . . . . Subsp. *paniculata*.
  Follicle strigose. Around the Caspian Sea and on the north side of the Black Sea. . . . . Subsp. *divaricata*.

Consolida regalis subsp. **regalis** FIG. 2, I.

Stem usually once or twice branched; flowers 22–35 mm. long; sepals 11–15 mm. long, usually light violet-blue, rather close together in the inflorescence; follicle glabrous, usually twice as long as broad.

TYPE LOCALITY: Britain.

DISTRIBUTION. Fallow fields, etc., largely below 1000 m., Europe, Caucasia, rarely in Turkey.

ILLUSTRATIONS. REICHENBACH, Icon. Fl. Germ. **4**: *pl. 66.* 1840; HEGI, Ill. Fl. Mittel-Eur. **3**: 487. *pl. 114.* 1909.

REPRESENTATIVE COLLECTION. *Davis 29695.*

Consolida regalis subsp. **paniculata** (Host) Soó, Österr. Bot. Zeitschr. **71**: 243. 1922. FIG. 2, K.

Delphinium paniculatum Host, Fl. Austr. **2**: 65. 1831.

Delphinium consolida L. subsp. *paniculatum* (Host) Busch in Kuznetzow, Fl. Cauc. Crit. **3**: 44. 1902.

Consolida regalis S. F. Gray subsp. *paniculata* Soó var. *paniculata*, Davis, Fl. Turkey **1**: 128. 1965.

Ceratosanthus paniculatus Schur, Verh. Siebenburg. Ver. Naturwiss. **4**: 47. 1853.

Delphinium consolida L. var. *micranthum* Boiss. Fl. Orient. **1**: 78. 1867. A new name for *D. paniculatum.*

Flowers widely scattered; spur 14–18 mm. long; sepals ca. 1 cm. long, to 6 mm. broad; "petal" ca. 15 mm. wide, the central lobe to 3.5 mm. long, the lateral 4.5–5 mm.; stamens 4–6 mm. long; anthers 0.6 mm. long; follicle 7–11 mm. long, excluding the style, glabrous; seeds angular obovoid, 1.75 mm. long.

TYPE: Jugoslavia, near Cattaro, *Tomasini.* Not seen.

DISTRIBUTION. Cultivated and disturbed places below 1000 m., southeastern Europe to Turkey and Caucasia.

ILLUSTRATIONS. CURTIS, Bot. Mag. **159**: *pl. 9435.* 1936; DAVIS, Fl. Turkey, **1**: 129. 1965.

REPRESENTATIVE COLLECTIONS. **Caucasus:** *Czerniakowska*, Aug. 28, 1936. **Turkey:** *Sintenis 4294*; *Bornmüller 13689*; *Bourgeau 10*; *Krause 3878*; *Balansa 595, 1134*; *Davis 32787, 13008, 13463, 38961.*

I have seen a number of cultivated specimens, some grown as *Delphinium consolida* some as *D. paniculatum.*

Consolida regalis subsp. **divaricata** (Ledeb.) Munz, comb. nov. FIG. 2, J.

Delphinium consolida L. subsp. *divaricatum* (Ledeb.) Hossain & Davis, Notes Bot. Gard. Edinb. **22**: 424. 1958.

Delphinium divaricatum Ledeb. in Eichwald, Pl. Nov. Caspio-Cauc. **2**: 16. *pl. 16.* 1831.

Consolida divaricata (Ledeb.) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 25. 1909.

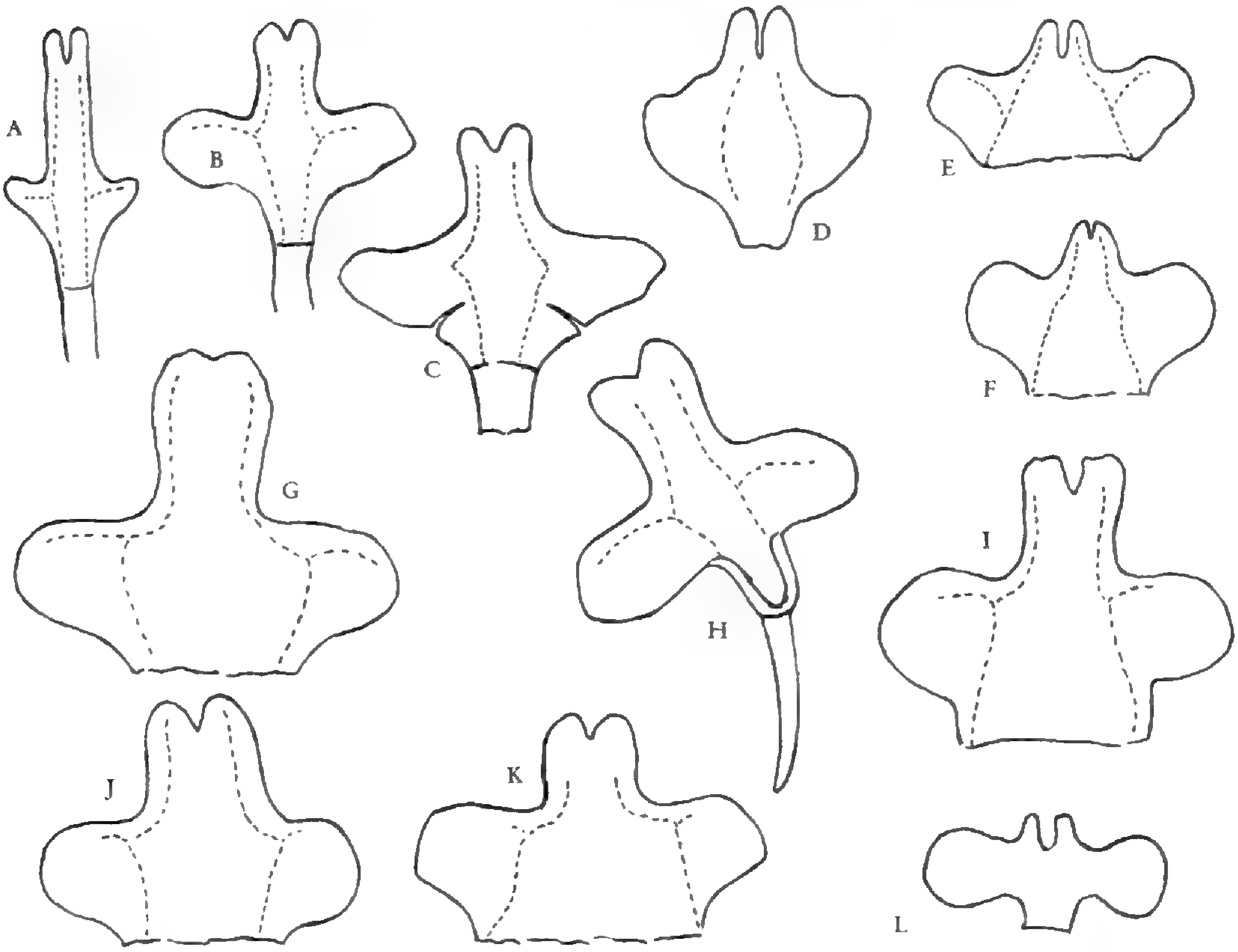

FIGURE 2. **Consolida** species. Drawings show lamina of "petal" of 3-lobed type with lateral lobes perpendicular to terminal lobe, the latter somewhat divided at tip; dotted lines, when shown, indicate principal veins. A. *C. raveyi*, lamina 6 mm. wide; base of spur indicated. B. *C. cruciata*, lamina 11 mm. wide; drawn from *Siehe 362* (GH). C. *C. axilliflora*, lamina 12 mm. wide; from *Balansa 729* (US). D. *C. gombaultii*, lamina 10 mm. wide; from *Gombault 1717* (P). E. *C. stocksiana*, lamina 11 mm. wide; from *Beach 5029* (US). F. *C. stocksiana*, lamina 11 mm. wide; illustrating the form known as var. *kabuliana*. G. *C. ambigua*, lamina 15 mm. wide; from *Levine 824* (GH). H. *C. orientalis*, lamina 13 mm. wide. I. *C. regalis* subsp. *regalis*, lamina 15 mm. wide; from *Taccan* in 1926 (NY). J. *C. regalis* subsp. *divaricata*, lamina 14 mm. wide; from *Rubtzova*, Nov. 3, 1934 (CAS). K. *C. regalis* subsp. *paniculata*, lamina 13 mm. wide; from *Sintenis 4294* (US). L. *C. incana*, lamina 8 mm. wide; from *Post* at Beirut (F).

Consolida regalis S. F. Gray subsp. *paniculata* (Host) Soó var. *divaricata* (Ledeb.) Davis, Notes Bot. Gard. Edinb. **26:** 174. 1965.

Delphinium divaricatum Ledeb. var. *gilliati* Turrill, Kew Bull., 1929, according to Parsa, Fl. de l'Iran **1:** 432. 1951, but I find no such reference.

Essentially like subsp. *paniculata* in habit and flowers, the central lobe of the violet "petal" 3–4 mm. long; sepal spur 17–20 mm. long; follicle strigose.

TYPE: Near Astrachan, at mouth of the Volga, *Eichwald* (LE); seen.

DISTRIBUTION. Northern Balkans to Iran and Transcaspia, especially in the region surrounding the Caspian and on the north side of the Black Sea.

ILLUSTRATION. EICHWALD, Pl. Nov. Caspio-Cauc. **2:** *pl. 16.* 1831.

REPRESENTATIVE COLLECTIONS. **Transcaucasia:** *Hejdeman*, May 22, 1930; *Rubt-*

zova, Nov. 3, 1934; *Hohenacker*, 1834; *Koenig 66b*. **Iran:** *Miss Lindsay 1424*; *Rechinger 6678*; *Harrington 205*; *Furse & Synge 799/16*.

I have seen cultivated specimens of subsp. *divaricata* grown as *Delphinium parryi, D. paniculatum*, and *D. divaricatum*.

18. **Consolida incana** (E. D. Clarke) Munz, comb. nov. FIG. 2, L.

Delphinium incanum E. D. Clarke, Travels **2:** 451. 1812–16.
Delphinium rigidum DC. Syst. **1:** 344. 1817. Type "in Oriente," *Labillardière* (G?) not seen, but well illustrated in Delessert, Icon. Pl. **1:** *pl. 52*. 1820.
Consolida rigida Hayek, Prodr. Fl. Penins. Balcan. **1:** 315. 1924. Bornm., Beih. Bot. Centralbl. **31**(Abt. 2): 181. 1914, not valid.
Delphinium exsertum DC. Syst. **1:** 345. 1817. Based on a *Labillardière* collection which I have not seen, but the 1820 plate (Delessert, Icon. Pl. **1:** *pl. 53*) does not reveal any differences from *D. rigidum* except that it is more glabrous.

Divaricately stiff-branched from the base, 2–6 dm. tall, pubescent throughout with short stiffish hairs, some of these in the upper parts gland-tipped, some with yellow swollen bases; lower leaves long-petioled, middle cauline subsessile; blades commonly 2–3 cm. long, multifid into linear-oblong segments, more or less mucronate and ca. 1 mm. wide, pubescent; racemes lax, rather few-flowered; bracts mostly 3–5-lobed, 3–10(–25) mm. long; pedicels commonly 1–2 cm. long, spreading to more or less decurved in fruit; bracteoles 1–3 mm. long, mostly remote from the flower; flowers 12–18 mm. across; sepals dirty white to pale violet to rose, elliptic-ovate, subobtuse, narrowed toward a clawlike base, ca. 5–7 mm. long, somewhat pubescent without, especially on the upper sepal and the lower pair; spur 5–7 mm. long, pubescent; "petal" ca. 8 mm. wide, 3-lobed, pale, the middle lobe 1.5 mm. long, divided three-fourths way to the base, the lateral lobes rounded, ca. 3 mm. in diameter; stamens to 5 mm. long, the filaments glabrous, dilated below; anthers 0.6 mm. long, dark; follicle flattened, more or less reflexed, pubescent, transversely ridged, 7–10 mm. long, 3–3.5 mm. wide, the style an additional 4 mm.; seeds 1.5 mm. long, obpyramidal, dark brownish, with transverse rows of broad scales.

TYPE: The E. D. Clarke collections are at the British Museum (Natural History), but nothing of his material for this species seems to be extant. Huth (Bot. Jahrb. **20**: 365. 1895) reduced the name *Delphinium incanum* to synonymy under *D. aconiti* L. However, that is a species endemic to the Dardanelles region of Turkey, while Clarke says he found his *D. incanum* at Cana. His description seems best to fit *Consolida rigida* of that region in the opinion of Miss Dorothy Hillcoat and Dr. N. K. B. Robson of the British Museum, to both of whom I am indebted and with whom I agree. It would seem, then, that a neotype must be chosen and I propose: Migdal, Lower Galilee, June 13, 1942, *Peter H. Davis 4819* (neotype, BM; isoneotypes E, K), from the Cana region.

DISTRIBUTION. Below 1500 m. elevation; Israel and Lebanon, western Jordan.

REPRESENTATIVE SPECIMENS of *C. incana* may be cited. **Israel:** *Field & Lazar 314*; *F. T. Meyers 30.* **Lebanon:** *Ehrenberg 193*; *Blanche 348*; *Berton 222*; *Bornmüller 30.*

19. **Consolida glandulosa** (Boiss. & Huet) Bornm. Fedde, Repert. Sp. Nov. Beih. **89**: 13. 1936. FIG. 3, A.

Delphinium glandulosum Boiss. & Huet in Boiss. Diagn. II. **5**: 11. 1856.

Delphinium glandulosum vars. *lasiostemon* and *leiostemon* Boiss. Fl. Orient. **1**: 80. 1867, the former with sparsely ciliate filaments, the latter with them glabrous.

Rather freely and divaricately branched, erect, 3–6 dm. high, finely retrorse-strigulose below, short yellowish-pubescent above, many of these hairs gland-tipped, some stiff and enlarged at the base; lower leaves largely gone by anthesis, petioled, multifid; cauline leaves sessile or subsessile, commonly 2–3 cm. long, the ultimate linear lobes ca. 1.5 mm. broad, pubescent with more or less crisped hairs; racemes rather many, lax, few-flowered; bracts mostly simple, lance-linear, to 5 mm. long; pedicels divaricate, slender, 1–4 cm. long; the bracteoles 2–3 mm. long, near the middle of the pedicel; sepals oblong-spatulate to obovate, scarcely unguiculate, blue-violet with light median strip, crisp-pubescent especially along the middle, 9–10 mm. long, the lateral pair broadest, rounded at the apex, to 7 mm. wide and least hairy; others more pointed and narrower; spur strigose, ca. 2 cm. long, 3 mm. wide at base, horizontal, flexuous, slender; "petal" whitish with violet tinge at apex, ca. 17–18 mm. wide, with 2 lateral rounded lobes ca. 5 mm. wide and curved slightly upward, the median lobe ca. 3 mm. high, bifid at the tip into lobules about 1 mm. long; stamens 5–8 mm. long, abruptly broadly dilated on lower half, whitish, glabrous or nearly so; anther yellow, ca. 1 mm. long; follicle oblong, with transverse elevated lines, appressed-pubescent, 9–11 mm. long, 3.5–4 mm. wide, the style an additional 4 mm. long; seeds grayish, narrowly obpyramidal, ca. 2 mm. long, with several transverse rows of contiguous scales.

TYPE: Fields near Maimansour between Baibout and Erzerum, Turkish Armenia, at 6000 ft., Aug., 1853, *Huet du Pavillon* (G) not seen, but isotypes (BM, K, P, MO, UC) have been examined.

DISTRIBUTION. Open places, 800–1600 m., central and eastern Anatolia excluding Mesopotamia and Kurdistan.

ILLUSTRATION. DAVIS, Fl. Turkey **1**: 129. 1965.

REPRESENTATIVE SPECIMENS. **Turkey:** *Balansa 854*; *Romia 510* and *Bornmüller 1724* — all labeled var. *leiostemon. Sintenis 1286* (labeled var. *lasiostemon*). Other collections *Davis 32616, 31983, 31968, 32715, 31732, 31860*; *Bourgeau 6.*

20. **Consolida oliveriana** (DC.) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 3, B.

Delphinium oliverianum DC. Syst. **1**: 341. 1817.

Delphinium cappadocicum Boiss. Ann. Sci. Nat. II. **16:** 367. 1841. Based on *Aucher 74* (P) which I have seen.
Delphinium oliverianum DC. var. *cappadocicum* (Boiss.) Huth, Bot. Jahrb. **20:** 389. 1895.
Delphinium hispidum Boiss. Fl. Orient. **1:** 82. 1867, in synonymy.

Branched throughout, 1–5 dm. high, glabrous to pubescent with white spreading hairs above, the branches divergent, somewhat angled, often with some hairs with yellow bases; lower leaves petioled, the blades 1–3 cm. long, trifid, the petiolulate divisions multifid into acute, lance-linear lobes 1–2.5 mm. wide; upper leaves sessile, passing gradually into 3–5-lobed bracts 8–20 mm. long; flowers loosely racemose with long intervals between; pedicels mostly 1–4 cm. long, glabrous except at the summit; bracteoles linear, subopposite, 2.5–3 mm. long, with a few hairs near the summit; flowers bluish purple, almost 2 cm. in diameter; sepals at first cream, later bluish purple, loosely white-pubescent, especially on the greenish median strip, 8.5–14 mm. long, narrowed into broad clawlike bases, the upper sepal and lower pair ca. 4 mm. wide, narrowed apically, the lateral pair 5 mm. wide, rounded at the tip; spur straight, 13–17 mm. long, 2.5 mm. wide at the base, pubescent; "petal" cream with purplish tinge at the margin, 3-lobed, 15–18 mm. wide, 10–12 mm. high, the lateral lobes 4–5 mm. broad, upturned, the middle lobe ca. 3 mm. high, cleft almost to the base into 2 oblong lobules; stamens 5–8 mm. long, glabrous, somewhat dilated below; anthers yellow, ca. 0.8 mm. long; follicle appressed-pubescent, more or less compressed, 10–16 mm. long, 3–3.5 mm. wide, transversely nerved, the style an additional 2.5 mm., somewhat curved; seeds obpyramidal, ca. 1.7 mm. long, with transverse rows of scales.

TYPE: Fields between Bagdad and Vermancha, Iraq, *Olivier* (P); seen.
DISTRIBUTION. Hills and fields, 600–1400 m., Turkey, Iraq, and Iran.
ILLUSTRATIONS. DELESSERT, Icon. Pl. 1: *pl. 51.* 1820; DAVIS, Fl. Turkey 1: 129. 1965.

REPRESENTATIVE SPECIMENS. **Turkey:** *Sintenis 1187, 2732; Davis 28669, 28406, 31026; Kotschy 416* (labeled *D. hispidum*, sp. nov.); *Strauss 3.* **Iraq:** *Field & Lazar 52, 770, 741; Gillett 8305; Guest 2757, 3742; Rawi 8540.* **Iran:** *Gilliat-Smith 1734; Koelz 18202.*

For some time I separated these as two species on the basis of a spur 13 mm. long and flowers at first cream in *Consolida cappadocicum* and spur 15–20 mm. long and flowers more purplish in *C. oliveriana*, but a reexamination of the situation seems to indicate that the two are scarcely separable taxa.

21. **Consolida flava** (DC.) Schröd. Ann. K. K. Naturh. Hofmus. Wien 27: 43. 1913. FIG. 3, C.

Delphinium flavum DC. Syst. **1:** 346. 1817.
Delphinium flavum DC. var. *velutinum* DC. *loc. cit.* (pubescent throughout; bracteoles in middle of pedicel) and var. *glaucum* DC. *loc. cit.* (glabrous below; bracteoles at base of pedicel). Not typified.

Plant 1.5–4 dm. high, branched from base, densely retrorse-strigose below, more or less spreading-pubescent above; lower leaves petioled, the blades 2.5–5 cm. long, ternately divided into segments with linear lobes; cauline leaves palmately multipartite, the final divisions linear, very short; bracts entire, short-linear, 4–5 mm. long; pedicels 12–20 mm. long; bracteoles 2, minute, linear-lanceolate; racemes lax, short; sepals 4–5 mm. long, oblong-elliptical, yellow to brown or purplish; spur 4–5 mm. long, straight, bent upward; "petal" wider than long, truncate, 3-lobed, the lateral lobes semiovate, longer than broad, the short-lobulate middle lobe with crimson spots; filaments densely hirsute, 3–4 mm. long; anthers rounded, yellow; follicle cylindrical, strict, viscid-hairy, linear-oblong, attenuate at both ends, many seeded, 10–12 mm. long; style 3–4 mm. long; seeds small, angulate, with separate scales.

TYPE: "In Oriente, verosimiliter in Archipelago. *Olivier*" (P). Seen, the label reading "de Bagdad a Kermancha, Voyage d'Olivier et Bruguière en Orient"; stem very retrorse-hairy below, glandular above only.

DISTRIBUTION. Apparently below 1000 m., Iraq and, less frequently in Syria.

EXAMPLES SEEN. **Iraq:** *Rechinger 148, 9907, 19357*; *Guest 787*; *Rawi 22859, 21097, 21258, 21070, 20995, 20427*. **Syria:** Mayadine (Meyadin), *E. S. Brown*, May 26, 1946; *Post*, July 4, 1890.

22. **Consolida deserti** (Boiss.) Munz, Jour. Arnold Arb. **48**: 51. *fig. 17*. 1967. FIG. 3, D.

Delphinium deserti Boiss. Fl. Orient. **1**: 83. 1867.

Delphinium flavum DC. var. *deserti* (Boiss.) Finet & Gagnep. Bull. Soc. Bot. France **51**: 468. 1905.

Plant 5–30 cm. tall, diffusely branched from below, short viscid-hairy; leaves 5–25 mm. long, short hairy, palmately parted into oblong-linear segments, these again laciniate in the main leaves, the tips sharp; bracts 5–8 mm. long, oblong-linear; pedicels 1.5–3 cm. long; bracteoles near middle of pedicel, 3–5 mm. long; flowers small, yellow; sepals hairy, oblong, 4–6 mm. long; spur straight, 5–6 mm. long; "petal" obcordate, ca. 6 mm. wide, apparently 4-lobed, since the middle lobe is deeply divided, the outer lobes are longer, semi-ovate; "petal" with a row of brownish red spots across the base of the lobes; spur horizontal, equaling the blade, i.e., 5–6 mm. long; filaments sparsely hairy; anthers yellow, rounded, 0.5 mm. long; follicle oblong, viscid-hairy, 6–10 mm. long, 2–2.5 mm. wide, the beak slender, ca. 2 mm. long; seeds oblong, with densely imbricate scales about the cupuliform center.

TYPE: *Bové 131*, from desert between Suez and Gaza, July 1832; this number seen (K, P). It is spreading-hairy throughout on both those sheets. At GH are two *Bové* specimens of July, 1832, from between Suez and Gaza: *131* is virgate, few-branched, ca. 3.5 dm. tall, strigulose and with a spur ca. 1 cm. long. It bears only one flower which seems to have the 2 lower petals unguiculate and with round limb. It is *Delphinium peregrinum* L. There is also at GH a sheet *130*, much branched, spreading pubescent, spur

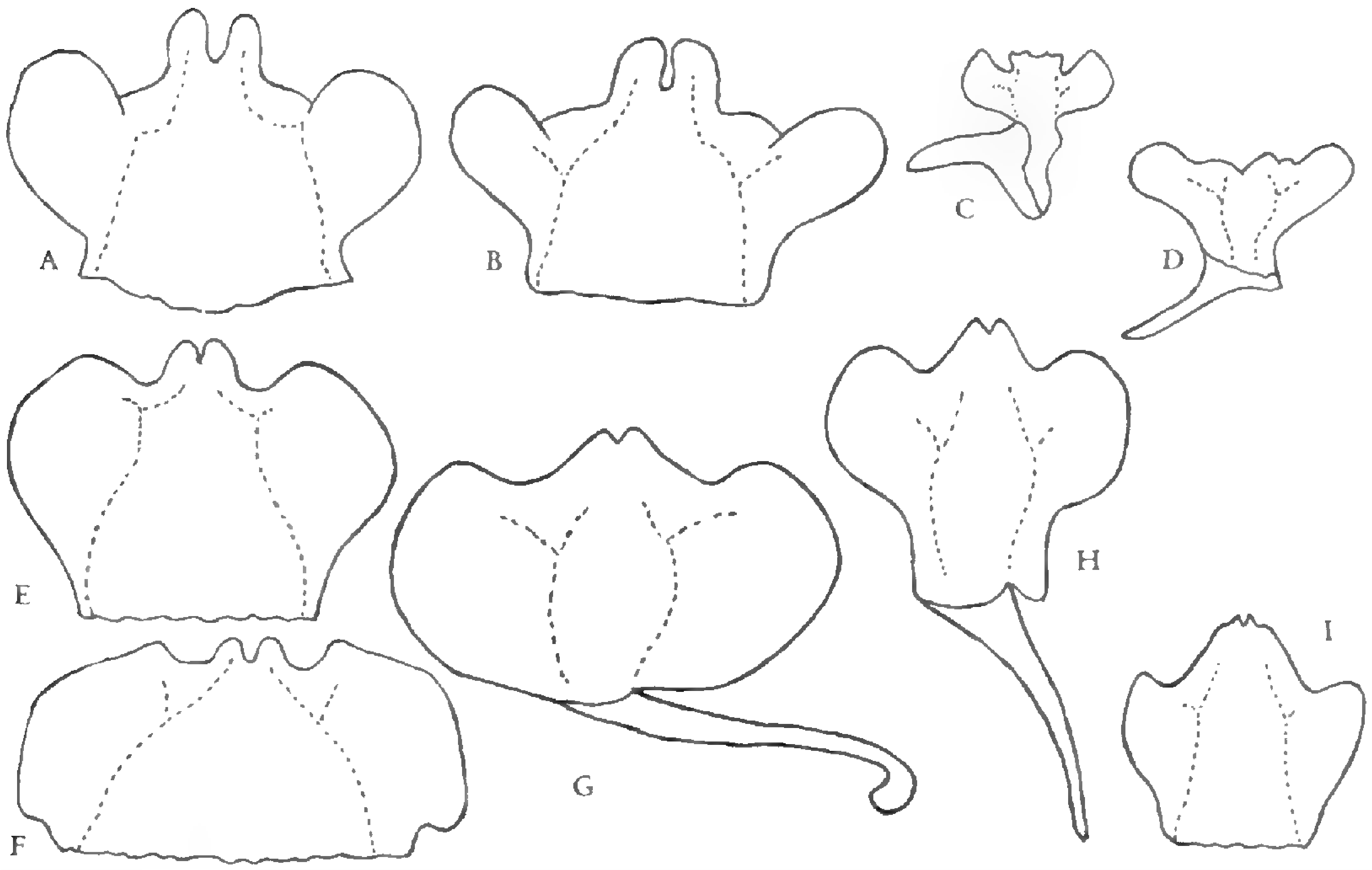

Figure 3. **Consolida** species. Drawings show lamina of "petal" of 3-lobed type, with lateral lobes projecting toward the tip of the "petal". A. *C. glandulosa*, lamina 18 mm. wide; drawn from *Huet* in 1853 (US). B. *C. oliveriana*, lamina 16 mm. wide; from *Strauss* in 1896 (US). C. *C. flava*, lamina 6 mm. wide; from *Olivier & Brugière* (P). D. *C. deserti*, lamina 8 mm. wide; from *Uvarov* in 1932 (BM). E. *C. leptocarpa*, lamina 15 mm. wide; from *Sintenis 283* (GH). F. *C. persica*, lamina 17 mm. wide; from *Herzfeld 4* (F). G. *C. deserti-syriaci*, lamina 18 mm. wide; drawn from *"V.C.R."*, from Jordan (K). H. *C. cornuta*, lamina 11 mm. wide; from *Davis 30855* (BM). I. *C. rugulosa*, lamina 8 mm. wide; from *Sintenis 143* (US).

4 mm. long. At K no. *130* is strigulose, with 1–3 carpels. Apparently labels have been exchanged at GH and their *Bové 130* should be *131*.

Distribution. Arabian Desert west of the Gulf of Suez and Red Sea to Iraq.

Representative specimens. **Egypt:** Sinai Desert, *M. F. White*, May, 1916. **Israel:** *Meyers & Dinsmore 7238*; *P. H. Davis*, 1942. **Iraq:** *Aucher 64*; *Uvarov*, May 26, 1932.

This species is near to *C. flava* in its low stature and yellowish flowers, but differs in its spreading pubescence and glandulosity.

23. **Consolida leptocarpa** Nevski, Acta Inst. Bot. Acad. Sci. URSS, **4**: 296. 1937. Fig. 3, E.

Delphinium leptocarpum Nevski in Komarov, Fl. U.S.S.R. **7**: 110. 1937.

Plant 1–6 dm. high, with several erect or upcurved branches from above the base and below the middle, strigulose below, more spreading-pubescent and more or less glandular above, leafy throughout, the lower leaves laciniate into segments 2–2.5 mm. wide; main cauline leaves oblanceolate, entire, 2–4 cm. long, 5–7 mm. wide; lower leaves petiolate, cauline gradually reduced upward, all somewhat pubescent; flowers subsessile, solitary in all but the lower leaf-axils; bracts 1–1.5 cm. long, trifid with obtuse, lance-oblong, lateral segments; pedicels 1–2 mm. long; bracteoles subulate; flowers pale cream-pink, the sepals not clawed, 9–11 mm. long, the upper lance-ovate, pubescent, the spur 22–24 mm. long, 3.5 mm. wide at the base, erect, flexuous; lateral sepals ovate, 5–6 mm. wide, hairy along the midrib; lower sepals lanceolate, more hairy, 3 mm. wide; "petal" trilobed, ca. 15 mm. wide, 10 mm. high, the terminal lobe ca. 2 mm. long, slightly divided at apex; lateral lobes round-truncate; stamens glabrous, 6–8 mm. long, dilated below; anthers yellow, 1 mm. long; follicle strict, scarcely curved above, ca. 2 mm. wide, cylindric, rugulose-veined, 17–25 mm. long, pubescent, the style an additional 3–4 mm.; upper follicles longer than subtending bracts; seeds 1.5 mm. long, obpyramidal, with pale overlapping scales.

TYPE: "Ad declivia argillosa gypsacea prope trajectum Ak-Davan, June 21, no. 364", collector's name not given, possibly Nevski. At K was seen a specimen labeled "Plantae montium Kuhitang (Turcomania orientalis)," again without collector, but treated as type material. In his description in Fl. U.S.S.R. 7: 110, Nevski cites as representative of the species: *Sintenis 283*, which I have seen (BH, BM, GH, MO).

DISTRIBUTION. Turkestan, northern Iran.

ILLUSTRATION. KOMAROV, Fl. U.S.S.R. 7: 107. *pl. 8, fig. 2.* 1937.

REPRESENTATIVE SPECIMENS. **Transcaspia:** *Sintenis 283*; *Michelson*, 1911. **Turkestan:** *Fedtschenko* at Tashkent; *Regel*, May 1882 at Samarkand; *Gontscharow, Grigoriev & Nikiton 114* near Bukhara [Bochara]. **Iran:** *Donaldson 48.*

Formerly treated as *Consolida persica* and *C. rugulosa,* but with longer sepals than the former and broader "petal" than the latter.

24. **Consolida persica** (Boiss.) Schröd. Abh. Zool.-Bot. Ges. Wien 4(5): 17, 162. 1909; Grossheim, Fl. Kavkaza **2**: 101. 1930.

FIG. 3, F.

Delphinium persicum Boiss. Ann. Sci. Nat. II. **16**: 362. 1841.

Plant 1–3.5 dm. high, widely and divaricately branched, ashy-strigulose throughout, also with some spreading and glandular hairs, especially in the upper parts; leaves small, scattered, strigulose or pubescent, the blades mostly scarcely 1 cm. long, parted into narrow fleshy segments; lower leaves petioled, upper reduced and sessile; flowers largely in upper half of plant; bracts trifid or the uppermost entire, pubescent, commonly 2–8 mm. long; pedicels 2–4 mm. long; the bracteoles subulate, to ca. 3 mm. long; sepals pinkish or whitish, or with a blue tinge, with greenish midribs, not clawed, 6–8 mm. long, the upper sepal lance-ovate, with steeply ascending spur 20–25 mm. long, 4 mm. wide at base, pubescent; lateral sepals oblong-obovate, 3.5 mm. wide, obtuse, pubescent on midrib; lower sepals broadly lance-oblong, 4 mm. wide, obtuse, rather generally pubescent; "petal" 3-lobed, ca. 17 mm. wide, the terminal lobe ca. 1 mm. high, with 2 short oblong lobules, the lateral main lobes rounded, reaching as high as the terminal one; stamens 6–7 mm. long, glabrous; anthers yellow, 0.8 mm. long; follicle on a pedicel to 5 mm. long, hairy, slightly compressed. ca. 10 mm. long, 2.5 mm. wide, not strongly reticulate, the beak an additional 3 mm. long.

TYPE: *Aucher 78,* Persia circa Amadan; probably at Paris. No. 78 seen (K, P).

DISTRIBUTION. At 1000–2000 m., Armenia to Turkestan, Iran, and Afghanistan.

REPRESENTATIVE COLLECTIONS. **Turkey:** *Demiriz 3412* (fide Davis). **Russian Armenia:** *Szovitz 420.* **Turkestan:** Herb. Fl. Ross. *no. 2751*; *Regel,* May, 1882. **Iraq:** *Field & Lazar 532*; *Haines W 1543*; *Haussknecht,* 1867; *Gillett 11207.* **Iran:** *Kotschy 442*; *Herzfeld 4*; *Lindsay 268, 329*; *Furse & Synge 625.* **Afghanistan:** *Clifford 14.* **West Pakistan:** *Crookshank 153.*

25. **Consolida deserti-syriaci** (Zohary) Munz, comb. nov. FIG. 3, G.

Delphinium deserti-syriaci Zohary, Palest. Jour. Bot. Jerusalem Ser. **2:** 155 1941.

Stem solitary, erect, branched, ca. 15 cm. tall, with spreading hairs and dense appressed short ones; cauline leaves petioled, ternate or bifid, the lobes further divided into linear segments 1–1.5 mm. wide and 10 mm. long, pubescent; bracts simple, minute, oblong, glandular-pubescent; pedicels 16–18 mm. long, glandular-pubescent, spreading; bracteoles spreading, oblong, 2 mm. long; flowers remote, 23 mm. long; sepals whitish, the upper ca. 8 mm. long, obtuse, the spur horizontal, narrow, ca. 18 mm. long, saccate-uncinate at apex, white to pink, puberulent; lower sepals oblong-lanceolate, acutish, green, apically scarious, ca. 8 mm. long; "petal" white, ca. 2 cm. wide when spread open, 10 mm. high; lateral lobes broad, rounded, separated from the upper by a rounded sinus 2.5–3 mm. deep; stamens 5–6 mm. long, whitish in dilated lower half, yellowish above, glabrous; anthers yellow, 0.8 mm. long; follicle ca. 17 mm. long, 3 mm. wide, canescent-strigulose and with spreading gland-based hairs. beak 4 mm. long.

TYPE: Between Azra and Damascus, western Syria, *Zohary 1931.* The type was destroyed during the war in Israel and all that remains is a slide with the flower parts spread out. Through the kindness of Professor Naomi Feinbrun of the Hebrew University at Jerusalem I have been sent a photograph of that slide. So far as I can tell, it and the original description agree with a collection from Jordan, without locality, made by "*V. C. R.*", Feb., 1954, Kew no. 47 (K).

26. **Consolida cornuta** (Hossain & Davis) Davis, Notes Bot. Gard. Edinb. **26**: 174. 1965. FIG. 3, H.

Delphinium cornutum Hossain & Davis, Notes Bot. Gard. Edinb. **22:** 424. 1958.

Erect, 1.5–4 dm. tall, sparsely branched, strigose below, with spreading yellowish pubescence above; leaves puberulent, the lower linear-multifid, with blades 12–15 mm. long and petioles 7–9 mm. long; upper blades 20–25 mm. long, the ultimate divisions linear, acute; raceme lax; pedicels 12–25 mm. long, densely pubescent; bracts linear, acute, the lower 9–12 mm. long and sometimes parted, the upper shorter, entire; bracteoles 2–3 mm. long, remote from the flowers; flowers bicolored when dry; sepals bluish, 8–10 mm. long, pubescent and greenish without along the median nerve, the lateral and lower alike, 8–9 mm. long, 4–4.5 mm. wide, ovate, obtuse; spur pubescent, 10–13 mm. long, with slightly decurved tip; "petal" 3-lobed, 11–12 mm. wide, 9–10 mm. long, the median lobe longer than the lateral, deeply emarginate at tip, the lateral lobes semilunate, 5–6 mm. long, rounded and wide at the base, attenuate into an upturned hornlike tip 2–2.5 mm. wide; filaments slightly pubescent, dilated below; anthers purplish-brown; follicle erect, densely strigose, obcompressed, semiovate-oblong, 9–10 mm. long, 3.5–4 mm. wide, with the style an additional 2 mm. long.

TYPE: Turkish Armenia, *Calvert & Zohrab* (holotype E).
DISTRIBUTION. Fields at 1800–1900 m., northern Armenia of Turkey.
ILLUSTRATION. DAVIS, Fl. Turkey **1**: 129. 1965.

SPECIMEN SEEN. **Erzurum:** west of Ilica, *Davis 30855*.

27. **Consolida rugulosa** (Boiss.) Schröd. Ann. K. K. Naturh. Hofmus. Wien **27**: 43. 1913. FIG. 3, I.

Delphinium rugulosum Boiss. Ann. Sci. Nat. II. **16**: 361. 1841.
Delphinium aucheri Boiss. *loc. cit.* 362. Based on *Aucher 4030* from south Persia. I would interpret the specimen at Paris to be the type. I have seen it.
Delphinium persicum Boiss. var. *aucheri* (Boiss.) Boiss. Fl. Orient. **1**: 77. 1867.
Delphinium paradoxum Bunge, Arbeit. Nat. Ver. Riga **1**: 124. 1847. See discussion below.
Consolida paradoxa (Bunge) Nevski in Komarov, Fl. U.S.S.R. **7**: 113. 1937.

Simple or with simple branches from the base, erect, largely 1–3 dm. high, with some appressed hairs and numerous spreading ones, especially in the upper part (many hairs glandular at the base); stems rather equally leafy throughout; lower leaves petioled, the cauline largely subsessile and to 4 cm. long or the uppermost sessile, all more or less fleshy, 4–3-partite, then again divided into narrow segments more or less dilated upward and to 2.5 (–4.5) mm. wide, subglabrous to somewhat pubescent, acute; flowers solitary in most leaf axils, almost sessile or the pedicels to 2 mm. long; bracteoles 2, entire, 2–3 mm. long; sepals pinkish or greenish white, 7–10 mm. long, the spur more or less flexuous, ascending to erect, pubescent, slender, 17–18 mm. long (rarely lacking); lateral sepals narrowly oblong-ovate, obtuse, scarcely clawed, 3.5–4 mm. wide, pubescent only along the median strip; lower sepals linear-oblong, ca. 2 mm. wide, rather generally pubescent; "petal" 3-lobed, ca. 9 mm. long, the broad more or less blunt-deltoid terminal lobe more or less erose, the rounded-deltoid lateral lobes almost straight on the upper edge, obtuse, slightly rounded on the outer edges; stamens 6–9 mm. long, the filaments glabrous; anthers yellow, ca. 1 mm. long; follicle erect, shorter than the bracts, subcompressed, hairy, reticulate-veined, 10–15 mm. long, ca. 3 mm. wide, the beak an additional 3 mm.; seeds brownish, obovoid, somewhat angled, ca. 1.6 mm. long, with short pale scales not in very regular transverse rows.

TYPE: *Aucher 4028*, from Lake Urmiah (Ourmiah), Iran; I would suppose the holotype is the specimen at P, isotypes BM, K. All seen.

DISTRIBUTION. At 600–1400 m., Transcaucasia and Transcaspia to northern Iran and to Afghanistan.

ILLUSTRATION. KOMAROV, Fl. U.S.S.R. 7: *pl. 8, fig. 4*. 1937.

REPRESENTATIVE SPECIMENS. **Transcaspia:** *Sintenis 143, 283*; *Litwinow 440*. **Turkestan:** *Sovetkina 131*; *Kusckokewicz*. **Iran:** *Rechinger 1011, 789*; *Merton 3884*. **West Pakistan:** *Lace 3338*. **Afghanistan:** *Aitchison 310*.

In genera like *Consolida, Delphinium*, and *Aquilegia* spurlessness occurs apparently as a mutation, not only in cultivation, but also in nature. For example, in *Aquilegia*, refer to Munz, Gentes Herb. 7: 134. 1946, for its appearance in spurless garden plants of *A. caerulea* James. Sometimes in nature spurless forms have been given varietal status, as *A. micrantha* var. *mancosana* Eastw. In *Delphinium* I have found the spurless condition in a number of specimens, as in a collection by *H. B. Morse* (NY) from Lungchow, Kwangsi Prov., China and belonging to *D. anthriscifolium* Hance. It lacks both spur and petals. From Africa I have seen a collection of *D. macrocentron* Oliver, *Bally 1205* (K), with 4 sepals, 2 upper petals without spurs, but with well developed stamens and carpels. In other cases I have noticed plants with both normal flowers and abnormal, sometimes on separate branches. Since *Consolida paradoxa* resembles *C. rugulosa* in its vegetative characters, so far as I can see, I agree with the possibility expressed before (Huth, Bot. Jahrb. **20**: 373. 1895) that it is simply a spurless form of the latter. Its sepals are a trifle smaller; it lacks petals altogether, but stamens and follicle and seeds are well developed. The type number is *Lehmann 36* from Turkestan. I have seen specimens (GH, K, P, LE). Another collection, from northern Iran is *Polak*, 1882 (K).

28. **Consolida halophila** (Huth) Munz, comb. nov. FIG. 4. A.

Delphinium halophilum Huth, Bot. Jahrb. **20**: 487. 1895. New name for *D. freynii* Huth.

Delphinium freynii Huth, *loc. cit.* 372. April, 1895; not Conrath, Bull. Herb. Boiss. **3**: 36. Jan. 1895.

Delphinium laxiflorum Freyn, Denkschr. Akad. Wien Math. Naturw. **51**: 293. 1886; not DC. 1817.

? *Delphinium freynii* Huth var. *hirtum* Freyn ex Huth, *loc. cit.* 372. No specimens cited.

Stem flexuous, simple or openly branched below, 6–45 cm. tall, ashy-strigose, leafy throughout; lower leaves trifid, the parts petiolulate and divided into narrow, obtuse, tripartite lobes; main cauline leaves 1–3 cm. long, the lobes to 2.5 mm. wide; branches floriferous from near the base, more or less glandular-pubescent in the upper parts; bracts sessile, 3-parted, ca. as long as the flowers, the lobes subacute; pedicels to ca. 5 mm. long; bracteoles lanceolate, 2–3 mm. long; sepals elliptic, glabrescent, pale violet-pink to creamy-yellow, 2 mm. wide, obscurely dotted, 5–7 mm. long; spur directed upward, 15–24 mm. long, 5–6 mm. wide at base, obtuse; "petal" 3-lobed, ca. 8 mm. wide, 10 mm. long, the middle lobe emarginate, slightly longer and much narrower than the lateral lobes which are directed slightly forward; follicle erect, 10–13 mm. long, straight, cylindric, veined, tomentose and spreading-hairy, the beak an additional 2–3 mm.; seeds scaly, transversely angular, 1.5 mm. long, 1 mm. thick.

TYPE: N. Iran, Gussediche on the Teheran road, *Pichler* 1882; holotype, Barbey Herbarium (G) not seen; isotype (K) seen.

DISTRIBUTION. At about 1600–2000 m., northern Iran.

EXAMPLES SEEN. *Furse 3301*; *Bunge*, March 1859; *Gilliat-Smith 1724, 1914*; *L. S. Grown 1923.*

29. **Consolida trigonelloides** (Boiss.) Munz, comb. nov. FIG. 4, B.

Delphinium trigonelloides Boiss. Ann. Sci. Nat. II. **16:** 366. 1841.

Bushy, 3–15 cm. tall, branched at base, gray with short spreading pubescence; leaves canescent-pubescent, the cauline with 2–3 linear or linear-spatulate lobes 6–12 mm. long, obtuse or rarely bifid; upper leaves entire, oblong, 4–6 mm. long; bracts oblong, entire, 5 mm. long, 1–1.5 mm. wide; pedicels at tips of branches, remote, 10–12 mm. long at anthesis, 25–30 mm. in fruit; bracteoles oblong, opposite, entire, 4–5 mm. long; flowers bluish; sepals ca. 8 mm. long, oblong-spatulate, obtuse, the upper acute, with a straight pubescent attenuate spur 16 mm. long; "petal" obtusely 3-lobed, the middle lobe subtruncate, slightly 3–5-lobulate, smaller than the short rounded lateral lobes; filaments glabrous; follicle cylindric, appressed-canescent, incurved, 10–12 mm. long, 3 mm. thick, the beak ca. 1.5 mm. long; seeds ca. 1.6 mm. long, pyramido-pentagonal, basally truncate, with transverse white scales in rather irregular arrangement.

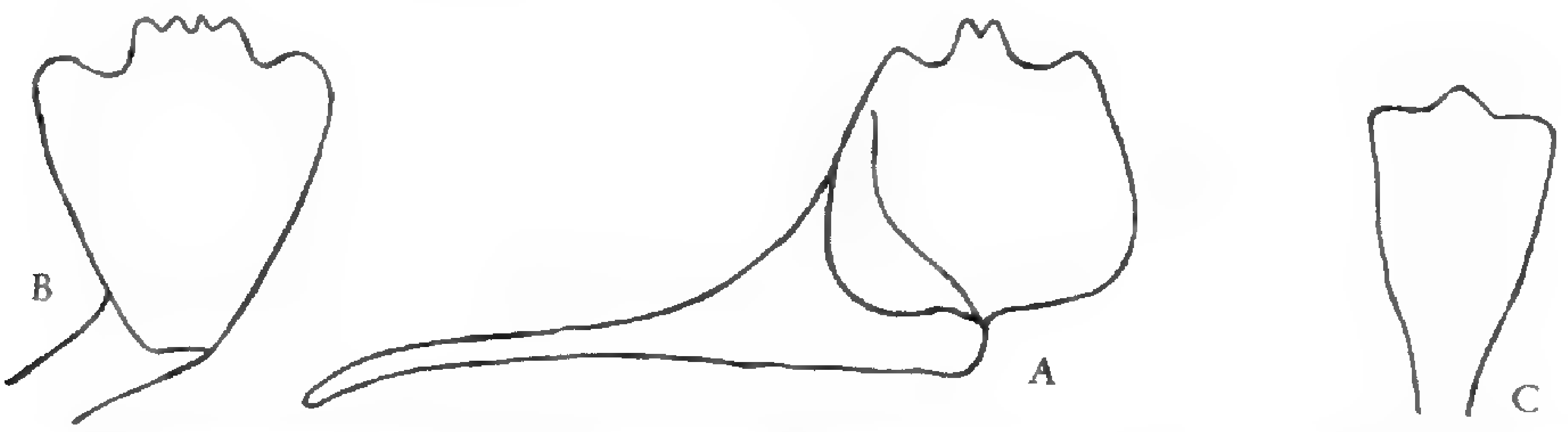

FIGURE 4. **Consolida** species. Drawings show lamina of "petal" of 3-lobed type (and in one case the spur) with lateral lobes greatly reduced. A. *C. halophila*, lamina 8 mm. wide; drawn from *Pichler* in 1882 (K). B. *C. trigonelloides*, lamina 8 mm. wide; from *Aucher 4033* (P). C. *C. linarioides*, lamina 5 mm. wide; from *Aucher 4029* (P).

TYPE: Southern Iran, *Aucher 4033* presumably P, isotypes BM, G, K. All these seen. There are no flowers on the BM and K specimens.

No other material seen.

30. **Consolida linarioides** (Boiss.) Munz, comb. nov. FIG. 4, C.

Delphinium linarioides Boiss. Ann. Sci. Nat. II. **16:** 368. 1841.

Branched at the base, with spreading soft white pubescence, to 1.5 dm. tall; lower petioles ca. 1 cm. long, the laminae 3–4-parted, the segments with linear-obtuse lobes 0.5–1.5 cm. long; upper leaves sessile, subentire or with 2 lateral lobes, 1–1.2 cm. long; racemes laxly 3–4-flowered; bracts broadly linear, 8–10 mm. long, 1.5–2 mm. wide; pedicels 1–2.5 cm. long; bracteoles 6–8 mm. long, linear, at base of flower; sepals violet, oblong, obtuse; upper sepal acute, 8 mm. long; spur subincurved, ca. 4 mm. long; "petal" scarcely longer than the sepals, tricrenate at apex, the 3 lobules rounded, equal; filaments glabrous, dilated at base, ca. 5 mm. long; anthers yellow, ca. 1 mm. long; follicle densely white-strigose.

TYPE: Ispahan, Iran, *Aucher 4029*; holotype (P) seen; isotype (K) seen. Known only from the type collection; at least to me. There is some question about how normal the plants of this collection are. The specimen at Kew seems to have one normal flower with oblong sepal and "petal" ca. 1 cm. long and with 3 minute lobes as in my figure, but the other flowers have an abortive spur (2 mm. long, crinkled) and the upper sepal more or less petal-like, but no "petal" developed. Obviously the species is near *C. trigonelloides*, but with quite a different "petal" and with the sepal spur shorter than the sepal-blade instead of twice as long.

31. **Consolida schlagintweitii** (Huth) Munz, comb. nov. FIG. 5, A.

Delphinium schlagintweitii Huth, Bull. Herb. Boiss. **1:** 329. 1893.

Plant glabrescent below, pubescent above with some hairs having swollen yellow bases; stem slender, branched, apparently several dm. tall; cauline leaves largely 2–5 cm. long, subsessile, multipartite into linear lobes 0.5–1.5 mm. wide, 1–3 cm. long, more or less strigulose; lower bracts pluripartite, upper entire, subulate, ca. 5 mm. long; racemes rather few flowered, rather dense, the pubescence short, stiffish, much of it more or less retrorse; pedicels suberect, 1–1.5 cm. long at anthesis, to ca. 5 cm. in fruit; bracteoles 2.5–3 mm. long, almost or quite touching the flower; spur straightish, 6–7 mm. long, 1.5 mm. thick at the base, somewhat strigose; sepals 6–7 mm. long, deep violet, oblong to ovate, definitely unguiculate, the lateral pair subglabrous except for the ciliate claw, ovate; lower pair narrowed, more generally pubescent, rather pointed; "petal" 3-lobed, the middle lobe ca. 3 mm. high, with 2 lobules, the lateral lobes spreading, the whole "petal" ca. 11 mm. wide; follicle oblong, more or less flattened, densely hairy, ca. 1 cm. long, 3.5 mm. wide; style ca. 1 mm. long.

TYPE: Kashmir, prov. Balti, near Skárdo, at 2300–2500 m., *Schlagintweit 821*, 1856, William Barbey Herbarium (G); isotypes (BM, US) seen.

This is the only material I have seen of this species which is remote in its eastern range for the genus *Consolida*. It somewhat resembles *C. orientalis*, but is much smaller-flowered.

32. **Consolida phrygia** (Boiss.) Soó, Österr. Bot. Zeitschr. **71**: 245. 1922. FIG. 5, B.

Delphinium phrygium Boiss. Ann. Sci. Nat. II. **16**: 363. 1841.
Delphinium ajacis L. var. *phrygium* (Boiss.) Finet & Gagnep. Bull. Soc. Bot. France **51**: 467. 1904.
Consolida orientalis (Gay) Schröd. ssp. *phrygia* (Boiss.) Chater, Feddes Repert. **68**: 193. 1963.

Plant 2–5 dm. tall, simple or few branched above, with short spreading, often gland-tipped hairs and rather densely leafy at least in the lower half; basal leaves withered at time of anthesis, with petioles to ca. 2 cm. long, blades 1–1.5 cm. across, multifid into linear, pubescent, mucronate segments ca. 0.5 mm. wide; cauline leaves rather crowded, mostly sessile, with numerous narrow linear segments; racemes 2–10-flowered, to ca. 1 dm. long in fruit, many of the hairs papillose at the base; pedicels mostly 5–7 mm. long, erect; bracts largely linear, entire, 3–6 mm. long, the basal sometimes divided; bracteoles linear, 1–2.5 mm. long, near the base of the flower; flowers violet, rose or white, 10–13 mm. in diameter; sepals somewhat unguiculate at the base, ovate, acutish, pubescent at least along a greenish median strip, ca. 6–9 mm. long; spur straight, pubescent, horizontal, 9–10 mm. long, slender, ca. 1.5 mm. wide at base; "petal" 3-lobed, the central lobes ca. 6 mm. high, rather deeply divided with a broad sinus, lateral lobes rounded-reflexed; spur ca. 9 mm. long; stamens ca. 5 mm. long, the filaments rather abruptly dilated, glabrous; follicles appressed-pubescent, cylindric, 10–18 mm. long, ca. 4 mm. thick, subterete, the style 2 mm. long; seeds with transverse rows of connate scales.

TYPE: Phrygia (Turkey), *Aucher 71*, not seen.

DISTRIBUTION. Fields in Phrygia and Anatolia, as well as Cyprus, Rhodes.

REPRESENTATIVE SPECIMENS. **Turkey:** *Pinard*, 1843; *Sintenis 843*.

33. **Consolida pusilla** (Labill.) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 5, C.

Delphinium pusillum Labill. Icon. Pl. Syr. Rar. Dec. IV. **5**: *pl. 2, fig. 2*. 1812.
Delphinium pygmaeum Poir. in Lam. Encycl. Bot. Suppl. **2**: 458. 1812.

Plant 2–8 cm. high, densely soft-pubescent, canescent, simple or divaricately short-branched only near the top; leaves small, to 15 mm. long, 3–5-parted, the lobes lance-linear, obtuse; lower leaves short-petioled; bracts 3-parted, ca. 6 mm. long; pedicels ca. 1 cm. long; racemes dense, with 3–5 violet flowers; bracteoles linear, 6–7 mm. long, extending to above the base of the calyx; sepals elliptic-oblong, obtuse, 8–9 mm. long, the lateral pair obtuse, 2 mm. wide, soft-hairy especially along the midrib;

upper sepals 9–10 mm. long, 4 mm. wide, the spur 5–8 mm. long, horizontal, pubescent, curved; lower sepals 3 mm. wide; "petal" rhombic, ca. 9 mm. wide and high, the middle lobe ca. 3 mm. long, subtruncate and erose at tip, the lateral pair ca. 3 mm. wide; stamens 3–4 mm. long, the filaments broadly winged at base, glabrous; anthers yellow, 0.7 mm. long; follicle oblong, compressed, strigose, 13 mm. long, 2.5 mm. wide, the beak 2 mm. long.

TYPE: Near Damascus at base of Mt. Djebel Cher; an isotype seen (K).

ILLUSTRATION. LABILLARDIÈRE, Icon. Pl. Syr. Rar. Dec. IV. **5**: *pl. 2, f. 2*. 1812.

DISTRIBUTION. Rocky places, Lebanon and Syria to Jordan.

REPRESENTATIVE MATERIAL. **Syria:** *Post*, May 1, 1900. **Lebanon:** *Peyron 1453*. **Jordan:** *Kotschy 737*; *Boissier*, June 1846.

34. **Consolida camptocarpa** (Fisch. & Meyer ex Ledeb.) Nevski in Komarov, Fl. U.S.S.R. **7**: 106. 1937. FIG. 5, D, E.

Delphinium camptocarpum Fisch. & Meyer ex Ledeb. Fl. Ross. **1**: 58. 1842.

Delphinium camptocarpum Fisch. & Meyer var. *dasycarpum* Ledeb. *loc. cit.* Not typified. A collection by *A. Regel* from Turkestan, prope pudicum Rafotak, in 1884, was sent from Leningrad as representing this taxon; (BM, US) seen.

Delphinium camptocarpum Fisch. & Meyer var. *leiocarpum* Ledeb. *loc. cit.* Not typified. A specimen by *A. Regel* (P), collected much later, seems to be this.

Delphinium camptocarpum Fisch. & Meyer *β songoricum* Kar. & Kir., Bull. Soc. Nat. Mosc. **15**: 136. 1842. A collection "in arenosis Songoriae ad fl. Lepsa," (se. of Lake Barkasch), *Karelin & Kiriloff 1165* (NY, K, P) seems to be the original one.

Delphinium songoricum (Kar. & Kir.) Nevski in Komarov, Fl. U.S.S.R. **7**: 109. 1937. *Consolida songorica* (Kar. & Kir.) Nevski in the same reference.

Delphinium camptocarpum Fisch. & Meyer var. *turkomanicum* Bunge, Arbeit. Naturforsch. Ver. Riga **1**: 125. 1848. Type uncertain, may have been the Karelin collection. But a specimen at Kew from the Bunge Herbarium is labeled as this var. and surely shows what Bunge had in mind.

Delphinium camptocarpum Fisch. & Meyer var. *robustum* Bunge, *loc. cit.* 126. Referred to synonymy by Nevski, Fl. U.S.S.R. **7**: 109. 1937.

Delphinium camptocarpum Fisch. & Meyer var. *brevipedunculatum* Boiss. Fl. Orient. **1**: 77. 1867. Type collected in northern Iran, near Schahrud, *Bunge* (G); not seen.

Delphinium stocksianum Boiss. var. *obovatum* Huth, Bot. Jahrb. **20**: 373. 1895. Based on *Aitchison* from Afghanistan; may belong here.

Delphinium persicum Boiss. var. *regelianum* Huth, *op. cit.* 370. Referred here by Nevski in Komarov, Fl. U.S.S.R. **7**: 109. 1937. Based on a specimen by *Regel* from Bochara (Bukhara); not seen.

Plant 2–6 dm. tall, erect, mostly with few ascending branches from above the base, with short retrorse-appressed or spreading hairs, not very densely leafy; leaves largely in lower half of plant, mostly petioled, trifid, the segments with 2–3 parts, each of which has 2–3 large coarse terminal subacute teeth; blades mostly 1–2 cm. long, strigose, the lower petioles longer than the blades, the upper leaves passing into subsessile bracts, the uppermost 3–5 mm. long; flowers ca. 5–15 in terminal racemes; pedicels 2–20 mm. long, even longer in fruit; bracteoles setaceous, minute; flowers blue or blue-violet, ca. 17–19 mm. in diameter; upper sepal lanceolate, pubescent, 10–11 mm. long, 2.5–3.5 mm. wide, the spur ca. 18 mm. long, suberect, 4–4.5 mm. wide at the base; lateral sepals rhombic-ovate, 10 mm. long, not unguiculate; lower sepals asymmetrical, ca. 10 mm. by 5 mm., rather well covered with pubescence; "petal" 3-lobed, 10–14 mm. wide when expanded, 8–12 mm. high, the lobes broadly triangular, obtuse, the terminal ca. 3 mm. high, shallowly 2-lobed at apex, the two lateral ca. 4 mm. long, spreading; stamens 6–8 mm. long, glabrous; anthers yellow, 1 mm. long; follicle declined by the recurved tip of the pedicel, curved, more or less pubescent, reticulate-veined, compressed, ca. 10 mm. by 2–3 mm., the style an additional 2–3 mm.

TYPE: Turcomania: "ad latus orientale maris caspii," *Karelin* (LE); seen.

DISTRIBUTION. Transcaspia and Turkestan to Afghanistan, at 1000 m. or thereabouts.

ILLUSTRATIONS. NEVSKI in Komarov, Fl. U.S.S.R. 7: *pl. 8, fig. 1a, 1b, 1c.* 1937.

REPRESENTATIVE COLLECTIONS. **Transcaspia:** *Dimo 130*; *Litwinow 4380*; *Sintenis 1301*. **Turkestan:** *Androsow 2218*; *Schischkin*, June 4, 1913. **Afghanistan:** *Aitchison 1002*.

The recognition of *C. songorica* as distinct does not seem to hold. The chief difference seems to be in the more spreading pubescence and perhaps smaller flowers. It occupies the same region as *C. camptocarpa* and there is great variability in amount and mixture of appressed and spreading hairs.

At Kew is a set of five sheets "Afghanistan, Griffith", some with "Herb. Lehmann, 1852," some with no. 1377 and 1377a written on them; all are labeled with a name apparently never published. One sheet has "No. 42". The plants seem to be unusually robust *camptocarpa*, one with sort of a woody base (long tap root), branching new shoots with broken leaves. The blades are 3–4 cm. long. They are in a type cover, with the unpublished name on the outer folder. More material may reveal a distinct taxon.

35. **Consolida oligantha** (Boiss.) Schröd. Ann. K. K. Naturh. Hofmus. Wien **27**: 43. 1913. FIG. 5, F.

Delphinium oliganthum Boiss. Fl. Orient. **1**: 80. 1867.

Consolida tomentosa (Aucher) Schröd. subsp. *oligantha* (Boiss.) Davis, Notes Bot. Gard. Edinb. **26**: 175. 1965.

Delphinium oliganthum Boiss. var. *brachycentrum* Huth, Bot. Jahrb. **20**: 381. 1895. Not typified, but the shortness of the spur would seem to place it here.

Divaricately branched from the base, 1.5–3 dm. high, more or less densely canescent-strigose; lower leaves 1.5–3 cm. long, ternate then divided into mostly linear lobes scarcely 1 mm. broad; upper leaves less divided; racemes dense, mostly 4–5-flowered; lower bracts trisect, 5–15 mm. long, the upper entire, linear; pedicels 1–3 cm. long; bracteoles 2, linear, 8–14 mm. long, exceeding the base of the flowers; sepals violet or blue, 10–12 mm. long, oblong-elliptical, the upper pointed, pubescent, the spur ca. 6 mm. long, pubescent, bent upward; lateral sepals ca. 12 mm. by 4 mm., obtusish, pubescent on midrib and part of upper edge, narrowed to a long lower part; lower sepals narrower, more pointed and pubescent; "petal" ca. 15 mm. long, purple-striped, rhombic, the terminal lobe triangular, the lateral lobes triangular, spreading; follicle oblong-linear, pendent, strigose, 10–14 mm. long, ca. 2.5 mm. wide, subterete, with some transverse veining, the style an additional 2 mm.; seeds about 1 mm. long, subglobose, with 4–5 rows of more or less contiguous scales.

LECTOTYPE: "Ad segetes prope Aintab, Syriae Bor." *Haussknecht* (G, not seen; K, P, isolectotypes, seen). The Kew specimen is a mixture of *Consolida oligantha* and *C. hellespontica*. Aintab is, of course, now in Turkey.

DISTRIBUTION. Grain and fallow fields, 600–1000 m., Mesopotamian region of Turkey and northern Iraq.

ILLUSTRATION. HOSSAIN & DAVIS, Notes Bot. Gard. Edinb. **22**: 419. *fig. 2, C.* 1958.

REPRESENTATIVE COLLECTIONS. **Turkey:** *Davis 22106*; *Sintenis 1131*. **Iraq:** *Field & Lazar 830, 586, 538*; *J. B. Gillett 8011*; *Wheeler & Haines W 1063*; *Rawi 21818*.

There is a question as to whether this species is distinct from *C. tomentosa*, of which it was made a subspecies (Davis, Fl. Turkey **1**: 132. 1965). It is supposed to have the sepal blade about twice as long as the spur but, as Davis points out, this condition does not hold for some collections from Iraq. The more erose and plicately folded tip of the terminal lobe and the more spreading lateral lobes of the "petal" seem to me to distinguish it; indeed, to put it very close to *C. hellespontica*.

36. **Consolida tomentosa** (Aucher ex Boiss.) Schröd., Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 5, G, H.

Delphinium tomentosum Aucher ex Boiss. Ann. Sci. Nat. II. **16**: 365. 1841.

Simple or branched from the base, 5–15 cm. high, more or less appressed-canescent; lower leaves short-petioled, with 3 linear lobes; upper leaves sessile, 5–8 mm. long; racemes short, lax, 2–6-flowered; bracts 2-parted or entire, 5–6 mm. long; pedicels ca. 1 cm. long, apparently refracted in fruit; bracteoles 2, linear, 4–10 mm. long, at middle of pedicel or above; flowers deep violet to mauve; sepals oblong, acutish, grayish-strigose, ca. 1 cm. long, 3 mm. wide, narrowed rather abruptly to a claw 3–4 mm. long; spur usually 6–8 mm. or more long; "petal" 3-lobed, ca. 1 cm. long and wide, the upper lobe with dark stripes, truncate at apex, the lateral lobes round, somewhat reflexed-spreading.

TYPE: Aleppo, Syria, *Aucher 76* (P, presumable holotype; seen).

DISTRIBUTION. Dry fields and open places, 500–1200 m., Syria and Lebanon.

ILLUSTRATION. HOSSAIN & DAVIS, Notes Bot. Gard. Edinb. **22**: 419. *fig. 2, D.* 1958.

REPRESENTATIVE MATERIAL. **Lebanon:** *Bornmüller 11326*; *Fox*, June, 1866; *Trench*, May 25, 1945. **Syria:** *Haradjian 1849.*

37. **Consolida hellespontica** (Boiss.) Chater in Heywood, Feddes Repert. **69**: 55. 1964. FIG. 5, I, J.

Delphinium hellespontica Boiss. Ann. Sci. Nat. II. **16**: 366. 1841.

Delphinium hellesponticum Boiss. subsp. *campylopodum* (Freyn) Hossain & Davis, Notes Bot. Gard. Edinb. **22**: 419. 1958.

Delphinium campylopodum Freyn, Denkschr. Akad. Wien Math. Naturw. **51**: 368. 1856.

Consolida hellespontica (Boiss.) Chater subsp. *macedonica* (Hal. & Charrel) Chater in Heywood, Feddes Repert. **69**: 55. 1964.

Delphinium hellesponticum Boiss. subsp. *macedonicum* (Hal. & Charrel) Hossain & Davis, Notes Bot. Gard. Edinb. **22**: 419. 1958.

Delphinium macedonicum Hal. & Charrel, in Abdur Rahman Hadji Effendi, Empire Ottoman Géogr. Bot., Faites Nouv. Relatifs à la Prov. Salonique 8. 1892. Based on *Frivaldsky*, Macedonia; seen from NY.

Delphinium paphlagonicum Huth, Bull. Herb. Boiss. **1**: 328. 1893. Based on *Sintenis 4547* (BH, K, NY, P, US; seen).

Delphinium holopetalum Boiss. var. *paphlagonicum* (Huth) Huth, Bot. Jahrb. **20**: 381. 1895.

Delphinium oliganthum Boiss. var. *ponticum* Huth, *loc. cit.* Type from Pontus: Amasya, *Bornmüller*, 1889. I do not know whether *Bornmüller 970*, 1889, from Pontus (BM, K, PH; all seen) is the actual type number or not.

Delphinium hellesponticum Boiss. subsp. *aintabense* Hossain & Davis, *loc. cit.* Based on *Post*, June, 1889, from Aintab (Gaziantep), Turkey (BM, MO; seen).

? *Delphinium tomentosum* Auch. in Boiss. var. *longecalcaratum* Post, Fl. Syr., Pal., Sinai, ed. 2, **1**: 22. 1932. Apparently based on the same *Post* collection from Aintab, as was subsp. *aintabense* above.

Corymbosely divaricately branched, 1–4 dm. tall, sometimes simple, strigulose throughout; leaves divided into long linear lobes, the lower leaves petioled, withered by anthesis, the middle leaves gradually reduced and subsessile, the upper becoming bracts and the uppermost entire; flowers violet or violet-blue inside, more or less silvery-gray with appressed pubescence outside and with some green on the midribs of the sepals, rather few in number and in fairly lax to rather dense racemes; pedicels 1–4 cm. long, upwardly spreading-incurved; bracteoles 2, linear, 4–15 mm. long, placed just below the flower and growing up around it; sepals more or less lance-ovate, not unguiculate, 10–14 mm. long; spur 12–20 mm. long, slender, pubescent; "petal" light blue to yellowish and violet-nerved, 9–15 mm. long, triangular in outline, 3-lobed, either gradually narrowed toward the more or less erose apex or the upper lobe subequal to the lateral lobes; stamens glabrous; anthers yellow; follicles subterete, strigose, 10–13 mm. long.

TYPE: Ad Hellespontum [Dardanelles], *Aucher 67* (P, K); seen.

DISTRIBUTION. Grain and fallow fields below 1200 m., Anatolia to northeastern Greece and northwestern Syrian desert.

ILLUSTRATIONS. HOOKER, Icon. Pl. **32**: *pl. 3152.* 1932; DAVIS, Fl. Turkey **1**: 126. 1965.

In 1958, Hossain and Davis (Notes Bot. Gard. Edinb. **22**: 418) recognized four subspecies in *Delphinium hellesponticum* which they keyed out as follows:

"Petal" 13–15 mm. long, 12–13 mm. wide; plants mostly 2.5–4 dm. high; racemes rather lax. Northern Greece, Paphlagonia, Galatia, etc. in Turkey. .... subsp. *macedonicum.*

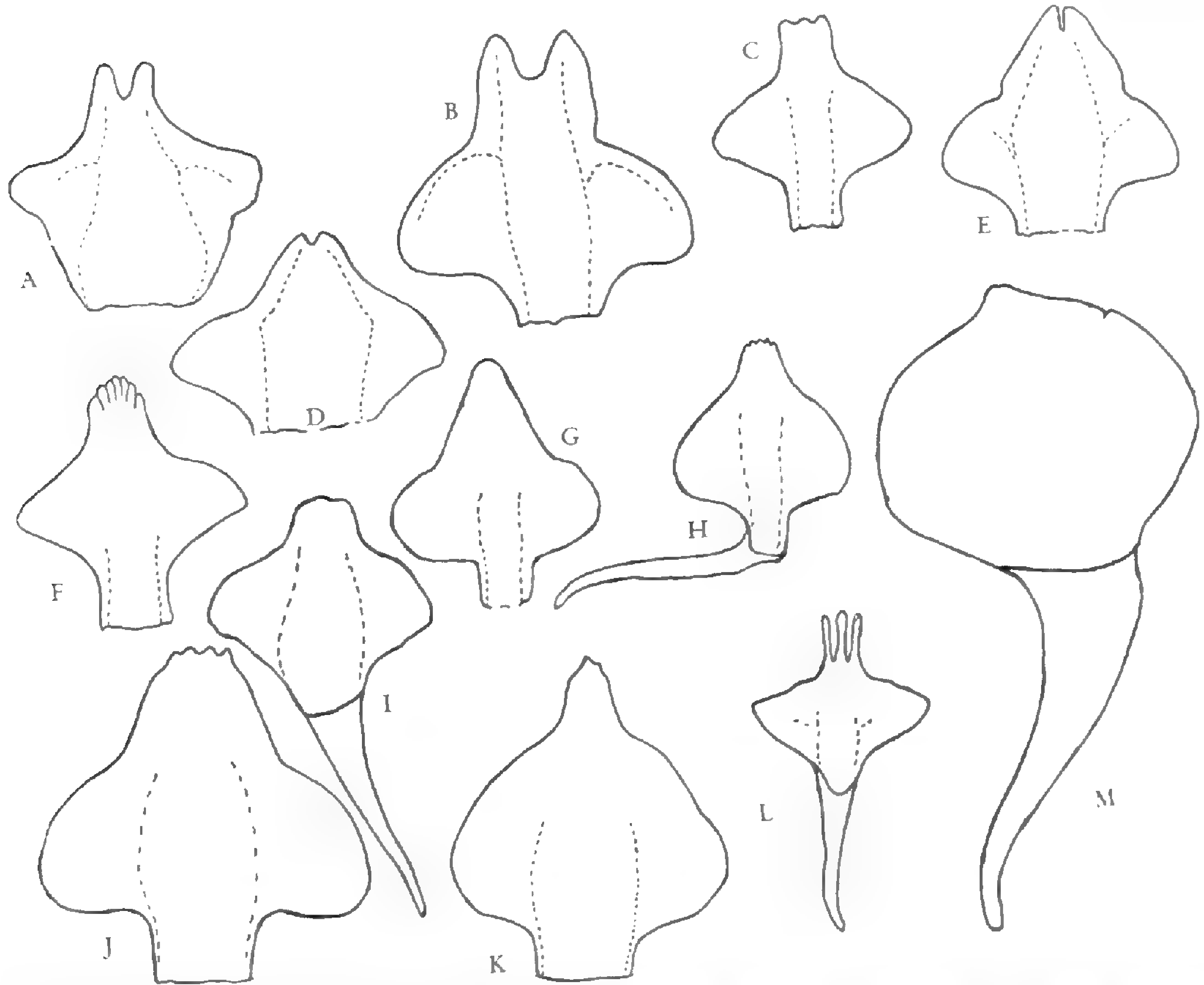

FIGURE 5. **Consolida** species. Drawings show lamina of "petal" in those 3-lobed species in which the lateral lobes turn toward the base of the lamina. A. *C. schlagintweitii*, lamina 11 mm. wide; drawn from *Schlagintweit 821* (US). B. *C. phrygia*, lamina 12 mm. wide; from *Sintenis & Rigo 852* (GH). C. *C. pusilla*, lamina 9 mm. wide; from *Boissier* in 1846 (GH). D. *C. camptocarpa*, lamina 14 mm. wide; from *Dimo 130* (NY). E. *C. camptocarpa*, the form often called *songorica*; lamina 11 mm. wide; from *Regel* (US 2090341). F. *C. oligantha*, lamina 10 mm. wide; from *Field & Lazar 586* (US). G. *C. tomentosa*, lamina 10 mm. wide; from *Iraq Petroleum Co. no. 3* (F). H. *C. tomentosa*, lamina 9 mm. wide; from *Trent* in 1945 (BM). I. *C. hellespontica*, typical form, lamina 10 mm. wide; from *Davis 31010* (BM). J. *C. hellespontica*, the form known as *macedonica*, lamina 15 mm. wide; from *Sintenis 4547* (NY). K. *C. armeniaca*, lamina 13 mm. wide; from *Balls 1756* (US). L. *C. sulphurea*, lamina 8 mm. wide; from *Haussknecht* at Maras (K). M. *C. olopetala*, lamina 15 mm. wide; from *Davis 30951* (BM).

"Petal" 9–12 mm. long, ca. 10 mm. wide; plants mostly 1–2 dm. high; racemes rather dense.
  Bracteoles 10–15 mm. long; lowest pedicel 25–40 mm. long; raceme of main stem pyramidal, prominent. Aintab [Gazianteb] (Turkey), Aleppo (Syria). .... subsp. *aintabense.*
  Bracteoles 4–8 mm. long; lowest pedicel ca. 15–20 mm. long; raceme of main stem seldom prominent.
    "Petal" yellowish when dry, often with pinkish shades, 10–11 mm. long; sepals violet inside. Lycia, Caria, Phrygia (Turkey). .... subsp. *campylopodum.*
    "Petal" usually light blue when dry, often pinkish white, 9–10 mm. long; sepals violet-blue inside. Mostly central Anatolia. .... subsp. *hellesponticum.*

In the *Flora of Turkey* 1: 133. 1965, Davis says "Additional material breaks down the distinctions between the subspecies previously recognized by the author." I am following him because of his great knowledge of the area involved, but the herbarium specimens that I have studied seemed to fit pretty well into his original four concepts. Of this herbarium material I give some examples using the *Delphinium* names, since some have never been transferred to *Consolida*:

(1) Subsp. *macedonicum.* **Paphlagonia:** *Sintenis 4547.* **Galatia:** Ancyra, *Bornmüller 13693.* **Pontus:** Amasya, *Manisdjian 652*; Sankiri *Bornmüller 13695, 970.*

(2) Subsp. *aintabense.* **Turkey:** Mt. Dülük, n. of Aintab, *Haradjian 1415.* **Syria:** Aleppo, *Kotschy*, May 20, 1841.

(3) Subsp. *campylopodum.* **Phrygia:** *Balansa 1132.* **Caria:** *Pinard*, 1843. **Lycia:** *Bourgeau 7.* **Cappadocia:** *Balansa 855.*

(4) Subsp. *hellesponticum.* **Central Anatolia:** *Uvarov 22*; *Davis 31010, 36538, 36430A*; *McNeill 336*; *Ratcliffe 414, 352*; *Sintenis 4979.*

38. **Consolida armeniaca** (Stapf ex Huth) Schröd. Abh. Zool.-Bot. Ges. Wien **4**(5): 62. 1909. FIG. 5, K.

Delphinium armeniacum Stapf ex Huth, Bot. Jahrb. **20:** 380. *pl. 7, fig. 9.* 1895.

Simple or with few, open branches from near the base, 1–3 dm. tall, strigulose, pale in upper parts; leaves multipartite into rather few narrowly linear lobes ca. 0.5 mm. wide, the laminae to 2 or more cm. broad; bracts tripartite or the upper entire, narrow; inflorescence racemose, few- and open-flowered, more or less cinereous, some of the retrorse-appressed hairs with glandular swollen bases; pedicels mostly 1–4 cm. long, curved-ascending; bracteoles 2, linear, near and surpassing the base of the deep blue to violet-blue flowers; upper sepal ca. 14 mm. by 3 mm., lanceolate, not unguiculate, acute, strigose without, the spur 17–24 mm. long, ca. 3 mm. wide at the base, curved, very slender at the tip; lateral sepals ca. 13 mm. by 6 mm., subobtuse, strigose along the midrib; lower sepals 14 mm. by 4.5 mm., acute, strigose; "petal" ca. 13 mm. wide, 14 mm. high, the tip a narrowed beaklike lobe 3.5–4 mm. long, 2–3 mm. wide, the lateral lobes rounded, the whole rather dome-shaped; stamens 5–10 mm. long, the filaments tinged bluish, glabrous; anthers bluish, 1 mm. long; follicle 12–13 mm. long, appressed-pubescent with long hairs, beak 2.5 mm. long.

Type collection: Sipikordagh toward Bendola, Turkish Armenia, *Sintenis 3177*, 1890 (K, P), seen.

Distribution. Dry igneous places, 1200–1800 m., Turkish Armenia.

Illustration. Davis, Fl. Turkey **1**: 129. 1965.

Representative material. **Turkish Armenia:** *E. K. Balls 1756*; *Davis 31941*; *Sintenis 1320*; *H. de Lesse*, July 26, 1956; *Guichard T/50/60.*

39. **Consolida sulphurea** (Boiss. & Hausskn.) Davis, Notes Bot. Gard. Edinb. **26**: 175. 1965. Fig. 5, L.

Delphinium sulphureum Boiss. & Hausskn. in Boiss. Fl. Orient. **1**: 81. 1867.

Strigose, slender, 1–2 dm. tall, divaricately few-branched at or near the middle; lowest leaves largely withered by anthesis, midcauline trifid into revolute, strigulose lobes 8–20 mm. long; racemes lax, 2–5-flowered, strigulose; bracts linear, mucronate, 5–6 mm. long; pedicels 7–15 mm. long, the bracteoles near the flower, 4–6 mm. long; flowers sulphur colored; sepals 9–10 mm. long, oblong, strigose, obtuse; spur subcylindric, 5–7 mm. long; "petal" 3-lobed, ca. 8 mm. wide when opened, the median lobe with 3 lobules at the tip, the whole longer and narrower than the lateral lobes; stamens 5–6 mm. long, very wide at the base of the apparently glabrous filaments; anthers 0.6 mm. long, apparently yellowish; follicle on a recurved pedicel, pendulous, white appressed-hirsute, lance-oblong, 8 mm. long, 2.5 mm. wide; seeds with distinct scales.

Type: Turkey, near Marasch (Maras) at 1300 m., *Haussknecht*, presumably (G), not seen, but apparent isotypes (P as of July 11, 1865, at 4100 ft., and K) were seen.

Distribution. Grassy places and clearings, 750–1300 m., western Mesopotamia, Turkey.

Specimen seen. **Turkey:** Maras-Gaziantep road, June 18, 1960. *K. M. Guichard T/25/60* (K).

40. **Consolida olopetala** (Boiss.) Hayek, Fedde, Repert. Sp. Nov. Beih. **30**: 313. 1924. Fig. 5, M.

Delphinium olopetalum Boiss. Ann. Sci. Nat. II. **16**: 364. 1841.
Delphinium holopetalum in Huth, Bot. Jahrb. **20**: 381. 1965.
Delphinium holopetalum Boiss. var. *Boissieri* Huth, Bot. Jahrb. **20**: 381. 1895. From Armenia, for which were cited: *Sintenis* 1890 and *Bourgeau* 1862. Both are *C. olopetala*.

Plant to 3 dm. tall, 3–4-branched above the base, strigulose; lower leaves short-petioled, the main cauline 1–3 cm. long, 3-parted to base, the divisions with numerous setaceous lobes scarcely 0.5 mm. wide; bracts 3-parted into bifid lobes, or entire, 8–12 mm. long; raceme 15–20-flowered, 10–12 cm. long; pedicels arched spreading, 2–4 cm. long; bracteoles 2, near the flower, linear-subulate, 7–10 mm. long; sepals oblong, obtuse, violet-blue, strigose without, 12–15 mm. long, the lateral sepals strigose only on the midrib; spur incurved, longer than the "petal", i.e. 15–20 mm. long and 3 mm. wide at the base; "petal" more or less entire and subcircular, pale, ca. 15 mm. in diameter, the spur ca. 16 mm. long; filaments violet, to 8 mm. long; anthers rounded, pale, 1 mm. long; follicle strigose, oblong, straight, erect, to ca. 1 cm. long, 3 mm. wide, the beak 3 mm. long.

TYPE: *Aucher* in herb. Mus. Paris, "probably from Persia" (P); seen.

DISTRIBUTION. Upper Euphrates, probably confined to Turkey.

ILLUSTRATIONS. HUTH, Bot. Jahrb. **20**: *pl. 7, fig. 10*. 1895; DAVIS, Fl. Turkey **1**: 129. 1965.

SPECIMENS SEEN. **Turkey:** *Davis 30951, 31909*; *Bourgeau 3*.

REPRESENTATIVE EXSICCATAE OF ASIAN SPECIES OF CONSOLIDA

Agnew Sept. 1, 1961, *saccata*
Aitchison *145 & 310*, *rugulosa*; *1002*, *camptocarpa*
Androsow *2218*, *camptocarpa*
Antonow April 25, 1889, *leptocarpa*
Aucher *64*, *deserti*; *65*, *hohenackeri*; *66*, *aconiti*; *67*, *hellespontica*; *71*, *phrygia*; *72*, *axilliflora*; *73*, *incana*; *74*, *oliveriana*; *76*, *77*, *tomentosa*; *78*, *persica*; *4029*, *linarioides*; *4028*, *rugulosa*; *4031*, *regalis* subsp. *divaricata*; *4032*, *anthoroidea*; *4033*, *trigonelloides*
Balansa *595*, *1134*, *regalis* subsp. *paniculata*; *599*, *719*, *856*, *1135*, *raveyi*; *729*, *axilliflora*; *730*, *scleroclada*; *854*, *glandulosa*; *855*, *1132*, *hellespontica*; *857*, *stenocarpa*; *1133*, *orientalis*
Balls, E. K. *1441*, *hohenackeri*; *1756*, *armeniaca*; *2243*, *axilliflora*
Beach, Kay *5029*, *stocksiana*
Becker *30*, *camptocarpa*
Berton *222*, *incana*
Blanche *348*, *incana*
Boissier June 1842, near Aphrodisias, *raveyi*; June 1842, near Laodicea, *regalis* subsp. *paniculata*; June 1846, near Raschaya, *incana*; June 1846, in Antilibanus, *pusilla*; May 1863, *orientalis*; May 1866, *axilliflora*
Bornmüller *30*, *11324*, *incana*; *32*, *scleroclada* var. *pumila*; *970*, *13693*, *13695*, *hellespontica*; *1724*, *glandulosa*; *4029*, *13692*, *13698*, *orientalis*; *1719*, *4027*, *13690*, *raveyi*; *3221*, *scleroclada* var. *rigida*; *4031*, *13696*, *thirkeana*; *11326*, *tomentosa*
Bourgeau *3*, *olopetala*; *6*, from Elmalu, *glandulosa*; *6*, from Baiboul, *orientalis*; *7* (July 4, 1860), *hellespontica*; *7* (July 12, 1862), *hohenackeri*; *8*, *raveyi*; *10*, *regalis* subsp. *paniculata*
Bové *131*, *deserti*
Bunge *372*, *camptocarpa*; March 1859, *halophila*; April 1859, *rugulosa*; 1858–9, *orientalis*; between Tehran and Tabris, *regalis* subsp. *divaricata*
Capus *54*, *barbata*; *55*, *56*, *rugulosa*; May 1886, *camptocarpa*
Chung *1608*, *ambigua*
Crookshank, Helen *155*, *414*, *orientalis*; *153*, *persica*
Davis, P. H. *4819*, *incana*; *3221*, *6477*, *9992*, *10030*, *30973*, *31592*, *31688*, *35878*, *scleroclada* var. *rigida*; *13010*, *36622*, *raveyi*; *16638*, *16643*, *32810*, *stenocarpa*; *13463*, *37229*, *38698*, *39136*, *39207*, *regalis* subsp. *paniculata*; *16678*, *22026*, *25080*, *31017*, *31732*, *31860*, *31983*, *glandulosa*; *18721*, *19918*, *33881*, *regalis* subsp. *divaricata*; *18878*, *31010*, *36430A*, *36538*, *37241*, *hellespontica*; *21041*, *28406*, *28669*, *31026*, *oliveriana*; *22106*, *oligantha*; *23802*, *anthoroidea*; *22135*, *28680*, *28753*, *axilliflora*; *29695*, *regalis* subsp. *regalis*; *28945*, *30079*, *30598*, *31992*, *orientalis*; *30855*, *cornuta*; *30076*, *30825*, *32613*, *hohenackeri*; *30951*, *31909*, *olopetala*; *35960*, *ambigua*; *31941*, *armeniaca*
Dimo *130*, *camptocarpa*
Dinsmore *6030*, *incana*

Donaldson *48, leptocarpa*

Falconer *59, ambigua*

Fedtschenko July 5, 1897, *barbata*; at Tashkent, *leptocarpa*

Field & Lazar *52, 371, 741, 770, oliveriana*; *314, incana*; *532, 1020, persica*; *538, 586, 691, 830, oligantha*

Furse *2459, orientalis*; *3254, 3283, 3297, anthoroidea*; *3301, halophila*; *2907, teheranica*; *5341, 5360, camptocarpa*; *5942, 5943, 6469, stocksiana*

Furse & Synge *292, orientalis*; *625, 777, persica*; *799, regalis* subsp. *divaricata*; *911, glandulosa*

Geld *4268, camptocarpa*

Gillett, J. B. *8305, oliveriana*; *8011, 11171, oligantha*; *11207, persica*; *11210, flava*

Gillett & Rawi *11621, oliveriana*

Gilliat-Smith *1575, orientalis*; *1724, 1914, halophila*; *1734, oliveriana*

Gontscharow & Grigoriev *114, leptocarpa*; *871, barbata*

Görz *857, 866, regalis* subsp. *paniculata*

Griffith *42, stocksiana*; *1376, rugulosa*

Grown, L. S. *1923, halophila*

Guest *787, flava*; *2470, 2757, 3742, oliveriana*

Guichard *142/62, aconiti*; *T 50/60, armeniaca*; *25/1960, sulphurea*

Haines, R. N. *W 1543, persica*

Haradjian *1263, 2266, axilliflora*; *1415, hellespontica*; *1524, sulphurea*; *1849, tomentosa*

Harris, R. Wheeler *467, 2100, oliveriana*; *1218, saccata*

Haussknecht, in Luristan in 1868, *hohenackeri*; in Kurdistan in 1867, *anthoroidea*; Aleppo in 1865, *axilliflora*; in Ghilan in 1868, *regalis* subsp. *divaricata*; fl. Chabur, May 1867, *oliveriana*; between Erbil & Kirkuk in 1867, *persica*; Kirkuk, May 1867, *oligantha*; Marasch in 1865, *sulphurea*

Hay *210, 282, stocksiana*

Hohenacker, Helenendorf in 1838, *ambigua*; Helenendorf in 1838, *orientalis*; Caucasus in 1834, *regalis* subsp. *divaricata*; pagum Kaelaechan, July 1837, *hohenackeri*

Horner, S. *155, oliveriana*

Huet du Pavillon, near Erzeroum in 1853, *orientalis*; Maimansour in 1853, *glandulosa*

Jacobs, M. *6812, oliveriana*

Karelin in Turcomania, *camptocarpa*

Karelin & Kiriloff *1165, camptocarpa*

Khan, Prance & Ratcliffe *352, 414, hellespontica*; *759A, glandulosa*

Koelz, W. *18202, oliveriana*

Komarov, V. L., Varsaminor, Aug. 18, 1893, *barbata*; Pendjakent in 1892, *rugulosa*

Kotschy *23, 34, 222, axilliflora*; *103, scleroclada* var. *pumila*; *351, regalis* subsp. *paniculata*; *416, oliveriana*; *737, pusilla*; Aleppo, May 20, 1841, *hellespontica*; Raschaya to Palmyra in 1855, *incana*

Kraschennikov *146, camptocarpa*

Krause *3397, 3723, orientalis*; *3488, regalis* subsp. *paniculata*; *3828, anthoroidea*; *5126, hellespontica*

Lace *3338, rugulosa*

Lazar, Y. *371, oliveriana*; June 13, 1933, *orientalis*

Lehmann *32, 36, paradoxa*; *38, barbata*. I am not certain whether these were collected by Lehmann or are his herbarium numbers.

Letourneaux, June 22, 1881, *oligantha*

Levine *823, 952, ambigua*

Lindsay, Miss, *260, 1151, orientalis*; *268, 329, persica*; *1424, regalis* subsp. *divaricata*

Litwinow *440, rugulosa*; *442, orientalis*; *4380, camptocarpa*

Manisdjian *652, hellespontica*

McNeill *336A, hellespontica*; *336B, raveyi*

Meade, E. *171, oliveriana*

Merton *3884, rugulosa*

Meyer, F. N. *541, 572, orientalis*

Meyer & Dinsmore *4030, incana*; *7238, deserti*

Meyers, F. T. *30, incana*

Peyron, at Zaur, May 24, 1890, *oligantha*; *1453, pusilla*; Tarsous, June 6, 1896, *axilliflora*

Pichler *22, raveyi*; in 1882, *halophila*

Pinard, Syria, in 1846, *hohenackeri*;

Caria in 1843, *phrygia*; Caria in 1843, *hellespontica*

Post, E. E., at Beirut, in 1876 & 1877, *incana*; *213*, *218*, *823*, *axilliflora*; Mardin in 1899, *oligantha*; Aintab, June 1889, *hellespontica*; Isriyeh, May 1, 1900, *pusilla*

Radi *307*, *hohenackeri*

Radde in 1867, *orientalis*

Rawi *8540*, *oliveriana*; *21818*, *oligantha*; *20427*, *20708*, *20995*, *21070*, *21097*, *21258*, *22859*, *flava*

Rechinger *148*, *9907*, *19357*, *flava*; *383*, *4173*, *5220*, *orientalis*; *6678*, *regalis* subsp. *divaricata*; *1011*, *789*, *rugulosa*; *2015*, *teheranica*

Regel at Tashkent, May 1880 and *52* in June 1881, *barbata*; Samarkand, May 1882 and Tschardschuia, Sept. 21, 1884, *stocksiana*; Samarkand, May 1882, *leptocarpa*; Samarkand, May 1882, *persica*; Turkestan in 1884, *rugulosa*; Turkestan, *camptocarpa*

Richter *263*, *camptocarpa*

Schischkin, June 4, 1913, *camptocarpa*; June 16, 1916, *oliveriana*

Schlagintweit *821*, *schlagintweitii*

Siehe *135*, *orientalis*; *362*, *403*, *cruciata*; *175*, *548*, *550*, *raveyi*; *387*, *scleroclada* var. *rigida*

Sintenis *143*, *rugulosa*; *301*, *1301b*, *camptocarpa*; *678*, *aconiti*; *283*, *leptocarpa*; *832*, *axilliflora*; *843*, *phrygia*; *1320*, *3177*, *armeniaca*; *1336*, *hohenackeri*; *1131*, *oligantha*; *1186*, *saccata*; *961*, *1187*, *2732*, *oliveriana*; *2965*, *olopetala*; *420*, *522*, *1746b*, *4137*, *orientalis*; *4293*, *raveyi*; *2969*, *scleroclada* var. *rigida*; *4547*, *4979*, *hellespontica*; *4882*, *thirkeana*

Sovetkina *131*, *rugulosa*

Strauss, Th., *3* and July 15, 1896, *oliveriana*

Uvazov, B. P., Jezireb, June 2, 1932, *oligantha*; Kirkuk, May 27, 1932, *rugulosa*; Khanagin, May 26, 1932, *deserti*; *95*, *regalis* subsp. *paniculata*

Wiedemann, Anatolia, *regalis* subsp. *paniculata*; Zejradin, in 1932, *rugulosa*

Wight *18*, *ambigua*

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With affection and appreciation this number of the Journal of the Arnold Arboretum is dedicated to LAZELLA SCHWARTEN, *friend and colleague, on the occasion of her retirement from the staff. The assistance and the friendship which she has extended to all in her role as Librarian of the Arnold Arboretum and her special efforts in the circulation of this Journal will be greatly missed.*

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PRELIMINARY INVESTIGATIONS OF HYMENAEA COURBARIL AS A RESIN PRODUCER

JEAN H. LANGENHEIM

DATA HAVE RECENTLY BEEN PRESENTED to suggest that Oligo-Miocene amber from Chiapas, Mexico, was produced by an ancestral population of the leguminous genus *Hymenaea* (Langenheim, 1963; Langenheim & Beck, 1965; Langenheim, 1966). Evidence for this source was obtained through comparison of infrared spectra of the amber and resin from living populations of *Hymenaea courbaril* L., and supported by the presence of *Hymenaea* leaflets in the amber. The evidence was further corroborated by the discovery that the amber had been deposited at or near mangrove vegetation, a habitat in which *H. courbaril* occurs commonly today (Langenheim, Hackner, & Bartlett, 1967). This determination of a leguminous source is in contrast to the classic concept of amber as generally derived from pines or at least from conifers.

The usual preconception of pine origin of amber results from relatively detailed studies of the extensive early Tertiary amber deposits along the Baltic coast (Conwentz, 1890; Schubert, 1953, 1961; Langenheim, 1964). Inclusions in the Baltic amber of needles and staminate cones of pines usually have been cited as a basis for origin, although other coniferous remains, as well as certain angiospermous ones, are more abundant than those of pines. The most convincing evidence for pine origin is droplets of amber found in resin canals in the xylem and around parenchymatous cells of the inner living bark (Schubert, 1953, 1961). Several species of pines were thought to have been involved in production of the Baltic amber but these are now all treated as a single species, *Pinus succinifera* (Conw.) Schubert.

The great quantities of amber found in these Baltic deposits, sufficiently extensive to have been mined for centuries on the Samland Peninsula, opened questions as to how so much resin was produced. Because pines commonly do not exude this quantity of resin "naturally," it was assumed that a pathological condition known as "succinosis" must have existed (Conwentz, 1890). Not only did Conwentz and his followers think that pathological conditions were necessary, but that the entire forest must have been diseased to have produced such deposits of amber, "Es gab kaum einen gesunden Baum im ganzen Bernsteinwald — das Pathologische war die Regel, das Normale die Ausnahme!" Czeczott (1960) has pointed out that this picture of the "sick amber forest" was so masterfully presented by Conwentz that his view has "hypnotized" workers for almost 60 years. Schubert (1953, 1958, 1961) thought that the abnormally intensified resin production might have been caused by a "strong disturbance of physiological balance," some of which might possibly have resulted from trees being exceptionally susceptible to injury near the periphery of their distribution. Only a few investigators such as Klebs (Kunz, 1903) and Bachofen-Echt (1930, 1949) have indicated that the Baltic amber accumulations could have resulted from normal production of resin. They thought that pines, dominant in forests over extensive areas for millions of years, could account for the large quantities of amber found in the Baltic deposits.

Although the flora occurring in the Baltic amber has been known to contain a large tropical element, except for Schubert's (1958) reference to warm temperate pines, no one seems to have recognized that trees produce more copious amounts of resin in tropical environments than in temperate ones. Likewise it has not been pointed out that angiosperms belonging to such families as Leguminosae, Burseraceae, Guttiferae, Anacardiaceae and Dipterocarpaceae can produce as much or more resin than gymnosperms. Moreover, many of these angiosperms seem to produce large quantities of resin under natural forest conditions. At least resin accumulates in the soil today in sufficient amounts to justify collection for commercial purposes. Thus the Chiapas amber project has directed our attention to a tropical angiosperm which has produced sufficiently large quantities of resin in an environment where it could become incorporated into the geologic record. The Chiapas amber likewise has an advantage in being chemically stable enough to allow comparison with resin from living populations. The opportunity to compare the fossil and modern resins has brought up various questions, such as what genetic and environmental conditions control chemical composition as well as yield of resin. What are the conditions in tropical environments that result in active biosynthesis as well as exudation of resin to the surface of the plant where large quantities may accumulate? In what tissues does biosynthesis occur and what are the variations in production during the ontogeny of the plant? To answer these questions, resin production in populations of *Hymenaea courbaril* is being studied ecologically in the field and morphogenetically in the laboratory. This paper constitutes a preliminary report on field studies and initial morphogenetic considerations of a planned long-range investigation.

TAXONOMIC AND ECOLOGIC PERSPECTIVE

The genus *Hymenaea*, subfamily Caesalpinioideae, family Leguminosae, has the center of its distribution in the Brazilian Amazonian region (Record & Hess, 1943). East African and Asiatic species of *Trachylobium* resemble *Hymenaea* and sometimes have been included in the genus, as have some South American species of *Peltogyne*. Twenty-seven species are commonly recognized; the number can be greater if several varieties of *H. courbaril* are considered worthy of specific recognition. Twelve species (*H. davisii* Sandwith, *H. microcarpa* Huber, *H. palustris* Ducke, *H. oblongifolia* Huber, *H. parvifolia* Huber, *H. pororoca* Huber, *H. velutina* Ducke, *H. reticulata* Ducke, *H. intermedia* Ducke, *H. floribunda* HBK., *H. venosa* Vahl, *H. rubriflora* Ducke) have their distribution centered in northern South America. They generally occur in the Amazonian region and adjacent areas in northern Brazil, Peru, Colombia, Venezuela, and the Guianas. Five species (*H. stigonocarpa* Mart., *H. stilbocarpa* Hayne, *H. martiana* Hayne, *H. splendida* Vogel and *H. eriogyne* Benth.) generally occur in southeastern Brazil (from Bahia to Rio Grande do Sul) as well as in adjacent Paraguay and Bolivia. Six species (*H. adenotricha* Ducke, *H. multiflora* Kleinh., *H. sellowiana* Hayne, *H. chapadensis* Barb.-Rodr., *H. correana* Barb.-Rodr., *H. olfersiana* Hayne) are recorded only locally.

Hymenaea courbaril L. has a wide range of distribution, occurring in all of the South American countries except Argentina, Uruguay and Chile, on most of the islands of the West Indies, and along the Pacific drainage throughout Central America to central Mexico. Although this species generally appears to be distinctive from the other described species, confusion apparently does exist in distinguishing it from *H. oblongifolia* which occurs in the Amazonian area. *H. altissima* Ducke is often recognized as a variety of *H. courbaril* in southeastern Brazil. *Hymenaea candolliana* HBK. in Central America is so close morphologically that it frequently is considered either synonymous with or a variety of *H. courbaril*. Ducke (1949) indicates that the typical form of *H. courbaril* occurs in Colombia, Venezuela, the Guianas, the Antilles, and Central America as well as in the lower Amazonian area to the tributary Rio Tapanjós. However, he described the variety *subsessilis* from the region of Manaus and the variety *obtusifolia* from northeastern Brazil, particularly in Ceará and Bahia.

Hymenaea courbaril is commonly called Locust or Algarroba in the West Indies, Guapinol in Central America, and Jutahy or Jatobá in Brazil. This is the species of *Hymenaea* that produces the largest quantity of resin; therefore, it is the one from which resin has been collected for commercial usage. Other species of *Hymenaea* reported to yield resin in varying amounts are *H. intermedia, H. parvifolia, H. velutina*, and *H. stigonocarpa* (Tschirch & Stock, 1936). Detailed statements regarding resin production for the other species are not known to the author.

Hymenaea courbaril can reach a large size, i.e., 100 to 180 feet high, with a spreading crown supported by a large trunk sometimes more than six feet in diameter. The trees are taprooted when young but later develop a considerable ramifying root system. The tree reproduces extensively from root suckers and thus persists following cutting. In secondary vegetation in Central America it commonly attains only 40 to 60 feet in height and a diameter of 2 to 3 feet. Rarely today can one see the few remaining relatively undisturbed areas where these trees attain the large sizes reported by Freise (1934), Record and Hess (1943), et al.

This species, *Hymenaea courbaril*, seems to occupy a relatively wide range of habitats throughout its extensive distributional pattern. In Mexico and Central America it occurs in moist evergreen forests as well as seasonally dry ones (Miranda 1952–53; Miranda & Hernandez-X., 1963; Gómez-Pompa, 1965; Langenheim, 1966). The moist evergreen forest in Mexico (Selva Alta Perennifolia *sensu* Miranda) occurs where the median annual temperature is greater than 20° C., the annual precipitation greater than 1500 mm., and where there is a short dry period. Where precipitation is greater than 2000 mm., the dry period can be longer. Variations in this type of forest are numerous and characterized by some of the components tending to dominate in certain zones. *Hymenaea courbaril* occurs only sporadically in this forest type except in flooded areas or where soil moisture is abundant. For example, it grows amid such populations as *Ficus* spp. and *Andira* spp. which occur along banks or lowlands with rapid movement of water during flooding, with *Tabebuia pentaphylla* (L.) Hemsl. in lowlands with little movement of water during flooding, and with *Pachira aquatica* Aubl. on banks of muddy rivers which are flooded frequently. Some of these same riparian species also occur in the semideciduous types of forest (Selva Alta or Mediana Subcaducifolia *sensu* Miranda & Hernandez-X., 1963). These forests are characterized as ones in which 50 to 75 per cent of the trees lose their leaves during the peak of the dry season. The climate, like that of the Selva Alta Perennifolia, is characterized by a median annual temperature greater than 20° C. The annual precipitation is above 1200 mm., but there is an accentuated dry season. On the Pacific slopes in Mexico *H. courbaril* is one of the most characteristic trees in this forest type. Other populations occurring frequently with it are *Enterolobium cyclocarpum* (Jacq.) Griseb., *Cedrela mexicana* Roem., *Licania arborea* Seem., *Cybistax donnell-smithii* Rose, and *Hura polyandra* Baill. (Miranda & Hernandez-X., 1963). Actually "selvas de guapinol" occur along rivers or arroyos where soil is deep in southern Mexico (Miranda, 1952–53). Commonly occurring with *H. courbaril* are *Andira inermis* (Sw.) HBK., *Nectandra* spp., *Ficus glabrata* HBK., *Calophyllum brasiliense* Camb., *Brosimum costaricanum* Liebm. and *Tabebuia pentaphylla*. Among smaller trees (6–15 m.) the following are most frequent: *Trichilia cuneata* Radlk., *T. hirta* L., *Coccoloba cozumelensis* Hemsl., *Annona reticulata* L., *Swietenia humilis* Zucc., *Bursera simaruba* (L.) Sarg., *Psidium sartorianum* (Berg.) Nied., *Inga laurina* (Sw.) Willd., *Styrax argenteus* Presl, *Genipa americana* L. and *Karwinskia calderoni* Standl.

Hymenaea courbaril often occurs in Sabanas, i.e., grassy areas with scattered trees, in either the Selva Subcaducifolia or Selva Baja Subperennifolia. Here the soil is usually characterized by deficient drainage, i.e., muddy in the rainy season and parched in the dry season. *Licania* *arborea* and *Bursera simaruba* are common associates of *Hymenaea* in these habitats.

In certain stands of Selva Mediana Subcaducifolia *Hymenaea courbaril* can be sufficiently dominant to form essentially a consociation. It occurs in this manner along the Guerrero coast in Mexico on sandy soils derived from granitic parent materials. It likewise can appear in coastal sites on sandy plains or beach ridges intermingling with Selva Baja Caducifolia, i.e., with *Bursera* spp., *Pistacia mexicana* HBK., *Ceiba* sp., *et al.* In coastal areas such as these in Mexico, *H. courbaril* commonly comes in contact with mangrove swamps (Manglares). *Hymenaea* apparently grew near mangrove swamps during the Oligo-Miocene also in the Chiapas, Mexico, area, as evidence from a palynological study indicates that the Chiapas amber was deposited in or adjacent to mangrove vegetation (Langenheim, Hackner & Bartlett, 1967).

In Costa Rica *H. courbaril* also occurs in moist to relatively dry forest types. In the province of Guanacaste, it is an important element in the forest classified as Tropical Dry (Holdridge, 1964). The dry sites in Costa Rica, however, are considerably more mesic than those in Mexico. It generally grows on fertile, well-drained soils and is frequent along rivers with such associates as *Anacardium excelsum* (Bert. & Balb.) Skeels, *Enterolobium cyclocarpum*, *Cedrela mexicana*, *Tabebuia chrysantha* (Jacq.) Nichols., and *Achras* sp.

Hymenaea courbaril is a common component of the Subtropical or Premontane Moist forests (*sensu* Holdridge) in Costa Rica. Plots were made in this forest type near Villa Colón in the province of San José at approximately 900 m. altitude. Here the median temperature is above 20° C; the precipitation is about 2000 mm. annually, but there is a pronounced dry season from mid-November through April. The forest studied was near a river where the vegetation has been disturbed by long human occupation. The dominant trees are *H. courbaril*, *Brosimum* sp., *Tabebuia pentaphylla*, *Luehea candida* (DC.) Mart. and *Cupania guatemalensis* Radlk. (Fournier, personal communication).

On the Osa Peninsula of Costa Rica, *H. courbaril* occurs in a dense mixed forest (Tropical Wet *sensu* Holdridge or Lower Montane Rain Forest *sensu* Allen) where it reaches a height of over 120 feet and with a buttressed base 4 to 6 feet in diameter. Here it grows with *Virola* spp., *Vantanea* sp., *Vochysia* spp., *Carapa* sp., *Calophyllum brasiliense*, and *Copaifera trapezifolia* Hayne. This forest type develops where the median annual temperature is greater than 24° C and annual precipitation is greater than 4000 mm.

It is reported that *Hymenaea courbaril* occurs in both moist and dry coastal forests in Puerto Rico, as well as on other islands of the West Indies (Little & Wadsworth, 1964).

Despite the abundance and economic importance of *H. courbaril* in Brazil, little ecologic information seems available. Freise (1934) does state that in Brazil it occurs in a variety of habitats, from sterile, sandy soils along the coast to well-drained soils in the midst of Amazonian forests. In the Amazonian region difference in size of the trees apparently can be correlated with edaphic conditions (Rodrigues, personal communication). The trees attain a greater diameter, although not necessarily greater height, on fertile floodplain soils than on relatively more sterile upland soils.

One would expect *Hymenaea courbaril* to be differentiated into ecological races, since it has occupied different climatic and edaphic conditions over a wide distributional range probably for long periods of time. Morphological differences have been recognized by description of varieties, but no evaluation of the variation pattern has been attempted, as is true for most genera from this part of the world. Nor are data available regarding genetic and physiological differences which might provide illumination concerning both chemical composition and yield of resin.

Even though *H. courbaril* probably is ecotypically differentiated, what effect this might have on resin composition is not definitely known. Investigations present varying results for species populations within different genera. Baker and Smith (1901, 1920) in pioneer studies of the chemical composition of *Eucalyptus* oils found that generally, except for perhaps half a dozen, all species possess comparatively constant chemical characteristics throughout their geographical distribution. Penfold and Morrison (1927), however, discovered some forms of *Eucalyptus dives* Schauer in which the essential oils varied in composition, and they concluded that these variations were due to genetic rather than environmental differences. In a later study, Penfold and co-workers (1948) also showed differences in the composition of the oils in physiological races of *Leptospermum citratrum* Shallinor.

Krestinsky et al. (1952), found that turpentine of *Pinus sylvestris* L. from different ecological sites in forests possessed the same physical properties and chemical composition. Mirov (1948), however, indicates that *P. sylvestris* has several physiological races and questions whether or not Krestinsky dealt with only one of these. Mirov further points out that when the physical characters (reflecting the chemical composition) of turpentine of the genus *Pinus* are studied, some species vary but little throughout their range, whereas others vary a great deal. *Pinus merkusii* De Vries, which grows over a wide range in Burma and Indonesia, varies but little in the physical characters of its turpentine. On the contrary, the chemical composition of the turpentine of *Pinus ponderosa* Laws. (Mirov, 1958, 1961) varies with the several physiological races which have been identified. Mirov also noted that variation in chemical composition of the turpentine may be a result of hybridization in some cases.

CHEMICAL COMPOSITION OF THE RESIN

The pale yellow to reddish resin (sometimes referred to as a resin-like gum) produced by *Hymenaea* has been known in the commercial trade as "South American Copal" to distinguish it from various copals from other parts of the tropics (Tschirch & Stock, 1936). As a result of the varied usage in literature two semantic confusions need to be clarified. First is the distinction between gums and resins. These products are synthesized through different metabolic pathways. Chemically gums are hydrophilic polysaccharides. Resins (often called oleoresins or balsams) are complex mixtures of mono-, sesqui-, and di- and triterpenoids. These terpenoids are built on a fundamental isoprenoid pattern regarded as evolutionary modifications of a primeval mevalonic acid pathway (Robinson, 1963). Gums are readily distinguished from resins by their ability to dissolve in water or to absorb water to form a jelly or gelatinous paste, and by their inability to dissolve in hydrocarbons which are solvents for resins. Although a small polysaccharide fraction is present in the product from *Hymenaea*, this material primarily is composed of terpenoid constituents. In order to indicate this polysaccharide component, the product from *Hymenaea* justifiably can be called a gum-resin, but not a gum *per se*. Part of the confusion with the term "gum" results from lax usage in the commercial literature, but it also may be due to the tendency of some botanists to refer to resinous secretions from angiosperms as "gums."

Confusion also exists with the term "copal," as it is used to connote resins from different plant families. The word probably has a Mexican origin, being derived from "copalli," meaning incense. In Mexico, however, the natives do not use "copal" or "copalli," to refer to resins from members of the Leguminosae but rather to those from the Burseraceae. In the commercial resin literature, nonetheless, "copal" certainly is more commonly used for resins of various leguminous genera, particularly the African *Trachylobium*, *Copaifera* (including *Guibourtia*), *Daniellia* et al., as well as *Hymenaea* in Central and South America. Copal also is used for resin from the gymnospermous *Agathis alba* (Lamb.) Foxw. in the East Indies and Philippines.

Throughout the wide distributional range of *H. courbaril*, natives use the resin for incense and generally as a cement. Extensive commercial usage, however, seems to have developed primarily in Brazil. Here it has been employed chiefly in the manufacture of special grades of varnish and to a limited extent for medicinal purposes. Howes (1949) reports that Brazilian copal is recovered frequently from water courses and varies in size from a pea to that of a man's fist. When dug from the ground, it may be in large, irregularly shaped pieces. Record and Hess (1943) indicate that "the gum gatherers dig around the roots and sometimes obtain a barrelful of copal lumps in a place, while the former site on a big tree, long since decayed, may yield several barrels of so-called fossil copal." Although resin apparently has been collected from various areas in Brazil, the great collection center seems to have been in the Amazonian region — the Ilha do Marajó near Belém and along Amazonian tributaries such as the Tapanjós and Xingu. *Hymenaea* resin also was collected and used by pre-Columbian aborigines in southern Costa Rica and Panama (Balser, 1960). Noriega (1918) likewise reports the economic value of *Hymenaea* resin in Oaxaca, Mexico, where large masses again are found in the soil.

Early chemical analyses of *Hymenaea* resin have been made in this commercial context. Freise (1934) analyzed resin from *H. stilbocarpa* in three conditions: 1) freshly flowing, 2) fresh resin from a recent cut in bark, 3) buried in the soil. The terms "fossil" and "subfossil" are used frequently in the commercial literature to refer to resins buried in the soil. This is a different connotation from that generally employed by geologists in which prehistoric conditions are at least implied. At our present state of knowledge, the processes involved in fossilization of resin appear to be progressive oxidation and polymerization. At what point a resin actually is considered to be fossilized has not yet been defined. Freise discovered that between the free-flowing and the buried states, the resin becomes harder, darker in color, and considerably more insoluble in alcohol. The melting point range increases from 180 to 192° C. for fresh resin from a bark wound to 265° C. plus, for an old, buried resin. The resin acid content varies from 8 to 16 per cent in the fresh, flowing resin, 32 to 38 per cent from the wound in the bark, 50 to 55 per cent in young, buried resin to 55 to 68 per cent in the old, buried resin. This increase in resin acid content may be due to volatilization of components initially present. Nakano and Djerassi (1961) have made the only modern analyses known to the author on the resin acid constituents of *H. courbaril*. They investigated a single sample from Brazil and did not indicate whether or not it came from the tree or was buried in the ground. They reported that the acidic fractions of this sample consist largely of a diterpene acid which they named copalic acid. Copalic acid has the same carbon skeleton of agathanedicarboxylic acid and related diterpene acids (cativic, eperuic and labdanolic) and appears to correspond in absolute configuration to dehydroeperuic acid. These latter resin acids occur in *Prioria copaifera* Griseb., *Eperua falcata* Aubl., and *Cistus ladanum*[1] Le Maout & Dcne.

Corroborative evidence that an ancestral population of *Hymenaea courbaril* is the source of Oligo-Miocene amber from Chiapas, Mexico, was provided by comparing infrared spectra of the amber with spectra of resin from trees living today (Langenheim & Beck, 1965; Langenheim, 1966). Infrared spectrophotometry offers a simpler means of relating chemical composition to the botanical origin of amber than other techniques now recorded. Because amber is so highly polymerized, only small percentages of the material are readily soluble. The infrared technique provides a means whereby the whole amber can be analyzed in the solid state by dispersing it in potassium bromide pellets. Also the large number of absorption bands that amber and modern resin show offer a multiplicity of parameters from a single experiment.

In the study of the Chiapas amber, spectra were made from living trees whose ancestors might have produced the amber, such as: *Styrax*, *Amyris*, *Myroxylon*, *Guaiacum*, *Pistacia*, *Bursera*, *Hymenaea*, *Protium*, *Pinus*, *Taxodium*, etc. The spectrum for each genus was clearly distinguishable

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[1] This name, supplied by a colleague in chemistry, was used by LeMaout and Decaisne in the legend to an illustration and is cited in Index Londinensis. It is probable that the name *Cistus ladaniferus* L. was intended.

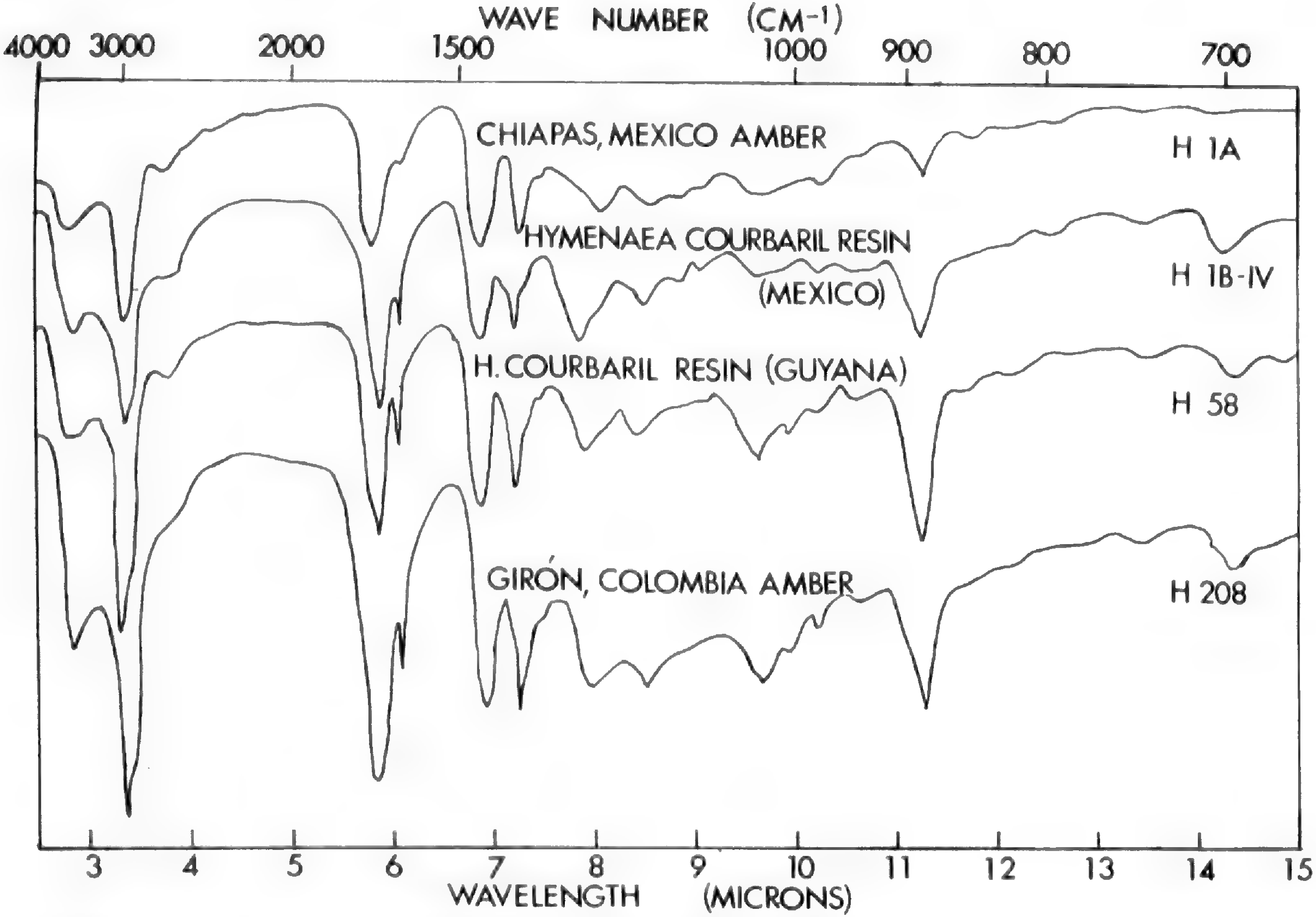

Fig. 1. Infrared spectra of Oligo-Miocene amber from Chiapas, Mexico, and resin from extant *Hymenaea courbaril* from Mexico; amber from Girón, Colombia, and resin from extant *Hymenaea courbaril* from Guyana.

(Langenheim & Beck, 1965; Langenheim, 1966). Populations of certain species, as well as closely related species within a genus, were found to have characteristic, reproducible spectra. Also all of the spectra of the Chiapas amber specimens analyzed are similar to spectra from *H. courbaril* (FIG. 1), although some samples are more closely correlated than others. Langenheim and Beck (1965) indicate that the differences may be explained by the progressive effects of both oxidation and polymerization.

In order to try to assess the variability in chemical composition of the hardened present-day resin, as expressed in infrared spectra, samples of *H. courbaril* resin were obtained from various localities throughout its wide distribution. Problems exist in obtaining resin samples that have adequate information substantiating their determination. Samples and voucher specimens were collected in the field in Mexico, Costa Rica, and Brazil by the author. Specimens were also obtained from resin collections of the Chicago Museum of Natural History and the Botanical Museum of Harvard University, from Guatemala, Guyana, Venezuela, Brazil, Ecuador, and Dominica. There is no absolute assurance that the resin specimens from the museums were produced by *H. courbaril*, as no voucher collections are available. Within the risk of a possible error, however, these resins are assumed to be properly identified. Samples also have been analyzed from different trees in the same local populations in the states of Guerrero and Chiapas in Mexico, and the provinces of San José and Puntarenas in Costa Rica. Likewise spectra of samples of oxidized resins have been run from different parts of the tree, i.e., trunk, branches, and roots, in addition to pieces buried in the soil. FIGURE 2 presents a representative spectrum for samples taken from Mexico, Guatemala, Costa Rica, Dominica, Ecuador, Brazil, Guyana, and Venezuela. The spectra are generally similar to one another, although certain differences are apparent. As Langenheim and Beck (1965) have stated, the identity of two infrared spectra of pure compounds can be taken as proof of the identity of the compounds. But for resins, which consist of mixtures of components of high average molecular weight, two restrictions must be made: 1) only major constituents can be expected to give strong absorption bands, so that differences in minor constituents may not be apparent at all; 2) identity of spectra can never be expected even from samples from a single specimen, but the presence of similarities, particularly in the upper "fingerprint" region is evidence for structural similarity of major constituents. The variations displayed may possibly be a reflection of a slightly different chemical composition due to ecotypic differentiation of the various populations. Certainly from the indications of Mirov's work, ecotypic differentiation and consequent variation in composition might be expected in a species with such a wide distributional range and occurrence in different environmental conditions. Fresh resin, however, might reflect ecotypic variation better than the resin changed by oxidation and polymerization. In pines, the mono- and sesquiterpene fractions (turpentine) are useful, in some cases, in indicating racial differences (Mirov, 1961), whereas a large portion of the remaining resin fraction

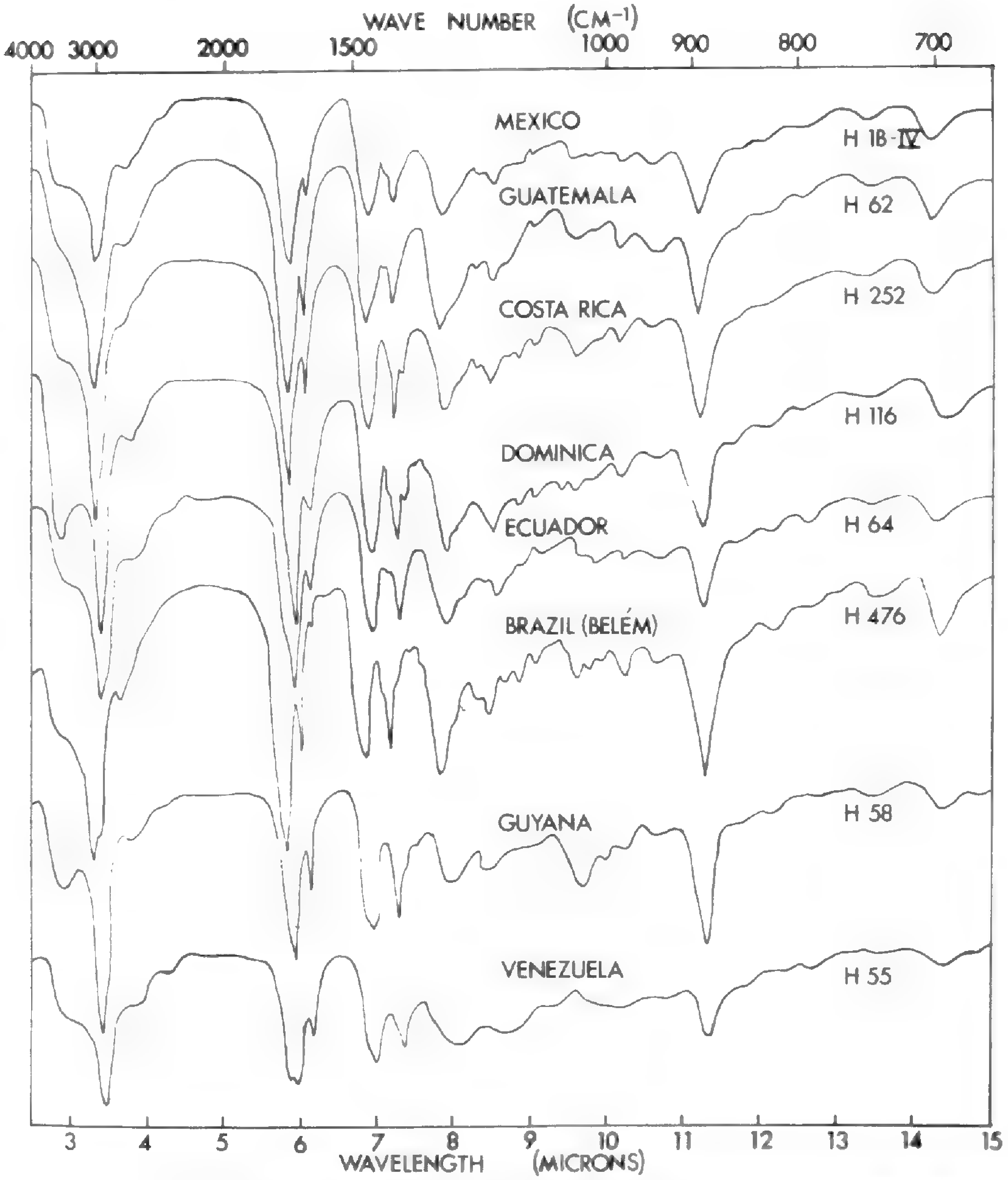

FIG. 2. Infrared spectra of resin specimens from *Hymenaea courbaril* populations in Mexico, Guatemala, Costa Rica, Dominica, Ecuador, Brazil, Guyana, and Venezuela.

has converted to relatively stable diterpene resin acids of the abietic type (Lawrence, 1959). For possible use of the oxidized resin in reflecting specific or subspecific biochemical variation, further chemical analyses are needed.

Apart from the possible influence of ecotypic variation, Beck (personal communication, 1967) indicates that the general similarity of the spectra are in accord with the expectations raised by the gross structure of copalic acid proposed by Nakano and Djerassi (1961). The strongest carbonyl absorption in all cases lies at a wave number (1700 cm.$^{-1}$) as would be expected for α, β-unsaturated carboxylic acids, but there is evidence of lesser amounts of saturated carboxylic acids in all the samples. In most of them, this evidence is limited to changes in slope at the edge of the carbonyl band toward higher wave numbers but variations exist in some of the samples. This is in agreement with the opinion of Nakano and Djerassi, that the resin acids of *H. courbaril* are mixtures not only of stereoisomers, but of double-bond isomers.

Beck likewise states that "a remarkable and quite unexpected feature of all the *H. courbaril* spectra is the weak but unmistakable absorption at approximately 700 $cm.^{-1}$ and 750 $cm.^{-1}$. This pair of bands is associated with mono-substituted benzenes. Their low intensity might lead one to suspect that these resins contain minor amounts of relatively simple aromatic compounds, but to our knowledge none have been isolated from copals by conventional chemical means." Considerable variation in intensity of these presumably aromatic absorption bands also occurred in all samples tested. These possible chemical differences in the oxidized resin of *H. courbaril* are currently being investigated in more detail by analyzing extracts of the soluble fractions.

Amber from three other localities in South America gives spectra that likewise are similar to resin from *H. courbaril.* Amber from Girón, Colombia (near Bucaramanga) occurs in goldbearing alluvium and hence its geologic age is unknown. The spectra from six samples fall into two types, one of which is presented in FIGURE 1. Six spectra of amber from Medellín, Colombia, also of unknown geologic age, were run and five are similar to the pattern indicated for the Girón amber. In both of these cases the amber spectrum was more similar to the resin spectrum of *H. courbaril* from Guiana than to other spectra run. No spectra of resin of *H. courbaril* from Colombia are available.

Another amber sample was run from Capanêma, Pará, Brazil, from strata which are considered early Miocene in age. The spectrum is similar to resin from extant *H. courbaril,* especially from Pará, Brazil, as well as from Costa Rica (FIG. 3).

Variation in spectra shown through the geographic distribution of *H. courbaril* is also reflected in the amber. The spectra of the Chiapas amber are related more closely to spectra of *Hymenaea* resin from populations in Mexico and Guatemala than to those resins from populations with a more southern distribution. Therefore, it was not surprising when the spectra of amber from Girón and Medellín, Colombia, compared closely with *H. courbaril* resin from Guiana, and that the amber from Pará, Brazil, was more comparable to the resin from Pará, Brazil, than from other areas.

PRODUCTION OF RESIN

The location of the cells and tissues in which the resin is synthesized and the anatomical mechanism for its internal collection, as well as the manner of exudation, have not been adequately investigated in *Hymenaea courbaril.* Because secretion of the resin occurs in a different manner in

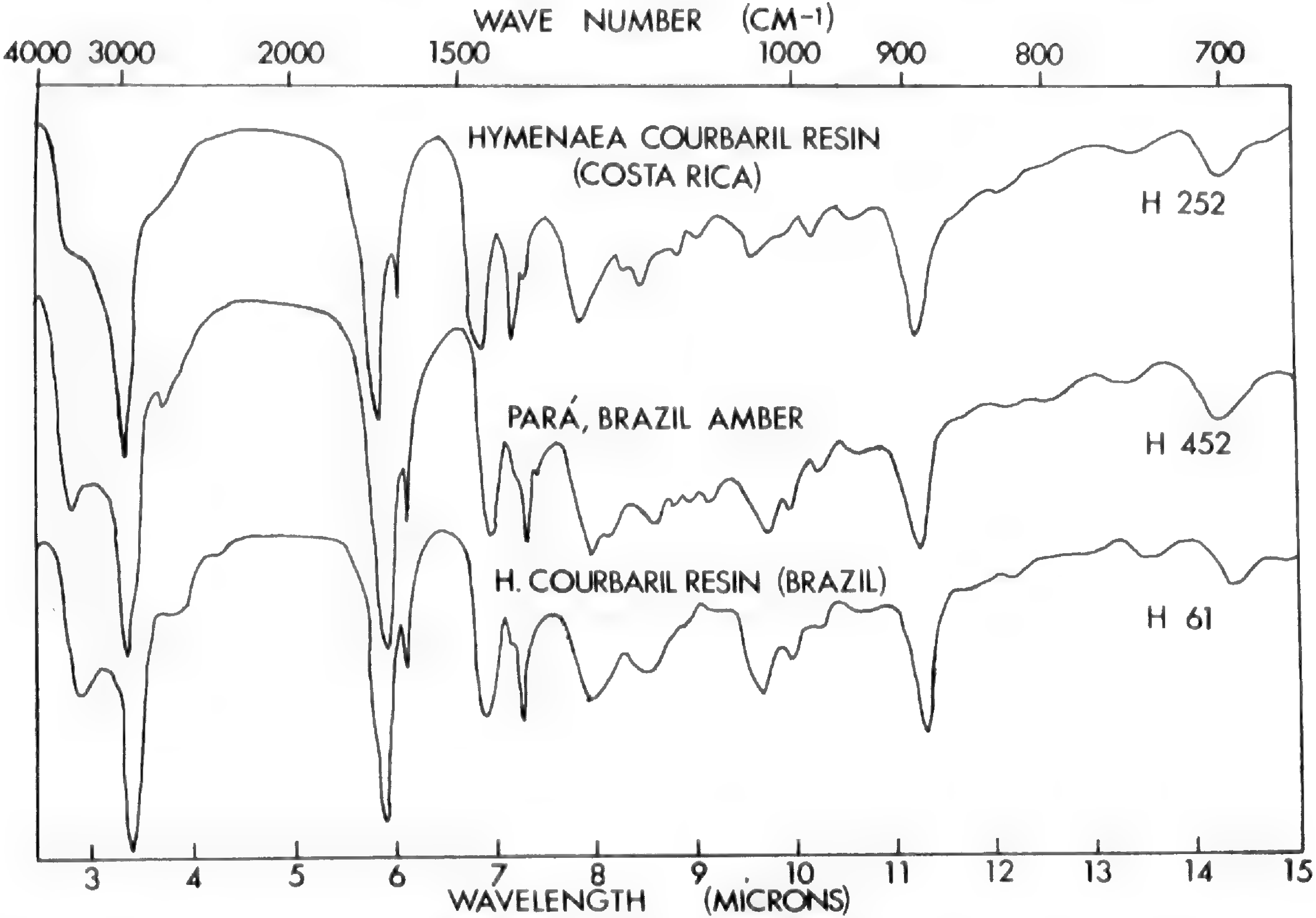

FIG. 3. Infrared spectra of Miocene amber from Pará, Brazil, and resin from extant *Hymenaea courbaril* from Pará, Brazil, and from Costa Rica.

young plants and mature trees, the secretory system is being studied from time of germination to year-old plants in the laboratory, and in older trees in the field.

MATERIALS AND METHODS

In order to study the secretory system in the young plants, seeds from Mexico, Puerto Rico, Panama, and Costa Rica were scarified, planted in sand or vermiculite and put in growth chambers (16 hour day length) at temperatures of 25° C. during the day and 21° during the night. After three months of growth in the control chambers, the plants were removed to the greenhouse. All tissue specimens of seedlings grown in either the growth chamber or greenhouse were fixed in 10 per cent aqueous acrolein (Feder, 1960) or in 3 to 6 per cent glutaraldehyde. The fixed specimens were dehydrated in a series of methoxyethanol, ethanol, n-propanol, and n-butanol, and then embedded in a monomer mixture of glycol methacrylate according to the technique of Ashley and Feder (1966). Sections were stained in aqueous 0.05 per cent toluidine blue O; in some cases they were counterstained with 1 per cent acid fuchsin or periodic acid-Schiff reagent. All sections were mounted in Permount.

Samples of branches and root suckers taken in the field in 1965 were fixed in FAA, dehydrated in an alcohol series and embedded in the previously mentioned monomer mixture of glycol methacrylate. Samples of the mature tree taken in 1966 were fixed in 10 per cent formalin in the field and post-fixed in 10 per cent acrolein upon return to the laboratory. They were taken through the dehydration schedule discussed above, except that the final changes were made in anhydrous ether. Extreme difficulty in obtaining sections of the cambial zone in *Hymenaea* had been encountered previously. Therefore a modification of the previously reported embedding mixture of glycol methacrylate was devised by Feder. The monomer mix consists of: 1) glycol methacrylate, 91.85 per cent, 2) polyethylene glycol 400, 5.0 per cent, 3) ethylene glycol dimethacrylate, 5.0 per cent and a-azodiisobutyronitrile, 0.15 per cent. The specimens then were polymerized in ¾ fl. oz. aluminum weighing pans at 60° C. overnight, followed by a 12-hour period at 100° C. It was possible to section blocks as large as 2 cm. × 1 cm., containing both wood and bark. Sections were stained with 0.05 per cent toluidine blue O and mounted in indopol polybutene H-1900, thinned to about 25 per cent in xylol in order for the sections to adhere firmly to the slide. If allowed to air dry, as with smaller sections, considerable curling and wrinkling occurred. With this technique it was possible to obtain intact sections of the cambial zone between 1 to 6 μ thick with metal knives on a Leitz rotary microtome. It also provided means of sectioning the heterogeneous cell types of phloem and xylem tissue adjacent to the cambium.

OBSERVATIONS AND RESULTS

Seedling plant: Seedlings are not commonly observed in the field.

although seeds appear to be produced abundantly. Seeds often are reported to be slow to germinate in the forest, but seedlings grow rapidly (Record & Hess, 1943). The author has observed seeds germinating in semideciduous, seasonally dry forests in both Mexico and Costa Rica just after the rainy season had begun. Seedlings were observed neither in the tropical wet forest on the Osa Peninsula of Costa Rica nor in the Amazonian forests near Belém or Manaus in Brazil. In none of these sites had trees obviously developed from seedlings. All small trees excavated were attached to roots from a large tree; thus they appear to be root suckers. Root grafts may have occurred, but this has not been substantiated. Record and Hess suggest that, because the seedlings are bushy and succulent at first, they are attractive to browsing animals. Grazing could account for lack of survival of seedlings in some sites, but seems improbable in others. Explanation for the striking lack of *H. courbaril* seedlings in the forest awaits further observation and study.

Time required for germination of seeds in the growth chambers varied considerably from the same locality as well as from different localities from Mexico, Puerto Rico, Panama, and Costa Rica. No attempt had been made to keep seeds from individual trees separate, although seeds were segregated by local populations in Mexico and Costa Rica. For example, the time of germination varied from 9 to 18 days from seeds from the same population in Guerrero, Mexico, under the same controlled conditions. Seeds from a population in Panama which germinated in 12 days in the 16 hour chamber in January, 1965, took two months in November, 1965. If germination studies per se were done, some care probably should be given to segregating seeds from individuals within a local population and to knowing the age of the pods which are collected.

At germination, the hypocotyl emerges and fleshy cotyledons are pushed above the ground. The root begins to develop rapidly, constituting approximately two-thirds of the growth for about two weeks. At this point the stem portion of the hypocotyl starts to elongate, and the epicotyl and juvenile leaves begin to develop. By 16 days the stem above the juvenile leaves has developed as well as the first pair of leaves. Although there are some differences in the length of time for development of stem and leaf, by the twenty-first day their pattern is generally developed.

Schizogenous pockets of limited size, not canals, occur in the epicotyl and in the hypocotyl to the place where root tissue begins. The pockets appear as early as three days after germination or, since the growth rate may vary, when the hypocotyl is approximately three cm. in length. In the cortex they occur one to two cells under the epidermis. They vary in number, sometimes being scattered through the cortex (Fig. 4), at other times being closely packed next to each other at least in portions of the hypocotyl or epicotyl. One to two layers of epithelial cells are common with another layer of "collapsed" cells often outside the functional layer. The pockets also occur commonly in the pith, apparently scattered at random. The pockets vary in size, but the variation in a single section may be due to cutting the pockets at different levels. Because they have an ovoid shape, a cross-sectional diameter will vary in any given section.

Petioles also present a similar morphological topography to that of the hypocotyl and epicotyl. Resin seems to be synthesized early and more of it actually appears to issue from cells in the petiole than from the hypocotyl and epicotyl. FIGURE 8 shows the general topography of the petiole. In the petiole, as well as the hypocotyl and epicotyl, the actively secreting cells are densely cytoplasmic and appear to be metabolically active (FIGS. 6 and 7). In some cells, an expansion of the cell wall is evident (FIG. 5). This expansion suggests that the resin has been secreted but not yet passed through the cell wall. Unfortunately, in these sections most of the terpenes may have been dissolved in the dehydration sequence. Also no specific stain has presently been developed which is unique for the lower terpenes, so that their presence can be substantiated. Considerably more cytological study is needed to determine the site of biosynthesis of resins in cells such as these.

Year-old plant: Periderm is initiated in the cell layer adjacent to the epidermis and forms inward into the cortex. Therefore, the secretory pockets formed early in the cortical region are preserved after the periderm has developed (FIG. 12). The extent of cortical parenchyma has decreased, however, with considerable development of phloem fibers. Pockets are not apparent either in phloem or xylem tissue, although some pockets have been maintained in the pith. Camargo (1960) noted a similar anatomical pattern for one- to two-year old stems of *H. stilbocarpa.*

The epithelial cells surrounding the pockets in year or year-and-a-half old plants do not appear to have the dense cytoplasm characteristic of the epithelial cells of younger tissue. These epithelial cells possibly are no longer synthesizing resin, but have already emptied their product into the pocket.

Resin exudes from the cortical region when the stem is cut or scraped. Wound experiments, in which pin pricks and razor slashes were made on stems of one-year old plants, were carried out. Care was necessary in any wounding experiment not to destroy completely the narrow cortical zone containing the secretory pockets. Four months following the wounding, samples of the stem were fixed, embedded, and sectioned. No evidence for an increased number of pockets was noted, nor was it possible to determine with existing techniques if additional resin synthesis was initiated.

Resin pockets have not been observed in root tissue of year-old plants.

Root suckers: As previously mentioned, all of the young trees seen in Mexico and Costa Rica appeared to have developed as root suckers. Sections of these suckers present a general anatomical pattern similar to that in the one- to two-year old stems developed from seeds. The secretory pockets, however, appear more numerous, particularly in the pith, than in the seedlings. Also considerably more resin seems to be secreted from a sucker than from a seedling stem of the same diameter. This increased production may result from the stem being attached to an extensive root system of a mature tree, where more reserve carbohydrates might be available for biosynthesis than in the seedling.

Branches: In the field, resin which had exuded in small globules along the branch was commonly observed (FIG. 15). Similar to the one-year old stem, the pockets which had their origin in the cortex have been preserved after periderm formation (FIG. 11). The resin appears superficially to be issuing through lenticels; however, in sections the pockets are not shown to have an obvious relationship to lenticels. Von Höhnel (Kisser, 1954) suggests that with increase in size of the pockets (which has been observed) the resin spontaneously bursts out of the container which is close to the periderm. As the branch enlarges, considerable cortical parenchyma is replaced by sclerenchyma, and resin is produced from cells in the cambial zone.

Globules of resin also frequently appear near the attachment of branches to the trunk. Larger masses occur associated with larger branches. These masses seem to have occurred where breaks, due to strain at the point of attachment, allow issuance of the resin which probably is produced in the cambial zone.

Fruit: Young fruits have been observed to produce such large masses of resin that they often encase the pods. Sections of fruits have not been made by the author. Ribiere (Moens, 1955) reports that fruit of *Hymenaea courbaril* contains abundant resin pockets which form in the vicinity of the epidermis in the young ovary. These pockets persist and often are engorged with resin in the wall of the older fruit.

Mature tree: The schizogenous pockets which develop in the cortex progressively disappear with the secondary development of the bark. The bark in older *H. courbaril* trees can be one to two inches thick or more. For the greater part of its thickness, the bark is highly sclerenchymatous, has relatively narrow rays, and a thin periderm. The tree can be sufficiently large and the bark so "tough" in the Amazonian region that canoes with a carrying capacity of 25 to 30 men can be made from a single tree (Record & Hess, 1943). External bark character varies in individuals. Most commonly the bark has been observed to be smooth with little rugosity (FIG. 13); sometimes a buttressing develops at the base of the tree with indication of growth stresses. In these smooth-barked trees, most of the resin seems to issue from a rupture in the bark producing vertical fissures which may be due to release of tension during rapid growth. In some cases, the smooth bark is interrupted by rugose patches (FIG. 14) and resin commonly is found in these ridges and furrows.

If a cut is made into either the trunk or root of the mature tree, resin exudes from the cambial zone. Resin is exuded in different amounts from trees of essentially the same size in the same general region, but growing in habitats with different availability of moisture. For example, resin was viscous and scantily produced from machete cuts in a tree on a dry, upland site near Villa Colón, Costa Rica. On the other hand, it was produced more abundantly and was considerably less viscous from a similar-sized tree which grew in more mesic conditions along the river near Villa Colón. Resin begins to issue soon after cutting occurs. Flowage has been observed to occur for at least six weeks, and probably longer periods could be recorded if there were opportunity for observation. Quantity of exudation depends not only on the capacity of the tree to synthesize the resin, but upon the viscosity of the resin. Also humidity conditions in the forest, which determine the rate of drying of the outer surfaces of the resin masses, are critical. In cases where the resin continues to flow for long periods despite drying conditions, sufficient pressure exists to force the mass with the oxidized surface outward. Concentric flow layers are formed within the resin mass. Often during the rainy season, the resin is beaten from the surface almost as soon as it is exuded, unless a well-oxidized crust is rapidly formed.

Although resin pockets were not noted in sections of root in the young plant, production of resin in the cambial zone of the mature root was observed. Numerous instances of small lumps of resin associated with breaks in the bark of the root were found (FIG. 16). Large masses, however, were not discovered by the author to be associated with the roots. Cuts made in excavated roots produced resin copiously and the mature root appears to have a capacity to synthesize the resin similar to that of the trunk. Questions have arisen as to the role of resin production from the roots in accounting for the large accumulations of resin in the soil around the tree. The location of resin three feet or more beneath the soil surface has been cited by Noriega (1918), Record and Hess (1943), and others as indicating that resin production underground by roots is likely. Yet it seems difficult to understand the mechanism whereby large masses of resin are produced underground, unless considerable pressure pushes the resin out into the surrounding soil. From both observation and wounding experiments no doubt exists that roots have the capacity for synthesis, and that they are highly susceptible to types of injury that would result in exudation. Adequate assessment, however, has not yet been made of the relative roles of resin production by trunk and root and subsequent accumulation of resin in the soil. Since extensive accumulations of resin occur primarily around large trees, it might be assumed that these are old trees. Thus time would have been provided for resin that had fallen from the tree to have become incorporated in the soil. In tropical areas where *Hymenaea* grows, however, the trees do not develop annual growth layers so that determination of the age of trees is difficult. Also, little is known about the rate of soil formation in these types of forest. Leaf litter is strikingly lacking and there is no basis for knowing how long it would take to incorporate lumps of resin that have fallen from the tree to any depth within the soil. In areas in Chiapas, Mexico, the resin was observed to have flowed into sand, cementing the grains into large lumps to a depth of at least six inches. On the Osa Peninsula of Costa Rica large pieces of resin had obviously fallen from long (up to 2 feet) resin stalactites hanging from the trunk and other masses incrusting the bark around fissures. Some resin lumps were incorporated in the surface of the soil above the level of the roots and hence were probably produced from the trunk.

Sections made initially of trunk and root tissue where resin was issuing did not show evidence of pockets; probably as a result of separation of the samples at the delicate cambial zone. Sections using the methods developed by Feder show the development of pockets or cavities of varying size in the cambial zone (FIGS. 9 and 10). These pockets form between the rays in a zone of undifferentiated xylem tissue. The cells in the zone where the cavities develop appear not to have become lignified as indicated by the red-violet color of the staining of the toluidine blue O. Lignified walls are blue-green in color and occur in tracheid and vessel cells just inward from the zone where the pockets form. The pockets apparently develop by cells breaking down and releasing resin into the cavity which is being enlarged, with subsequent breakdown of additional cells. The origin of these cavities would probably be considered lysigenous as compared with schizogenous separation of cells in the young plant (Esau, 1964). These pockets apparently can merge to form larger cavities, a process shown beginning in FIGURE 10. Longitudinal sections of the particular specimens examined thus far have not shown if these cavities can attain any sizable vertical extent. The particular secreting layer of cells with characteristically dense cytoplasm that occurs in schizogenous pockets of the young plant, is not evident in the lysigenous pockets. These cavities apparently develop when a sufficient break in the bark has disturbed the cambium. As yet it is not known if resin production in the mature tree is restricted to this cambial zone or if individual parenchyma cells are capable of production in the newly differentiated phloem as well as in the rays. The relatively quick exudation of the resin after cutting seems to indicate that individual cells have already synthesized the resin or that precursors are present so that the final stages of synthesis are accomplished rapidly following injury. It seems unlikely that the large quantities of resin observed can be produced from a single, relatively narrow zone of pockets along the cambium as shown from the sections presented here. More extensive cavities probably are developed or at least biosynthesis must be kept in a very active state for a relatively long period to produce the large accumulations of resin found. These conditions need further investigation before an understanding of the anatomical organization for resin production in *Hymenaea courbaril* is reached.

A pressing question raised at this point is whether or not pathological conditions are necessary for production of resin in the mature tree. As just pointed out, schizogenous resin pockets arise early as a part of the normal pattern of development in the young plant, but disruption of tissues in the cambial zone seems necessary for development of pockets in the mature plant. Even though disturbance of the cambial tissue occurs, diseased or physiologically weakened conditions are not indicated. On the contrary, the largest, most vigorous trees growing in what appear to be the most favorable environmental conditions (i.e., excellent water relations and fertile soils) are clearly those observed to be producing the most resin.

Insect damage has often been suggested to account for injury that might increase resin production. Stephen L. Wood, a specialist in the study of Central American bark beetles, reports that beetles of the Scolicidae are the most likely to produce damaging effects on a tree such as *Hymenaea* (personal communication, 1966). He, however, has not witnessed these beetles injuring *H. courbaril* in his experience in Central America. In fact, on the Osa Peninsula of Costa Rica he has observed a species of *Platypus* (a platypodid ambrosia beetle) that started tunnels it never completed, having been forced out by resin. He also noted that profuse quantities of resin were produced in large trees. In one case he states that deposits "more than an inch deep, four inches wide and a foot or two in length" were removed from an area of longitudinal furrows and ridges (Wood, personal communication, 1966). He further indicates that all tissues were healthy, with no hint of insect, fungal or other damage than forced separation of tissues from internal pressure. He offers the explanation that *H. courbaril* appears to grow slowly as a subdominant, but when an opening occurs, growth is extremely rapid until maturity is reached. During this period growth might be so rapid that the bark cannot accommodate the expansion in certain areas of stress and bark ruptures. Thus Wood's observations support those of the author's in that the large quantities of resin appear to be produced by healthy trees growing rapidly, and that insect damage apparently does not play a role in inducing pathological conditions.

The apparent individual variation in resin production in *Hymenaea courbaril* might be explained from evidence on comparative yields in certain pine populations. Resin yields have been shown to be under genetic control in *Pinus palustris* Mill., *P. caribaea* Morelet and *P. elliottii* Engelm. Snow (1949, 1954) reports that certain individuals of *P. caribaea* and *P. elliottii* yield two and one-half times as much resin as that of the average tree of the same size growing under similar conditions. No single or combined external characteristics, or environmental conditions, were discovered to set these trees apart. Squillace and Dorman (1961) and Squillace (1966), in breeding experiments on the variation and inheritance of resin yield in *P. elliottii*, have shown that this trait not only varies highly among individual trees, but is strongly inherited in comparison with most biological traits. A strain of slash pine has been developed that will yield about twice the normal amount of resin of average trees. Their results also suggest that resin yield is positively correlated with growth rate. Squillace points out that, although they selected mainly for resin yield in their experiments, the high resin producing strain also yields about 12 per cent more volume growth than normal strains. Dyer (1963) states that the quantity of resin manufactured is directly proportional to the size of the crown of slash pine.

Boudreau and Schopmeyer (1958) have noted that physical factors relating to resin flow from wounds in *Pinus elliottii* are number and size of resin ducts, pressure, and viscosity. Both resin pressure and viscosity are under strong genetic control. Duct size and number vary with stem age. Pressure and viscosity seem unaffected by stem size above 5 cm. diameter but the ratio of pressure to viscosity accounts for a substantial amount of yield variation. They also indicate that resin pressure in trees varies with environmental conditions, particularly with water relations.

Thus these studies on some pines indicate that resin yield is under genetic control, but likewise environmental conditions are important in producing favorable growth conditions that affect pressure and viscosity. These data also suggest that vigorously growing trees, rather than diseased, physiologically weakened ones, give the greatest resin yields.

DISCUSSION AND SUMMARY

Preliminary investigations of *Hymenaea courbaril* have provided evidence that at least some angiosperm resin producers living under tropical conditions do not need to be diseased or physiologically weakened by insect, fungal or other attacks to produce large quantities of resin. Resin is produced and can accumulate in sufficient quantity to account for large deposits of amber. Although these studies do not necessarily provide answers to the accumulation of the Baltic amber deposits, they do turn our attention to certain important aspects of resin production by angiosperms as well as gymnosperms. In order to assess the capacity of members of various species of *Hymenaea* to produce resin, as well as to account for differences in chemical composition of the resin, further systematic analysis of the group is needed. Particularly, more ecologic and genetic data in terms of the development of physiological races would be valuable. Studies of the unoxidized resin (i.e., the volatile terpene fractions) from populations of *H. courbaril* might show differences in composition related to ecotypic differentiation. Striking similarity of infrared spectra of oxidized resin from specimens throughout the wide range of distribution of *H. courbaril* may result from chemical stability of the diterpene copalic acid constituent. This copalic acid also may provide the basis for relating the present-day *H. courbaril* resin to amber of Oligo-Miocene age from Mexico, Miocene from Brazil, and unknown age from two localities in Colombia.

In the anatomical adaptation for resin production in *Hymenaea courbaril*, schizogenous pockets form in cortical and medullary tissue of the epicotyl and stem (but not the root) portion of the hypocotyl soon after germination. These pockets persist until bark formation finally obliterates them. In the older plant, lysigenously developed cavities appear in the cambial zone of the trunk or root. It seems unlikely that the narrow zone of pockets in the cambial zone can entirely account for the large quantities of resin that are produced, even allowing considerable time for production. Although not observed yet, more extensive cavities may be formed by enlargement of the existing ones. Whether or not parenchyma cells in the living phloem or in the xylem rays also synthesize resins is still questionable. There also is question as to whether continual stress of some sort is needed to keep the enzymes active for continued biosynthesis when lysigenous breakdown is involved.

Although not demonstrated as yet, it seems likely that resin yield in *Hymenaea courbaril* is under strong genetic control, as has been shown for several species of pine. Local populations of *H. courbaril* in particular geographic regions have been noted for outstanding resin yields by commercial resin collectors. This fact, however, does not sort out the genetic factors from the environmental ones. The largest, most vigorously growing trees have been observed to produce the greatest amounts of resin, which possibly may be due to excess carbohydrate available for synthesis of a secondary product. Therefore, superimposed upon genetic capacity, all environmental factors that result in greater net photosynthesis, and hence possible higher growth rates, may increase synthesis. Partial explanation for the large number of different kinds of trees producing resin, which occur in tropical regions, as well as particularly high resin yields, may be provided by the favorable growth conditions throughout the year. Experimental work is needed to substantiate these possibilities. Likewise, vigorous growth activities of these tropical trees may help account for means of exudation which augment those resulting from injuries due to storms, insect and fungal infestations, etc. This leads then to the *raison d'être* for biosynthesis of resin and its possible evolutionary significance. The metabolic role of these terpenoids which constitute resins still is obscure; the prevailing idea is that they simply represent ways of disposing of excess acetate. Thus the primary significance of these terpenoids may be ecologic, in providing protective adaptation against such damage as is inflicted by insects and fungi. Abnormal flows of resin are known to be stimulated by wounds and by the presence of fungal disease. Also terpenoids can act as excellent fungicides and insecticides and their presence in a tropical environment, where both fungi and insects are abundant, could provide a selective advantage. With more studies of the chemistry of these terpenoids making up resins, their biogenesis, and their discharging processes, however, a metabolic role may possibly be discovered that would augment the ecologic, protective role.

ACKNOWLEDGMENTS

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EXPLANATION OF PLATES

PLATE I

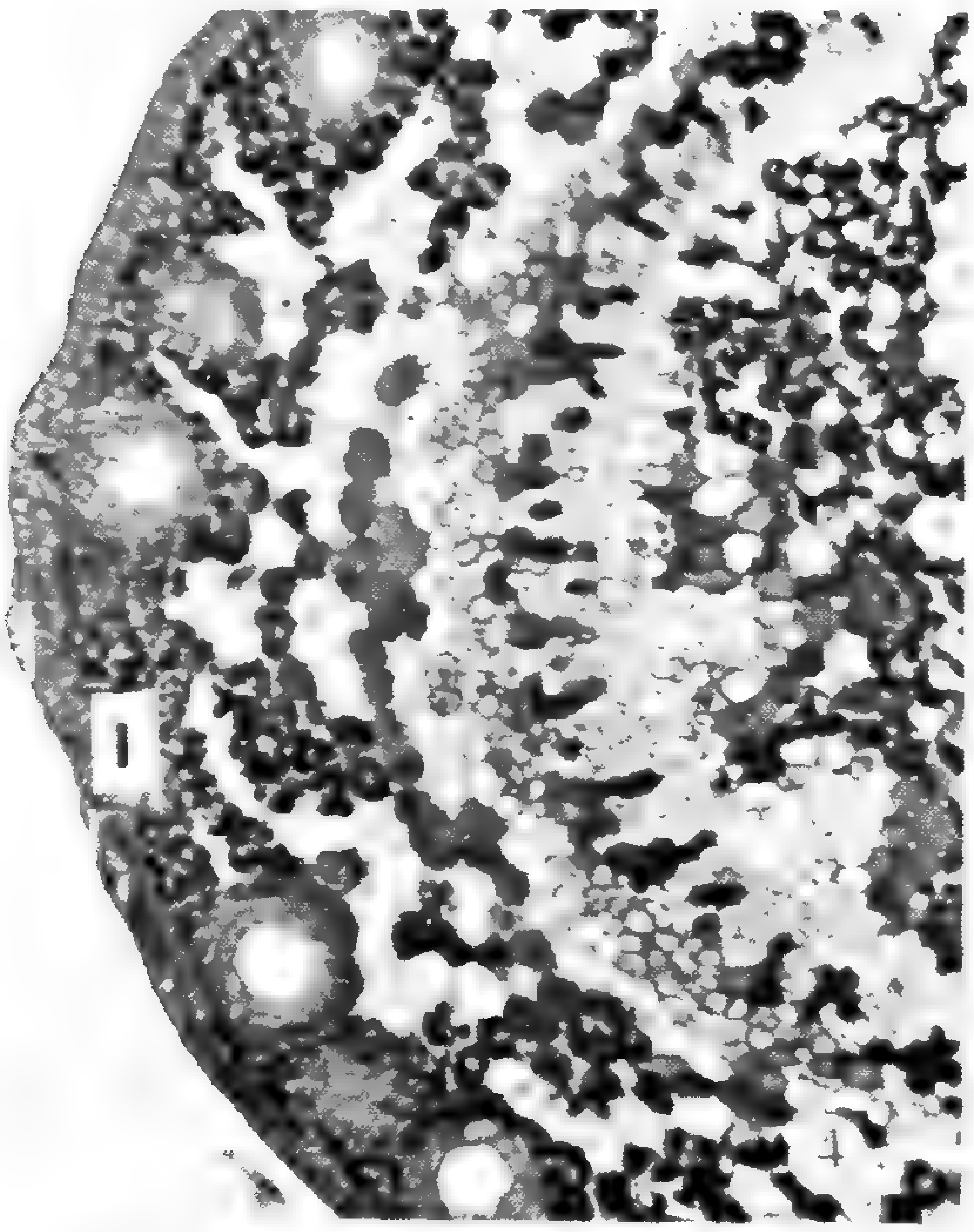
FIGS. 4–8. Transverse sections of *Hymenaea courbaril* (Mexico). 4, topography of epicotyl, 21-day old plant, showing location of resin pockets in cortex near epidermis; 5, resin pocket from epicotyl (FIG. 4) near epidermis, with distention of cell walls in secreting cells; 6, resin pocket in pith of petiole, (FIG. 8) showing densely cytoplasmic secreting cells; 7, resin pocket from cortex of petiole; 8, topography of petiole showing extensive development of resin pockets in cortex and pith. Line scale on all figures is 50μ.

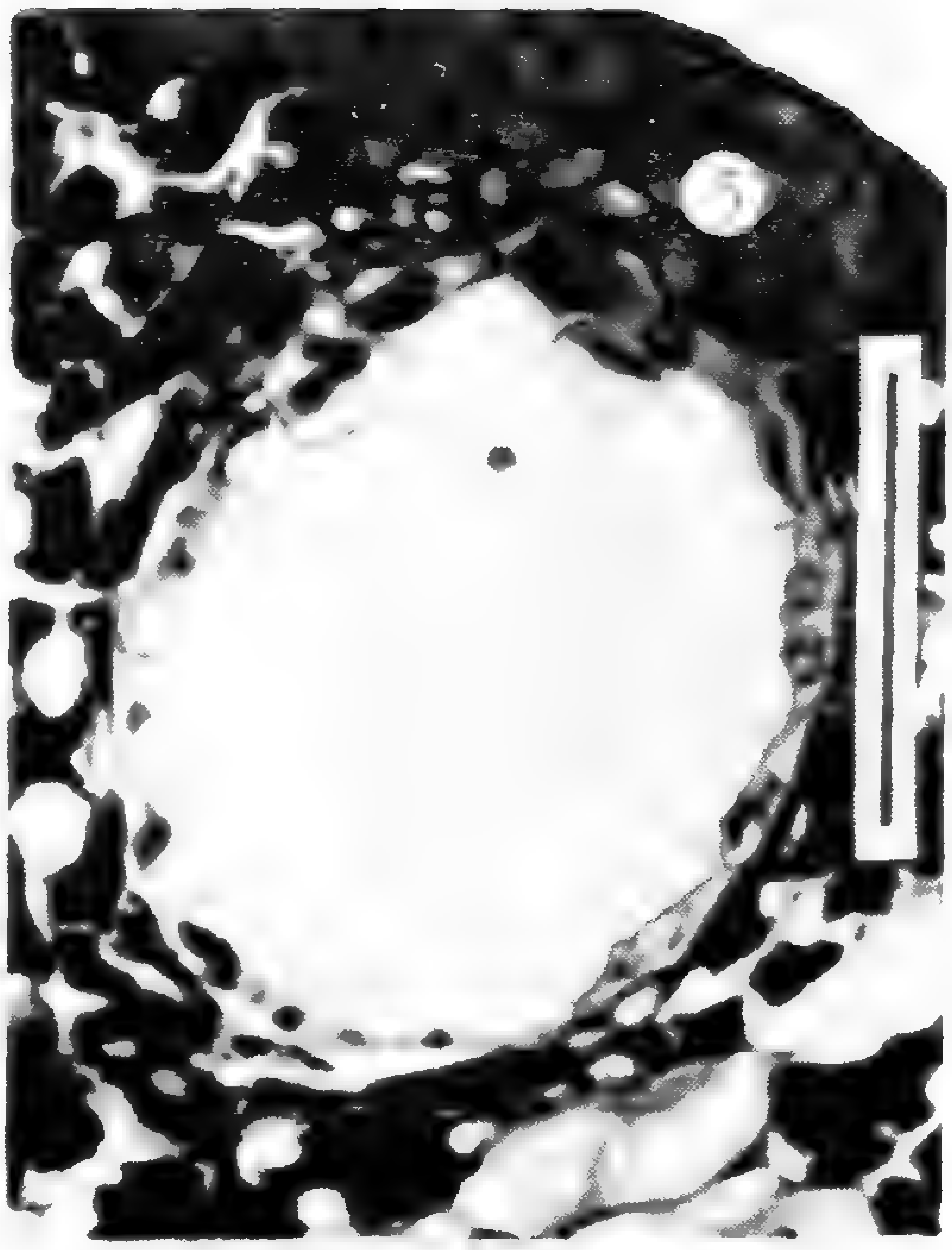
PLATE II

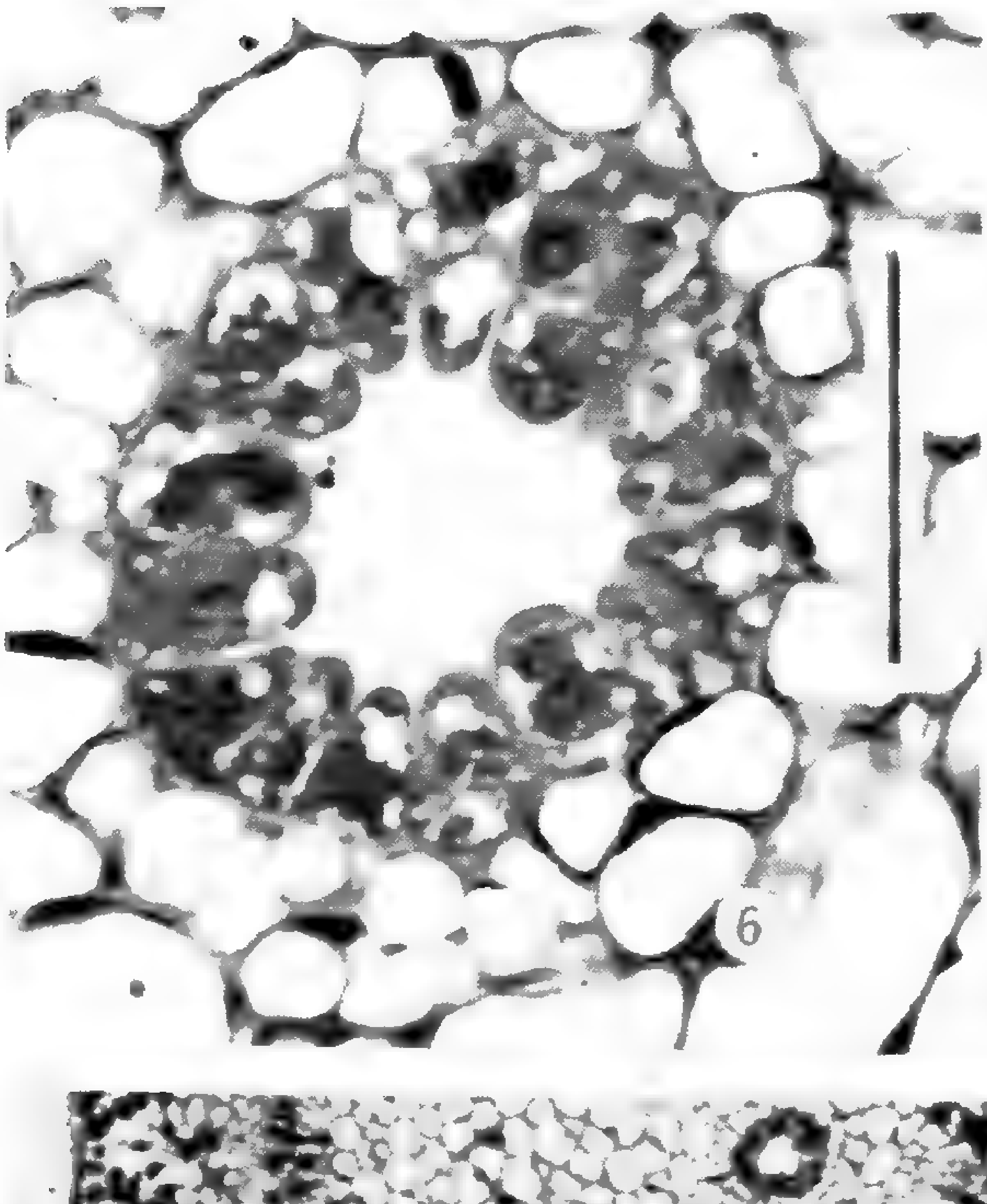
FIGS. 9–12. Transverse section of *Hymenaea courbaril*. 9, pockets developed in cambial zone of trunk of mature tree, Belém, Brazil; 10, pockets similar to FIG. 9 but showing coalescence to form cavities; 11, branch, Manaus, Brazil, showing preservation of pockets in the cortex amid extensive development of sclerenchyma; 12, one-year old stem, Mexico, showing preservation of pockets after the periderm starts to develop. Line scale on all figures is 50μ.

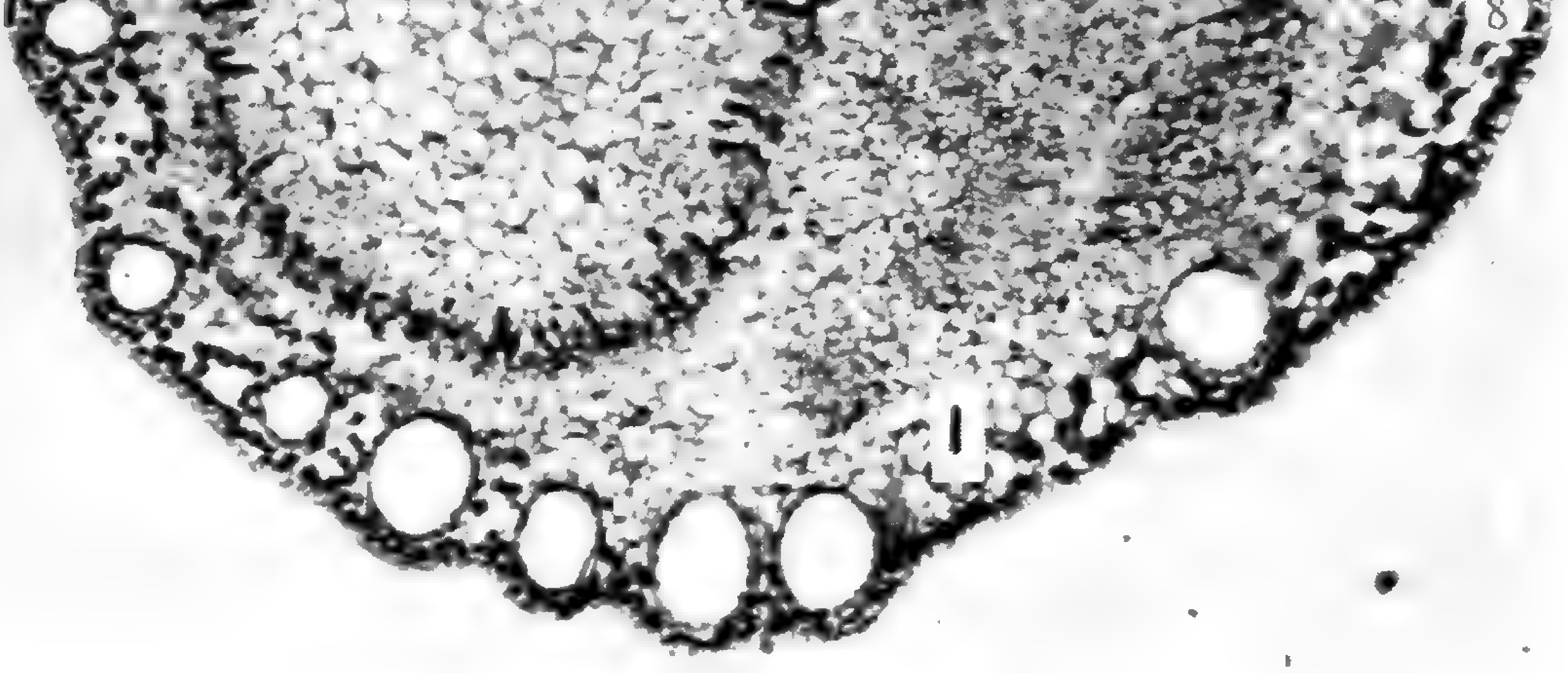
PLATE III

FIGS. 13–16. Field conditions in which *Hymenaea courbaril* is found. 13, typical mature tree with smooth bark, tropical dry forest, Guanacaste, Costa Rica; 14, tree with rugose patches in bark, subdeciduous forest, Guerrero, Mexico; 15, branch showing exuded balls of resin, Guerrero, Mexico; 16, injured root with associated small masses of resin, Guerrero, Mexico.

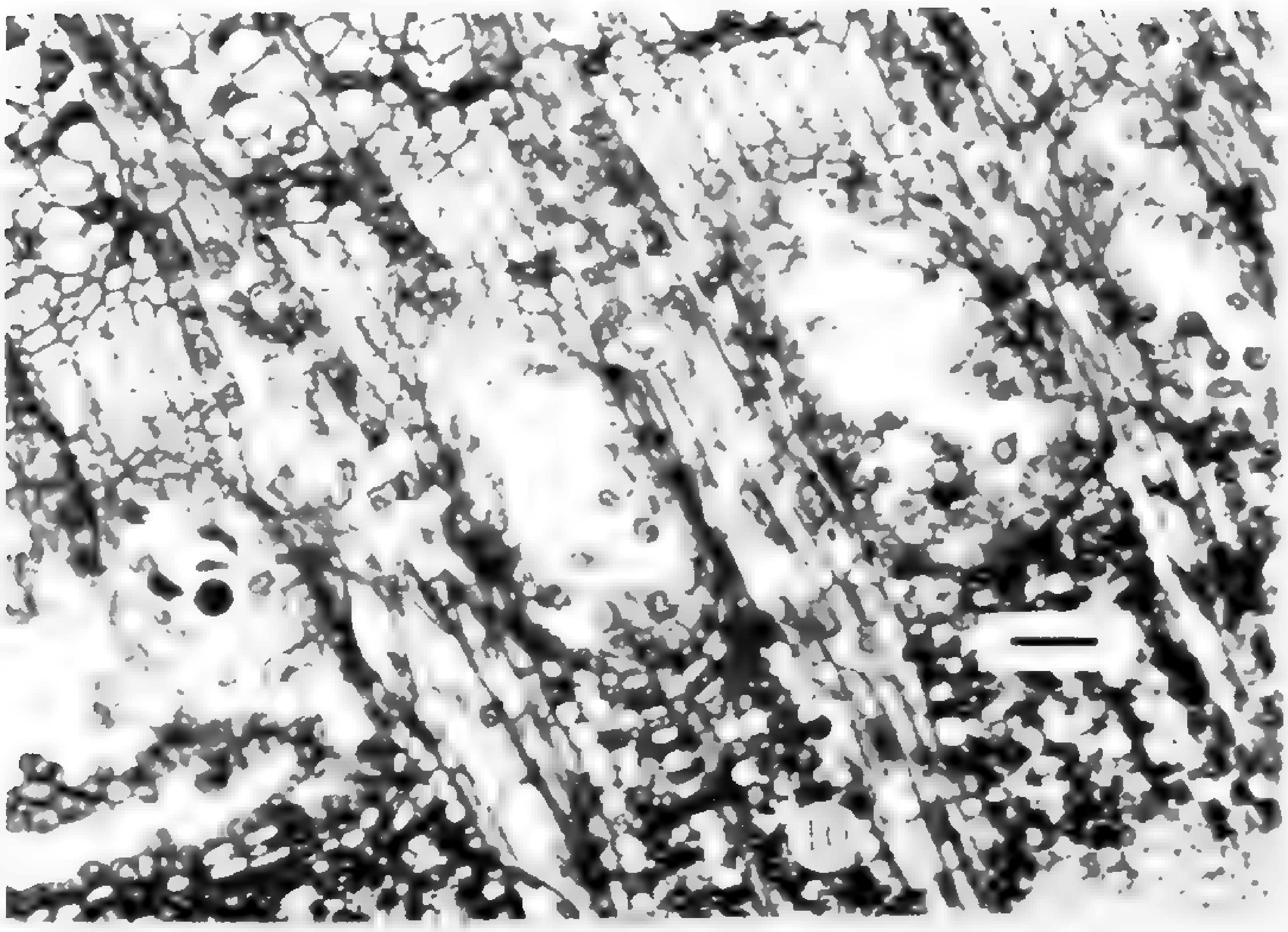


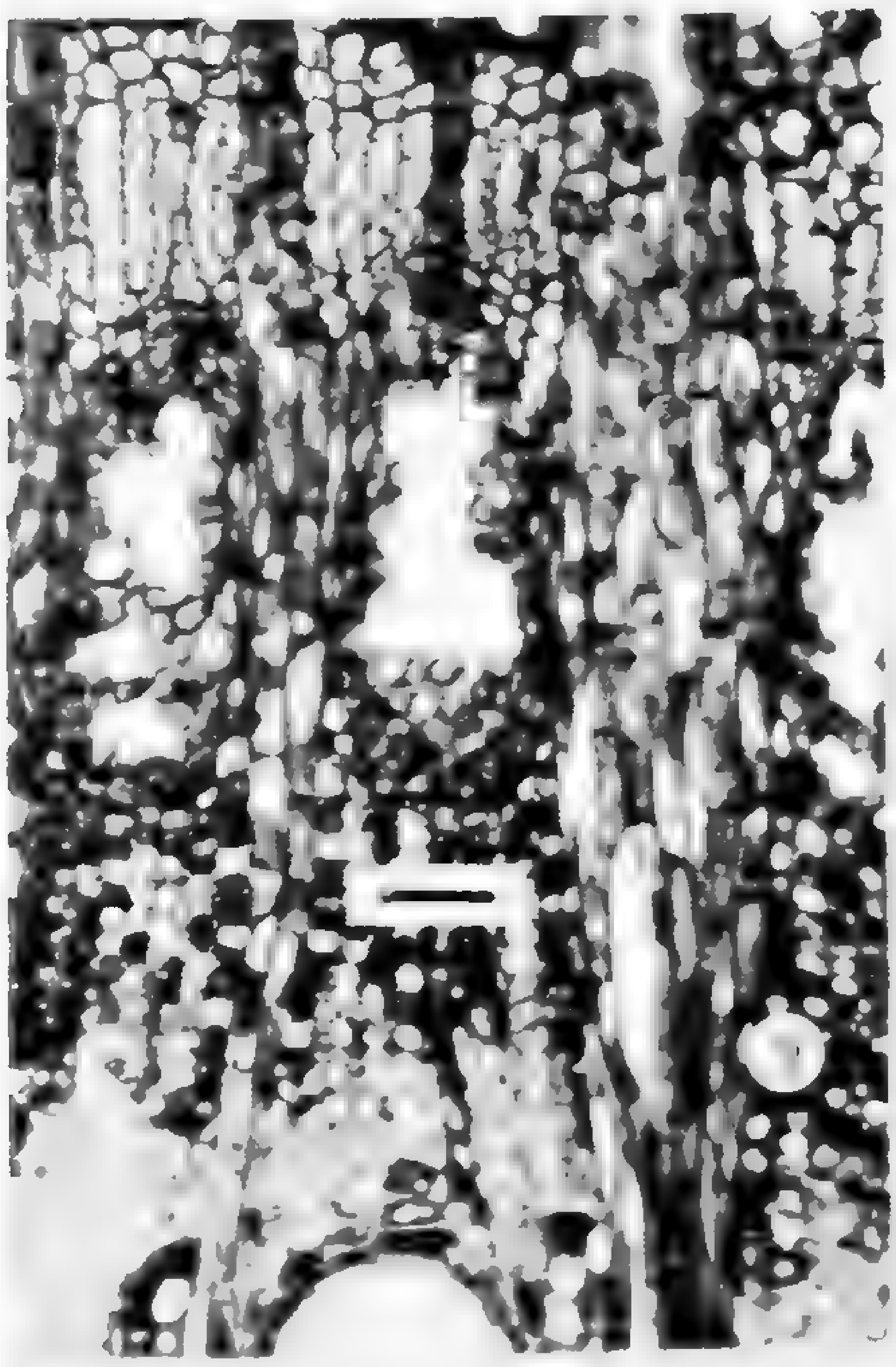


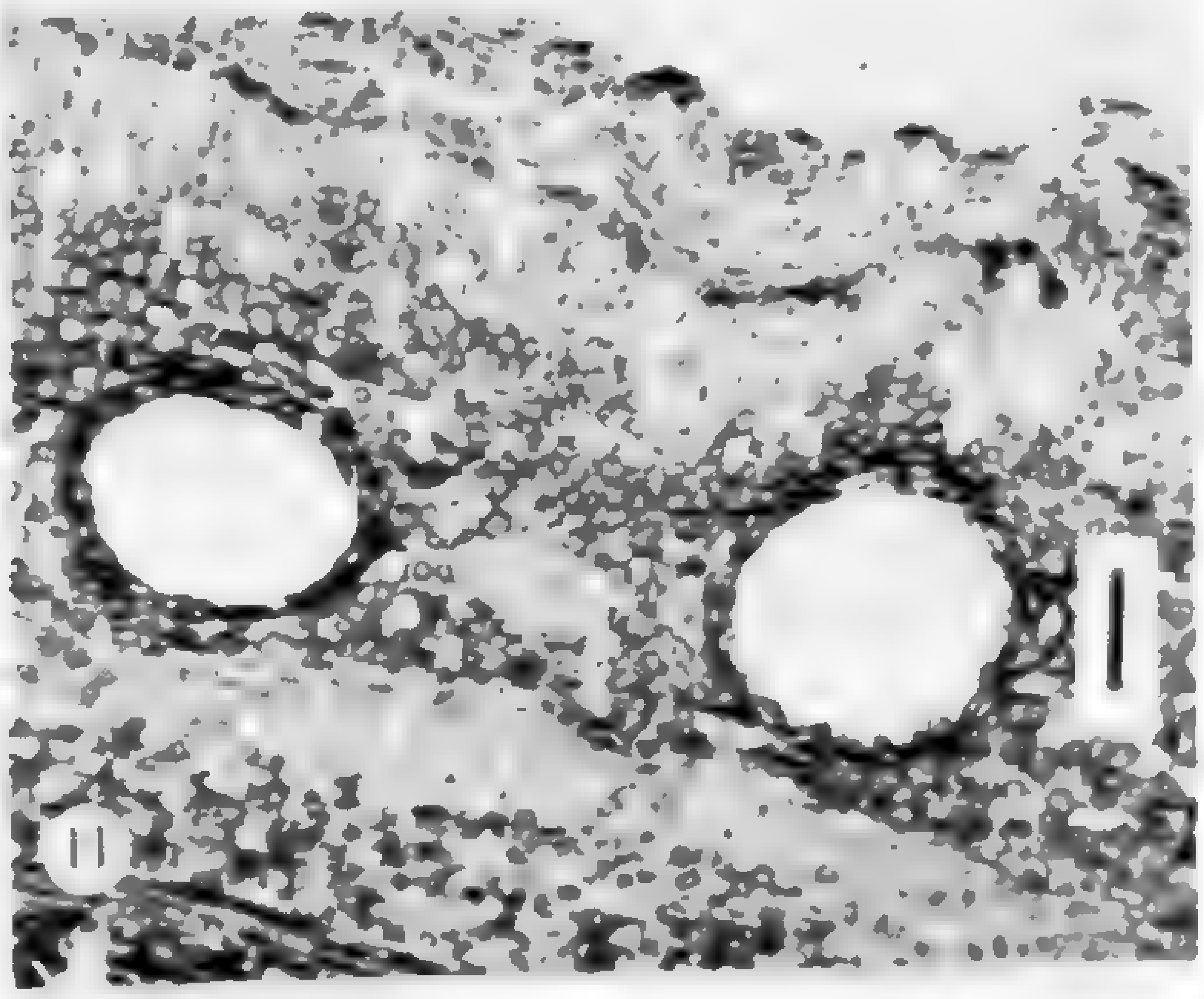


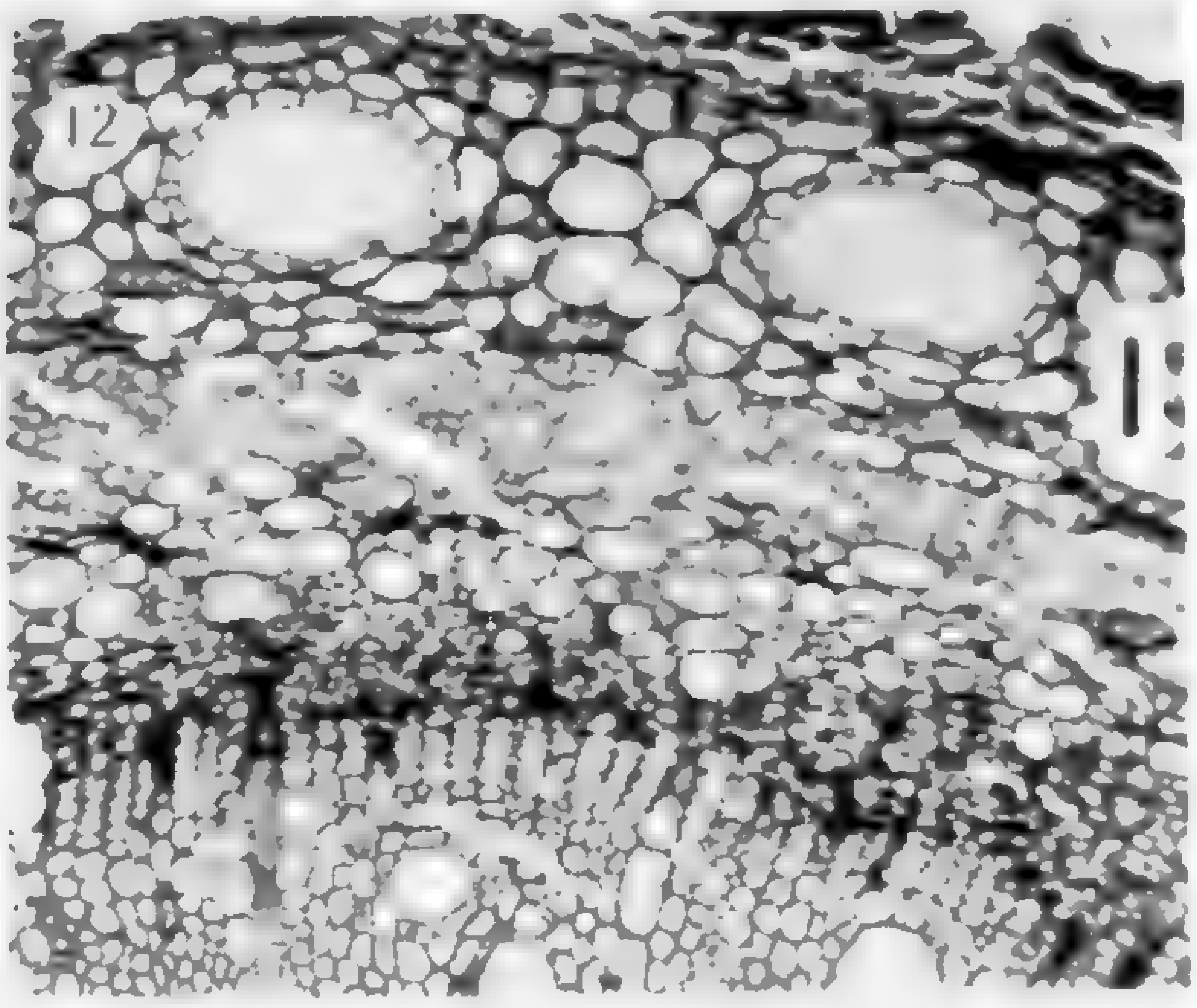


Langenheim, Hymenaea courbaril









LANGENHEIM, HYMENAEA COURBARIL

LANGENHEIM, HYMENAEA COURBARIL

COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, II. THE POLLEN

William C. Dickison

In a previous paper (Dickison, 1967) it was indicated that since a comprehensive comparative morphological investigation of the Dilleniaceae had never been undertaken, such a study might prove very rewarding in the attempt to discover the phylogenetic relationships of this interesting tropical family. The lack of prior morphological work on the Dilleniaceae is particularly evident in the area of pollen morphology. This can be attributed, in part, to the comparatively recent application of palynological data in solving taxonomic problems.

Erdtman (1952) gives a limited description of three genera and seven species of Dilleniaceae. From this treatment he concluded that "pollen morphology seems to support the assumption that Dilleniaceae should be related to Polycarpicae."

In the only other significant reference to dilleniaceous pollen, Barth (1962) described in detail the pollen of four species belonging to the genera *Davilla*, *Doliocarpus*, and *Tetracera*. It was this worker's opinion that the family represented a parallel group to the Magnoliaceae from which it had previously been thought to be derived.

The present study was carried out in order to provide evidence to be evaluated from all organs and parts of the plants in an effort to determine the affinities of the Dilleniaceae.

MATERIALS AND METHODS

Pollen of all ten dilleniaceous genera was examined. The source of material was basically threefold: (1) liquid preserved (FAA) or dried specimens sent to the author; (2) exchange slides from the Harvard Pollen Collections (HPC), Pan American Oil Co., and the Rancho Santa Ana Botanic Garden (RSA) and (3) herbarium specimens obtained from the University of California, Berkeley (UC); Missouri Botanical Garden, St. Louis (MO); New York Botanical Garden (NY); and the United States National Herbarium, Washington (US) to whom I am especially grateful for providing material of the rare genus *Acrotrema*.

Pollen was prepared by the standard acetolysis method outlined by Erdtman (1960). Material was subsequently mounted in glycerine jelly. This procedure generally left grains with a darkened exine which made staining unnecessary. In a few cases, however, a basic fuchsin dye was employed with good results. Difficulty was encountered in removing the protoplasm from grains preserved in formalin-acetic acid-alcohol (FAA). In some samples there was a tendency for the protoplasm to become plasmolyzed into a sphere which was never successfully removed.

The fact that pollen prepared by the acetolysis method is larger than pollen prepared by other means (e.g., lactic acid, KOH, etc.) is now well established (see Canright, 1953). Carlquist (1961) is of the opinion that not enough emphasis has been placed on the fact that pollen morphology is highly influenced by methods of preparation. In a recent discussion of this problem, Whitehead (1965) also stresses the need for a uniform mounting medium; however, he does not recommend glycerine jelly.

Despite opposition to the acetolysis-glycerine jelly method, the ease of preparation, wide application in palynological research, and generally excellent results obtained, justify its employment in comparative morphological investigations.

With the above discussion in mind, in addition to personal experience, I concur with Canright (1963) that pollen size and shape are the most unreliable of diagnostic features.

In order to minimize usage of complex and confusing terminology, the suggestions of Faegri and Iversen (1964) are followed. All measurements and descriptions were made under oil immersion (× 1000). Size dimensions were determined by measuring at least twenty grains from each sample. No effort was made to treat the numerical data statistically. The dimensions are, accordingly, only intended to indicate relative size ranges. Pollen descriptions of putatively related families were obtained for the most part from Erdtman (1952).

OBSERVATIONS

1. **Dillenia** L. (FIGS. 1–3)

The pollen grains of *Dillenia* are the most variable in the family with respect to both sculpturing and aperture type. SHAPE: Oblate, oblate-spheroidal or spheroidal; circular to semiangular in polar view. SIZE:[1] Avg. dimensions for all species examined, ca. 21.7μ (P) × 24.9μ (E). The largest grains were recorded for *D. reifferscheidia* ($25.2\mu \times 32.2\mu$). STRUCTURE: Tectate or rarely semitectate. Endexine generally equal in thickness to ektexine. SCULPTURE: Scabrate to reticulate-rugulate to most frequently reticulate. APERTURE: Triporate in *D. indica* and *D. philippinensis*; tricolpate in *D. turbinata*, *D. reifferscheidia*, *D. alata*, *D. excelsa*, and *D. papuana*; tricolpate with rare or occasional tetracolpate grains in *D. suffruticosa*, *D. ovata*, and *D. luzoniensis*. Triporate grains have elongate pores and are provided with a well-defined annulus. Tricolpate and tetracolpate forms have granular furrows which may or may not have opercular membranes and margo. Furrows extend about three-fourths the length of the polar axis.

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[1] P refers to dimension of polar axis, E the length of equatorial axis.

2. **Hibbertia** Andr. (Figs. 4–6, 21)

Shape: Oblate to spheroidal to prolate spheroidal; circular to subangular in polar view. Size: The smallest grains were recorded for *H. salicifolia* ($18.9\mu \times 17\mu$) and the largest for *H. stricta* ($34\mu \times 32.2\mu$). Avg. size for all species examined, ca. 25.2μ (P) $\times$ 27μ (E). Structure: Tectate; endexine equal in thickness to ektexine. Sculpture: Foveolate (e.g., *H. stellaris* and *H. salicifolia*) to most frequently reticulate. Aperture: Tricolpate, furrows granular, often provided with opercular membrane and margo. Furrows either quite distinct and wide (10μ), in which case they extend the entire length of polar axis (e.g., *H. cuneiformis* and *H. tetrandra*), or else, not well defined and extending about two-thirds the length of polar axis (e.g., *H. hexandra*). Erdtman (1952) describes *H. acicularis* as tricolporate, a condition which was not observed in any of the samples examined in this study.

3. **Pachynema** R. Br. (Fig. 9)

Shape: Spheroidal to prolate spheroidal; circular in polar view. Size: ca. 16.4μ (P) $\times$ 16.1μ (E). Structure: Tectate or semitectate; endexine equal in thickness to ektexine. Sculpture: Foveolate to reticulate. Aperture: Tricolpate, furrows granular and not well defined, extending entire length of polar axis.

4. **Schumacheria** Vahl (Fig. 8)

Shape: Oblate spheroidal; mostly rectangular to spheroidal in polar view. Size: ca. 15μ (P) $\times$ 16.5μ (E). Structure: Tectate; endexine equal in thickness to ektexine. Aperture: Tetracolpate, rarely tricolpate; furrows poorly defined and extending about one-third the length of polar axis. Slight thickening of ektexine at margins of furrows.

5. **Acrotrema** Jack (Fig. 7)

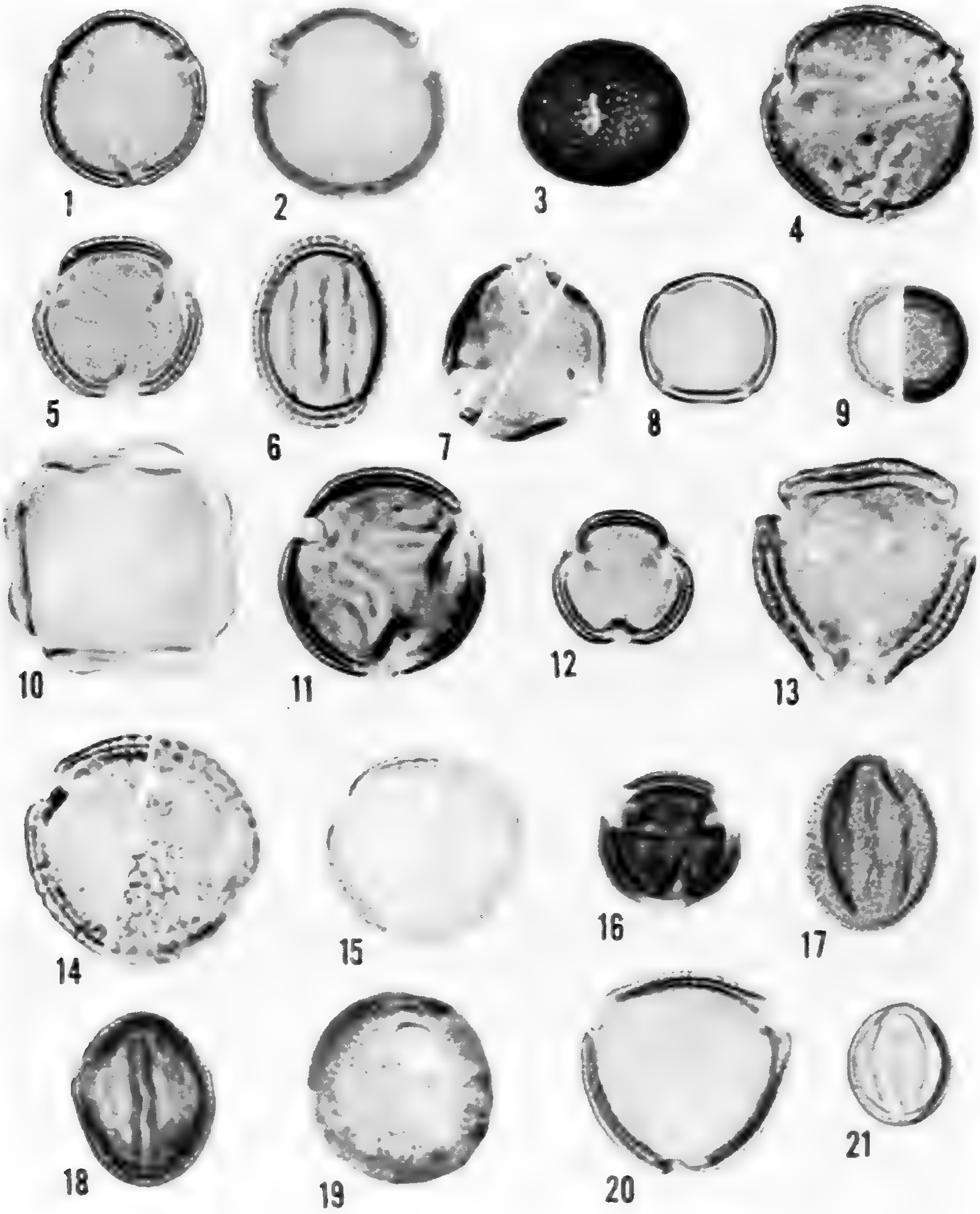
Shape: Oblate spheroidal; semiangular in polar view. Size: ca. 18μ (P) $\times$ 21μ (E). Structure: Tectate; endexine equal in thickness to ektexine. Sculpture: Finely reticulate. Aperture: Tricolpate, furrows granular and provided with opercular membranes.

6. **Didesmandra** Stapf (Fig. 10)

Shape: Oblate spheroidal; mostly rectangular to subangular in polar view. Size: ca. 25.7μ (P) $\times$ 28μ (E). Structure: Tectate; endexine equal in thickness to ektexine. Sculpture: Reticulate. Aperture: Tetracolpate, occasionally tricolpate; furrows extend about one-third the length of polar axis.

7. **Curatella** Loefl. (Figs. 16, 17)

Shape: Spheroidal to prolate spheroidal to occasionally prolate; circular in polar view. Size: ca. 23μ (P) $\times$ 20μ (E). Structure: Tectate;



FIGS. 1–21. Dilleniaceous pollen (all ca. × 1000). 1. *Dillenia suffruticosa* (cult. SING *s.n.*), polar view showing tectate structure. 2. *Dillenia indica* (cult. BRI *s.n.*), polar view. 3. *the same*, equatorial view of elongate pore. 4. *Hibbertia stricta* (HPC *2981*), polar view depicting tectate structure and prominent opercular membranes. 5. *Hibbertia scandens* (cult. K *s.n.*), polar view. 6. *the same*, equatorial view. 7. *Acrotrema bullatum* (US *1576874*), polar view in two focal levels, note granular membranes. 8. *Schumacheria castaneifolia* (*Abeywickrama s.n.*), polar view of tetracolpate grain. 9. *Pachynema dilatatum* (NT *6129*), polar view in two focal levels showing reticulate exine. 10. *Didesmandra aspera* (*Burtt 2540*), polar view showing reticulate exine. 11. *Tetracera fagifolia* (HPC *6270*), polar view showing tectate structure. 12. *Tetracera asiatica* (HPC *1835*), polar view, note opercular membranes. 13. *Davilla rugosa* (HPC *2953*), polar view of tricolporate grain. 14. *Davilla kunthii* (UC *963504*), polar view in two focal levels showing nature of reticulum. 15. *Doliocarpus dentatus*

endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate. APERTURE: Tricolpate, furrows provided with opercular membranes and margo, extending entire length of polar axis. A limited number of grains observed were questionably tricolporate but the occurrence of this feature could never be satisfactorily proven.

8. **Davilla** Vandelli (FIGS. 13, 14)

SHAPE: Spheroidal to subspheroidal; circular to semiangular in polar view. SIZE: Avg. size for all species examined, 26.2μ (P) × 25μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Reticulate to coarsely reticulate (e.g., *D. kunthii*). APERTURE: tricolporate; furrows provided with an operculum. Pores granular, spheroidal to slightly elongate. The pollen of *D. rugosa* has previously been described and diagrammed as tetraporate (Barth, 1962). My observations show that this species possesses three well-defined furrows and is, therefore, tricolporate.

9. **Doliocarpus** Roland. (FIGS. 15, 19, 20)

SHAPE: Spheroidal to prolate spheroidal to prolate; circular to semiangular in polar view. SIZE: Avg. size for all species examined, 24μ (P) × 20.6μ (E). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate to reticulate. APERTURE: Tricolporate, furrows may or may not be provided with a margo extending three-fourths the length of polar axis. Pores indistinct due to opercular membrane, generally circular in outline.

10. **Tetracera** L. (FIGS. 11, 12, 18)

SHAPE: Spheroidal, prolate spheroidal or prolate; circular in polar view. SIZE: Avg. pollen size in this genus can be correlated with geographical distribution. The largest grains occur in the New World species (ca. 26.5μ (P) × 22.7μ (E)), the smallest in the Indo-Malayan species (diam. ca. 18.5μ), whereas African forms are intermediate (ca. 22.8μ (P) × 20.4μ (E)). STRUCTURE: Tectate; endexine equal in thickness to ektexine. SCULPTURE: Finely reticulate to reticulate. APERTURE: Mostly tricolporate, tricolpate in *T. alnifolia*; furrows and pores granular, provided with opercular membranes, pores generally circular in outline.

SUMMARY OF POLLEN MORPHOLOGY OF DILLENIACEAE

The pollen grains of the Dilleniaceae vary in shape from oblate to spheroidal to prolate. The smallest grains were recorded for *Schumacheria castaneifolia* (15μ × 16.5μ), while the largest occurred in *Hibbertia*

(HPC *2962*), polar view in two focal levels. 16, *Curatella americana* (*Irwin 5470*), polar view. 17, *the same*, equatorial view. 18, *Tetracera alnifolia* (MO *1598748*), equatorial view of tricolpate grain with prominent margo. 19, *Doliocarpus major* (HPC *6272*), equatorial view showing well defined pore in granular furrow. 20, *the same*, polar view. 21, *Hibbertia stellaris* (HPC *1837*), equatorial view showing elongate furrows.

stricta ($34\mu \times 32.2\mu$). The median size for all genera examined was ca. 22.4μ (P) $\times$ 21.7μ (E). Pollen was exclusively tectate or rarely semitectate, with no significant difference in thickness between endexine and ektexine. Sculpturing is predominantly reticulate or a modification of reticulate. Four basic aperture types can be recognized as existing within the family: triporate, tricolporate, tricolpate and tetracolpate. Segregation of tricolpate and tetracolpate genera is not always strict because of species in which both conditions exist. Likewise, separation of tricolpate and tricolporate aperture types is often difficult owing to the presence of granular opercular membranes.

DISCUSSION

Dilleniaceous pollen is characterized by a relatively large number of morphological types. Unfortunately, the family cannot be successfully divided into tribes or subfamilies on the basis of pollen morphology. This is due to the variation within and overlap between genera in diagnostic features.

Briefly stated, morphologists now generally agree that the monosulcate pollen grain, with a distal solitary furrow, represents the primitive condition in dicotyledons (Eames, 1961, p. 161). Pollen of this nature is found only in dicot families which are known to have general ranalian affinities. In contrast, the more common tricolpate dicotyledonous grain has three meridional furrows or modifications thereof. It has long been difficult for botanists to explain the derivation of tricolpate pollen from the monosulcate type. Wodehouse (1936) suggested a derivation from a spore bearing a triradiate crest. Such an origin was originally supported by the morphology of certain ranalian pollen grains (*Schisandra*). Wilson (1963) has offered an alternative explanation by theorizing that the tricolpate grain may have resulted from a trichotomosulcate condition (as found in some Canellaceae) by loss of furrow contact at the distal pole. Meeuse (1965) believes that the distal extension of the furrows in some tricolpate dilleniaceous pollen supports the latter hypothesis. Since trichotomosulcate pollen was not observed in any Dilleniaceae, such presumptions can only be looked upon with skepticism.

There are at present no widely accepted trends for pollen specialization above the tricolpate level, although some have been suggested for individual families (e.g., Dahl, 1952). Therefore, it is difficult to assess phylogenetic relationships within the Dilleniaceae on this basis.

If it is assumed, however, that the tricolpate grains with very extended, wide furrows (as illustrated in the woody hibbertias) are the most primitive pollen types in the family, phylogenetic specializations could be hypothesized. Advancement in one line could possibly have led to the tricolporate grain, while in another direction a continuing reduction of furrow length would arrive at the triporate condition. It might also be suggested that there was a trend for the addition of an extra furrow which culminated in the tetracolpate forms. Species with both tricolpate and tetracolpate pollen stand as intermediate in this advancement.

Admittedly, there is no sound basis for this sequence. Since it would be dangerous to correlate pollen morphology with data derived from other parts of the plant, it should be emphasized that the data obtained from palynology alone does not provide evidence for any trends of pollen specialization in the Dilleniaceae.

Few similarities can be observed between the pollen of the Dilleniaceae and that of the ranalian complex of families. This is opposed to the opinion of Erdtman (1952) who advanced such an alliance on the basis of palynological evidence. Pollen grains of the Magnoliaceae and Canellaceae are monosulcate or modifications of monosulcate types (trichotomosulcate and dichotomosulcate). Pollen of the Calycanthaceae varies from monosulcate to zonaperturate (belted) to bicolpate to infrequently tricolpate (Bailey, 1960) and is reticulated or baculate. Winteraceae pollen is shed in tetrahedral tetrads whereas that of Annonaceae is nonaperturate, monosulcate, or occasionally shed in coherent tetrads. A survey of other ranalian pollen forms reveals not a single family which closely approximates the Dilleniaceae in aperture type, size, and/or sculpturing.

Within the Parietales (sensu Engler & Prantl, 1893), the eurypalynous Sterculiaceae and the Eucryphiaceae with bicolpate (syncolpate), very small grains offer no foundation for considering these families closely allied to the Dilleniaceae.

The relationship of the Dilleniaceae to the Brunelliaceae, Ochnaceae, Connaraceae, and Theaceae is not as conclusive. These families all resemble the Dilleniaceae in pollen morphology in having either tri (tetra) colpate or tricolporate pollen, although unusual bilateral, subisopolar, tetracolpate grains are encountered in one subfamily of Connaraceae. Pollen exines in these families are psilate to reticulate with the exception of the baculate Brunelliaceae. Size dimensions are also in approximate agreement.

Information gathered from pollen morphology in determining the affinities of *Actinidia* and *Saurauia* is likewise inconclusive. *Actinidia* is characterized by tricolporate pollen which has an indistinct psilate exine. *Saurauia* pollen is quite variable as evidenced by the occurrence of tricolporate, triporate, and tetra (col) porate grains, as well as coherent tetrahedral tetrads. Exines are all predominantly psilate.

The pollen of *Crossosoma* is tricolporate or bicolporate, prolate, and the grains have reticulated exines. *Paeonia* pollen is tricolporate, with smooth furrows but pores covered by granular membranes, prolate spheroidal and reticulated. The size of the pollen in these two genera closely approximates that of the pollen of Dilleniaceae.

In conclusion, the data presented from pollen morphology does not provide a definite clue to the phylogenetic relationships of the Dilleniaceae. Nevertheless, I believe the comparatively specialized tricolpate, tricolporate, triporate, tetracolpate, and reticulated pollen of the Dilleniaceae clearly shows more resemblances to that of members of the Theales (or Guttiferales) than it does to ranalian families.

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I am extremely thankful to the following individuals who provided me either with preserved or dried specimens and thus made my study of the Dilleniaceae possible: Prof. B. A. Abeywickrama (Peradeniya, Ceylon), Dr. P. S. Ashton (Kuching, Sarawak), Dr. O. M. Barth (Rio de Janeiro, Brazil), Mr. B. L. Burtt (Edinburgh, Scotland), Mr. G. Chippendale (Alice Springs, Australia), Dr. Hj. Eichler (Adelaide, Australia), Dr. S. L. Everist (Brisbane, Australia), Dr. G. W. Gillett (Honolulu, Hawaii), Dr. R. D. Hoogland (Canberra, Australia), Dr. H. S. Irwin (New York, U.S.A.), Dr. H. Keng (Singapore), Mr. M. R. Monsalud (Laguna, Philippines), Dr. J. V. Pancho (Laguna, Philippines), Dr. J. M. Pires (Brasilia, Brazil), Dr. R. L. N. Sastri (Waltair, India), Mr. T. Smitinand (Bangkok, Thailand), Dr. B. C. Stone (Kuala Lumpur, Malaya), Sir George Taylor (Kew, England), Dr. C. L. Wilson (Hanover, New Hampshire, U.S.A.), Mr. J. S. Womersley (Lae, New Guinea), also the Directors of the Singapore Botanical Gardens and of the Forest Research Institute, Kepong, Malaya.

In addition, I am grateful to the various institutions who loaned the herbarium material used in this study.

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MATERIAL EXAMINED[2]

Acrotrema bullatum Thw. CEYLON: US *1576874*.

Curatella americana L. BRAZIL: *Irwin 5470* (NY). PANAMA: *J. F. McBride 2825* (US). MEXICO: UC *1249323*. GUATEMALA: MO *1091094*.

Davilla aspera (Aubl.) Benoist. BRITISH GUIANA: *A. C. Smith 2184* (GH), HPC *1836*. TRINIDAD: *W. E. Broadway 6836* (POM). PANAMA: MO *906390*.

Davilla elliptica St. Hil. BOLIVIA: MO *1810332*.

Davilla kunthii St. Hil. COSTA RICA: *A. F. Skutch 4091* (GH), HPC *2949*. COLOMBIA: UC *963504*.

Davilla multiflora (DC.) St. Hil. MEXICO: MO *1278423*.

Davilla rugosa Poir. MEXICO: *E. Matuda 0902* (GH), HPC *2953*. PERU: MO *1082135*.

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[2] In addition to these institutions previously mentioned, material studied was obtained from the Arnold Arboretum, Harvard University (A); The Forest Herbarium, Bangkok (BKF); Botanic Museum and Herbarium, Brisbane (BRI); Commonwealth Scientific and Industrial Research Organization, Canberra (CANB); Forest Products Research Institute, Laguna (CLP); Royal Botanic Garden, Edinburgh (E); Gray Herbarium, Harvard University (GH); Royal Botanic Gardens, Kew (K); Forest Research Institute, Kepong (KEP); Animal Industry Branch, Northern Territory Administration, Alice Springs (NT); Herbarium of Pomona College, Claremont (POM); Sarawak Museum, Kuching (SAR); and the Botanic Gardens, Singapore (SING).

Didesmandra aspera Stapf. Sarawak: *Burtt & Woods B.2540* (e). Sarawak: SAR *18297.*

Doliocarpus dentatus (Aubl.) Standl. Mexico. Yucatan: *Gentle 1418* (gh), HPC *2962.* Costa Rica: *Skutch 3829* (gh), HPC *6271.* Colombia: UC *584948.* Bolivia: UC *954321.* Costa Rica: MO *1147852.*

Doliocarpus guianensis (Aubl.) Gilg. Costa Rica: MO *1152277.*

Doliocarpus lasiogyne Benoist. Brazil: *Hatschbach 3580* (us). Brazil: UC *1088323.*

Doliocarpus major Gmel. Panama Canal Zone: *P. White 127* (gh), HPC *6272.* Panama: MO *1189259*; MO *1758246.* Brazil: MO *1255920.*

Doliocarpus olivaceus Sprague & Wms. Panama: Yale *11.*

Dillenia alata (DC.) Martelli. Papua: *Brass 7571* (a), HPC *2996. Hoogland 8521* (canb).

Dillenia excelsa (Jack) Gilg. Borneo: *Castillo 619* (a), HPC *2954.* North Borneo: *Cuadra A1019* (us). KEP *s.n.*

Dillenia indica L. Australia: Cult. BRI *s.n.*

Dillenia luzoniensis (Vidal) Martelli ex Dur. & Jacks. Philippines: *J. P. Rojó* (clp) *s.n.*

Dillenia megalantha Merr. Philippines: *Sulit* PNH *6377* (a), HPC *2957.*

Dillenia ovata Wall. ex Hook.f. & Thoms. Indochina: *Squires 775* (a), HPC *2958.* Singapore: Cult. SING *s.n.*

Dillenia papuana Martelli. New Guinea: *Darbyshire & Hoogland 8039* (canb).

Dillenia parviflora Griff. Thailand: BKF *s.n.*

Dillenia philippinensis Rolfe. Philippines: *Lambert & Brunson 39* (us); US *1861993*; *J. V. Pancho s.n.*

Dillenia reifferscheidia Villar. Philippines: *Paniza* PNH *9407* (a), HPC *2960.*

Dillenia suffruticosa (Griff.) Martelli. Philippines: *Fenix 92* (gh), HPC *2961.* North Borneo: *Clemens 9504* (a), HPC *2999.* Singapore: *Canright 978*; Cult. SING *s.n.*

Dillenia turbinata Finet & Gagnep. Hainan: *Ko 52211*, HPC *1838.*

Hibbertia acicularis (Labill.) F. Muell. Australia: *Camfield* (pom).

Hibbertia baudouinii Brongn. & Gris. New Caledonia: US *2192565.*

Hibbertia cuneiformis (Labill.) Gilg. Cult. K *s.n.*

Hibbertia dentata R.Br. Cult. K *s.n.*

Hibbertia hexandra C. T. White. New South Wales: *Hoogland 8585* (canb).

Hibbertia linearis R.Br. ex DC. New South Wales: *Hoogland 7747* (canb).

Hibbertia salicifolia F. Muell. New Caledonia: *Viellard 62* (a), HPC *2968.*

Hibbertia scandens (Willd.) Dryand. Australia: *C. T. White 8237* (a), HPC *2979.* Cult. K *s.n.*

Hibbertia stellaris Endl. Australia: *Pritzel 268* (gh), HPC *1837.*

Hibbertia stricta (DC.) R.Br. ex F. Muell. Australia: *Giblin H19* (a), HPC *2981.*

Hibbertia tetrandra (Lindl.) Gilg. Cult. E *C3544.*

Hibbertia vestita A. Cunn. Australia. New South Wales: *Boorman* (pom).

Pachynema junceum Benth. Australia. Northern Territory: NT *6750.*

Pachynema dilatatum Benth. Australia. Northern Territory: NT *6129.*

Schumacheria castaneifolia Vahl. Ceylon. Waga: *Abeywickrama s.n.*; HPC *2983.*

Tetracera alnifolia Willd. Congo: MO *1598748.*

Tetracera arborescens Jack. Borneo: UC *267698.*

Tetracera asiatica (Lour.) Hoogl. Formosa: HPC *1835.*

Tetracera boiviniana Baill. Tanganyika: UC *1219019.*

Tetracera euryandra Vahl. Malaya: UC *390344.*

Tetracera fagifolia Willd. ex Schlecht. PANAMA: *I. M. Johnston 624* (A), HPC *6270.*

Tetracera indica (Houtt. ex Christm. & Panz.) Merr. SINGAPORE: *H. Keng s.n.*

Tetracera korthalsii var. **subrotunda** (Elm.) Hoogl. BORNEO: NY *21376.*

Tetracera macrophylla Wall. ex Hook.f. & Thoms. MALAYA: UC *243404.*

Tetracera nordtiana F. Muell. PAPUA: NY *5938.*

Tetracera ovalifolia DC. PANAMA: MO *1240100.*

Tetracera podotricha Gilg. NIGERIA: MO *1608756.*

Tetracera portobellensis Buerl. MEXICO: MO *1810305.*

Tetracera scandens (L.) Merr. PHILIPPINES: *Ahern's Coll. 104* (A), HPC *2991.* HAINAN: UC *278563.*

Tetracera volubilis L. PERU: *Schunke 168* (A), HPC *2995.* BRITISH HONDURAS: MO *1065132.*

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THE CHROMOSOMES OF AUSTROBAILEYA

Lily Rüdenberg

The phylogenetic relationships among the families of the primitive Ranales of Engler and Prantl have been of great interest to systematic botanists. A comprehensive knowledge of this group is vital for an understanding of the evolution of early angiosperms. The relative taxonomic position of the families and their included genera within the Ranales has been difficult to determine primarily because the primitive characteristics of these plants are often paired with advanced or reduced specialized ones. To the present, a majority of studies on the group has been concerned with and based on macroscopic observations and on anatomical-morphological features. Now, it is important to supplement this information by an investigation of the chromosome numbers and karyotypes of some of these plants.

No karyological studies exist for some of the families of this complex. No chromosome counts have been published for any members of the Amborellaceae, Austrobaileyaceae, Gomortegaceae, Gyrocarpaceae, and Trimeniaceae (Raven & Kyhos, 1965). The present note is a report on the chromosome number and karyotype of *Austrobaileya.*

Plants of *Austrobaileya* were first collected in 1929 by Kajewski in Northern Queensland. White (1933) described *A. scandens* from this material. From the beginning, the taxonomic position of this plant posed difficult problems. It was studied by White (1933, 1948) and Croizat (1941, 1943) and its taxonomic position was changed several times. Bailey and Swamy (1949) discussed the merits of these changes on the basis of detailed investigations on the morphology and anatomy of the plant. Their material included specimens from the two species *A. scandens* and *A. maculata* C. T. White. The genus is composed of only these two species and is placed in a separate family, the Austrobaileyaceae, which is considered an independent ranalian family with close affinity to the Monimiaceae.

MATERIALS AND METHODS

Seeds of *Austrobaileya* sp. were collected near Ravenshoe, North Queensland, Australia, *Webb & Tracy 6301.* Four seeds of this collection were sown at the Arnold Arboretum in 1964. Only one seed germinated almost a whole year later. The seedling was potted in 1965 and cuttings made in 1966.[1] It must be mentioned that there is some difficulty in

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[1] The assistance of A. J. Fordham, propagator of the Arnold Arboretum, is gratefully acknowledged. The author is greatly indebted to Dr. L. I. Nevling, Jr., for his advice and reading of the manuscript.

species determination and in Bailey and Swamy's opinion there is a question ". . . . whether there actually are two distinct species of overlapping ranges." On the basis of vegetative characteristics, our plants seem to resemble most closely the isotype of *A. scandens*; up to now these plants have not flowered.

Squashes were prepared from actively growing roots. The root-tips were pretreated for four hours in cold oxyquinoline (0.002 Mol.) or, for the purpose of comparison, in 0.05 per cent colchicine. They were fixed overnight in three parts absolute ethyl alcohol to one part glacial acetic acid, hydrolyzed in 1 N. HCl for 25 minutes, stained with leuco-basic fuchsin and squashed in diluted aceto-carmine. Slides were made permanent following the freezing technique of Conger and Fairchild (1953). Observations were made with a Zeiss phase microscope.

CYTOLOGY

A somatic chromosome number of $2n=44$ for *Austrobaileya* is shown in FIGURE 1. In the cell photographed most chromosomes are clearly visible, only one of them, probably the shortest one, lies across another chromosome of median length and is somewhat obscured. In the karyotype the homologues have been arranged in pairs, each pair in sequence according to decrease in length. The two longest pairs are approximately 8 and 6.4μ long, the shortest pair only 2.6μ.

Some of the chromosomes have a distinctive morphology and are definitely present only in duplicate. Most conspicuous in this respect is the longest pair with submedian centromere and the pair next in length, also submedian, with a long satellite. The satellite has the same width as the chromosome and is about one half as long as the chromosome arm to which it is attached. In several other cells the satellites became detached from the chromosomes at the secondary constrictions. Furthermore, there are two metacentric chromosome pairs in the somatic complement, each pair of a different length. The majority of the remaining chromosomes have subterminal centromeres. However, the proportion of short arm to whole chromosome length is not the same in all of them. A comparison of the individual lengths of some of the homologues may be slightly misleading because of the high magnification of the photograph by which small differences due to pressure and stretching are greatly multiplied. Nevertheless, based solely on observations of their similar morphology some of the subterminal chromosomes appear to be present in fours.

DISCUSSION

The chromosomes of *Austrobaileya* are highly asymmetrical and represent a specialized karyotype in their unequal size. Most woody angiosperms have small chromosomes with relatively few variations in size. The chromosomes of a number of ranalian families are generally larger

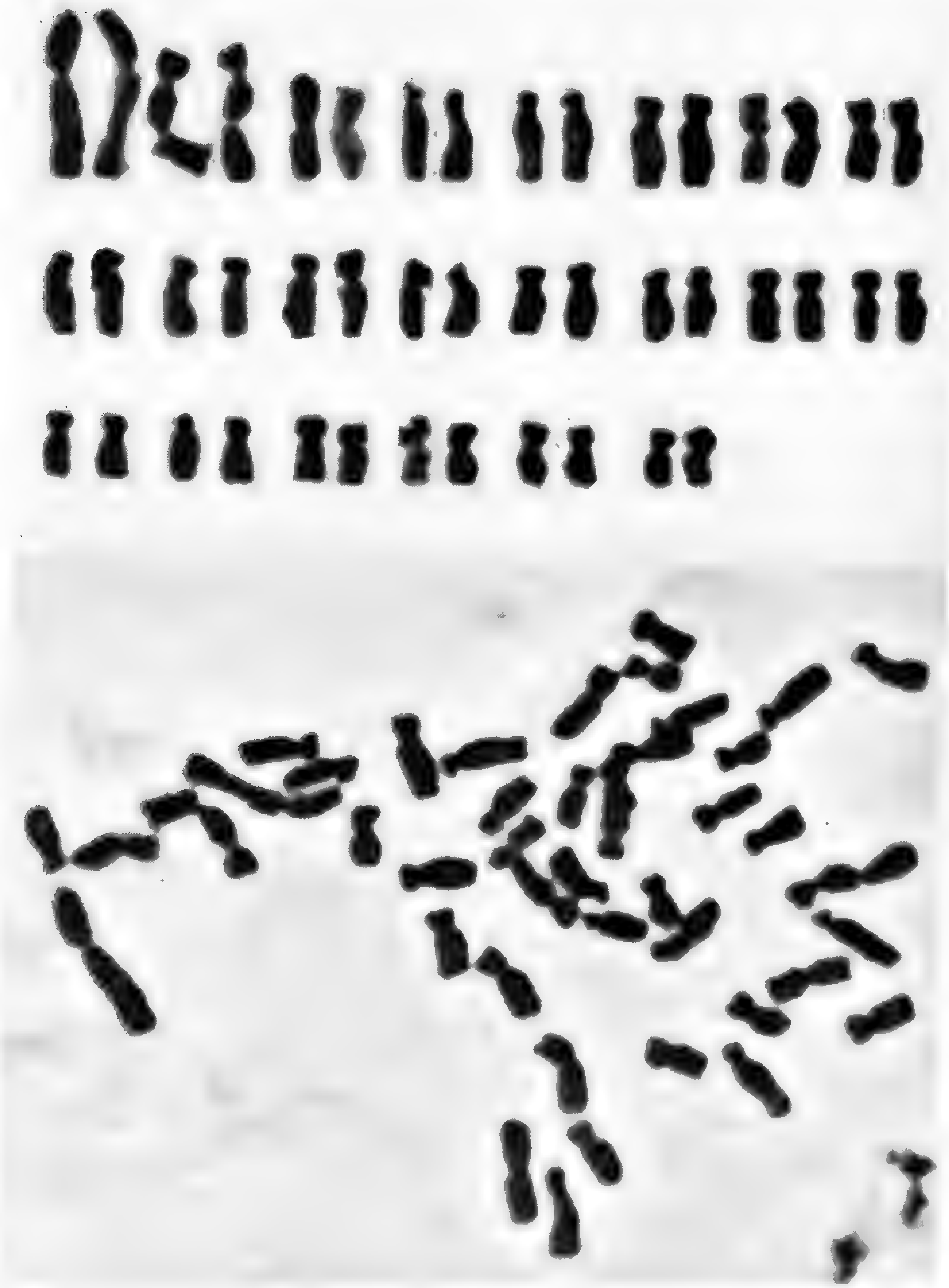

FIG. 1. ABOVE: Karyotype reconstructed from a cell of *Austrobaileya*. BELOW: This cell at mitotic metaphase with 2n = 44 chromosomes. × 2,500.

(Stebbins, 1938). Still larger chromosomes, however, of more equal size are found in Gymnosperms, Gnetales, and Cycadales. Many specialized monocots have relatively large chromosomes of unequal morphology in the same gametic complement together with much smaller chromosomes.

Such size differences are in some cases greater than those observed in *Austrobaileya*.

A chromosome count of $2n=44$ is rare among families of the ranalian complex. For two genera of the Monimiaceae this chromosome number has been reported. In pollen mother cells at meiosis the chromosomes pair to form 22 bivalents in *Laurelia novae-zelandiae* A. Cunn. (Hair & Beuzenberg, 1959). A species of the genus *Kibara* from East New Guinea has $2n=44$ chromosomes (Borgmann, 1964). No karyotype of this species has been published and, therefore, it is not yet possible to determine whether the chromosome complements of *Austrobaileya* and *Laurelia* and *Kibara* show an affinity or whether their equal numbers represent an insignificant coincidence. A similarity of karyotype and number could reflect a taxonomic relationship of these genera which would be particularly meaningful in woody plants which are cytologically more stable than herbaceous plants.

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CORONANTHERA GRANDIS (GESNERIACEAE), A NEW SPECIES FROM THE SOLOMON ISLANDS

GEORGE W. GILLETT

THE GENUS *Coronanthera* C. B. Clarke includes eleven species, ten of which are restricted to New Caledonia. A single species, *C. australiana* C. T. White, was described from material collected in Queensland. However, S. L. Everist (personal communication) indicates that White in a later collection (*White 10548*, Sept., 1936) confirmed that the Queensland species has fleshy, indehiscent fruits. This character would exclude it from *Coronanthera* and also from the tribe Coronanthereae, as delineated by Burtt (1962). Therefore, the presence of the genus in Australia may be questioned.

The tribe Coronanthereae is assigned by Burtt (*op. cit.*) to the subfamily Gesnerioideae, and is comprised of *Coronanthera*, *Rhabdothamnus* A. Cunn. (1 sp., New Zealand), *Negria* F. Muell. (1 sp., Lord Howe Island), and *Depanthus* S. Moore (based on *Coronanthera glabra* C. B. Clarke, New Caledonia). These four genera, in addition to the genus *Fieldia* F. Muell. (1 sp., S. E. Queensland) of the tribe Mitrarieae, constitute the total representation in the Old World of the large (over 70 genera) New World subfamily Gesnerioideae. It is perhaps noteworthy that this representation occurs in a somewhat limited phytogeographic area that includes New Zealand, Lord Howe Island, New Caledonia, and Queensland. The additional species of *Coronanthera* described in this paper is a first record for the Coronanthereae in the Solomon Islands. It is significant that the area of distribution presently excludes New Guinea, but it probably would not be excessively speculative to predict the representation of the Coronanthereae on that island.

The Coronanthereae are characterized by dehiscent fruit and cymose inflorescences. In the genus *Coronanthera*, the fruit dehisces along the sutures of the four apically coherent valves (FIG. 1, H). Dispersal, apparently, is by means of the shaker action of the capsule and the subsequent transport, by wind, of the very light seeds. It is this highly distinctive fruit that enabled me to recognize specimens of the new species in a survey of South Pacific material of the genus *Cyrtandra*.

Coronanthera grandis G. W. Gillett, sp. nov. FIG. 1.

Frutex procerus vel arbor ad 15 m. alta. Folia, ramuli et inflorescentia pilis velutinis septatis non capitatis 50–100μ diametro, 1–2 mm. longis. Ramulis teretibus, 3–6 mm. diametro. Folia opposita, in eodem pari aequalia, petiolus gracilis, velutinus, 2–5 cm. longus, lamina elliptica

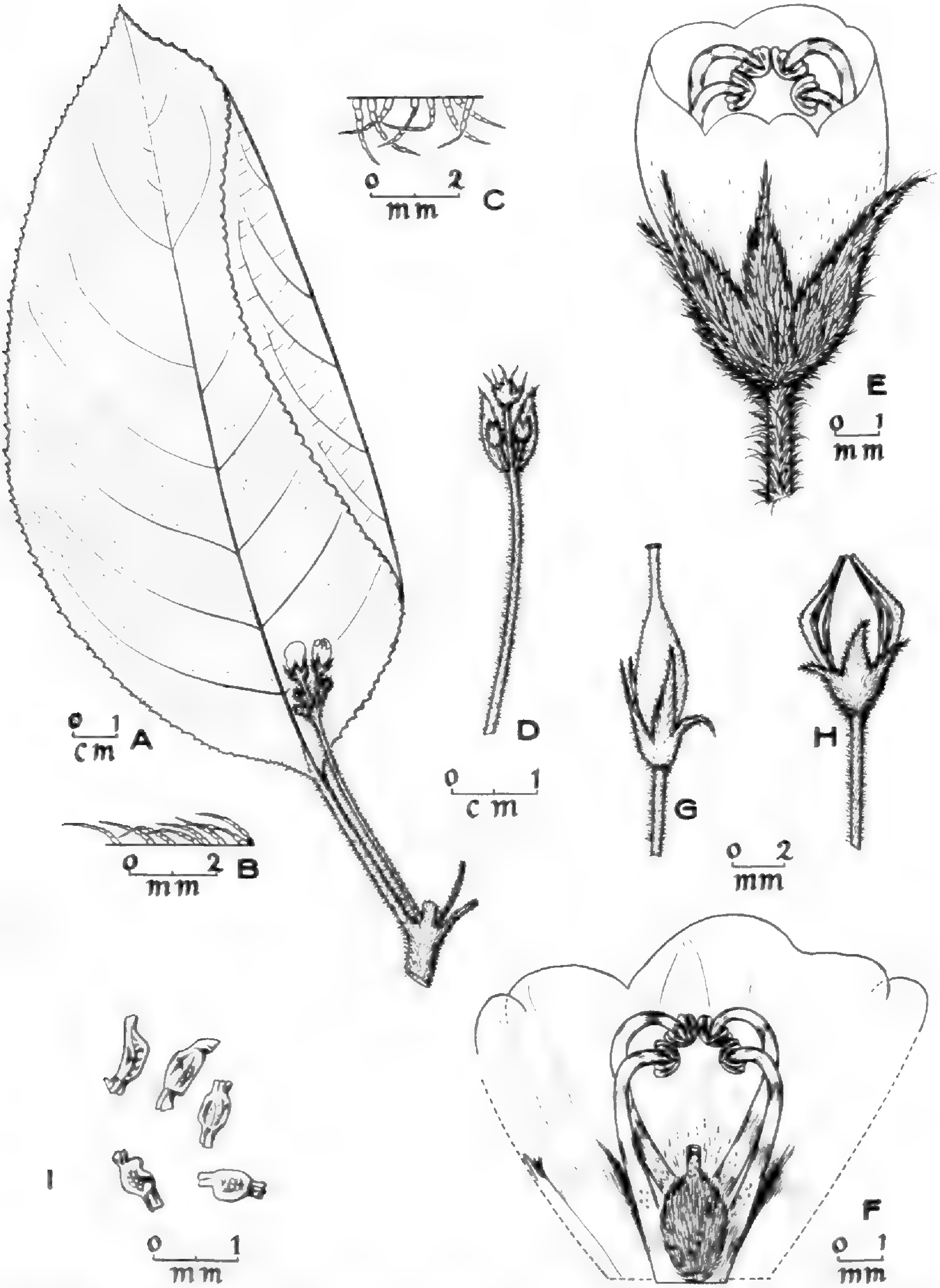

FIG. 1. *Coronanthera grandis* G. W. Gillett. All drawings from *Kajewski 1749*. A, leaf and axillary inflorescence; B, upper leaf surface showing antrorsely appressed sericeous hairs; C, lower leaf surface showing spreading hairs; D, cymose inflorescence, bracts, and peduncle; E, posterior view of flower; F, flower with corolla opened out on the posterior sinus; G, capsule prior to dehiscence; H, dehiscent capsule showing longitudinal fissures; I, seeds.

usque ovata, 12–20 cm. longa, 7–12 cm. lata, basis rotundata usque acuta, apex acutus usque acuminatus, margines serrati usque serrulati (3–8 dentibus in quoque cm.), superne pubescentia appressa sericea instructa, inferne dense villosa, nervi secondarii in quoque latere 6–8, curvi sursum, subter prominulis, venulae reticulatae supra obscurae, subter prominulae. Cicatrices foliorum conspicuae in ramulos, obtriangulares, infra rotundatae, 2–3 mm. latae, cicatrice fasce magna centrali. Inflorescentia axillaris cyma, floribus 3–8, pedunculus gracilis, 1 mm. diametro, 3–10 cm. longus, dense pilosus, ad apicem bracteatus, bracteae duae, aequales, lanceolatae vel ovatae, 10–15 mm. longae, 2–5 mm. latae, pilosae, caducae, pedicelli inaequales, 1–2 cm. longi per anthesin, crescens ad 2–4 cm. quum capsulae maturae. Calyx 1 cm. longus, fissus per ⅔ longitudinis sua in lobos lanceolatos, aequales, acuminatos, extus intusque sericeus. Corolla urceolata, flavovirens, 8–10 mm. longa, 4–5 mm. lata, fissa inaequalis 1–3 mm. in lobos rotundatos, extus sericea intus superne glabra, inferne pilosa rare, limbus corollae bilabiatus, recurvus, labio superiore lobis duobus aequalibus 1 mm. longis, 1 mm. latis instructo, labio inferiore lobis tribus inaequalibus 1.5–2 mm. longis, 2–4 mm. latis. Stamina 4, filamenta aequalia, 6 mm. longa, 2 mm. ad tubum corollae affixa, 4 mm. liber, curvata superne versus centrum floris, superne glabra, inferne indumento sparso pilorum capitatorum instructa, antherae aequales, sagittatae, cohaerentes, facientes figura lunata adversus basem labi inferni corollae. Staminodium 1, 4 mm. longum, 3 mm. ad tubum corollae affixa, 1 mm. liber, pars libra portata ad altitudinem stigmatis, adversus sinum superum corollae. Gynoecium 5 mm. longum, ovarium ovoideum, 3 mm. longum, 1.5 mm. latum, piloso pilorum non capitatorum ascendentium instructo, uniloculare, placentis 2 parietalibus instructo, stylus 1 mm. longus, cylindraceus, superne glaber, inferne indumento sparso vel denso pilorum capitatorum instructus, stigma peltatum integrum, in centro depressum. Fructus capsula fusca, ovoidea, subulata, tomentosa, 8–10 mm. longa, 3–5 mm. lata, quadrivalvis, valvae ad apices connatae, inferne fissuris tenuibus longitudinalibus separatae, fissurae 5–6 mm. longae, 0.5–1 mm. latae, seminibus per fissuras laterales elapsis. Semina numerosa, fulvo-brunnea, ovoidea, fusiformes, 0.75 mm. longa, 0.4 mm. lata, testa reticulato-foveolata. Holotypus *Kajewski 1749* (A), insula Bougainville.

Solomon Islands (Australian Territory of Papua and New Guinea). BOUGAINVILLE ISLAND, Crown Prince Range: Kupei Gold Fields, 900 m. (Rupei, near Kieta), April 22, 1930, *Kajewski 1749* (A, holotype; BISH, isotype); Koniguru, 950 m. (near Buin), *Kajewski 2122* (A, BISH). SANTA YSABEL ISLAND (British Solomon Islands Protectorate): Kakatio, 900 m., *Brass 3252* (A, BISH).

The local name on Bougainville Island is "Coru-cokor" (*Kajewski 2122*), while on Santa Ysabel Island it is "Momona" (*Brass 3252*).

Appreciation is extended to Drs. Richard A. Howard, Director of the Arnold Arboretum of Harvard University, and Roland Force, Director of the Bishop Museum, who permitted me to examine specimens under

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A SYNOPSIS OF THE ASIAN SPECIES OF DELPHINIUM, SENSU STRICTO

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As IN THE PAPER on the Asian species of *Consolida* (Jour. Arnold Arb. **48**: 159–202. 1967), the present article deals with plants from the Asian mainland and does not include the islands to the west in the Aegean and Mediterranean seas. The same herbaria, for the most part, have made loans and furnished material, as indicated in that paper (pp. 159, 160). I again acknowledge my indebtedness for and express my appreciation of the many courtesies and much help received. Additional aid is recorded from time to time in the body of this paper under individual species concerned.

It is a pleasure, too, to acknowledge obligations to National Science Foundation funds for Grant Number GB-2716, which very greatly helped, especially in work in European and British centers, and in partly meeting the cost of publication.

A discussion in the earlier paper presented the characters of the segregate genus *Consolida* (pp. 160, 161). There follow now a description of *Delphinium* in the more restricted sense and a synoptical treatment of the large number of Asian species. Unfortunately, herbarium material has not been available for all of those described, especially many first proposed by W. T. Wang (Acta Bot. Sinica **10**: 59–89, 137–165, 264–284. 1962). Fortunately, the Royal Botanic Garden at Edinburgh received photographs of types of some of these species and I have found isotypes and other cited material in various American herbaria, especially in the large collection of unidentified Chinese specimens at the Arnold Arboretum. I am very much indebted to Dr. Shiu-Ying Hu of the Arboretum staff for translating critical passages and otherwise helping me with the Wang paper. In the same way, I gladly acknowledge the aid received from Mrs. Myra White, librarian of the Rancho Santa Ana Botanic Garden, whose ability to read Russian has helped with many passages in books dealing with the plants of the U. S. S. R. and with deciphering herbarium labels.

Since the publication of the monograph on *Delphinium*, sensu lato, by E. Huth (Bot. Jahrb. **20**: 322–499. *pls. 6–8.* 1895), which has to be the basis for all subsequent study of the group, many students have expressed their dissatisfaction with two principal features.

(1) *The subdivisions of the genus as set up by Dr. Huth.* The genus *Delphinium* has some quite natural and well characterized subgroups or botanical sections. Others, both of Huth and Wang, seem meaningless to me and separate related species rather widely. For my purpose, therefore, I have keyed out the Asian species into ten Groups which I shall treat, in sequence, as Group I, Group II, etc. Where these seem to be of botanical

significance I shall so indicate. In most cases they may be quite artificial assemblages. For the most part, to facilitate finding the descriptions, the species under the larger groups are treated alphabetically. In some cases the same species is keyed out in more than one group.

(2) *Typification of some of Huth's varietal proposals.* Quite often no specimen is cited under a new variety and there is doubt as to what the taxon was meant to include and where it should come in the synonymy.

A paper, such as mine, is obviously a tentative treatment. Lack of more herbarium material, inability to do field work, recognition of the fact that the species of *Delphinium* hybridize freely, all such matters preclude the possibility of a truly monographic treatment. It is hoped, however, that the more than two years spent in this study and the examination of perhaps 6000 herbarium sheets make possible a more precise treatment for identification of Asian collections than we have yet had.

DELPHINIUM L.

Delphinium, as a genus, L. Sp. Pl. 1: 530. 1753; Gen. Pl. ed. 5. 236. 1754. E. Huth, Bot. Jahrb. **20**: 322–499. *pls. 6–8.* 1895. As a subgenus, *Eudelphinium* (Huth) Dalla Torre & Harms, Genera Siphonogamarum 165. 1901.

Mostly perennial, more rarely biennial or annual, herbs; if perennial, with tuberiform compact roots or a woody deep-seated rootcrown or rhizome-like base with fibrous roots. Stems erect or ascending or much reduced. Leaves basal or cauline or both, persistent or withering early (especially the basal ones), palmatifid or lobed, often further divided or dissected. Flowers mostly in terminal racemes or panicles, sometimes only 1 or 2 on a stem. Pedicels subtended by more or less foliose bracts and bearing bractlets, the latter usually reduced and often two in number. Flowers zygomorphic. Calyx colored, of 5 sepals, the upper or posterior one spurred, the 2 lateral alike and the 2 lower alike. Petals 4, in 2 unlike pairs, the upper pair produced into nectariferous spurs that extend into the sepal spur and the upper part or lamina more or less cleaver-shaped; the lower pair with a slender claw and an expanded lamina which is often vertical to the claw. Stamens usually included, in 8 spiralled series, with filaments somewhat broadened and anthers short. Carpels 3–5, usually free, becoming follicles. Seeds mostly obpyramidal, winged or wingless at the angles, the surface variously beset with overlapping scales in transverse rows or ridged.

Type species, *Delphinium peregrinum* L.

KEY TO GROUPS OF ASIAN SPECIES OF DELPHINIUM

A. Plants annual or biennial; petals glabrous and not ciliate.
    B. Limb of upper petals with a lateral wing on one side and not clawed.
        C. Leaf-blades palmately divided; lower petals not deeply divided. .... GROUP I.

C. Leaf-blades pinnately divided; lower petals usually deeply divided. .... GROUP III.

B. Limb of upper petals not winged on one side; upper petals with short claw. .... GROUP II.

A. Plants perennial; lower petals bearded and/or ciliate.
  D. Roots tuberous, clustered, short, vertical; flowers small (the sepals to ca. 1 cm. long), usually rather crowded in short-pedicelled (mostly to 1 cm.) often dense racemes; at least the upper leaves dissected into linear or oblong laciniae. Plants of rather arid regions, Mediterranean Region to Turkestan, Afghanistan, West Pakistan. .... GROUP IV.
  D. Roots not tuberous, but mostly slender or cylindrical, rhizome-like; flowers mostly larger and often on longer pedicels.
    E. Plants mostly very hairy; flowers mostly large, the sepals 2 cm. or more long, veiny, dry and papery in age, more or less persistent; plants low; spur thick, 4–10 mm. in diameter at its base, conical to decurved. Largely central Asia. .... GROUP V.
    E. Plants usually less hairy; sepals not so veiny and papery, caducous; spur more slender.
      F. Leaves dissected into linear, more or less oblong ultimate segments 1–3 mm. wide.
        G. Stems with some well developed leaves. .... GROUP VI.
        G. Stems without leaves or with 1 or 2 reduced ones. GROUP VII.
      F. Leaves with broader, lanceolate to ovate ultimate divisions that are mostly over 5 mm. wide.
        H. Spur not or scarcely uncinate.
          J. Petals not darker than the sepals. .... GROUP VIII.
          J. Petals darker than sepals, almost black. .... GROUP IX.
        H. Spur uncinate, often forming a half circle. ...... GROUP X.

It is my feeling that the present knowledge of the species of *Delphinium* growing in Asia is entirely inadequate in most cases to make any attempt whatsoever to recognize subspecies or varieties, at least by a person like myself whose work on the group has had to be entirely in the herbarium and not at all in the field. In the first place, I am confident that many of the taxa which I am recognizing as species will not retain that status. In the case of those, and of many others, no specimens were actually seen by me, although altogether I have probably had the opportunity of studying more than 6000 sheets. In some cases letters asking for loans or bits of material have not been answered up to now. In others, so few specimens were available that it was impossible to get the feel of the species, its variability or the geographical or zonal range for these variations. I am therefore, almost without exception, attempting only to differentiate what seem to me to be possible species, keying them and describing them as well as the scanty material allows, and not attempting to treat their subdivisions.

GROUP I

Mostly annual or biennial. Petals glabrous, the upper winged on one side, not clawed. Limb of lower petal not deflexed. Seeds numerous, rounded, with transverse rows of closely overlapping scales.

This group happens to coincide with the section *Delphinium,* as recognized by Pawlowski, Fragm. Flor. et Geobot. 9(4): 437. 1963, and with the section *Delphinellum* DC. Syst. **1**: 346. 1817. The type species is *D. peregrinum* L., the type of the genus *Delphinium.*

KEY TO SPECIES

1. Limb of lower petals longer than wide, cuneate at base, gradually narrowed into a claw.
    2. The limb of the lower petals obovate, ca. as long as the claw; limb not or scarcely exserted. Eastern Mediterranean. .... 1. *D. peregrinum.*
    2. The limb of the lower petals elliptic-ovate, shorter than the claw and more or less exserted.
        3. Claw of lower petals ca. 6 mm. long; plant glabrous to strigulose. Turkey to Jordan and Palestine. .... 2. *D. virgatum.*
        3. Claw of lower petals ca. 4 mm. long; plant hirtellous or spreading-pubescent. Sinai Peninsula. .... 3. *D. nanum.*
1. Limb of the lower petals more or less rounded to quadrate, abruptly narrowed into a longer claw, the limb more or less exserted.
    4. Mature follicles sublinear, closely parallel, 10–12 mm. long; spur up to one and one-half times as long as the sepals. Turkey. .. 4. *D. cinereum.*
    4. Mature follicles broadly oblong, 5–8 mm. long; spur ca. twice as long as sepals.
        5. Racemes lax, linear, several-flowered; median cauline leaves thick in texture, with cuneate lobulate lobes. Turkey. ..... 5. *D. venulosum.*
        5. Racemes dense, oblong, many-flowered; median cauline leaves thin, with lance-linear ultimate divisions. Turkey. .... 6. *D. davisii.*

1. **Delphinium peregrinum** L. Sp. Pl. 1: 531. 1753. FIG. 1, A.

Delphinium forskölii Reichb. Illustr. Sp. Acon. **5**: 68, *t. 5.* 1823–27. Type material seen (BM).

Delphinium junceum DC. Fl. France **5**: 641. 1815.

Delphinium peregrinum subsp. *junceum* Batt. Fl. Alg. 16. 1888.

Delphinium peregrinum var. *junceum* Huth, Bot. Jahrb. **20**: 475. 1895.

Delphinium peregrinum var. *subvelutinum* DC. Syst. **1**: 348. 1817. Pubescent form based on Italian material.

Delphinium bovei Decaisne, Ann. Sci. Nat. II. **4**: 356. 1835. Type *Bové 130* from between Suez and Gaza. This number seen (K).

Delphinium peregrinum var. *eriocarpum* Boiss. Fl. Orient. **1**: 87. 1867. Based on plants from Caucasus with pubescent fruits.

Delphinium eriocarpum (Boiss.) Halacsy, Consp. Fl. Graeca **1**: 32. 1901.

Delphinium junceum DC. var. *subvelutinum* Ledeb. Fl. Ross. **1**: 59. 1841.

Delphinium peregrinum var. *eriocalyx* Post, Fl. Syria, Palestine Sinai. 46. 1896.

Delphinium subvelutinum Heldr. ex Boiss. Fl. Orient. Suppl. 19. 1888.

Annual, more or less gray-pubescent on stems with short stiff, often retrorse hairs, plant 2–7 dm. tall, usually virgately branched from below, the branches stiff, straight, or sometimes spreading, ridged; lower leaves 3–5-parted, the parts cut into 3 or more lance-linear lobes; blades 1–3 cm.

long, often wider, longer than the petioles, glabrous, coriaceous; basal and middle leaves deciduous at anthesis; upper entire, linear, much reduced on upper stems, sessile; racemes terminal, many flowered; bracts subulate, 3–6 mm. long; pedicels stiff-pubescent, to almost 1 cm. long; bracteoles 2, to ca. 3 mm. long; flowers violet; upper sepal 7–8 mm. long, pubescent, the spur straight, pubescent, ascending, 15–20 mm. long and 3.5 mm. wide at its base; lateral sepals lance-oblong, pubescent, 5–7 mm. long; lower pair more pointed and with pubescence more median; upper petals appearing bilobed because of the broad ovate to elliptical lateral wing, the lamina ca. 7 mm. long, yellowish at base, violet toward apex; lower petals 8–10 mm. long, the blade longer than wide and gradually narrowed into the slender claw; stamens 5–8 mm. long, with somewhat lavender filaments; follicles 3, pubescent to glabrous, 7–8 mm. long (including the style); seeds rounded, ca. 1 mm. long, the scales united into transverse rows.

TYPE: Specimens in Clifford Herb. (BM), probably originally from Italy, Sicily or Malta.

DISTRIBUTION. Largely at elevations below 2000 m., fallow fields, calcareous places, etc., from type region to Egypt, Turkey, Jordan, and Iran.

ILLUSTRATIONS. SIBTHORP & SMITH, Fl. Graeca **6**: *t. 506.* 1826; DAVIS, Fl. Turkey **1**: 129. 1965.

REPRESENTATIVE SPECIMENS of the species complex are: **Turkey:** *Kotschy 1*; *Balansa 728*; *Sintenis 1207*; *Balls 1207*; *Davis 13567*. **Lebanon:** *Gaillardot 52* and *367*; *Davis 9913*. **Israel:** *F. S. Meyers 99*; *Davis 4801*; *Boissier*, April. 1846. **Iraq:** *Field & Lazar 730* and *850*. **Iran:** *Layard*, ex Herb. J. Ball. **Egypt:** *Bové 130*.

Plants from Asia tend to have pubescent follicles and constitute the var. *eriocarpum* Boiss., if this variety is tenable. Those with the inflorescence condensed have been called var. *densum* Post, Fl. Syria, Palestine Sinai 46. 1896.

2. **Delphinium virgatum** Poir. in Lam. Encycl. **10**: 458. 1811.
FIG. 1, B.

Delphinium peregrinum var. *virgatum* (Poir.) Huth, Bot. Jahrb. **20**: 475. 1895.
Delphinium peregrinum var. *laxum* Post, Fl. Syria, Palestine Sinai 46. 1896.

Much like *Delphinium peregrinum*, but glaucous, glabrous to strigulose; lower leaves cuneate-obovate, short-petioled, the blades with 3–5 coarse mucronate teeth at apex; midcauline leaves subentire, subsessile, sharply acute, passing upward into lanceolate bractlike leaves ca. 1 cm. long; flowers deep blue, strigulose, 20–22 mm. long; sepals lanceolate, 8–10 mm. long; spur 14–18 mm. long, spreading-curved; upper petal with glabrous winged blade ca. 10 mm. long, the spur 14 mm.; lower petals with ovate, slightly exserted limb ca. 3 mm. long, broadly cuneate at base, gradually contracted into a claw 6 mm. long; carpels glabrous.

TYPE: Syria, *Labillardière* (FI); not seen.

ILLUSTRATION. DELESSERT, Icon. Pl. **1**: *t. 55.* 1820.

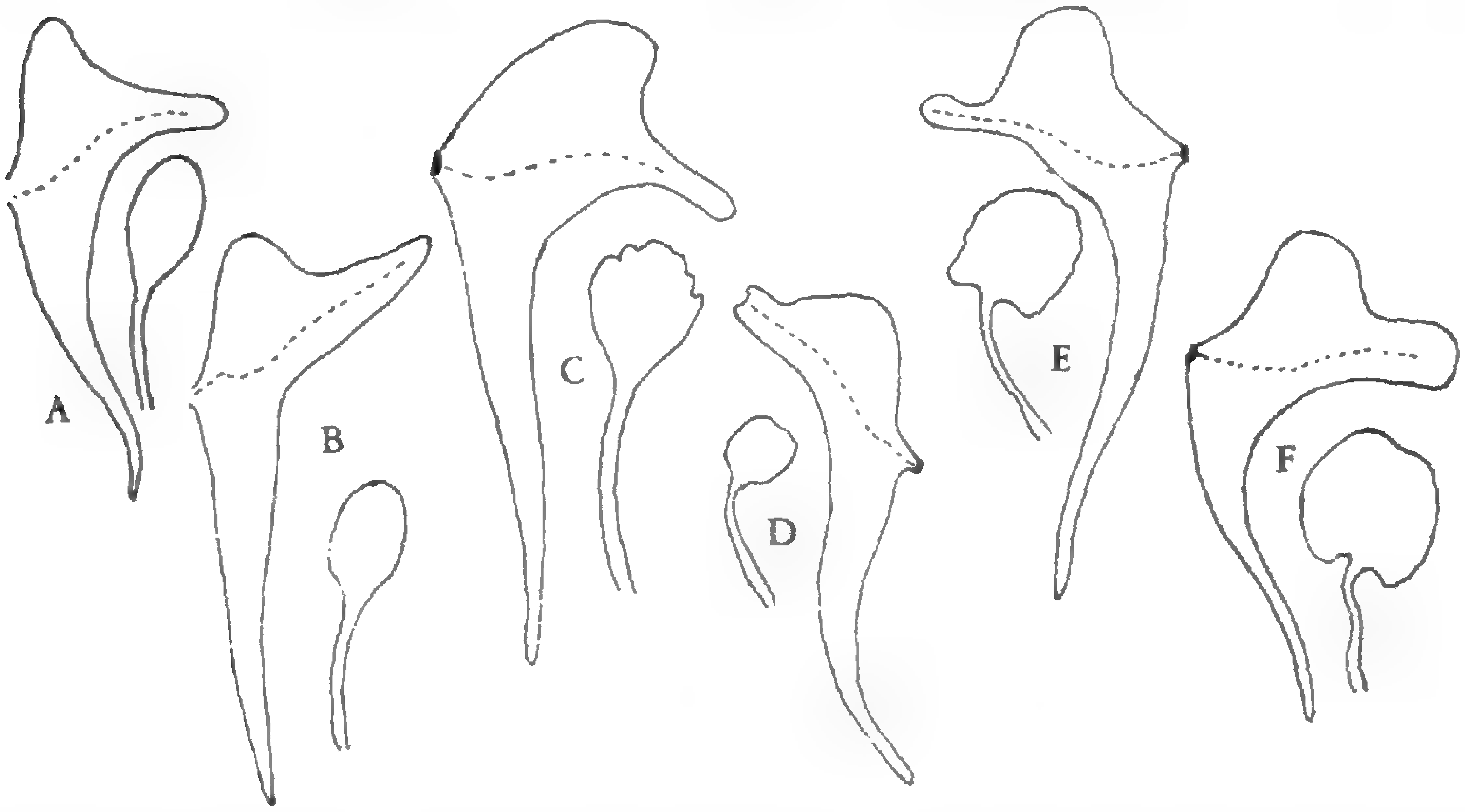

FIGURE 1. **Delphinium**, GROUP I. Petals, the upper spurred and with wing of lamina on side away from spur, the dotted line indicating position of main vein toward lamina tip. Lower petal clawed. A. *D. peregrinum*; spur 13 mm. long, lower petal 9 mm.; drawn from *Balansa 728* (A). B. *D. virgatum*; spur 15 mm. long, lower petal 9 mm.; from *Marsh* in 1851 (MO). C. *D. nanum*; spur 18 mm. long, lower petal 12 mm.; from *Letourneux* in 1877 (M). D. *D. cinereum*; spur 12 mm. long, lower petal 7.5 mm.; from *Boissier* in 1842 (GH). E. *D. venulosum*; spur 18 mm. long, lower petal 10 mm.; from *Bornmüller 3093* (BH). F. *D. davisii*; spur 15 mm. long; lower petal 8.5 mm.; from *Sintenis 4979* (K).

DISTRIBUTION. Limestone hills to ca. 1000 m., southern Anatolia to Jordan and Lebanon.

REPRESENTATIVE COLLECTIONS. **Turkey:** Kara Da, *Little*; *Davis 35701*. **Lebanon:** *Kotschy 227*. **Jordan:** *Marsh* in 1851; *F. Meyers 99*.

3. **Delphinium nanum** DC. Syst. **1**: 349. 1817. FIG. 1, C.

Delphinium peregrinum ssp. *nanum* (DC.) Graebner in Asch. & Graebn. Syn. 5. **2**: 701. 1929.

? *Delphinium peregrinum* var. *boissieri* Huth, Bot. Jahrb. **20**: 475. 1895. Not typified.

? *Delphinium peregrinum* var. *subsaccatum* Huth, *loc. cit.* Not typified.

Delphinium grandiflorum Forsk. Fl. Aegypt. Arab. 212. 1775, not L., 1753.

Annual, widely and stiffly branched from base to subsimple, the branches simple or nearly so, more or less hirtellous or spreading-pubescent throughout or especially on the sepals, the hairs sometimes somewhat interwoven, plants 3–15 cm. high; lower leaves obovate in outline, broadly 3-lobed, long-cuneate at base, 4–6 mm. long, the lobes broad, undivided; main cauline leaves largely simple, narrowly oblanceolate, 1–2.5 cm. long, narrowed at base into a broad petiole, gradually reduced up the stems and sessile, the upper lanceolate, sessile, bractlike, 2–6 mm. long; racemes short, loose; flowers few; pedicels 1–5 mm. long; bracteoles 2, lance-linear, 3–4 mm. long; flowers bluish purple to brownish violet with yellow base;

lower sepals oblong-lanceolate, 6–7 mm. long, grayish tomentulose-pubescent; lateral pair subovate, 6–7 mm. long, with median strip of pubescence; dorsal sepal 6–7 mm. long, densely pubescent as is the horizontal or ascendant spur which is 3–4 mm. wide at base and 15–20 mm. long; petals pale, the upper pair glabrous, lamina winged on the side, 7–8 mm. long, 8–10 mm. wide; lower petals to ca. 1 cm. long, the blade roundish-oblong, ca. 4 mm. wide, narrowed to a linear claw 4 mm. long; stamens 5–8 mm. long, filaments apparently bluish; carpels 3, sparsely pubescent, to ca. 8 mm. long and 2 mm. wide, the beak an additional 2–2.5 mm.; seeds 1 mm. long, almost round, dark brown with very closely appressed overlapping scales.

TYPE: Near Alexandria, Egypt, *Delile*. An 1803 collection seen (BM).
DISTRIBUTION. From between Suez and Gaza, Egypt, *Bové*; otherwise in African Egypt.
ILLUSTRATION. TÄCKHOLM, Students' Flora Egypt *Pl. 57.* 1956.

4. **Delphinium cinereum** Boiss. Diagn. I. 1: 67. 1842. FIG. 1, D.

Erect annual, divaricately branched from near the base, 1.5–2 dm. tall, densely cinereous-strigose with retrorse hairs, the branches several, rather coarse, simple or few branched, stiff, leafy to the racemes; lower leaves tripartite, 1–2.5 cm. long, short-petioled, the parts cuneate, 3–5-fid, more or less strigose, 2–5 mm. broad; upper subsessile, 3-lobed; uppermost simple, passing into bracts 3–20 mm. long; flowers 5–12, rather closely placed; pedicels 2–5 mm. long, pubescent; the bracteoles 2, linear, 5–7 mm. long; flowers pale blue, densely pubescent; upper sepal 7–8 mm. long, the spur straight, horizontal, pubescent, ca. 10 mm. long, 3 mm. wide at base; lateral sepals 6 mm. long, oblong, pubescent along midrib, the margins hyaline; lower sepals more pointed, pubescent over whole outer surface; upper petals about as long as sepals, 4–5 mm. wide, broadly emarginate; lower petals ca. 7 mm. long, the limb rounded, abruptly narrowed into a slender claw; stamens almost equaling sepals, dilated and glabrous at base; carpels 3, cylindrical, closely parallel, hirsute-pubescent, 10–12 mm. long in maturity; seeds globose, umbilicate, the scales in rows.

TYPE: Turkey: "in collibus Lydia circa Laodiceam." *Boissier*, June, 1842, according to the original description. But in his Fl. Orient. 1: 86. 1867, Boissier said "Fl. July." The specimens seen (BM, GH, K, P), all give July, 1842, and I take them to be isotypes, the holotype being at Geneva.

COLLECTIONS SEEN. **Turkey:** Caria, *Pinard* in 1843; Cilicia, *Persnin 170*.

A rare and rather local endemic.

5. **Delphinium venulosum** Boiss. Fl. Orient. 1: 86. 1867. FIG. 1, E.

Delphinium halteratum Sibth. & Smith var. *venulosum* (Boiss.) Finet & Gagnep. Bull. Soc. Bot. France **51**: 470. 1904.

Robust annual, 4–10 dm. tall, strigulose below, subglabrous above, with open ascending branches; stem leaves tripartite into broad segments, or the upper entire, elliptic-oblong, 3–20 mm. broad, subglabrous, 1–3 cm. long; those below the inflorescence deciduous by flowering time; racemes rather open, mostly several flowered; bracts linear or wider, 3–10 mm. long; pedicels strigulose, commonly 4–5 mm. long, bibracteolate; flowers violet-blue to deep blue-purple, the upper sepal ca. 7 mm. long, very finely strigulose, the spur straightish, subhorizontal, mostly ca. 1.5 cm. long, scarcely 3 mm. wide at base; lateral sepals narrowly oblong-ovate, ca. 7 mm. long, with strigulose median band; lower sepals lance-ovate, rather generally strigulose; upper petals apically blue, ca. 7 mm. wide; lower petals well exserted, ca. 9 mm. long, the rounded lamina abruptly contracted to a longer slender claw; stamens 5–6 mm. long; follicles 5–6 mm. long, 2.5 mm. thick, with a few scattered hairs; seeds rounded, the apex narrowed, deeply umbilicate.

TYPE: Turkey: "in cultis Cappadociae circa Caesaream," in 1856, *Balansa 858*; isotype seen (K).

DISTRIBUTION. Inner Anatolia in fallow places below 1200 m.

ILLUSTRATION. DAVIS, Fl. Turkey **1**: 129. *fig. 2* (*12*). 1965.

REPRESENTATIVE SPECIMENS. **Turkey:** *Bornmüller 2674*, *3093*, and *1529*; *Sintenis 4627*; *Davis 32782*, *32778*, *32813*; *Uvarov 98*; *Khan, Prance & Ratcliffe 759*.

An endemic Turkish species.

6. **Delphinium davisii** Munz, nomen novum. FIG. 1, F.

Delphinium sintenisii Freyn, Österr. Bot. Zeitschr. **43**: 374. 1893, not Uechtr. (1880).

Delphinium bithynicum Davis, Notes Bot. Gard. Edinb. **26**: 172. 1965, not Grisebach, 1839.

Plant 1–4 dm. tall, divaricately branched from base or middle, glabrous except for the strigulose pedicels and calyx; leaves round in outline, palmately parted, the segments cuneate, parted into mucronate lanceolate lobules 1–2.5 cm. long, 1–3 mm. wide; racemes densely few to many flowered, 5–15 cm. long; bracts simple, entire, lance-linear, 3–12 mm. long, mucronate, to ca. 1.5 mm. wide; pedicels 2–3-bracteolate, strict, 1–2 cm. long; bracteoles lanceolate, near middle of pedicel, 2–3 mm. long; sepals blue-violet, minutely strigulose, the upper sepal 9–11 mm. long, more or less oblong, rounded at apex; spur ascending, curved, ca. 15 mm. long, 3 mm. wide at base, subcylindric, rather blunt; lateral sepals oblong, 7 mm. long, 3 mm. wide, rounded at apex; lower sepals lance-ovate, 8 mm. long, obtuse; upper petals with blade 9.5 mm. long, bent at right angle to spur, the lateral wing broad, the apex entire, round-oblong, the spur 15 mm. long; laminae of lateral petals cordate-orbicular, 4 mm. in diameter, the glabrous claw 5 mm. long; stamens 5 mm. long, dilated at base, glabrous; anthers yellow, almost round, 1 mm. long; follicles erect, 3, short, oblong, parallel, torulose, glabrous, veined, 7–9 mm. long, the beak an additional 2 mm.; seeds black, almost 2 mm. long, depressed spherical, transversely lamellate-rugose, the lamellae imbricate.

TYPE COLLECTION: Turkey: Paphlagonia near Kastemuni [Kastamboli] in valley Kara Dere near Kady Oghbi Chan, Aug. 15, 1892, *Sintenis 4979*; isotypes seen (BM, K).

DISTRIBUTION. Disturbed places, 850–950 m., edge of scrub, Paphlagonia and Bithynia.

REPRESENTATIVE COLLECTIONS. **Bithynia:** *Grisebach.* **Paphlagonia:** *Davis 39053.*

Related to *D. **halteratum*** of the western Mediterranean, but tending to be more glabrous vegetatively and on the follicles, the plant of lower stature, etc. It is a pleasure to name this Turkish species for Dr. Peter H. Davis in recognition of the contribution he has made to an understanding of the genus ***Delphinium*** in Turkey.

UNCERTAIN SPECIES

7. **Delphinium syncarpum** Freyn ex Stapf, Denkschr. Akad. Wien Math. Naturw. **51**: 26. 1886. FIG. 2, E.

Simple erect, apparently annual, to ca. 2 dm. high, leafy, cinereous-strigulose and with short stiff spreading glandular hairs; lower petioles to ca. 1 cm. long; blades 8–12 mm. long, trisect, then again lobed into oblong, mucronate, obtusish parts to ca. 1 mm. wide; flowers few, in a close simple raceme; bracts commonly trifid, 5–8 mm. long; pedicels 3–6 mm. long; bracteoles linear, 2–3 mm. long, at about the middle of the pedicel; sepals white with upper midrib greenish, mostly elliptic, 8–9 mm. long, attenuate into a claw, the spur descending, ca. 8 mm. long; upper petals sepal-like, but without the green midrib, clawed, ca. 11 mm. long, apparently spurless, hence nectarless; lower petals with blade ca. 8 mm. long and wide, shortly 2-lobed, glabrous, the claw 4 mm. long; stamens 3.5–4.5 mm. long, the filaments broadly dilated, glabrous; anthers pale, 1 mm. long; follicles 3, hairy, united at the base.

TYPE: "ad portum Moschdiser," northern Iran, legit *Th. Pichler* (WU); seen.

A very doubtful species. The type consists of a single one-stemmed plant, with a few broken flowers; the carpels are very undeveloped. The flowers seem abnormal, the upper petals apparently not spurred, sepal-like, but lacking the dorsal green midrib of sepals. I believe it is annual and has lower petals glabrous, hence must be in my Group I, although I first placed it in Group IV.

I have seen a collection from Luristan, Iran, namely *Koelz 18519* (MICH), which may represent this species. It has no flowers; the follicles are united about half way.

I am very grateful to Professor Lothar Geitler, Botanical Institute, University of Vienna, for his kindness in loaning me the type of *D. syncarpum*.

GROUP II

Plants biennial. Leaves palmately 5–7-partite into entire or incised segments. Petals glabrous, the upper short clawed, not winged on the side. Seeds few, reticulate-foveolate, not squamate.

This group, in which three species are recognized in Europe (Tutin et al., Fl. Europaea **1**: 216. 1964) is the same as Section *Staphisagria* DC. Syst. **1**: 362. 1817, and Tribus *Staphisagria* Huth, Bot. Jahrb. **20**: 481. 1895. In Asia there is one species.

8. **Delphinium staphisagria** L. Sp. Pl. **1**: 531. 1753. FIG. 2, A.

Staphisagria macrosperma Spach, Hist. Nat. Vég. Phan. **7**: 348. 1839.

Biennial, usually one stemmed, simple or few branched above, 3–12 dm. tall, leafy, soft-hairy with fine rather long spreading hairs and densely covered also with short retrorse hairs; leaves large, the blades rounded or broader, to 2 dm. in diameter, more or less finely strigose and with longer hairs, the usually 5–7 segments entire or 2- or 3-lobed, these ultimate divisions broadly lanceolate, sharply acute, 3-veined, often entire or with few large teeth; petioles mostly longer than blades, dilated at base, with both kinds of pubescence; racemes terminal, dense or lax, usually many flowered on the main stem, few flowered on branches; lower bracts foliose, 3-parted or entire, sessile or petioled, from half as long to as long as the pedicels which are 0.5–5 cm. long, densely hairy and strigose, bibracteolate near the base; flowers mostly deep blue, 2–3 cm. in diameter; calyx fine-hairy, the upper sepal oblong-ovate, 1–2 cm. long, the spur saccate, 2–3 mm. long and wide; lateral sepals ovate, ca. 15 mm. long, rounded at apex; lower sepals similar but slightly shorter; upper petals white or bluish, pubescent, obtuse, simple or some bilobed at summit, 10–12 mm. long, short-spurred at base; lower petals glabrous, subspatulate or obovate-cuneiform, somewhat asymmetrical, 14–16 mm. long; stamens 8–10 mm. long, ciliate above, glabrous and dilated below; carpels 3, long-pubescent, inflated, 12–20 mm. long at maturity; seeds few, 5–6 mm. long, blackish, obpyramidal, 3-angled, reticulate-foveolate.

TYPE LOCALITY: Described from Istria, Dalmatia, Calabria, Apulia, S. France (LINN. 694/12).

DISTRIBUTION. Found mostly in woods and waste rocky places below 300 m., Mediterranean region from southern Europe and Morocco to Turkey, Syria, etc.

ILLUSTRATIONS. SIBTHORP & SMITH, Fl. Graeca **6**: *t. 508*. 1826; COSTE, Fl. France **1**: 51. 1901; MAIRE, Fl. de l'Afrique du Nord **11**: 84. *fig. 39*. 1964.

REPRESENTATIVE SPECIMENS. **Turkey**: *Persnin 1*; *Sintenis 444*; *Little 52*. **Syria**: *Egger 68*; *Haradjian 2138*.

GROUP III

Leafy annuals with leaves subpinnate into more or less ovate, cuneate segments. Petals glabrous, the upper sessile, with a wing opposite the spur so as to appear bilobulate. Lower petals more or less deeply divided. Seeds with a spiral band of 5–6 turns of confluent scales.

This group is the section *Anthriscifolium* W. T. Wang, Acta Bot. Sinica **10**: *277. 1962*, and is quite distinct in its characters. It ranges widely over China. As I understand it, it consists of a single variable species, varying in length and coarseness of spur, flower size, size of leaf lobules, lobing of both pairs of petals, slenderness, and shape of follicles. Occasional plants lack spur and petals (*H. B. Morse 553*, Lungchow, Kwangsi (NY). Variations do not seem to be geographic and I am treating them simply as varieties.

9. **Delphinium anthriscifolium** Hance, Jour. Bot. **6**: 207. 1868.

Annual, the stems rather slender, more or less flexuous, grooved when dry, simple to openly branched, mostly 1–7 dm. tall, subglabrous below to short- or long-retrorse-strigulose, more densely so above, sometimes with some spreading hairs; stems leafy almost to the inflorescence, the basal leaves gone by anthesis, the cauline little reduced upward, petioled, ternate, the 3 main divisions short petiolulate, becoming pinnate into several more or less ovate cuneate segments 1–3 cm. long and in turn pinnatifid into few to several lanceolate lobules usually 2–3 mm. wide, the terminal acuminate; leaf blades commonly 3–10 cm. long, somewhat strigulose; inflorescence short- to long-pedunculate, rather few flowered, racemose; bracts from tripartite to simple and linear, mostly 3–10 mm. long; pedicels about as long as the flower; bracteoles linear, usually near the middle of the pedicel; flower violet to blue; upper sepal 5–11 mm. long, 1.5–3 mm. wide, usually acute, pubescent, usually spurred, the spur 5–22 mm. long, rather straight, very slender to somewhat coarse; lateral sepals asymmetrical, more or less unguiculate, 5–10 mm. long, 3–6 mm. wide; quite membranous near the edges; lower sepals more elliptic, 2.5–4.5 mm. wide; petals often purplish or veined with purple, glabrous, the upper with the lamina 7–11 mm. long, winged on one side and appearing bilobed, with a spur mostly 5–20 mm. long; lower petals somewhat asymmetrical, usually deeply 2-lobed, sometimes only emarginate, unguiculate, the lamina 4–5 mm. long, the claw 3.5–5 mm. long; stamens unequal, 3.5–7 mm. long, the filaments glabrous, not strongly dilated below; anthers usually dark, 0.6–0.8 mm. long; follicles 3, rarely 5, inflated, divergent, usually rather abruptly narrowed at apex, 8–14 mm. long, 3–4.5 mm. wide, the style slender, 2–3 mm. long; seeds brownish, almost 2 mm. long, with a spiral band of 5–6 turns of confluent scales.

Spur often longer than sepals, 10–22 mm. long; sepals 9–11 mm. long. .... Var. *anthriscifolium*.

Spur often equal to sepals, shorter than above.

The spur 7–10 mm. long; sepals mostly 6–8 mm. long. ...... Var. *callerii.*
The spur 5 mm. long; sepals ca. 5 mm. long. .... Var. *savatieri.*

Delphinium anthriscifolium Hance var. **anthriscifolium.** FIG. 2, B.

Delphinium anthriscifolium Hance, Jour. Bot. **6:** 207. 1868.

? *Delphinium anthriscifolium* var. *majus* Pamp. and var. *ramosum* Pamp. Nouv. Giorn.-Bot. Ital. (n.s.) **22:** 288. 1915.

Delphinium cavaleriense Lévl. & Vaniot, Bull. Acad. Geogr. Bot. **11:** 49. 1902 and **15:** 711. 1905. Type, *Cavalerie 2344* from Pin-fa do Lofou (E, K) seen.

Delphinium cerefolium Lévl. & Vaniot, Bull. Acad. Geogr. Bot. **11:** 49. 1902. Type, *Chaffanjon*, June 2, 1898, Mont du College, Kouy-Tcheou (E), seen. Cf. Lauener & Green, Notes Bot. Gard. Edinb. **23:** 584. 1961.

Flowers usually several; sepals 9–11 mm. long; spur 10–22 mm. long.

LECTOTYPE: "prope rupem calcaream Kai-kun-shek," Kwantung prov., China, June, 1867, *Sampson*, Hance no. 10125 (holotype K; isotypes BM, GH); chosen since original description mentions this collection as having "afforded excellent material for the above diagnosis."

DISTRIBUTION: Widely distributed in China.

REPRESENTATIVE COLLECTIONS. **Hupeh:** *Henry 5862, 1348, 1966*; *Wilson 95*; *H-Ch'ang Chow 89*; *Watters* in 1879. **Szechwan:** *Fang 758*; *Farges 1146, 1441, 1440*; *Faber 725*; *Yang 58311.* **Anhwei:** *Fan & Li 98.* **Yunnan:** *Tsai 50809*; *Cavalerie 2957.* **Hunan:** *Handel-Mazzetti 11802.* **Fukien:** *Metcalf & Chang 797*; *Tang Siu Ging 13795.* **Kwangtung:** *Chun 6276*; *Lamont 1065.*

Delphinium anthriscifolium Hance var. **callerii** (Franchet) Finet & Gagnep. Bull. Soc. Bot. France **51:** 471. 1904. FIG. 2, C.

Delphinium callerii Franchet, Bull. Soc. Linn. Paris **1:** 329. 1882; Bull. Soc. Philom. Paris **5:** 161. 1893.

Delphinium exiguum E. Pritzel ex Diels, Bot. Jahrb. **29:** 327. 1900. Type from Szechwan: Nan ch'uan, *von Rosthorn 2022*; not seen.

Delphinium robertianum Lévl. & Vaniot, Bull. Acad. Geogr. Bot. **11:** 49. 1902. Type, near Kauy Yang, Kwangtung, Sept. 12, 1897, *Bodinier* ? (E); seen.

Delphinium minutum Lévl. & Vaniot, Bull. Herb. Boiss. II. **6:** 505. 1906. Based on *Esquirol 24*, Kouy-tchéou (printed as *23* in original description) (E, K, UC); seen. Cf. Lauener & Green, Notes Bot. Gard. Edinb. **23:** 584. 1961.

Delphinium kweichowense W. T. Wang, Acta Bot. Sinica **10:** 283. 1962. Based on *Y. Tsiang 8571* from Tenfan, Kweichow. Seen (NY, US). Somewhat intermediate between vars. *anthriscifolium* and *callerii.*

Flowers one to few; sepals mostly 6–8 mm. long; spur 7–10 mm. long.

TYPE: Near Macao, China, *Callery 6*, in 1841 (P), photo. (E), seen; and *Callery 51*, in 1844, photo. (E), seen.

RANGE. Widely distributed in China.

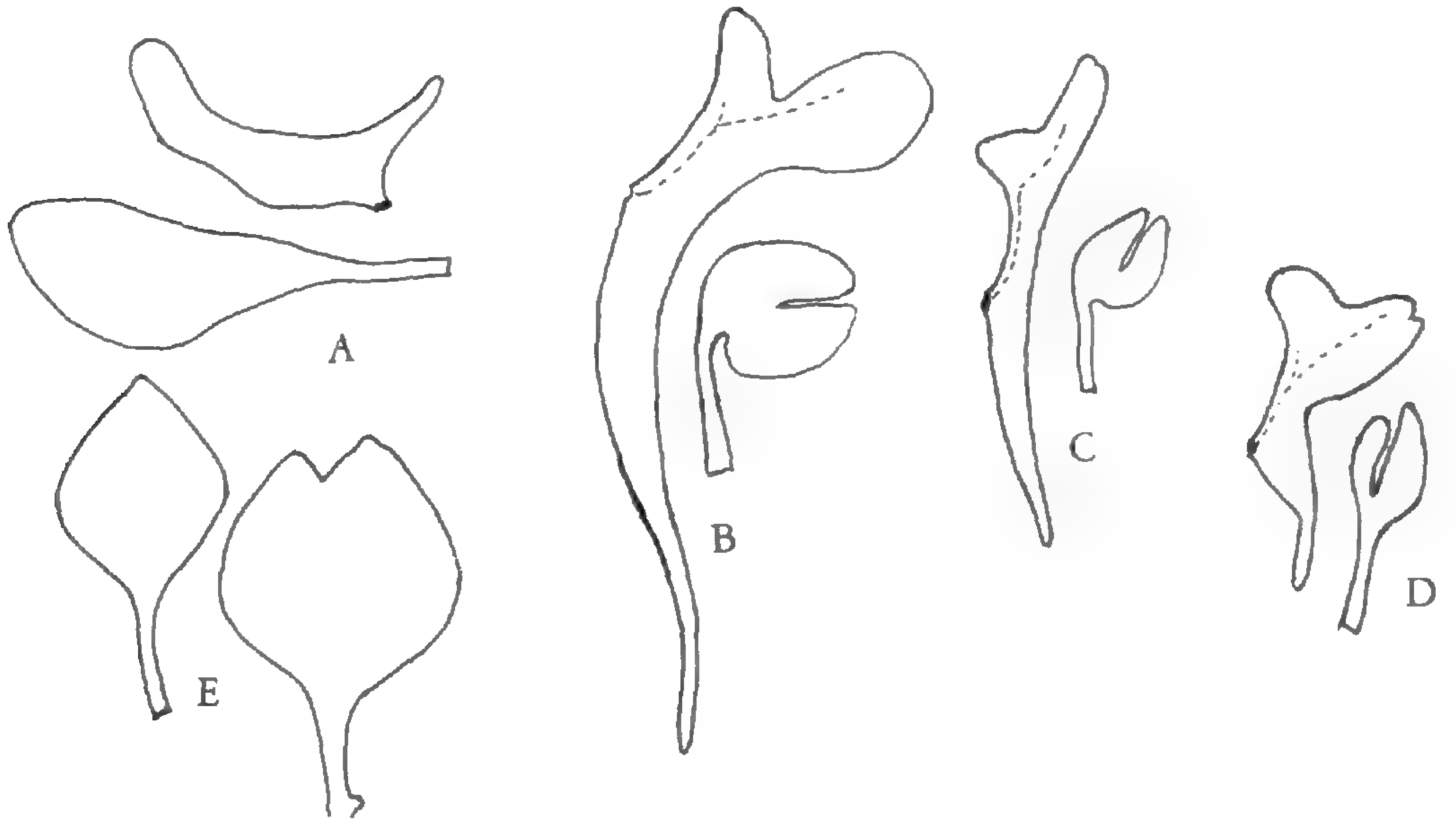

FIGURE 2. **Delphinium**, GROUP II. Petals, the upper with short spur to upper right, the lower asymmetrical. A. *D. staphisagria*; upper petal 10 mm. long, lower 16 mm.; drawn from *Alleizetti* May 1, 1853 (MO).

GROUP III. Upper petal with a wing opposite the base of the spur. B. *D. anthriscifolium* var. *anthriscifolium*; upper lamina 11 mm. long, lower lamina 5 mm. long; drawn from *Henry 5862* (GH). C. *D. a.* var. *callerii*; lamina of upper petal 9 mm. long, of lower petal 4 mm. long; drawn from *Cavalerie 2822* (UC). D. *D. a.* var. *savatieri*; lamina of upper petal 7.5 mm. long, of lower petal 4.5 mm. long; drawn from *Beach 20* (US).

GROUP I. E. *D. syncarpum*; lamina of upper petal 7 mm. long, claw 4 mm.; lamina of lower petal 8 mm. long and wide; drawn from *Pichler*, Moschdiser (UW).

REPRESENTATIVE SPECIMENS. **Szechwan:** *Henry 7263*; *Wang 20450*; *Sun 1765*; *Fang 12258*; *Chien 5877*. **Kiangsu:** *Feng 112*; *Schindler 275 C*; *Stewart 2071*; *Merrill 11429*; *Keng 1311*; *Pei 2646*. **Fukien:** *Dunn 2321*; *Chung 2602*. **Kwangtung:** *Cavalerie 2169, 2822*. **Chekiang:** *Barchet 11*; *Ching 1363*; *Bullock 7*. **Anhwei:** *Ching 8442*.

Delphinium anthriscifolium Hance var. **savatieri** (Franchet) Munz, comb. nov. FIG. 2, D.

Delphinium savatieri Franchet, Bull. Soc. Linn. Paris **1**: 330. 1882; Bull. Soc. Philom. Paris **5**: 162. 1893.

Sepals ca. 5 mm. long; spur ca. 5 mm. long, subconic.

TYPE: China: Chekiang: "in siccis ad pedem montium Shao-Shin, prope Ning-po," May, 1863, *Lud. Savatier* (P?); not seen.

REPRESENTATIVE SPECIMENS. Less common than the other two forms. **Kiangsu:** *Teng 153*; *Chang 386*. **Chekiang:** *Kay Beach*; *Keng 580*. **Hupeh:** *Henry 200, 760*. **Anhwei:** *Bullock 10125* (BM), cited by Hance as *D. anthriscifolium*. A spurless form seen from Hupeh: *Morse 553* (K, NY).

GROUP IV

Plants perennial, with a cluster of short, tuberous, mostly vertical roots. Leaves palmatifid, at least the upper dissected into linear or oblong laciniae. Inflorescence usually a rather dense raceme with pedicels short (to 1 cm. long) and flowers small (sepals to 1 cm. long). At least the lower petals bearded. Plants of rather arid regions, largely from the Mediterranean to Turkestan and Afghanistan.

This group is in large part the Section DIEDROPETALA, Tribus *Macrocentra* of Huth, Bot. Jahrb. **20**: 341. 1895; or, in the text of his monograph on later pages of the same reference, it would fall into his Tribus *Gibberula*, p. 423, Tribus *Lasiocarpa*, p. 428, and Tribus *Leiocarpa*, p. 439. All of these categories proposed by him, however, include other species not in my Group IV. Since the fifty species which I recognize in this group do not fall into readily separable minor groups, I am treating them in alphabetical order, hoping that in this way their study will be facilitated.

KEY TO SPECIES

1. Bracts broad, ovate-lanceolate.
    2. Bracts longer than the pedicels.
        3. Stems terete below; sepals whitish to yellowish or pale blue; spur 8–10 mm. long. Northern Anatolia to Bulgaria. ...... 10. *D. albiflorum.*
        3. Stems angled and sulcate below; sepals bluish; spur 10 mm. long. Upper Euphrates. .... 20. *D. dasystachyum.*
    2. Bracts equaling pedicels; sepals bluish white to pale rose; spur 15 mm. long. Syria to Jordan, Israel. .... 27. *D. ithaburense.*
1. Bracts narrower, mostly linear.
    4. Spur definitely longer than its sepal blade.
        5. Sepals bluish to purple, occasionally rose.
            6. Stems strigulose with closely appressed hairs.
                7. Flowers purplish blue.
                    8. Sepals strigulose; spur 10–15 mm. long; blade of lower petal longer than wide. Iraqui Kurdistan. .... 37. *D. micranthum.*
                    8. Sepals with scattered spreading hairs; spur 20 mm. long; blade of lower petal about as wide as long. Afghanistan. .... 52. *D. tetanoplectrum.*
                7. Flowers pale blue to smoky gray.
                    9. Stem subglabrous below, strigulose above; lower petioles only subvaginate at base; spur usually curved; carpels hirsute-pubescent. Turkish Kurdistan. .... 21. *D. dolichostachyum.*
                    9. Stem strigulose throughout; lower petioles strongly vaginate; spur straight; carpels strigulose.
                        10. Bracteoles 3–6 mm. long, near the middle of the pedicel.
                            11. Upper petals glabrous at tip; spur 16–20 mm. long, the upper sepal ca. 12 mm. long. Tauria. .... 40. *D. pallasii.*

11. Upper petals often with some hairs at tip; spur 12–15 mm. long, the upper sepal 8–10 mm. long. Northern Iran. . . . . 53. *D. tuberosum.*

10. Bracteoles 1.5–3 mm. long, near the flower.

12. Upper petal notched at apex; spur 10–15 mm. long. Afghanistan, western Himalaya. . . . . 50. *D. suave.*

12. Upper petal entire; spur 17 mm. long. Turkestan. . . . . 13. *D. batalinii.*

6. Stems glabrous or with spreading hairs (at least above).

13. Sepals essentially glabrous, sometimes with minute puberulence near the tip.

14. Lower leaves with broad primary lobes (1 cm. or wider), some usually still evident at anthesis; sepals violet blue, the spur 11–12 mm. long.

15. Spur of upper petals ca. 3.5 mm. wide at base, 12 mm. long; lobes of lower petals lanceolate. Northern Iran. . . . . 12. *D. aquilegifolium.*

15. Spur of upper petals 2 mm. wide, 9 mm. long; lobes of lower petals oblong-ovate. Southern Iran. . . . . 46. *D. saniculifolium.*

14. Lower leaves with mostly narrower lobes and largely withered by anthesis.

16. Sepals pale blue, ca. 8 mm. long; spur 15 mm. long; bracts 5–8 mm. long. Turkey. . . . . . 22. *D. fissum.*

16. Sepals dark blue, 9–10 mm. long.

17. Bracts 3–5 mm. long; spur 11–13 mm. long. Turkestan. . . . . 34. *D. longipedunculatum.*

17. Bracts 8–12 mm. long; spur 14–15 mm. long. Tean Shan, middle Asia. . . . . 11. *D. albomarginatum.*

13. Sepals with hairs on the outside.

18. Upper parts of plant not glandular; sepals 8–10 mm. long. Persian Kurdistan. . . . . 44. *D. quercetorum.*

18. Upper parts of plant with some glandular hairs.

19. Spur steeply ascending; carpels glabrous; racemes elongate. Caucasus and beyond. . . . . 47. *D. schmalhausenii.*

19. Spur more or less horizontal.

20. Sepals pale blue.

21. Carpels subglabrous; lower petals not exceeding sepals.

22. Spur curved at apex, about twice as long as sepals. Hamadan, Iran. . . . . 53. *D. tuberosum.*

22. Spur straight, about one and one-half times as long as sepals. Mascate, Iran. . . . . 42. *D. penicillatum.*

21. Carpels pubescent; lower petals exceeding sepals. Persian Kurdistan. . . . . 44. *D. quercetorum.*

20. Sepals violet-blue to deep blue.

23. Spur 9–10 mm. long, the upper sepal 5–6 mm. long; upper stem glabrous below the inflorescence; carpels glabrous. Tean Shan, middle Asia. .... 11. *D. albomarginatum.*

23. Spur mostly 12–20 mm. long, the upper sepal 6–10 mm. long.

24. Stem 1–7 dm. tall; upper sepal 6–10 mm. long.

25. Spur 11–17 mm. long.

26. Pedicels 5–7 mm. long; stem 1.5–2 dm. tall. Kastamonu, Turkey. ... 25. *D. ilgazense.*

26. Pedicels mostly 8–20 mm. long.

27. Sepals 9–13 mm. long. Turkish Kurdistan. ...... 16. *D. carduchorum.*

27. Sepals 6–9 mm. long. Afghanistan. .... 31. *D. latesquamatum.*

25. Spur 16–22 mm. long; upper sepal 8–10 mm. long; pedicels 7–10 mm. long, Transcaspia. .... 54. *D. turkmemum.*

24. Stem ca. 1 m. tall; upper sepal 10 mm. long.

28. Racemes long-cylindrical; bracts divided into linear lobes; follicles glabrous. Caucasus. .... 47. *D. schmalhausenii.*

28. Racemes rather few flowered; bracts simple; follicles hairy. Afghanistan. .. 17. *D. centeteroides.*

5. Sepals yellowish to white.

29. Spur descending; young carpels united at base, hairy. Iran. (See Group I). .... 7. *D. syncarpum.*

29. Spur horizontal or erect; carpels separate.

30. Ultimate divisions of upper leaves 8–20 mm. wide; spur horizontal; carpels glabrous. Kurdistan. .... 30. *D. kurdicum.*

30. Ultimate divisions of upper leaves 1–7 mm. wide; spur suberect.

31. Sepals glabrous; spur erect. South of Caucasus. .... 39. *D. ochroleucum.*

31. Sepals pubescent.

32. Ultimate lobules of leaves 2–7 mm. wide; lobules at tip of upper petal 2–3 mm. long.

33. Calyx short-pilose without; upper sepal 9 mm. long; spur 10–12 mm. long. Daghestania. .... 35. *D. macropogon.*

33. Calyx strigulose without; upper sepal 11–12

mm. long; spur 13–15 mm. long. Turkestan. .... 14. *D. biternatum.*

32. Ultimate lobules of leaves 0.5–2 mm. wide; upper sepal ca. 8 mm. long, the spur 13 mm. Transcaucasia. .... 51. *D. szowitsianum.*

4. Spur not definitely longer than upper sepal blade.

34. Flowers white to yellowish.

35. Stems with spreading hairs in upper parts; sepals with long yellow or white hairs; follicles hairy. Armenia. .... 33. *D. longebracteatum.*

35. Stems glabrous or strigulose above, except on some pedicels.

36. Sepals glabrous; carpels glabrous. Turkestan. .... 48. *D. semibarbatum.*

36. Sepals not glabrous; carpels usually pubescent or hirsute.

37. Pedicels strigose, not glandular; upper petals bidentate. Daghestan. .... 35. *D. macropogon.*

37. Pedicels more or less glandular.

38. Upper petal entire; sepals puberulent; spur 9–12 mm. long. Iran. .... 23. *D. gorganicum.*

38. Upper petals bilobulate; sepals strigulose; spur 12–15 mm. long. Turkestan, Iran. .... 14. *D. biternatum.*

34. Flowers blue or bluish to rose or greenish.

39. Sepals glabrous without or nearly so.

40. Inflorescence with some glandular hairs.

41. Lamina of lower petals deeply divided into 2 more or less toothed lobes ca. 1 mm. wide, hairy; sepals 8–9 mm. long; spur 10–11 mm. long. Asia Media. .... 26. *D. inopinatum.*

41. Lamina of lower petals not as above.

42. Spur suberect; ultimate divisions of upper leaves 1–2.5 mm. wide.

43. Carpels strigose. Kurdistan. .... 57. *D. vanense.*

43. Carpels glabrous. Armenia. .... 41. *D. pallidiflorum.*

42. Spur horizontal; ultimate divisions of leaves 2.5–5 mm. wide. Afghanistan. . 38. *D. nuristanicum.*

40. Inflorescence without glandular hairs.

44. Upper sepal 7–8 mm. long.

45. Upper petals with a few hairs at the tip; lower petals completely covered with long hairs. Middle Asia. .... 15. *D. bucharicum.*

45. Upper petals glabrous; lower petals with few short hairs in distal part.

46. Spur of upper petals ca. 3.5 mm. wide, 12 mm. long; lobes of lower petals lanceolate. Northern Iran. ..... 12. *D. aquilegifolium.*

46. Spur of upper petals 2 mm. wide, 9 mm. long; lobes of lower petals oblong-ovate. Southern Iran. .... 46. *D. saniculifolium.*

44. Upper sepal 10–16 mm. long.
47. Flowers pale rose; plant glabrous throughout. Israel. . . . . 18. *D. chodatii.*
47. Flowers blue or violet.
48. Racemes dense, elongate, many flowered; sepals deep violet. Kurdistan. . . . . 36. *D. macrostachyum.*
48. Racemes lax.
49. Sepals deep blue; lower petals hairy. Kurdistan. . . . . 57. *D. vanense.*
49. Sepals sordid-lilac; lower petals almost glabrous. Asia Media. . . . . 49. *D. semiclavatum.*
39. Sepals with some pubescence.
50. Bracts inflated at base and with long narrow terminal lobes. Turkey. . . . . 20. *D. dasystachyum.*
50. Bracts not as above.
51. Pedicels with some spreading hairs.
52. Spur curved into a terminal hook; sepals bluish purple, sparsely villous. Western Himalaya. . . . . 55. *D. uncinatum.*
52. Spur not hooked at end.
53. Sepals intense blue to dark blue-violet, 7–13 mm. long.
54. Plant 26–60 cm. tall; sepals appressed-pubescent. Turkish Kurdistan. . . . . 16. *D. carduchorum.*
54. Plant 16–20 cm. tall; sepals viscid-pubescent. Kastamonu, Turkey. . . . . 25. *D. ilgazense.*
53. Sepals paler, the upper sepal 12 mm. long; carpels glabrous. Turkish Armenia. . . . . 41. *D. pallidiflorum.*
51. Pedicels with closely appressed hairs.
55. Axis of inflorescence glabrous; sepals 10–11 mm. long; spur spreading-upcurved, 12 mm. long. Turkestan. . . . . 28. *D. karategini.*
55. Axis of inflorescence more or less pubescent.
56. Upper sepal 6–9 mm. long.
57. Racemes to ca. 10-flowered, rather open; spur 5–7 mm. long; upper petal-blade with some hairs. Himalaya. . . . . 29. *D. kohatense.*
57. Racemes 20- or more-flowered; spur 8–10 mm. long; upper petal-blade glabrous or nearly so.
58. Raceme dense; spur 8 mm. long. Iran. . . . . 56. *D. ursinum.*
58. Raceme open; spur 10 mm. long. East Afghanistan. . . 24. *D. griseum.*
56. Upper sepal 10–13 mm. long.
59. Flowers blackish violet-purple; petals

purple. Georgia to the Volga River. . . . . 43. *D. puniceum.*

59. Sepals bluish; petals lilac.
    60. Lamina of lower petals longer than wide.
        61. Ultimate leaf segments 1–2 mm. wide; lamina of lower petals oblong, with 2 lanceolate divergent lobes. Russian Armenia, Transcaucasia. . . . . 32. *D. laxiusculum.*
        61. Ultimate leaf segments 2–3 mm. wide; lamina of lower petals elliptic, with 2 broader parallel lobes. Southern Iran. . . . . . . 19. *D. cyphoplectrum.*
    60. Lamina of lower petals roundish, lobed ca. 3 mm. Western Himalaya. 45. *D. roylei.*

10. **Delphinium albiflorum** DC. Syst. Nat. 1: 353. 1817. FIG. 3, A.

Delphinium hybridum Steph. ex Willd. var. *albiflorum* (DC.) Koch, Linnaea **15**: 247. 1841.

Delphinium ochroleucum auct. non Stev. ex DC.

Delphinium ponticum Hausskn. & Bornm. Österr. Bot. Zeitschr. **40**: 211. 1890. Based on *Bornmüller 972* from Amasia, Mt. Sana Dagh (BM, K, P). Seen.

Delphinium albiflorum var. *candolleanum* Huth, Bot. Jahrb. **20**: 439. 1895. Not typified.

Delphinium albiflorum var. *eginense* Huth, Bot. Jahrb. **20**: 439. 1895. Based on *Sintenis* 1890 from Egin, Armenia. Not seen.

Stem terete, 5–6 dm. tall, 2–5 mm. thick, simple, glabrous or glandular-pubescent above, glabrous and somewhat angled below; leaves petioled, multipartite into acute long linear lobes 1–3 mm. wide, the petioles strongly dilated at their base; lower leaf blades 4–7 cm. broad, strigose; racemes crowded, elongate, many flowered, pubescent or glabrous; bracts membrane margined, white to pale blue, broadly lanceolate, acuminate, longer than the pedicels; bracteoles membranaceous, 3–4 mm. long and just below the flowers; median pedicels shorter than the sepals, mostly ca. 5 mm. long; flowers, including spur, 19–22 mm. long; sepals white, or nearly so, to yellowish or pale blue, glabrous or pubescent; upper sepal oblong-ovate, 7–8 mm. long, the spur straight, horizontal, obtuse, 8–10 mm. long, 2–2.5 mm. wide at base; lateral sepals oblong, 8–10 mm. long, 3–4 mm. wide, rounded at apex, with greenish midrib; lower sepals ovate, obtuse, ca. 8 by 5 mm.; upper petals glabrous, bluish, bilobed, the lamina somewhat oblique, ca. 9 mm. high and with 2 short rounded apical lobes; the spur ca. 10 mm. long; lower petals bifid, the lobes subacute, unequal, bearded, the lamina 6 mm. long, elliptic rounded in outline, the claw 5 mm. long; stamens 5–6.5 mm. long, the upper part of the filaments bluish or whitish; anthers yellowish or blue, roundish, 0.6 mm. in diameter; follicles 3, pubescent, erect, ca. 8 mm. by 2.5 mm., the beak an additional 2–2.5 mm.

TYPE: Armenia, *Tournefort* (P). Seen.
DISTRIBUTION. Northern Anatolia, Turkey at 1800 to 2100 m., growing on limestone.
ILLUSTRATION. DELESSERT, Icon. Pl. 1: *t. 58.* 1820.

REPRESENTATIVE COLLECTIONS. **Paphlagonia:** *Sintenis 4883*; **Kars:** *Davis 30593*; **Tunceli:** *Davis 31305*; **Agri:** *Furse 3654*; **Erzerum:** *Furse 3785*; **Armenia:** *Calvert & Zohrab 1347.*

A species characterized by its broad bracts.

11. **Delphinium albomarginatum** Simonova, Key Pl. Environ. Tashkent, ed. Popov, 124. 1924.

Delphinium karataviense Pavlov, Bull. Soc. Nat. Mosc. sect. Biol. [Mosk. Obschch. Isp. Pri. Biol.] II. **47:** 80. 1938. Described as having *D. albomarginatum* as a synonym.

Stem 8–15 dm. tall, branched and glabrous above, with short white unequal hairs below; lowest leaves long petioled, strongly widened at the base, still present at time of flowering, when the laminae fall away; laminae trifid, the lobes unequally palmate; upper leaves less divided; flowers in a dense long raceme; lower bracts longer than the flower, the upper narrow-linear and equal to it; pedicels not more than half as long as the calyx; bracteoles near the middle of the pedicel or lower; sepals dark violet-blue, 9–10 mm. long, glabrous; spur almost one and one-half times as long as the sepals, straight; petals white, the upper notched; lower ciliate, but glabrous on the surface.

TYPE: Middle Asia, from Humsana in Umganski Mts. Type at Tashkent, but I was unable to see it or any other material. Apparently this plant is endemic in the western part of the Tean Shan region.

12. **Delphinium aquilegifolium** (Boiss.) Bornm. Bull. Herb. Boiss. II. **4**: 1083. 1904, reprinted as Fl. Elbursgeb. N.-Persiens 11. 1904. FIG. 3, B.

Delphinium saniculifolium Boiss. var. *aquilegifolium* Boiss. Fl. Orient. **1**: 91. 1867.

Delphinium aquilegifolium var. *hebecarpum* Bornm. Bull. Herb. Boiss. II. **4**: 1085. 1904, reprinted as Fl. Elbursgeb. N.-Persiens 13. 1904. Based on *Bornmüller 6062*, May 29, 1902, N. Persia, mts. Schimran. Seen (BM. P).

? *Delphinium aquilegifolium* vars. *glandulosissimum*, *longipedunculatum* and *violaceum* Bornm. *loc. cit.*

Stem more or less zigzag, 3–6 dm. tall, openly few branched, subglabrous except for small areas on one side of the pedicels or all the way around with dense spreading gland-tipped hairs inflated at the base; basal leaves palmately 3–5-lobed into broad obovate parts 1–2 cm. wide or shallowly lobed and toothed at the apex, the blades 3–4 cm. wide, subreniform in outline, subglabrous, on petioles 3–10 cm. long, vaginate at base; cauline leaves few, more deeply dissected into parts with lance-linear lobes; inflorescence an open panicle of ca. 5–20 flowers in rather lax racemes; bracts lance-linear, 3–5 mm. long; pedicels elongating in fruit, ascending and becoming 1–3 cm. long, with 2–3 linear bracteoles ca. 2 mm. long and near the middle; flowers violet-blue; sepals glabrous or pubescent, the upper sepal ovate, 8 mm. by 3 mm., subacute, the spur 11–12 mm. long, 3 mm. wide at the base, somewhat attenuate at the apex; lateral sepals 7 mm. by 3 mm., oblong-elliptic, rounded at the tip; lower sepals 8 mm. by 4 mm., elliptic, obtuse; blade of upper petals oblique, ca. 8 mm. long, short-lobed at the apex, the spur ca. 12 mm. long; lower petals ca. 8 mm. long, the claw 4 mm., the broadly elliptic-oblong blade 4 mm. long, lobed to ca. 2.5 mm., ciliate in the cleft and more or less bearded on the surface; stamens 4–5 mm. long, subglabrous; anthers bluish, 0.7 mm. long; follicles 3, divergent, pubescent, to ca. 10 mm. by 4 mm., the styles an additional 2 mm.

LECTOTYPE: northern Iran, Mount Elbrus near Derbend, *Kotschy 239* (holotype undoubtedly at G; isotypes seen at A, BM, K, P).

DISTRIBUTION. At 1900–2500 m., northern Iran and western Pakistan.

REPRESENTATIVE COLLECTIONS. **Iran:** *Rechinger 3838*; *Bornmüller 6060*; *Furse 2627*; *Trott 887*; *Furse & Synge 329* and *330*; *Koelz 18257*; *W. O. Douglas 236*. **W. Pakistan:** Chitral, *Bowes Lyon 25*; Swat, *Stewart & Rahman 25229*.

The species is distinguished by the broad basal lobes and is near *D. saniculifolium*, but with broader, somewhat longer petal-spur and more sharply pointed lobes on the lower petals. *D. saniculifolium* is a species of southern Iran.

13. **Delphinium batalinii** Huth, Bot. Jahrb. **20**: 432. *pl. 8*. 1895.

FIG. 3, C.

Stem erect, slender, subsimple, 2.5–7 dm. tall, short-strigulose throughout, scattered-leafy throughout; petioles dilated at base, 2–5 cm. long, ascending; leaves palmately parted into ultimate broad oblong lobes, the lower blades 2–3 cm. wide, the upper gradually widened from the petiole and with several lanceolate to sublinear ultimate lobes ca. 1 cm. long and 2–4 mm. wide; inflorescence racemose, branched at base or simple, elongate, with rather many, not crowded flowers; bracts all entire, the lower oblong-lanceolate, the upper linear, 5–8 mm. long; pedicels erect, adpressed to the axis, 10–15 mm. long, strigulose; bracteoles 2, linear, near the flower or more often 1/3–1/4 way below it, ca. 2 mm. long; flowers dilute blue; sepals strigulose, the upper sepal round-ovate, 9 mm. by 7 mm., apiculate, the spur straight, 17 mm. long, 3 mm. wide at the base; lateral sepals round-ovate, ca. 8 mm. long; lower sepals ca. 8 mm. by 5 mm.; upper petals yellowish or tinged blue, the lamina ca. 7 mm.

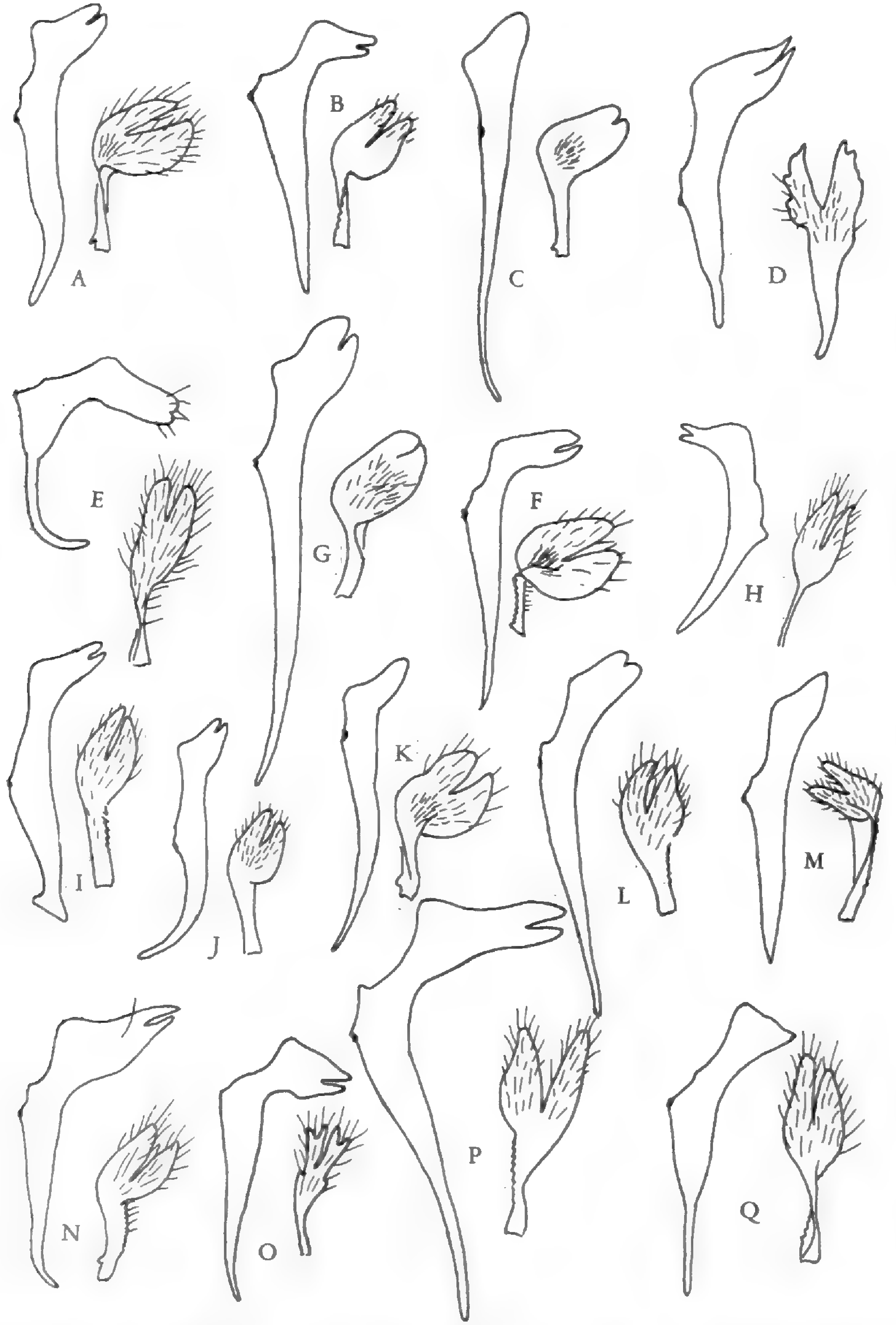

FIGURE 3. **Delphinium**, GROUP IV. Petals, the upper spurred, the lower clawed. A. *D. albiflorum*; upper lamina 9 mm. long, spur 5 mm.; lower lamina 6 mm. long, claw 5 mm.; drawn from *Davis 30593* (BM). B. *D. aquilegifolium*; upper lamina 8 mm. long, spur 12 mm.; lower lamina 4 mm. long, claw 4 mm.; drawn from *Kotschy 239* (A). C. *D. batalinii*; upper lamina 7 mm. long, spur 17 mm.; lower lamina 6 mm. long, claw 5 mm.; drawn from *Lipsky 1685* (BM). D. *D. biternatum*; upper lamina 11 mm. long, spur 11 mm.; lower lamina 6 mm.

long, slightly oblique, entire at the roundish apex, the spur 17 mm. long; lower petals short-bifid near the apex, sparsely pilose, blue or whitish, the blade strongly oblique, oblong, 6 mm. long, the claw 5 mm.; stamens ca. 6 mm. long, somewhat dilated at the base, glabrous, the round-oblong anthers bluish, 1 mm. long; carpels 3, short-hirsute, 9–10 mm. long.

TYPE: Huth cited four specimens, all in the Turkestan Herbarium in Leningrad. The one sent me on loan from Leningrad was "Trajectus montium Gasi Mailik, supra Choschbalak," 6000 feet, *Regel* in 1883 (LE). I therefore choose this as lectotype.

DISTRIBUTION. At about 2000–3000 m., Turkestan or Asia Media.

REPRESENTATIVE SPECIMENS. *Lipsky 1685*; *Lipschitz 685*; *Regel* at Chosch Rawat.

14. **Delphinium biternatum** Huth, Bot. Jahrb. 20: 422. 1895.
FIG. 3, D.

Delphinium floribundum Freyn & Sint. ex Freyn, Bull. Herb. Boiss. II. 3: 561. 1903. Based on *Sintenis 850*, Aschabad, Suluklii (seen at BM, E, MO, P).

Stems glabrous below, more or less strigulose above, branched at middle or above, 4–12 dm. tall; basal leaves gone by anthesis; cauline leaves subglabrous, short petioled, the petioles dilated at the base, the blades ternate with petiolulate segments cuneate at the base and divided into 3 subsessile, lanceolate, entire or lobed parts, mucronate, 2–5 mm. wide, the leaf laminae 4–10 cm. broad; terminal raceme to 30 cm. long, the lateral shorter, ascending; lowest bracts leafy, trifid, to ca. 1.5 cm. long, the upper entire, to 12 mm. long; pedicels densely glandular-pubescent, shorter than the flower, the lance-linear bractlets near the base of the flower, 2–3

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long, claw 6.5 mm.; drawn from *Rechinger 1416* (US). E. *D. bucharicum*; upper lamina 9 mm. long, spur 10 mm.; lower lamina 6 mm. long, claw 5 mm.; drawn from type (LE). F. *D. carduchorum*; upper lamina 7 mm. long, spur 11 mm.; lower lamina 5.5 mm. long, claw 4 mm.; drawn from *Davis 23954* (BM). G. *D. centeteroides*; upper lamina 9.5 mm. long, spur 20 mm.; lower lamina 7 mm. long, claw 4 mm.; drawn from *Griffith 45* (GH). H. *D. chodatii*; upper lamina 8 mm. long, spur 8 mm.; lower lamina 6 mm. long, claw 4 mm.; from drawings in original description. I. *D. cyphoplectrum*; upper lamina 9 mm. long, spur 10 mm.; lower lamina 6 mm. long, claw 5 mm.; drawn from *Kotschy 153* (MO). J. *D. dasystachyum*; upper lamina 8 mm. long, spur 9 mm.; lower lamina 4 mm. long, claw 4.5 mm.; drawn from *Balansa 859* (GH). K. *D. dolichostachyum*; upper lamina 7 mm. long, spur 11 mm.; lower lamina 5 mm. long, claw 4 mm.; drawn from *Davis 24566* (BM). L. *D. fissum* subsp. *anatolicum*; upper lamina 7 mm. long, spur 22 mm.; lower lamina 4.5 mm. long, claw 4.5 mm.; drawn from *Sintenis 589* (US). M. *D. gorganicum*; upper lamina 9 mm. long, spur 10 mm.; lower lamina 4.5 mm. long, claw 6 mm.; drawn from *Rechinger 6191* (US). N. *D. griseum*; upper lamina 10 mm. long, spur 10 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from type (W). O. *D. inopinatum*; upper lamina 8 mm. long, spur 12 mm.; lower lamina 5 mm. long, claw 3 mm.; drawn from TYPE (LE). P. *D. ithaburense*; upper lamina 10 mm. long, spur 18 mm.; lower lamina 6 mm. long, claw 6 mm.; *Douglas 39* (US). Q. *D. karategini*; upper lamina 8 mm. long, spur 10 mm.; lower lamina 7 mm. long, claw 6 mm.; drawn from TYPE (LE).

mm. long; sepals ochroleucous, strigulose, the upper 11–12 mm. long, ovate, subacute, the spur pointed, 13–15 mm. long; lateral sepals more or less oblong, strigulose on midrib and finely puberulent at apex; lower sepals elliptic-ovate, strigulose especially in upper parts; upper petals with lamina ca. 11 mm. long and with 2 lobes 2.5 mm. long, the spur 11 mm. long; lower petals ca. 12 mm. long, including a very short spur (1.5 mm. long), bearded, bilobed for ca. 4 mm.; stamens 4–6 mm. long, glabrous, dilated at base; anthers yellow, 0.7 mm. long; follicles 3, hirsute, 10 mm. by 2.5 mm., the style an additional 2 mm.; seeds obpyramidal, 1.2 mm. long, densely clothed with transverse rows of scales.

TYPE: (lectotype) in montibus Kuh-i-Frusch, Turkestan, 7000 ft., June, 1883, *Regel* (LE); seen.

DISTRIBUTION. At about 1700–2500 m., Turkestan, Transcaspia, Khorasan (Iran).

ILLUSTRATION. NEVSKI in Komarov, Fl. U.S.S.R. 7: *pl. 11, fig. 2a, 2b.* 1937.

REPRESENTATIVE COLLECTIONS. **Transcaspia:** *Sintenis 500.* **Turkestan:** *Socalski 292*; *Popov 259*; *Mikelson 2279*; *Chaffanjon 804*; *Komarov*, June 26, 1893. **Iran:** Khorasan, *Rechinger 1416.*

15. **Delphinium bucharicum** M. Popow in Korowin, Kultiasow & Popow, Descr. Pl. Nov. Turkestan. 49. 1916. FIG. 3, E.

Stem 3–4 dm. high, straight, very slender, sulcate, short-pubescent below, naked above; leaves 2–3 at base of plant, the petioles 4–5 cm. long, vaginate; lamina 3-lobed, the lobes sessile, many times dissected into long narrow, somewhat pubescent laciniae less than 1 mm. wide; racemes simple, with about 8 crowded flowers; bracts membranaceous on margins, linear-lanceolate, ca. 4 mm. long; pedicels 4–7 mm. long, glabrous; bracteoles small, below the middle of the pedicel; flowers pale, whitish-blue; sepals glabrous, with dark blue veins, elliptic-oblong, 7–8 mm. long, the spur 8–9 mm. long, curved upward and with a small hump near the tip; petals scarcely lobed at apex, bluish white, the upper laminae perpendicular to the spur, ca. 9 mm. long, with a few bristles near the tip, the spurs 10 mm. long; lower petals bearded throughout, the laminae 6 mm. long, oblong, bilobed 1/3 their length, the claw 6 mm. long; follicles 3, glabrous.

TYPE: In the Tashkent Herbarium. A specimen loaned me from Leningrad as type material was *Kultiasow 626*, April 29, 1914 (LE).

DISTRIBUTION. Endemic on mountain slopes, middle Asia; described from mountains west of Bishkent.

Popov in a corrected supplement to his work, reduced his species to *D. leiocarpum* Huth, but Nevski in Komarov, Fl. U.S.S.R. 7: 170. 1937. maintains it. It has the hairiest lower petals that I have seen.

16. **Delphinium carduchorum** Chowdhuri & Davis, Notes Bot. Gard. Edinb. **22**: 407. 1958. FIG. 3, F.

Stem 2.5–6 dm. tall, erect, acutely angled and subsulcate below, branched, leafy above, strigulose to subglabrous below, spreading glandular-pubescent above; lower petioles 4–8 cm. long, more or less vaginate, the blades orbicular, 3–6 cm. in diameter, palmately trisect into glabrous laciniate segments 2–4 (–5) mm. wide, linear-lanceolate to linear or oblong-lanceolate; upper cauline leaves short petioled, trisect, the linear segments entire or divided almost to the base; raceme terminal, 7- to 20-flowered, lax or somewhat dense, 8–15 cm. long, glandular-pubescent; lower bracts 2.5–5 cm. long, mostly deeply tripartite, strigose, equaling or surpassing pedicels; upper bracts entire, lance-linear, ciliate, shorter than flowers; pedicels 8–15, or the lower to 30 mm., strict; bracteoles in upper part of pedicel, 5–8 mm. long; sepals intense blue or somewhat violet, oblong-ovate or elliptic-obovate, acute or obtuse, 9–13 mm. by 5–7.5 mm., somewhat strigose; spur 11–16.5 mm. long, attenuate, horizontal or somewhat curved; petals included, the upper falcate, the lamina 7 mm., short-bifid, the spur 11 mm. long; lower 7.5–10 mm. long, the ovate limb 4–6 mm. by 3–3.5 mm., acutely lobed to about the middle, bearded; filaments glabrous; follicles 3, oblong, pubescent, 7 mm. by 3 mm.; seeds triquetrous, squamate.

TYPE: Turkey, prov. Hakkari, Cilo Dag above Diz deresi, 2400 m., *Davis 23954* holotype (E), isotypes (BM, K); seen.

DISTRIBUTION. Rocky places, 2250 to 2850 m., Turkish Kurdistan and adjacent Iran.

REPRESENTATIVE COLLECTIONS. **Turkey:** *Davis 24370, 23349, 23325, 22593, 22801, 23061, 22734.*

Related to *D. micranthum* of Iraq, which has a more panicled strigose inflorescence.

17. **Delphinium centeteroides** (Brühl) Munz, comb. nov. FIG. 3, G.

Delphinium saniculifolium Boiss. subsp. *centeteroides* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5:** 95. 1896.

Stem ca. 3–9 dm. high, openly and rather freely branched, sparsely pubescent above, the hairs short, thickened at base, apparently glandular; leaves mostly withered by anthesis, the lower long petioled (to 12 cm. and with long dilated base), the upper shorter, remote; lower laminae apparently with few broad cuneate lobes, the uppermost trisect, 2–5 cm. long, the ultimate divisions linear; inflorescence an open panicle of short, rather few flowered, compact racemes; bracts simple, lance-linear, 4–5 mm. long; pedicels ascending, pubescent, mostly 1–2 cm. long; bracteoles lanceolate, ca. 3 mm. long, near the middle of the pedicel; sepals blue, strigulose; upper sepal ovate, ca. 10 mm. by 4 mm., pointed; spur 16–20 mm. long, slender, subcylindric, more or less curved; lateral sepals broadly oblong-elliptic, 10 mm. by 4 mm., rounded at tip, strigose on mid-line; lower sepals asymmetrically oblong-obovate, 10 mm. by 4.5 mm.; upper petals with oblique glabrous lamina 9–10 mm. long, unequally shallowly bilobed; spur to 20 mm. long; lower petals with a claw ca. 4.5 mm. long, the oblong-ovate, bearded blade 7 mm. long, shallowly 2-lobed; stamens 6–7 mm. long, glabrous; anthers 1 mm. long; follicles hairy; styles 2.5 mm. long; seeds with short appressed scales.

TYPE: Afghanistan, *Griffith no. 45*, Herb. East India Co.; isotypes seen (GH, K).

DISTRIBUTION. At about 2200 to 3300 m., Afghanistan and West Pakistan (Baluchistan).

ILLUSTRATION of parts of flower, BRÜHL & KING, Ann. Bot. Gard. Calc. **5**: *pl. 117, fig. 4g, 5h, 6e.*

REPRESENTATIVE SPECIMENS: **Afghanistan:** *Hay 373.* **W. Pakistan:** *Helen Crookshank 324, 366*; *Lace 3862*; *Jafri & Akbar 2197*; *Nasir 28459.*

This proposed species is of slender, strigulose, and pale-flowered plants.

18. **Delphinium chodatii** Oppenheimer, Bull. Soc. Bot. Genève II. **26**: 94. 1936. FIG. 3, H.

Slender-stemmed, ca. 2.5 dm. tall, the stem sulcate, glabrous throughout; lower leaves 3–4, sparsely hirsute, the others glabrous, palmatifid, the segments divided into narrowly linear lobes, the blades ca. 2 cm. long; petiole somewhat dilated at the base, the lower longer than the upper; raceme leafless, rather lax, ca. 10-flowered; bracts lance-ovate, shorter than the pedicels; pedicels terete, recurved in flower, erect in fruit, thickened at summit; bracteoles basal, linear; sepals 9–10 mm. long, glabrous, pale rose; spur subattenuate, 9–12 mm. long; upper petals falcate, strongly oblique, the lamina ca. 8 mm. long, 2-toothed at apex, the spur 8 mm. long; lower petals obovate, the lamina densely bearded, divided 2/3 its length and ca. 6 mm. long, the claw 6–7 mm.; stamens glabrous; follicles 3, hairy; seeds obovoid-triquetrous, brown, winged.

TYPE: Ouadi Kelt, Palestine, "entre le Moulin et l'embouchure de la vallée de Jéricho," April 21, 1934, apparently at (G). Not seen.

ILLUSTRATION. Bull. Soc. Bot. Genève II. **26**: 94. *fig. 1, 2.* 1936.

No specimens seen. Drawings copied from those in original description. The glabrousness of the plants and the pale rose flowers seem distinctive.

19. **Delphinium cyphoplectrum** Boiss. Diagn. I. **6**: 7. 1845. FIG. 3, I.

Delphinium cyphoplectrum var. *micranthum* Boiss. Fl. Orient. **1**: 91. 1867.
Delphinium schroedingerianum Hand.-Mazz. Ann. K. K. Nat. Hofmus. Wien **27**: 44. 1913. Based on *Kotschy 393a* and *400*, near Persepolis. The latter seen (K).

Stem terete, branched above, 3–10 dm. tall, subglabrous to somewhat strigulose below, more loosely appressed-pubescent above; cauline leaves few, remote, with petioles to ca. 1 dm. long and somewhat vaginate at the base, the lower leaves palmately parted, then divided into oblong lobes 3–5 mm. or more wide, the laminae 5–8 cm. wide; racemes several, lax, several flowered; bracts mostly entire, the lower to 2 cm. long, 1.5–3 mm. wide, the upper much reduced; pedicels densely appressed-puberulent, 5–10 mm. long, the 2 bracteoles near the base of the pedicel, 2–3 mm. long; sepals blue to smoky gray, the upper 12 mm. by 7 mm., obtuse, strigose, the spur straight, obtuse, subcylindric, 10 mm. long, ca. 3 mm. wide at the base; lateral sepals subelliptic, ca. 12 mm. by 4.5 mm., rounded at apex, somewhat strigose near end of midrib; lower sepals elliptic-obovate, broadly obtuse, ca. 13 mm. by 5 mm.; upper petals blue, the lamina obliquely truncate, 9 mm. long, bilobulate; lower 10–11 mm. long, the claw 4.5 mm., the limb ca. 6 mm., elliptic, bearded, the 2 parallel lobes 2.5 mm. long; stamens 8–9 mm. long, glabrous, slightly dilated in lower half; anthers 0.8 mm. long; follicles 3, pubescent.

TYPE: Mt. "Kuh-Malo prope Dalechi Persiae australis," March, 1842, *Kotschy 153*, presumably (G); isotypes seen (A, BM, K, MO, P).
DISTRIBUTION. Between 2000 and 2700 m., southern Iran.

EXAMPLES. *Haussknecht*, April, 1868; *Furse 3061*; *Loftus*, May 3, 1852; *Horner 153*; *Kotschy 400*.

20. **Delphinium dasystachyum** Boiss. & Bal. in Boiss. Diagn. II. 6: 7. 1859. FIG. 3, J.

Delphinium dasystachyum var. *ochroleucum* Boiss. Fl. Orient. 1: 88. 1867. Based on Mt. Berit Da, *Hausskn.*, cited by Davis, Fl. Turkey 1: 113. 1965, as example of *D. dasystachyum*.

Plant cinerascent-strigulose throughout, the stem simple, more or less angled, 2–4.5 dm. tall, leafy to the inflorescence; lowest leaves 2–3 cm. broad, with petioles twice as long and vaginate at base, the laminae multifid into ultimate linear lobes ca. 1 mm. wide; upper cauline leaves more crowded, with short broad membranous petioles; inflorescence dense, many flowered, to ca. 1 dm. long; bracts 3–5-fid to the broad short petiole, strigulose, 1–2 cm. long; pedicels arcuate, 5–10 mm. long, the lanceolate acuminate bracteoles ca. 5 mm. long, 2 mm. wide, just beneath the flower; sepals broad based, bluish to dirty white, densely and loosely strigulose; upper sepal 8 mm. by 3 mm., obtuse, lance-ovate, the spur 10 mm. by 3 mm., acute, descending, slightly curved; lateral sepals 8 mm. by 3 mm., oblong, obtuse; lower sepals ca. 9 mm. by 3 mm., obtuse; upper petals glabrous, bluish to yellowish, oblique, ca. 8 mm. long, bidentate, the spur the same length; lower petals with claw 4–5 mm. long, lamina oblong-ovate, bearded, 4–5 mm. long, with terminal lobes ca. 2 mm. long; stamens yellow, 4–5 mm. long, glabrous, anthers 0.7 mm. long; follicles 3, ca. 6 mm. long, hairy, rugulose toward apex; seeds truncate, with transverse undulating rows of white lamellae.

TYPE: Summit of Ali-Dagh, at 1700 m., 7 km. se. of Caesarea, Cappadocia, Turkey, *Balansa 859* (probably G); isotypes seen (BM, GH, K, P).
DISTRIBUTION. Rocky slopes, 1500–2500 m., eastern Turkey.

EXAMPLES. *Davis 31669, 31999*; *Balls & Gourlay 1992, 1977*; *Furse 3732*.

21. **Delphinium dolichostachyum** Chowdhuri & Davis, Notes Bot. Gard. Edinb. **22**: 408. 1958. FIG. 3, K.

Plant 5–8.5 dm. tall, the stem erect, acutely angled, subsulcate, branched above the middle, strigulose above, subglabrous below; lower and median cauline leaves palmately 3–5-sect, 5–8 cm. broad, subglabrous, long petioled, the segments 3–5-parted into lance-linear or lanceolate ultimate parts 2–5 mm. wide; petioles subvaginate at the base; upper leaves few, trisect; terminal raceme 13–23 cm. long, dense, many flowered, longer than the lateral ones; bracts prominent, the lower 1–3 bracts foliaceous, plurisect, longer than the pedicels, the middle tripartite into linear segments, the upper entire, linear-subulate; pedicels 9–25 mm. long, ascending-erect; bracteoles linear-subulate, on upper part of pedicel; sepals pale blue, 6–9 mm. by 3–4 mm., oblong-obovate or elliptic-ovate, obtuse or rounded at tip, densely strigulose, the spur 9–12 mm. long, slender, attenuate, acute, usually curved; petals included, the upper glabrous, with a short-bifid almost straight lamina 7 mm. long, spur 10 mm. long; lower petals with broad-ovate limb 4–5 mm. long and broad, bearded, bifid above the middle, the claw puberulent; stamens 5–6 mm. long; anthers yellowish, rounded, almost 1 mm. long; follicles 3, mostly 7–9 mm. by 3–4 mm., hirsute-pubescent; seeds 1.5 mm. long, scaly, triquetrous.

TYPE: Turkish Kurdistan, prov. Bitlis, Karz Dag above Kamer, 2200 m., *Davis 24566* (*Davis & Polunin* 8–24–1954); holotype (E); isotypes (BM, K); seen.

A specimen collected by *Are Rowi 12213* and one by *Gillett 11782* from Iraq (K) seem to belong here.

The species resembles *D. dasystachyum* in its small pale flowers, but differs in its tall branching, strigosity, less vaginate petioles, and tripartite (not multi-) lower bracts.

22. **Delphinium fissum** Waldst. & Kit. subsp. **anatolicum** Chowdhuri & Davis, Notes Bot. Gard. Edinb. **22**: 404. 1958. FIG. 3, L.

Delphinium leiocarpum Huth, Bull. Herb. Boiss. **1**: 334. 1893, as to type: *Sintenis 589*, Kaz Da, near Kareikos, Turkey; isotype seen (K). Same as *anatolicum*.

Delphinium amani Post ex Huth, Bull. Herb. Boiss. **3**: 152. 1895. Based on *Shepard* (*Barbey 295*), in 1892, Gaiour Da (Amanus); isotype seen (K).

Stem 5–9 dm. tall, 3–6 mm. thick, sometimes with vertical lines of short spreading hairs above; leaves few, the lower glabrous, with petioles very slightly dilated at the base, to 1 dm. long, the blades 7–18 cm. wide, palmately multifid into ultimate lance-linear to oblong segments 2–8 mm. wide; upper leaves reduced; raceme dense, 5–10 or more cm. long, many flowered, subglabrous; bracts simple, linear, 5–8 mm. long; pedicels recurved and subclavate at summit, mostly less than 1 cm. long; bracteoles near middle of pedicel, linear, 2–3 mm. long; sepals pale blue, glabrous; upper sepal ovate, 8 mm. long, 4 mm. wide, obtuse, the spur often subvertical, straight, ca. 15 mm. long; lateral sepals oblong, obtuse, ca. 6 mm. by 2 mm.; the lower pair oblong-ovate, 6 mm. by 3 mm.; upper petals glabrous, pale, 7.5 mm. long, bilobulate, the spurs ca. 15 mm. long; lower petals with lamina ca. 4.5 mm. long, white bearded, the lobes 3.5 mm. long; stamens 5–6 mm. long, filaments dilated below, glabrous; anthers yellow, 0.8 mm. long; follicles 3, glabrous.

TYPE: Mt. Ida, near Kareikos, prov. Cannakale, Turkey, *Sintenis 589*, holotype (K), isotypes (BM, P, US); all seen.

DISTRIBUTION. Coniferous forest, 1000–1650 m., Anatolia. Subsp. *fissum* is European.

EXAMPLES. **Anatolia:** *Manissadjian 675*; *Davis 13140, 14703*; *Haradjian 571, 552, 2537.*

23. **Delphinium gorganicum** Rech. f. Ang. Österr. Akad. Wiss. Math.-Nat. **88**: 226. 1951. FIG. 3, M.

Stem erect, 1–1.3 m. high, subsimple or with few branches above, somewhat fistulose, scattered-leafy, pale green, striate, glabrous or sparsely strigulose, especially above; lower leaves gone by anthesis, the petioles apparently long, the upper much shorter, subglabrous, slightly dilated at the base; leaf blades angled-cordate in outline, to ca. 1 dm. broad, 2–3-palmatisect into petiolulate segments that are long-cuneate at the base, obovate above and divided into 5–7 lance-linear lobes 5–8 mm. wide, 2–4 cm. long, subglabrous, paler beneath than above, acute, submucronulate; uppermost leaves simpler, passing into leafy divided bracts 3–5 cm. long, upper bracts strigose, trifid to lance-linear, 5–10 mm. long; terminal raceme lax, many flowered, to 3 dm. long; pedicels suberect, 1–10 mm. long, with yellow glandular pubescence; bracteoles 2, subulate, near the base of the pedicels; sepals yellow, puberulent, the upper sepal broadly ovate, 10 mm. by 8 mm., acutish, the spur 9-12 mm. long, almost straight, ca. 3 mm. wide at base, narrowed rapidly to the narrow apex; lateral sepals elliptic-obovate, 12 mm. by 5 mm., obtuse; lower sepals 12 mm. by 7 mm., obovate, obtuse; petals yellowish, the lamina of the upper slightly oblique, entire at the obtuse tip, ca. 9 mm. long, the spur 10 mm. long; lower laminae bearded, ciliate, oblong, 4.5 mm. by 3 mm., deeply cleft, the lobes lance-oblong, claw 6 mm. long, serrulate on upper edge; stamens almost 8 mm. long, somewhat ciliate, moderately widened; anthers light in color, round-oblong, 0.8 mm. long; follicles 3, pubescent.

TYPE: Iran: prov. Gorgan (Asterabad), Mt. Shawar near Hadjilang, 2400–2600 m., *K. H. & F. Rechinger 6191* (W); isotypes seen (K, UC, US).

Very near *D. biternatum*; doubtfully distinct. No other collections seen.

24. **Delphinium griseum** Gilli, Repert. Sp. Nov. **57**: 96. 1955. FIG. 3, N.

Stem clothed at base with brownish black sheaths formed by old petiole bases, erect, angular-striate, subflexuous to bases of petioles, 6–7 dm. tall, with few short branches in upper part and with short retrorsely appressed pubescence; lower petioles to 13 cm. long, dilated into a sheathing base, short-puberulent; upper shorter; blades roundish in outline, the lower 5–8 cm. broad, 3-parted almost to base, the parts cuneate, 2–3 cm. wide, 3–4 cm. long, their upper part divided into lobes 1–1.5 cm. long, 3–15 mm. wide; bracts linear, strigulose, ca. 3 mm. long; terminal raceme lax, 2–3 dm. long, ca. 20-flowered, the lateral racemes 12–15 cm. long, 10-flowered; pedicels ca. 1 cm. long, elongating in fruit, bibracteolate, closely and finely strigulose; sepals gray-violet, oblong, attenuate at base, obtuse, 9 mm. long, 2 mm. wide, appressed-puberulent on whole outer face, the upper sepal with a slightly curved obtuse spur 1 cm. long, puberulent, somewhat gibbous above the base; petals whitish, the upper glabrous or nearly so, the blade and spur each 10 mm. long, the former with 2 lanceolate lobules; lower petals lanceolate-spatulate, long stipitate, deeply lobed into acutish lobes with long hair on both sides, blade and claw each about 5 mm. long; filaments gray violet, dilated at base, sparsely short-hairy; anthers dark brown; follicles 3, slightly pilose toward the tips to almost glabrous; immature seeds trigonous, squamate or rugulose.

TYPE: In Kabul Gorge, southeast of Surobi, east Afghanistan, at 1050 m., May 28, 1951, *Gilli 839* (W); seen.

Another collection from "Sarobi," May 12, 1951, *O. H. Volk 1873* (W).

This species is very near *Delphinium kohatense* of the northwestern Himalaya, but apparently has more flowers in a raceme and they are larger. I am greatly indebted to Professor Rechinger and Dr. Riedl of the Natural History Museum of Vienna for the loan of the two specimens cited above.

25. **Delphinium ilgazense** Davis, Notes Bot. Gard. Edinb. **26**: 169. 1965.

Stems 1.5–2 dm. tall, simple, terete, striate, sparsely strigulose below, with spreading glandular hairs in inflorescence; lower leaves long petioled, suborbicular, 2–3 cm. wide, palmatisect, strigose, the segments divided into ultimate linear laciniae ca. 0.5 mm. wide; inflorescence dense, 2.5–5 cm. long, 4- to 7-flowered; bracts viscid-pilose, the lower trisect or all entire, linear; pedicels erect, 5–7 mm. long; bracteoles in upper part of pedicel, lance-linear, 2.5–4.5 mm. long; sepals dark violet-blue, divergent, ovate-oblong, spreading-pilose, 7–10.5 mm. long; spur 13–14 mm. long, gradually attenuate, acute, horizontal; upper petals slightly exserted, the lamina glabrous, short-bifid; lower petals with a broadly ovate, deflexed, deeply bifid lamina bearded above and equal to the claw; follicles strigose.

TYPE: Kastamonu, Turkey, north side of Ilgaz Dag, 2200 m., on rocky limestone slopes, Aug. 28, 1962, *Davis 38373* (E) which I have not seen. Known from the type collection only; illustrated as *plate 17*, with the original description.

Endemic; Davis considers it near *D. cyphoplectrum*.

26. **Delphinium inopinatum** Nevski in Komarov, Fl. U.S.S.R. 7: 73, 727. 1937. FIG. 3, O.

Stem 7.5–8.5 dm. tall, leafy, almost wholly yellow glandular-pubescent; petioles 5–10 cm. long, widely dilated at base, densely pubescent; laminae of leaves 4–8 cm. broad, ternately parted, the first segments short petiolulate, divided bi- to triternately into terminal narrowly linear (1.25–2.5 mm. wide), densely pubescent laciniae; inflorescence mostly branched, the central raceme rather dense, 2.5–3.5 dm. long, the axis sparsely glandular-pilose; bracts minute, 2.5 mm. long, linear, glabrous or ciliolate; pedicels mostly less than 1 cm. long, glabrous; bracteoles linear-subulate, inserted above the middle of the pedicels; sepals pale, sordid bluish-lilac, 8–9 mm. long, 3.5–4 mm. wide, oblong-obovate, obtuse, glabrous, white-membranous on margins; spur nearly or quite straight, spreading to erect, glabrous, 10–11 mm. long, 2–2.5 mm. wide; petals whitish, the upper laminae perpendicular to the spur, glabrous, ca. 8 mm. long, bidentate, the spur 12 mm. long; lower laminae slightly oblique, long-hairy and ciliate, more or less laciniate, ca. 4 mm. long, the claw 4 mm. long; follicles 12–15 mm. long, 4 mm. wide, erect, glabrous; seeds pale, 2.5–3 mm. long, with transverse rows of scales.

TYPE: Asia Media, "in montibus Ak-Tau" (Kazakhskiy), May 19, 1932, *Russanov 119* (LE); seen. The type is the only specimen that I have seen.

This species differs from *D. bucharicum* in its indument of yellow glandular hairs.

27. **Delphinium ithaburense** Boiss. Diagn. I. 8: 9. 1849. FIG. 3, P.

Delphinium sulcatum Reichb. ex Hoffmannsegg, Verz. Pfl. Nachtr. 1: 132. 1824. *Nomen.*

Delphinium salmoneum Mouterde, Fl. Djebel Druse 98. *pl. III, no. 2.* 1953. No type cited, but in the illustration, the legend says "Tell Ahmar, 15 May. 1942." I have seen no specimen, and cannot separate it as a species from the description alone.

Stem 3–10 dm. tall, angled, simple, subglabrous to somewhat glandular-pubescent; leaves palmately 5–7-parted into cuneate segments, in turn coarsely toothed or lobed, the upper leaves laciniate into oblong-linear lobes ca. 2 mm. wide; petioles vaginate at base; raceme elongate, simple, rather many flowered, often rather dense at anthesis, lax in fruit; bracts lance-ovate, 5–10 mm. long, ciliate or glabrous; pedicels mostly 5–10 mm. long, the lance-ovate bractlets 2–3 mm. long and near the base of the pedicel; flowers bluish white to pink or yellowish green; sepals membranous margined; upper sepal lance-oblong, 9–10 mm. long, subglabrous except for the pubescent patch below the acutish tip, the spur straight, glabrous, horizontal, ca. 15 mm. long, 2.5 mm. wide at base; lateral sepals oblong, ca. 9 mm. by 3.5 mm., rounded at the apex, with broad base, slightly pubescent toward the tip of the midrib; lower sepals elliptic-oblong, 9 mm. long, 4 mm. wide, slightly asymmetrical; upper petals glabrous, obliquely truncate, the lamina 10 mm. long, 2-lobulate for 1 mm., the spur 15–17 mm. long; blade of lower petals 6–7 mm. long, bearded, with 2 lance-oblong lobes 3–4 mm. long, claw 3–4 mm. long; stamens 5–7 mm. long, lower half white, oblong, upper half yellow, narrow; anthers yellow, scarcely 1 mm. long; follicles 3, erect, hirsute, 13–16 mm. long, 4–5 mm. wide, the beak 3–5 mm. long; seeds ca. 2 mm. long, with several rows of scales.

TYPE: Mt. Thabor, Galilee, Palestine, *Boissier* in 1846 (G) not seen; isotype (P) seen.

DISTRIBUTION. Wooded places at 100–2000 m., mountains of Syria, Lebanon, Israel and Jordan.

ILLUSTRATION. MOUTERDE, Fl. Djebel Druse *Pl. III, no. 2.* 1953.

EXAMPLES. **Lebanon:** *W. O. Douglas 39.* **Jordan:** *Dinsmore 1864.* **Israel:** *Davis 4608a, 4894A, 4896, 4608*; *F. Meyers B4864*; *Egger* 6–29–1906.

28. **Delphinium karategini** Korsh. Bull. Acad. St. Pétersb. sér. 5. **9**: 402. 1898. FIG. 3, Q.

Stem 8–15 dm. tall, freely branched above, rather equably leafy, with scattered more or less retrorse short hairs; petioles vaginate at base, 5–12 cm. long, the blades to 15 cm. broad, parted into long-petiolulate segments, these in turn divided into petiolulate parts which are dissected into linear laciniae to 3 cm. long and 1.5–2 mm. wide, more or less pubescent; uppermost leaves reduced; inflorescence of several divergent strict branches 1.5–5 dm. long, each rather openly many flowered, the axis glabrous; lowest bracts trifid into linear segments, others linear-subulate, glabrous, 6–9 mm. long; pedicels erect-divaricate, to ca. 10 mm. long, glabrous, the bracteoles near or below the middle of the pedicel, lance-linear, ciliate, ca. 3 mm. long; sepals pale blue, somewhat strigose, membranous margined; upper sepal 10–11 mm. by 4–5 mm., acute, the spur spreading upcurved, 12 mm. long, 3 mm. wide at base, blunt; lateral sepals oblong-obovate, rounded at apex, ca. 9 mm. by 4 mm.; lower sepals ca. 10 mm. by 4 mm., acute; petals whitish, the upper laminae strongly oblique, 7 mm. by 3 mm., glabrous, entire, the spur 10–11 mm. long; lower laminae almost straight, oblong-ovate, 7 mm. by 3 mm., bifid over halfway into lance-oblong lobes, long-ciliate and bearded, the claw 6 mm. long; stamens 7 mm. long, glabrous, the anthers pale, oblong, 1 mm. long; follicles 3, glabrous.

TYPE: Turkestan: Karategia, "ad ostium fl. Muksi," June 23, 1897, *Korshinsky 80* (LE); seen.

29. **Delphinium kohatense** (P. Brühl) Munz, comb. nov. FIG. 4, A.

Delphinium saniculifolium Boiss. var. *kohatense* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 95. 1896.

Delphinium saniculifolium Boiss. var. *gilgitense* P. Brühl in Brühl & King, *loc.*

cit. Based on *J. L. Stewart*, Sept. 23, 1885, at 13,000′; Gilgit Expedition s. of Hindu Kush (K); seen.

Stem slender, terete, mostly few branched above, 2–5 dm. high, sparsely strigulose below, densely so in the inflorescence; lower leaves 2–4 cm. broad, subglabrous to somewhat strigulose, trifid to base into cuneate segments, of which the two lateral are deeply divided so as to make 5 subequal, pinnately few lobed or toothed parts, the ultimate divisions 1–3 mm. wide, mucronate; petioles 2–7 cm. long, slender, somewhat dilated at base; cauline leaves few, remote, reduced; racemes rather open, to ca. 10-flowered, slender, strigulose; bracts linear, 2–3 mm. long; pedicels ascending, 5–25 mm. long; bracteoles lanceolate, near the base of the pedicel; sepals pale blue, blunt, the upper 6–8 by 3 mm., strigulose, the spur cylindric, obtuse, 5–7 mm. long; lateral sepals 7.5–8 mm. by 2.5 mm.; lower sepals ca. 8 mm. by 3 mm., oblong-oblanceolate; upper petals ca. 7.5 mm. long, pale, oblique, the bearded lamina with terminal lobes 1 mm. long; spur 5 mm. long; lower petals ca. 8 mm. long, lamina and spur subequal in length, the former bearded, divided for 2.5 mm.; stamens 4.5–5.5 mm. long, the filaments bluish, somewhat ciliate on expanded lower part; anther 0.8 mm. long; follicles 3, pubescent at tip.

LECTOTYPE: Pakistan: Kohat & Wagiristan, *Drummond* (CAL), seen; but specimen old and almost without flowers. I am greatly indebted to Mr. K. S. Srinivasan for loan of the above and other specimens from the Calcutta Herbarium. What is apparently the same thing, collected by *J. L. Stewart*, at dry places up to 3500′, (K) was seen.

ILLUSTRATION. BRÜHL & KING, Ann. Bot. Gard. Calc. **5**: *pl. 117, fig. 1 & 2.* 1896.

DISTRIBUTION. Dry places, mostly below 3000 m., Afghanistan and West Pakistan to northwest India.

REPRESENTATIVE SPECIMENS. **Afghanistan:** *Herb. Griffith 43.* **Punjab:** *Aitchison 1004*; *Drummond 14811*; *R. R. Stewart 10936.* **West Pakistan:** Chitral, *Stainton 2529*; *Siddiqui & Arahman 26865*; *Toppin 370*; *Dr. Giles*, June 24, 1886.

30. **Delphinium kurdicum** Boiss. & Hohen. in Boiss. Diagn. I. 1: 67. 1842.

FIG. 4, B.

Delphinium kurdicum var. *elongatum* Freyn & Sint. Österr. Bot. Zeitschr. **41**: 363. 1891. Based on *Sintenis 2822* from Mt. Sokardidagh, Armenia; not seen, but cited by Davis as example of *D. kurdicum* in Fl. Turkey **1**: 116. 1965.

Stem somewhat zigzag, few branched, 3–5 dm. tall, more or less strigulose with very short hairs, many of which are enlarged at base; lower leaves withered by anthesis, upper multifid into few linear or lanceolate lobes 8–20 mm. wide, 3–8 cm. long; racemes in an open panicle, rather few to many flowered, more or less peduncled; bracts lance-linear, 5–10 mm., rarely to 30 mm. long; pedicels somewhat divaricate, 5–15 mm. long;

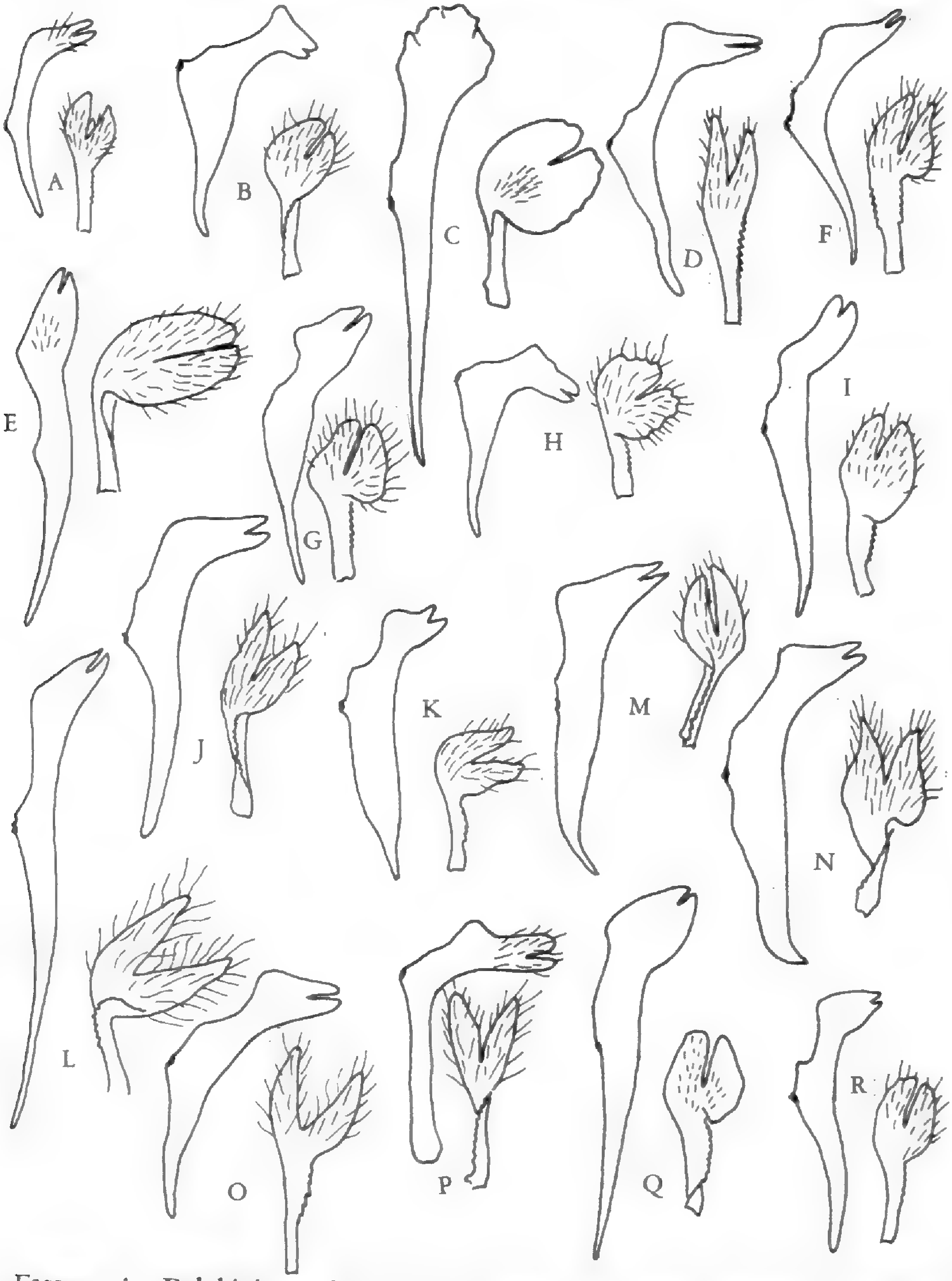

FIGURE 4. **Delphinium**, GROUP IV. Petals, the upper spurred, the lower clawed. A. *D. kohatense*; upper lamina 7.5 mm. long, spur 5 mm.; lower lamina 4 mm. long, claw 4.5 mm.; drawn from *R. R. Stewart* in 1936 (NY). B. *D. kurdicum*; upper lamina 7 mm. long, spur 10 mm.; lower lamina 4.5 mm. long, claw 4.5 mm.; drawn from *Kotschy 427* (MO). C. *D. latesquamatum*; upper lamina 11 mm. long, spur 16 mm.; lower lamina 6 mm. long, claw 4 mm.; drawn from *Gilli 840* (W). D. *D. laxiusculum*; upper lamina 8 mm. long, spur 10 mm.; lower lamina 5 mm. long, claw 4.5 mm.; drawn from *Sjovits* (GH). E. *D. longebracteatum*; upper lamina 12 mm. long, spur 10 mm.; lower lamina 8 mm. long, claw 5 mm.; drawn from *Balansa 1353* (US). F. *D. longipedunculatum*; upper lamina 8 mm. long, spur 11 mm.; lower lamina 7 mm. long, claw 5 mm.; drawn from Mo. Bot. Gard. 1.720.217. G. *D. macropogon*; upper lamina 7 mm.

bracteoles 3–4 mm. long, situated above the middle of the pedicel; sepals yellowish to dirty white, strigulose to glabrous, the upper sepal ovate, 7.5–8 mm. long, 3.5 mm. wide, acute, the spur horizontal, 10–11 mm. long, 3.5 mm. wide at base; lateral sepals 8 mm. by 3 mm., oblong, broadly unguiculate, pubescent on median line or more broadly; lower sepals 8 mm. by 3 mm., rather pointed, broadly unguiculate; upper petals glabrous, obliquely truncate, yellowish, the limb 7 mm. long, bidentate, the spur 10 mm. long; lower petals with claw 4 mm., blade 4.5 mm. long, the latter broadly elliptical, bearded, lobed ca. 2 mm. deep; stamens 4–5 mm. long, glabrous; anthers 0.8 mm. long; follicles 3, glabrous, 8 mm. by 3.5 mm., the styles an additional 2 mm.

Type: "Ad fontes montis Gara Kurdistaniae," *Kotschy 427* (originally published as 627) (G) not seen; isotypes (BM, K, MO, P) seen.

Distribution. Dry slopes and plains, 1000–1400 m., northern Iraq and eastern Turkey.

Examples. **Turkey:** *Kotschy 503*; *Sintenis 1185*; *Davis 31496*. **Iraq:** *Ali al-Rawi & Serhang 23807*; *R. Wheeler Haines 416*.

31. **Delphinium latesquamatum** Gilli, Repert. Sp. Nov. **57**: 94. 1955. Fig. 4, C.

Stem 2.5–6 dm. high, clothed at base with whitish sheaths of old leaves, terete, striate, erect, subflexuous, with divaricate branches 2–4 dm. long, with short retrorse pubescence throughout, mixed with glandular hairs in the upper parts; petioles 1.5–3 cm. long in lower leaves; blades cuneate, 3-parted to the lower third, 2–8 mm. wide, the parts incised into ultimate laciniae 0.5–2 mm. wide; cauline leaves with petioles 0.3–3 cm. long, the ultimate divisions of the laminae 0.5 mm. wide, acute; bracts linear, puberulent, 3–10 mm. long; pedicels 1–2 cm. long, bibracteolate mostly

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long, spur 10 mm.; lower lamina 4.5 mm. long, claw 4 mm.; drawn from TYPE (LE). H. *D. macrostachyum*; upper lamina 6 mm. long, spur 9 mm.; lower lamina 5 mm. long, claw 3.5 mm.; drawn from *Sintenis 1266* (PHIL). I. *D. micranthum*; upper lamina 7 mm. long, spur 12 mm.; lower lamina 6 mm. long, claw 4 mm.; drawn from *Gillett 9501* (US). J. *D. nuristanicum*; upper lamina 10 mm. long, spur 12 mm.; lower lamina 5 mm. long, claw 6 mm.; drawn from *W. E. Brown 804* (K). K. *D. ochroleucum*; upper lamina 7 mm. long, spur 8 mm.; lower lamina 5 mm. long, claw 4.5 mm.; drawn from *Hohenacker* at Schuscha (GH). L. *D. pallasii*; upper lamina 10 mm. long, spur 18 mm.; lower lamina 6.5 mm. long, claw 6 mm.; drawn from TYPE (LE). M. *D. pallidiflorum*; upper lamina 9 mm. long, spur 10 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Heideman* in 1932 (K). N. *D. penicillatum*; upper lamina 8 mm. long, spur 10 mm.; lower lamina 5 mm. long, claw 4 mm.; drawn from *Aucher 4034* (K). O. *D. puniceum*; upper lamina 10 mm. long, spur 9 mm.; lower lamina 6 mm. long, claw 6 mm.; drawn from *Hohenacker* in 1834 (CAS). P. *D. quercetorum*; upper lamina 9 mm. long, spur 11.5 mm.; lower lamina 5 mm. long, claw 5.5 mm.; drawn from *Haussknecht* in Kurdistan (BM). Q. *D. roylei*; upper lamina 8 mm. long, spur 14 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Koelz 9261* (GH). R. *D. saniculifolium*; upper lamina 7 mm. long, spur 9 mm.; lower lamina 5 mm. long, claw 4 mm.; drawn from *Rechinger 3364* (US).

above the middle, the bracteoles 2–3 mm. long; sepals blue, obovate, obtuse or acutish, 6–9 mm. long, 4–6 mm. wide, puberulent and glandular without, the spur slightly curved, not gibbous, 13–17 mm. long; petals somewhat yellowish below, bluish toward the tips, the upper lamina 10–11 mm. long, glabrous, almost round near the tip, where 5 mm. in diameter, crenulate, the spur ca. 12–13 mm. long; lower laminae 6 mm. by 5 mm., glabrous save for the patch of hairs near the base, with 2 lobes 1–2 mm. long, claw 3–4 mm. long; filaments glabrous; anthers dark brown; follicles 3, pilose, to ca. 8 mm. long; seeds with many tiers of broad scales.

TYPE: Afghanistan, near Bamian, 2950 m., Aug. 29, 1951, *Gilli 840* (W); seen.

REPRESENTATIVE COLLECTIONS. All from **Afghanistan:** prov. Orozgan, *Rechinger 18812*; *Lindberg 875, 964*; central Nuristan, *Kerstan 1399*, at 2600 m.; *Edelberg 1208* at 2000 m.; prov. Ghazni, *Rechinger 17552, 17629*, at 3300 m.; prov. Bamian, *Rechinger 18698, 18449, 18250.*

The species seems near *D. batalinii* of Turkestan, but has much wider petals. I am very grateful to Dr. K. H. Rechinger and Dr. H. Riedl of the Natural History Museum at Vienna for the loan of the material cited above.

32. **Delphinium laxiusculum** (Boiss.) Rouy, Fl. France **1**: 143. 1893. Nevski in Komarov, Fl. U.S.S.R. **7**: 175. 1937. FIG. 4, D.

Delphinium hybridum Willd. var. *laxiusculum* Boiss. Fl. Orient. **1**: 89. 1867.
Delphinium hybridum subsp. *laxiusculum* N. Busch in Fl. Cauc. Crit. III. **3**: 56. 1903.
Delphinium hybridum var. *gracillimum* Ledeb. Fl. Rossica **1**: 61. 1841. Placed here by Nevski in Komarov, Fl. U.S.S.R. **7**: 175. 1937.
Delphinium hybridum var. *hirtula* Trautv. Acta Horti Petrop. I. **1**: 21. 1878. Placed here by Nevski in Komarov, Fl. U.S.S.R. **7**: 175. 1937.
Delphinium cyphoplectrum Boiss. var. *stenophyllum* Boiss. Fl. Orient. **1**: 91. 1867. Isolectotype (Davis), Schambulagh, Iran, *Szowits* (K), seen.
Delphinium talyschense Tzvelev, Not. Syst. ex Hort. Inst. Bot. Komarovii **19**: 6. 1959. Type, Azerbaidschan, Talysch, *Matveeva 555* (LE), seen.

Stem 2–5.5 dm. tall, somewhat angled and sulcate, strigulose, quite densely so in the inflorescence, simple; lower leaves with petioles to 1 dm. long and vaginate at the base, blades 3–10 cm. wide; cauline leaves remote, the uppermost with shorter petioles, blades palmately 5-fid, the segments openly laciniate into few lobes 1–2 mm. wide; raceme 12–18-flowered, lax, strigose; bracts simple, lanceolate, 3–20 mm. long; pedicels mostly 5–15 mm. long; bracteoles 2, near base of pedicel, 2–3 mm. long; sepals blue, the upper strigulose, 12 mm. by 4 mm., lance-ovate, acute, the spur cylindrical, blunt, 12 mm. long, 2.5 mm. wide at the base; lateral sepals elliptical, 10 mm. by 4 mm., obtuse, strigose near the tip of midrib; lower sepals 12 mm. by 4 mm., acute, more generally strigose; upper petals bluish, oblique, ca. 8.5 mm. long, shallowly bilobulate, the spur 8.5–9 mm. long; lower petals bluish, claw 4.5 mm. long, blade 7.5 mm. long, bearded, narrow, with 2 lanceolate lobes 3–4 mm. long; stamens 6–7 mm. long, glabrous, dilated in lower half; anthers bluish, 0.7 mm. long; follicles 3, strigose, 11–20 mm. long, the beak an additional 2–3 mm.

TYPE: "Hab. inter segetes prope Elisabethpol," *Hohenacker in 1834* (G) not seen, isotypes (GH, K, LE, MO) seen.

DISTRIBUTION. Transcaucasia, northern Turkey, and northern Iran.

EXAMPLES. **Transcaucasia:** *Gurvitsch* in 1937. **Iran:** *Furse & Synge 784*; *Pichler*, in 1882. This plant is treated in Davis, Fl. Turkey **1:** 115. 1965, as *D. cyphoplectrum* var. *stenophyllum*.

33. **Delphinium longebracteatum** (Boiss.) Munz, comb. nov.

FIG. 4, E.

Delphinium dasystachyum Boiss. & Bal. var. *longebracteatum* Boiss. Fl. Orient. **1:** 89. 1867.

Delphinium szovitsianum var. *longebracteatum* (Boiss.) Huth, Bot. Jahrb. **20:** 438. 1895.

Stem simple, subterete, 2–3 dm. tall, substrigulose below, densely pubescent above with soft yellowish spreading hairs; lower leaves with petioles 4–7 cm. long, much dilated at base, middle cauline and upper petioles shorter, the broad base membranous, 1–1.5 cm. long, almost 1 cm. wide; blades 2–3 cm. wide, multifid into linear lobes to ca. 1 mm. wide; inflorescence dense, 4–8 cm. long, soft-hairy, many flowered; lower bracts to 3 cm. long, with long linear segments and dilated membranous base, the upper ca. 1 cm. long, simple, with dilated hairy base and long attenuate tip; pedicels to 1.5 cm. long, more or less curved; bracteoles to ca. 9 mm. long, membranous, with subulate tip and placed about the middle of the pedicel; flowers yellowish, the sepals with long yellow or white hairs, upper sepal 11 mm. by 5.5 mm., obtuse, the spur 12 mm. long, descending, acute; lateral sepals oblong-obovate, 10 mm. by 4.5 mm., rounded at apex; lower sepals elliptic-oblong, 10 mm. by 4.5 mm.; upper petals oblique, the blade 12 mm. long, somewhat bearded on inner face of lamina and with terminal lobules ca. 1 mm. long; lower petals unguiculate. the claw ca. 5 mm. long, the lamina bearded, oblong, 5 mm. long, the 2 parallel lobes ca. 3 mm. long; stamens glabrous, 5–6 mm. long; anthers 0.8 mm. long; follicles 3, hairy.

TYPE: Northeastern Turkey: "in monte Bingoldagh Armeniae alt. 6000′," *Kotschy 754* (G). Not seen.

DISTRIBUTION. At 1500 to 2200 m., northeastern Turkey.

EXAMPLES. *Balansa 1353*; *Balls & Gourlay 1977a*.

So far as I can see these collections are referred to *D. dasystachyum* by Davis, Fl. Turkey 1: 113. 1965, but the more spreading pubescence of the upper stems, more yellowish sepals, longer upper petals, etc., seem to me to separate *Delphinium longebracteatum* from that species.

34. **Delphinium longipedunculatum** Regel & Schmalh. Acta Horti Petrop. **5**: *226*. 1877. FIG. 4, F.

Stem slender, 3–6 dm. high, zigzag, slightly angled, sparsely pilose below, glabrous above, subdivaricately branched above; leaves remote, largely withered by anthesis, the petioles dilated at the base, 2–5 cm. long, the blades rounded-cordate, palmately lobed, the lobes incised into broadly oblong, obtuse lobules; inflorescence open, subpaniculate, the flowers on each branch rather few; bracts entire, lance-linear, 3–5 mm. long; pedicels stiff, slender, 2–6 cm. long; bracteoles opposite, ca. 3 mm. long, placed well below the flower; sepals deep blue, glabrous; upper sepals lance-ovate, 9 mm. long, 4 mm. wide, acute, spur straight, subcylindric, blue, horizontal, acute, 11–13 mm. long; lateral sepals oblong-ovate, 9 mm. by 5 mm., abruptly narrowed into an acute tip; lower sepals elliptic-obovate, 9 mm. by 5.5 mm., rounded apically; upper petals white with bluish tinge, 8–9 mm. long, the terminal lobules slightly more than 1 mm. long; lower petals bluish, white bearded, the lamina 7–8 mm. long, with divaricate lobes 3 mm. long and the claw 4.5 mm. long; stamens 5–6 mm. long, bluish, dilated below, glabrous; anthers 1 mm. long; follicles 3, glabrous, 10–12 mm. long, 2 mm. thick.

TYPE: "In montibus Karatau inter Turkestan et Tschemkent," *A. Regel*, May, 1876 (LE) seen; possible isotypes seen (BM, K, P).
DISTRIBUTION. Turkestan.

EXAMPLE. *Vnorrili 43*.

35. **Delphinium macropogon** Prokhanov, Not. Syst. ex Herb. Komarovii **21**: 417–437. 1961. FIG. 4, G.

Stem 2–10 (–14) dm. tall, 2–5 mm. thick, ridged, glabrous below, somewhat strigulose in inflorescence, more or less zigzag, remotely leafy, simple or few branched in inflorescence; lower leaves long petioled (14–25 cm.), cauline petioles to ca. 1 dm., somewhat vaginate; blades suborbicular, 7–15 cm. broad, pubescent on both surfaces, paler beneath, palmately 5–7-fid to base into obovate segments narrow-cuneate below, more or less trifid above into lance-linear lobes 13–30 mm. long, 2–7 mm. wide; racemes 5–12 cm. long, dense, many flowered; bracts linear, 5–15 mm. long, white margined, somewhat pubescent on margins; pedicels 5–8 mm. long, strigose; bracteoles linear, 3–6 mm. long, situated near middle of pedicel; sepals ochroleucous to whitish, pubescent; upper sepal 9 mm. by 5 mm., spur conic-cylindric, 10–12 mm. long; lateral sepals 7 mm. by 4 mm., elliptic, rounded at apex; lower sepals ca. 8 mm. by 4 mm.; petals white, the upper laminae strongly oblique, 7 mm. long, glabrous, bidentate, the spur 10 mm. long; lower laminae round-ovate, 4.5 mm. in diameter, bearded and ciliate in upper parts, bifid almost to base into approximate broad segments, claw 4 mm. long; stamens 6–7 mm. long, glabrous; anthers pale, elongate; follicles 8–10 mm. long, glabrous to strigose; seeds obovoid, to 2 mm. long.

TYPE: Daghestan: Kukurt-Tau, 2 km. from Mukku, *Prokhanov 43*, (LE) seen. No other material available.

36. **Delphinium macrostachyum** Boiss. ex Huth, Bot. Jahrb. 20: 441. 1895. FIG. 4, H.

Stem erect, flexuous, 6–15 dm. high, 3–4 mm. thick, glabrous below, sometimes puberulous above; leaves remote, long petioled, the petioles broadly vaginate at the base; lower leaf blades to 3 dm. across, subglabrous, multifid, the lobes broadly lanceolate; upper leaves 3–5-parted, the parts subentire; inflorescence simple and racemose or openly few branched, 3–5 dm. long, densely and many flowered; bracts entire, lance-subulate, 4–6 mm. long; pedicels 6–10 mm. long; bracteoles linear, 2–3 mm. long, near the middle of the pedicel; sepals deep violet to bronze-black, glabrous, the upper sepal ovate, 9 mm. by 4 mm., obtuse, the spur obtuse, straight, ca. 10 mm. long, 3 mm. wide at the base; lateral sepals 10–11 mm. long, 2.5 mm. wide, subobtuse; lower sepals 9 mm. by 4 mm., rounded at apex; upper petals violet, glabrous, ca. 7 mm. long, the 2 lobes 1 mm. long, the spur at right angles to the lamina and ca. 9 mm. long; lower petals violet, the claw 3 mm. long, the lamina roundish, white bearded, the lobes 3 mm. deep; stamens 5–6 mm. long, glabrous; anthers dark, 0.8 mm. long; follicles 3, erect, glabrous, 10 mm. long, the styles another 3 mm.

LECTOTYPE: Turkey: Bakakri near Mardin, July 2, 1888, *Sintenis 1266* (K); isotypes (P, PHIL); all seen.

DISTRIBUTION. Kurdistan from Turkey to Iran; on rocky limestone slopes at 1200–2000 m.

SEEN. **Iran:** *Furse 3404.* **Iraq:** *Wheeler Haines 513*; *Rami, Hoshen & Nuri 29481.*

37. **Delphinium micranthum** Boiss. & Hohen. in Boiss. Diagn. I. 1: 68. 1842. FIG. 4, I.

Stem angled, subglabrous to strigulose, slender, 3–5 dm. tall; petioles dilated-vaginate at base, the lower to 8 cm. long, the upper shorter; leaves 3–5-parted, then multifid into linear lobes ca. 1 mm. wide; racemes in loose panicles, but only 5–7-flowered; bracts linear (the lower trifid), 5–15 mm. long; pedicels 5–20 mm. long, bibracteolate just below the flower or lower, the bracteoles linear, 4–5 mm. long; sepals purple-blue, 7–10 mm. long, strigulose; spur straight, acute, 10–15 mm. long; upper petals glabrous, bluish, the blade about 7 mm. long, the spur 10–12 mm.; lower petals with the limb ovate, bifid to the middle and almost 6 mm. long; stamens somewhat bluish, 5–6 mm. long; anthers 0.6 mm. long; follicles 3, glabrous or glandular-pubescent, 6–8 mm. long, the styles an additional 1.5–2 mm.

TYPE: Iraq: Mt. Gara, Kurdistan, *Kotschy 610*, in 1843 (G), not seen. I have seen *Kotschy 410*, July 1841 (P) from same region.

DISTRIBUTION. At elevations below 2800 m., Iraqui Kurdistan.

EXAMPLES. *J. B. Gillett 9501, 11206, 12473*; *Gillett & Rawi 7404, 7223*; *Guest & Ludlow-Hewitt 2691*; *Lazar 118*; *Al-Rawi 24731*; *Wheeler Haines 1320*; *Guest 2916.*

38. **Delphinium nuristanicum** Tamura, Acta Phytotax. Geobot. **16**: 141. 1956. FIG. 4, J.

Stem 4–8 dm. tall, 3 or more mm. thick, simple or branched in inflorescence, sparsely white-hispidulous below, glabrous above the very base; radical and lower cauline leaves round-reniform in outline, 3–5 cm. long, 4–6 cm. wide, 3-parted almost to base, the lateral segments bipartite, all 5 parts incised-laciniate into lance-linear, obtuse lobes white-hispid on margins and lower surface; petioles 6–10 cm. long; upper cauline leaves glabrous, tripartite almost to base into linear-oblong segments 2–4 cm. long, 2.5–5 mm. wide, short petioled; raceme simple or branched below, 1–2 dm. long, few to many flowered; lower bracts to 18 mm. by 1.8 mm., petioled, the upper linear-filiform, 3–8 mm. long; pedicels 5–12 mm. long, more or less divaricate, elongating after anthesis, with some spreading, yellowish, glandular hairs near the summit; bracteoles near middle of pedicel, ca. 3 mm. long; sepals blue with pale median band, glabrous; upper sepals 12–13 mm. long, 4 mm. wide, obtuse, the spur horizontal with decurved tip, 12 mm. long, 2.5–3 mm. wide at base; lateral sepals 12 mm. by 4 mm., rounded at apex; lower sepals 10–12 mm. by 4–5 mm., oblong with rounded apex; upper petals whitish, the lamina strongly oblique, ca. 10 mm. long, glabrous, deeply bidentate, the spur ca. 12 mm. long; lower petals bluish, the oblong-obovate lamina ca. 6 mm. by 4 mm., bearded, cleft into 2 lanceolate divaricate lobes ca. 3 mm. long, the claw 6 mm. long; stamens 7–8 mm. long, glabrous, the roundish anthers 1 mm. long; carpels 3, said to be pilose in the type, glabrous in specimen cited below.

TYPE: Afghanistan: Nuristan: Chatras at 2100 m., *Kitamura*, Aug. 2, 1955 (KYO), not seen.

ILLUSTRATION. KITAMURA, Fl. Afghan. 126. *fig. 50.* 1960.

SPECIMEN SEEN. **West Pakistan:** Chitral, *W. E. Brown 804* (K).

Resembling *D. penicillatum* of southern Iran, but that species is viscid-pubescent, has shorter bracts and pedicels, smaller sepals.

39. **Delphinium ochroleucum** Stev. ex. DC. Syst. **1**: 353, 546. 1817. FIG. 4, K.

Delphinium hybridum var. *ochroleucum* Boiss. Fl. Orient. **1**: 89. 1867, as to type.

Delphinium hybridum ssp. *ochroleucum* Busch in Fl. Cauc. Crit. III. **3**: 54. 1903.

Delphinium ochroleucum var. *sulphureum* Regel ex Huth, Bot. Jahrb. **20**: 432. 1895. Not typified.

Stem slender, mostly 3–7 dm. tall, sparingly strigulose below, almost glabrous in inflorescence; lower leaves mostly withered by anthesis, long petioled, the petioles broad and vaginate at base, cauline leaves crowded, short-petioled, largely 2–4 cm. in diameter, 3–5-parted, then again divided into many narrowly linear lobes 0.5–1.5 mm. broad, strigulose; raceme generally simple, dense, many flowered, mostly 1–2 dm. long; lower bracts trifid, upper entire, linear, 8–15 mm. long; pedicels shorter than flowers, bibracteolate in middle; sepals ochroleucous, glabrous, the upper one ca. 7 mm. long, ovate, acute, its spur erect, 10–11 mm. long, 2 mm. wide at base; lateral sepals 5.6 mm. by 2 mm., more or less oblong; lower sepals 7 mm. by 3 mm.; upper petals with bluish tinge, glabrous, 7 mm. long, bidentate, the spur 10 mm. long; lower petals with blade ca. 5 mm. long, the 2 bearded lobes ca. 3.5 mm., the claw serrulate; stamens 4–5 mm. long, glabrous; anthers yellow, 0.8 mm. long; follicles 3, erect, 12–15 mm. long, 3 mm. thick, glabrous, the style an additional 2.5–3 mm.

TYPE: "Hab. in Iberia," now East Georgia (G) not seen. I have, however, seen a photograph of the Leningrad specimen "Iberia. comm. Steven" (K).

DISTRIBUTION. Apparently largely below 1000 m., mountains of Caucasus and Transcaucasia.

EXAMPLES SEEN. *Kolenati 1590*; *Hohenacker* near Schuscha; *Grossheim 37*; *Woronow 990*; *Davis 33907, 33853*; *Capus 50, 51, 53.*

40. **Delphinium pallasii** Nevski in Komarov, Fl. U.S.S.R. 7: 177. 727. 1937. FIG. 4, L.

Delphinium tauricum Pallas, Ind. taur. in Neueste Nordische Beiträge 3: 432. 1796; *nomen.*

Delphinium hybridum Willd. var. *debilius* Ledeb. Fl. Rossica 1: 61. 1841. Based on *Bieber*, Tauria. Not seen.

Stem 3.5–11.5 dm. tall, simple, densely strigulose throughout, more or less leafy; petioles strongly dilated at base, the lower 1–2 dm. long, the upper 1–3 cm.; blades of leaves 3-parted almost to base into cuneate-rhombic segments, these divided deeply into few divaricate, more or less falcate, linear-lanceolate lobes 1–3 cm. long, 1.5–4 mm. wide, somewhat pubescent especially beneath; raceme erect, dense, many flowered, 1–3 dm. long; bracts linear, the lower rarely 2–3-parted, 7–15 mm. long; pedicels suberect, 8–12 mm. long, strigulose; bracteoles at about the middle of the pedicel, linear-subulate, 3–6 mm. long; sepals lilac, obtuse, somewhat strigose, the upper oblong-ovate, ca. 12 mm. by 6 mm., the spur spreading, slightly curved, 16–20 mm. long; lateral sepals oblong-elliptic, 12 mm. by 6 mm., rounded-truncate; the lower 11 mm. by 5 mm., rounded-truncate; petals pale, the upper lamina almost straight, 10 mm. by 2 mm., glabrous, bidentate, the spur ca. 18 mm. long; lower laminae 6.5 mm. by 5 mm., bifid to near the base into acute lanceolate lobes, long-ciliate, the claw ca. 6 mm. long; stamens 5–6 mm. long, glabrous; anthers round-oblong, 0.8 mm. long; follicles 3, pubescent.

TYPE: Tauria (in Azerbaydzhan?), Herb. *Pallas* (LE); seen.
No other material seen.

41. **Delphinium pallidiflorum** Freyn, Bull. Herb. Boiss. II. **1**: 254. 1901. FIG. 4, M.

Delphinium cyphoplectrum Boiss. var. *pallidiflorum* (Freyn) Davis, Notes Bot. Gard. Edinb. **26**: 171. 1965.

Delphinium nachiczevanicum Tzvelev, Not. Syst. Leningrad **19**: 3. 1959. Based on *Egorova, Tzevelev & Czerepanov 418* (LE) from prov. Nachiezevan, Azerbaidshan. Seen.

Stem terete, zigzag, 3–8 dm. tall, simple or sparsely branched, retrorse-strigulose below, with longer spreading glanduliferous hairs below the inflorescence; leaves few, short strigulose, the long petioles vaginate at the base, the blades round in outline, 5–6 cm. in diameter, palmately many parted, the lower into lanceolate, the upper into ultimate lance-linear laciniae 1–3 mm. wide; raceme short to long, lax, with spreading more or less glandular hairs; bracts entire, linear to linear-lanceolate, 3–7 mm. long; pedicels glabrous or pubescent, 6–20 mm. long; bracteoles below middle of pedicel, 2–4 mm. long; sepals violet-blue, bluish or light lilac, subglabrous, 11–13 mm. long, the spur 10–13 mm. long, blunt; petals pale, the upper glabrous, with narrowly lanceolate, oblique, bilobed blade, the spur ca. 10 mm. long; lower blades long-pilose, 5–6 mm. long, 3 mm. wide, deeply cleft into parallel lobes, the claw 5–6 mm. long; filaments pale lilac, glabrous; anthers yellow, minute; follicles 3, glabrous.

TYPE: Turkey, Armenia, Wan, Warack-Dagh, 2700 m., June 27, 1899, *A. Kronenburg* (G?), not seen.

DISTRIBUTION. Steppes and rocky places, 1900–2400 m., Turkish and Russian Armenia, northern Iraq and northwestern Iran.

EXAMPLES. **Transcaucasia:** *Heideman*, May 27, 1932. **Russian Armenia:** *Besser*. **Iraq:** *Gillett 11782*; *Rawi 12213*. **Iran:** *Koelz 18015*.

42. **Delphinium penicillatum** Boiss. Ann. Sci. Nat. II. **16**: 369–370. 1841. FIG. 4, N.

Plant with short, viscid pubescence throughout; stem angled-striate, 2–3 dm. tall; leaves petioled, tripartite, the segments bipinnatifid into short linear setaceous lobes scarcely 1 mm. wide; lower blades roundish, to 5 cm. broad, upper smaller; racemes spiciform, strict, open, to 15-flowered, 5–12 cm. long; bracts deltoid-acute, 2 mm. long; pedicels 3.5–4 mm. long, bibracteolate below the middle; bracteoles linear, pubescent, ca. 2 mm. long; sepals hairy, oblong, pale blue, the upper sepal ovate, 6 mm. by 3 mm., subacute, spur straight, 9–9.5 mm. long, 2 mm. wide at base, gibbous at tip; lateral sepals oblance-spatulate, 6 mm. by 3 mm., pubescent along the middle line; lower sepals slightly wider, more pointed and pubescent; upper petals glabrous, the blades obliquely truncate, slightly divided, the lamina ca. 8 mm., the spur 10 mm. long; lower laminae ovate, bearded, penicillate, ca. 5 mm. by 3 mm., deeply divided into 2 divaricate pointed lobes, claw ca. 4 mm. long; stamens 4–5 mm. long, ciliate; anthers yellow, 0.6 mm. long; follicles 2–3, subglabrous.

TYPE: *Aucher 4034* from Mascate (Muscat?), Arabia?, (P); isotype (K); both seen.

RANGE. Apparently in arid places, Oman and southern Iran.

EXAMPLE SEEN. **Iran:** *Kotschy 393a.*

43. **Delphinium puniceum** Pallas, Reise **3**: 327. 1776. FIG. 4, O.

Delphinium hybridum Willd. var. *puniceum* Claus. Ind. des in Göbel It. **2**: 248. 1837.

Delphinium hybridum subsp. *puniceum* N. Busch in Fl. Cauc. Crit. III. **3**: 55. 1903.

Plant somewhat strigulose throughout; stem 3–8 dm. tall, slender, terete, simple or few branched above; leaves few, the lower long petioled, the upper with shorter petioles; petioles dilated at base; blades 3–15 cm. in diameter, 3–5-parted to base, the parts then divided into linear strigulose lobes mostly 1–3(–6) mm. wide and with 1–2 divergent lobules; racemes dense, many flowered, 5–30 cm. long, densely, sometimes loosely strigulose; bracts entire, lance-linear, 4–6 mm. long; pedicels ascending, 7–12 mm. long; bracteoles 3–4 mm. long, mostly near the base of the pedicel; sepals deep bluish-purple, strigulose; upper sepal ovate-lanceolate, ca. 12 mm. by 3 mm., acute, the spur straight, obtuse, 11–12 mm. long, 3 mm. wide at the base; lateral sepals lanceolate, 12 mm. by 2 mm., subobtuse, slightly narrowed at base; lower sepals lance-oblong, 13 mm. by 4 mm., acutish; upper petal lamina purple, ca. 9 mm. long, the terminal lobules 1.5 mm. long, spur 10–11 mm. long; lower petals purple, the blade 6 mm. long, white bearded, the lobes lance-oblong, 4 mm. long; claw 6 mm.; stamens 6–7 mm. long, glabrous; anthers dark, 0.8 mm. long; follicles 3, erect, 10 mm. by 3 mm., more or less reticulate and strigulose, the styles 2–2.5 mm. long; seeds obscurely angled, covered with scales.

TYPE: near Salinas Tschaptschatschi near "Volgam australem" in Sibiria, Pallas misit 1781, (LE), seen. Photographs (E, K), seen.

RANGE. Region of Volga River to Georgia and Asia Media (Pawlowski, Fragm. Fl. & Geobot. **9**: 437. (1963).

EXAMPLES. **Georgia:** *Hohenacker* in 1834; *Radde* in 1870.

44. **Delphinium quercetorum** Boiss. & Hausskn. in Boiss. Fl. Orient. Suppl. 20. 1888. FIG. 4, P.

Delphinium hybridum ssp. *laxiusculum* var. *pallidiflora* Busch in Fl. Cauc. Crit. III. **3**: 57. 1903.

Stem to 3 mm. thick, glandular-pubescent in upper half, 3–4 dm. tall, mostly simple; lower leaves suborbicular, 1.5–3 cm. in diameter, strigulose, palmatisect into short divergent linear or oblong lobes; petioles dilate-vaginate at base; raceme 7–12 cm. long, lax, 7–12-flowered, glandular-pubescent; bracts lanceolate, membranous, 4–7 mm. long, entire; pedicels pubescent, short; bracteoles near middle of pedicel, 2–3 mm. long; sepals pale bluish, somewhat pubescent; upper sepal lance-ovate, ca. 9 mm. by 3 mm., obtuse, the spur somewhat inflated at apex, 12–15 mm. long, 2.5 mm. wide at base, straight, horizontal; lateral sepals oblong-elliptic, 9 mm. by 4 mm., rounded-obtuse, pubescent on midrib; lower sepals pubescent, 7–9 mm. long, 4 mm. wide, subacute; upper petals whitish, the laminae 9 mm. by 2 mm., at right angles to the claw, with 2 short apical lobes, hirsute, the thick spur 11–12 mm. long; lower laminae 5.5 mm. long, heavily bearded, the linear-lanceolate lobes 5 mm. long, claw 5.5 mm. long; stamens glabrous, 5–6 mm. long; anthers bluish yellow, rounded, 0.8 mm. long; carpels 3, pilose their entire length.

TYPE: Mt. Pir Omar Gudrun, Persian Kurdistan, at 4000–5000′, June 1867, *Haussknecht* (G) not seen; isotypes (BM, K) seen.

DISTRIBUTION. At 600–2000 m., Iraq, Iran.

EXAMPLES. **Iraq:** *Rawi 23431, 22706, 22200*; *Kass & Nuri 27607.* **Iran:** *Merton 3935*; *Wheeler Haines 1712.*

There is some question as to the distinctness of this species, since there is considerable variation in the specimens. It is near *D. cyphoplectrum.*

45. **Delphinium roylei** Munz, nomen novum. FIG. 4, Q.

Delphinium incanum Royle, Illustr. Bot. Himal. 55. 1834, not E. D. Clarke, 1812.

Stem 5–10 dm. tall, simple or usually few branched above, terete, 3–5 mm. thick, closely and finely strigulose, so as to be more or less ashy, especially above; lower leaves withered by anthesis, 5–8 cm. in diameter, palmately multipartite into cuneate, deeply and sharply incised segments, the ultimate lobes sharp pointed, 1.5–3 mm. wide, greenish above, paler and closely strigulose beneath, the petioles to 1 dm. long, vaginate at base; middle cauline leaves remote, short petioled to subsessile; principal raceme commonly 1–2 dm. long, rather densely many flowered, the lateral racemes fewer and more loosely flowered; bracts linear, acuminate, 5–10 mm. long; pedicels commonly 1–2.5 cm. long, recurved at apex; bracteoles 2.5–3 mm. long, located near base of pedicel; sepals deep blue, densely strigulose; upper sepal 13–14 mm. by 8–9 mm., pointed, the spur horizontal, cylindric, straight, somewhat pointed, 15–16 mm. long, 3–3.5 mm. wide at base; lateral sepals broadly elliptic-ovate, obtuse, 15 mm. by 10 mm., strigulose on midline; lower sepals 15–16 mm. by 8–9 mm., subobovate, pointed; upper petals pale, the oblique glabrous lamina 8 mm. long, shallowly 2-toothed, spur ca. 14 mm. long; lower laminae deep blue, 6 mm. long, bearded, roundish, lobed for ca. 3 mm., the claw 5 mm. long; stamens 5–7 mm. long, subglabrous; anthers blue, 1 mm. long; follicles 3, strigose, 10–15 mm. long, 3–4 mm. wide; seeds ca. 1 mm. long, 3-angled, with ca. 5 transverse rows of scales.

TYPE: Kashmir: Purbunee, *R. Inglis* (LIV?); not seen.

RANGE. Grassy meadows and hillsides, 2000–5000 m., Kashmir.

ILLUSTRATIONS. BLATTER, Beautiful Fl. Kashmir 1: *pl. 4.* 1927; COVENTRY, Wild Fl. Kashmir **3**: *pl. 6.* 1930.

EXAMPLES. A few of the many specimens, apparently all from **Kashmir** or environs are: *R. R. Stewart 6530, 5694, 3156, 10546, 19586, 19693*; *Duthie 13440, 14091*; *Falconer 61*; *Dickason 365, 372*; *Koelz 9261*; *Lace 467*; *Ludlow 868, 8213*; *Ludlow & Sherriff 7560, 8238, 9376*; *Jacquemont 673/791*; *Schlagintweit 3066, 5171.*

The earlier use of the name *Delphinium incanum* by E. D. Clarke, Travels 2: 451. 1812, for a species from Cana, Israel, now referred to the genus *Consolida*, makes it necessary to give up Royle's later *Delphinium incanum*.

46. **Delphinium saniculifolium** Boiss. Diagn. I. **6**: 6. 1845. FIG. 4, R.

? *Delphinium saniculifolium* Boiss. var. *refracta* Brühl & King, Ann. Bot. Gard. Calc. **5**: 95. 1896. Not typified; no specimens cited.

Stem erect, terete, flexuous, mostly openly branched above, 3–8 dm. tall, glabrous or sparsely hairy (especially below); lower leaves with petioles 2–8 cm. long and more or less vaginate at the base, the blades palmately 5-lobed into broad cuneate divisions with few coarse terminal teeth, the laminae 2–5 cm. broad, glabrous or somewhat strigulose; cauline leaves few, smaller, palmately parted to the base; racemes lax, several flowered, in an open panicle, peduncled; bracts lance-linear, mostly 3–5 mm. long; pedicels divaricate, very slender, 5–25 mm. long; bracteoles 2 (3), ca. 2 mm. long, inserted near the base or the middle of the pedicel; sepals blue, subglabrous, the upper ovate, 7–8 mm. long, obtuse, the spur 7–9 mm. long, subcylindric, obtuse; lateral sepals elliptic-oblong, rounded at apex, 7 mm. long; lower elliptic, rounded at apex, 7 mm. long; upper petals bluish, the laminae oblique, glabrous, 7 mm. long, more or less bidentate, the spur ca. 9 mm. long; lower petals blue, the blades 4–5 mm. long, subovate, bearded, lobed for 2–3 mm., the claw 4 mm. long; stamens 4–5 mm. long, somewhat bluish, glabrous; anthers 0.6 mm. long; follicles 3, largely glabrous, 7–10 mm. by 3 mm., the styles ca. 2 mm. in addition; seeds scarcely 1 mm. long, obpyramidal, with several rows of scales.

TYPE: "In alpe Kuh-Delu Persiae australis," *Kotschy 536*, (G?), not seen; isotypes (A, BM, K, MO, UC) seen, but all in rather poor condition.

DISTRIBUTION. Southern Iran at 900–2400 m.

EXAMPLES. *Rechinger 3364*; *Haussknecht*, July, 1868; *Stapf 2300.*

47. **Delphinium schmalhausenii** Alboff, Trav. Soc. Hort. Odessa (Descr. nouv. esp. pl.) 1891; Huth, Bot. Jahrb. **20**: 441. 1895. FIG. 5, A.

Delphinium hybridum Willd. subsp. *schmalhausenii* (Alb.) Busch in Fl. Cauc. Crit. **3**: 53. 1903.

Delphinium hybridum Steph. ex Willd. Sp. Pl. **2:** 1229. 1799, not L., 1756.

Delphinium freynii Conrath ex Freyn, Bull. Herb. Boiss. **3:** 36. 1895. Based on *Conrath*, 1889, Somchetia, Lok. 2300 m. (G); not seen.

Delphinium somcheticum Conrath & Freyn, Bull. Herb. Boiss. **3:** 37. 1895. Based on *Conrath*, 1889, Somchetia, Tschatach (G); not seen.

Delphinium halophilum Huth, Bot. Jahrb. **20:** 487. 1895. New name for *D. freynii* Conrath.

Stem single, 2–10 dm. tall, more or less zigzag, striate and usually glabrous below, glandular-pubescent above; lower leaves gone at time of anthesis; cauline rather long petioled (1–2 dm.) and petioles with broad base, upper petioles almost lacking; blades to 2 dm. broad, palmately multifid, then pinnately dissected into numerous very narrow laciniae; raceme solitary, long-cylindrical, rather dense; lower bracts foliaceous, laciniate, the upper trifid or entire; pedicels 5–10(–18) mm. long, glandular pubescent; bracteoles linear in upper half of pedicels; sepals dark blue, strigulose, the upper sepal linear-elliptic, obtuse, 9–10 mm. long, 3.5 mm. broad, spur ascending, straight, 15–20 mm. long, 3 mm. wide at base, acute; upper petals blue, glabrous, ca. 8–10 mm. high, short lobed, the spur 15–16 mm. long; lower petals with roundish hairy lamina 5 mm. long, rather deeply bilobed, claw 5 mm. long; filaments yellowish; anthers blue; follicles mostly glabrous, 10–12 mm. long; seeds with numerous membranous scales.

TYPE: Transcaucasia, *Alboff 190*, Aug., 1893. Not seen.

DISTRIBUTION. At 2000 m. or above, northern Turkey, Transcaucasia.

EXAMPLES. **Turkey:** Prov. Kars, *Davis 32512*. **Transcaucasia:** *Radde 428*; *Radde*, June 16, 1867; *Szowitz 391*; *Hohenacker* in 1834.

Davis, Fl. Turkey 1: 112. 1965, unites the above three proposed species (*Delphinium schmalhausenii, D. freynii,* and *D. somcheticum*) into one. The variation in size of flowers, character of pubescence (whether glandular or not), and in division of bracts does not correspond with any distinction in geographical distribution.

48. **Delphinium semibarbatum** Bienert ex Boiss., Fl. Orient. **1:** 92. 1867. FIG. 5, B.

? *Delphinium semibarbatum* var. *hoeltzeri* Huth, Bot. Jahrb. **20:** 424. 1895. Based on a *Hoeltzer* collection from Persia (LE); not seen.

Delphinium hybridum var. *sulphureum* Regel, Acta Horti Petrop. **5:** 226. 1877.

Delphinium zalil Aitch. & Hemsl. Trans. Linn. Soc. II. **3:** 30. 1888–1894. Based on *Aitchison 671*, Khorasan, Iran; isotypes seen (BM, GH).

Delphinium biternatum Huth var. *leiocarpum* Freyn & Sint. ex Freyn, Bull. Herb. Boiss. II. **3:** 561. 1903. Aschabad, *Sintenis 383*; isotypes seen (BH, BM, E, K, MO, US).

Stem erect, 2–8 dm. tall, subglabrous to retrorse-strigulose, simple or few branched above; lower petioles to 1 dm. or longer, scarcely dilated at base, the cauline leaves several, gradually shorter petioled upward, the blades 3-parted, then again ternate, ultimately divided into long linear lobes mostly 1–1.5(–2) mm. wide, the blades 2–10 cm. in diameter, subglabrous to somewhat strigulose; inflorescence with rather open, rather many flowered racemes 1–3 dm. long, often with smaller supplementary racemes as side branches; bracts mostly lance-subulate, 3–8 mm. long; pedicels 2–10 mm. long, stout, more or less glandular pubescent; bracteoles lance-subulate, at about the middle of the pedicel, 2–4 mm. long; flowers yellow or with a greenish tinge; sepals glabrous, broadly ovate, obtuse, 9–10 mm. long, the spur subcylindric, yellow, 7–10 mm. long; upper petals with the laminae ca. 10 mm. long, 3 mm. wide, attenuate into a bidentate minutely puberulent tip; spurs ca. 8 mm. long; lower laminae almost as long, bifid, yellow bearded, subserrate on the claw; stamens yellow, 4–6 mm. long, glabrous; anthers 1 mm. long; follicles 3, glabrous, suberect, 10 mm. by 3.5 mm., the styles 2 mm.; seeds quadrate, transversely fimbriate-lamellate.

TYPE: "In montosis prov. Khorassan Persicae orient. ad orientem urbis Mesched" (*Bunge*) (G), not seen. Isotype seen (P).

DISTRIBUTION. Mountain meadows and grassy plains to 2000 m., Transcaspia to Turkestan and Iran.

ILLUSTRATIONS. Trans. Linn. Soc. II. **3**: *pl. 3.* 1888–1894; Bot. Mag. *pl. 7049.* 1889.

EXAMPLES. **Transcaspia:** *Litvinov 443*; *F. N. Meyer 626.* **Turkestan:** *Regel,* May 17, 1880; *Lipsky 1706*; *Sovetkina & Czausova 4267.* **Iran:** *Rechinger 1698, 4934*; *Merton 3888.*

49. **Delphinium semiclavatum** Nevski in Komarov, Fl. U.S.S.R. 7: 168, 726. 1937. FIG. 5, C.

Stem 5.5–7.5 dm. high, few branched with long virgate branches, densely retrorse-pubescent below, leafy at the base, the petioles 5–10 cm. long, dilated at their base, subglabrous; leaf blades suborbicular, almost glabrous, 3-parted to base, the segments sessile, the middle one obovate, cuneate at base, shallowly incised into 3–5 obtuse, oblong, rounded lobes 2–3 mm. broad, the lateral segments unequally incised into further divisions; raceme lax, few flowered, long and with a glabrous axis; pedicels glabrous, to 1.7 cm. long; bracts narrowly lance-linear, glabrous, 2–3 mm. long; bracteoles 1.5–2 mm. long, linear-subulate, inserted above the middle of the pedicels; sepals sordid lilac, glabrous, obtuse, 9–10 mm. long, 4.5 mm. wide; spur straight or nearly so, obtuse, gibbous below the tip, 10–12 mm. long, to 2.7 mm. wide at base; upper petals whitish, the laminae glabrous, oblique, bidentate, ca. 8 mm. long, the spur 9 mm. long; lower laminae round-ovate, 3 mm. long, bifid half its length, sparsely bearded, the claw 4 mm. long; follicles glabrous, 8 mm. long.

TYPE: Asia Media: Pamiro-Alaj occidentalis, Sangardak, June 20, 1896, *Lipsky 1887* (LE); seen.

Near *Delphinium saniculifolium*, but flowers sordid lilac, not blue, spur longer; pedicels shorter, petals subglabrous.

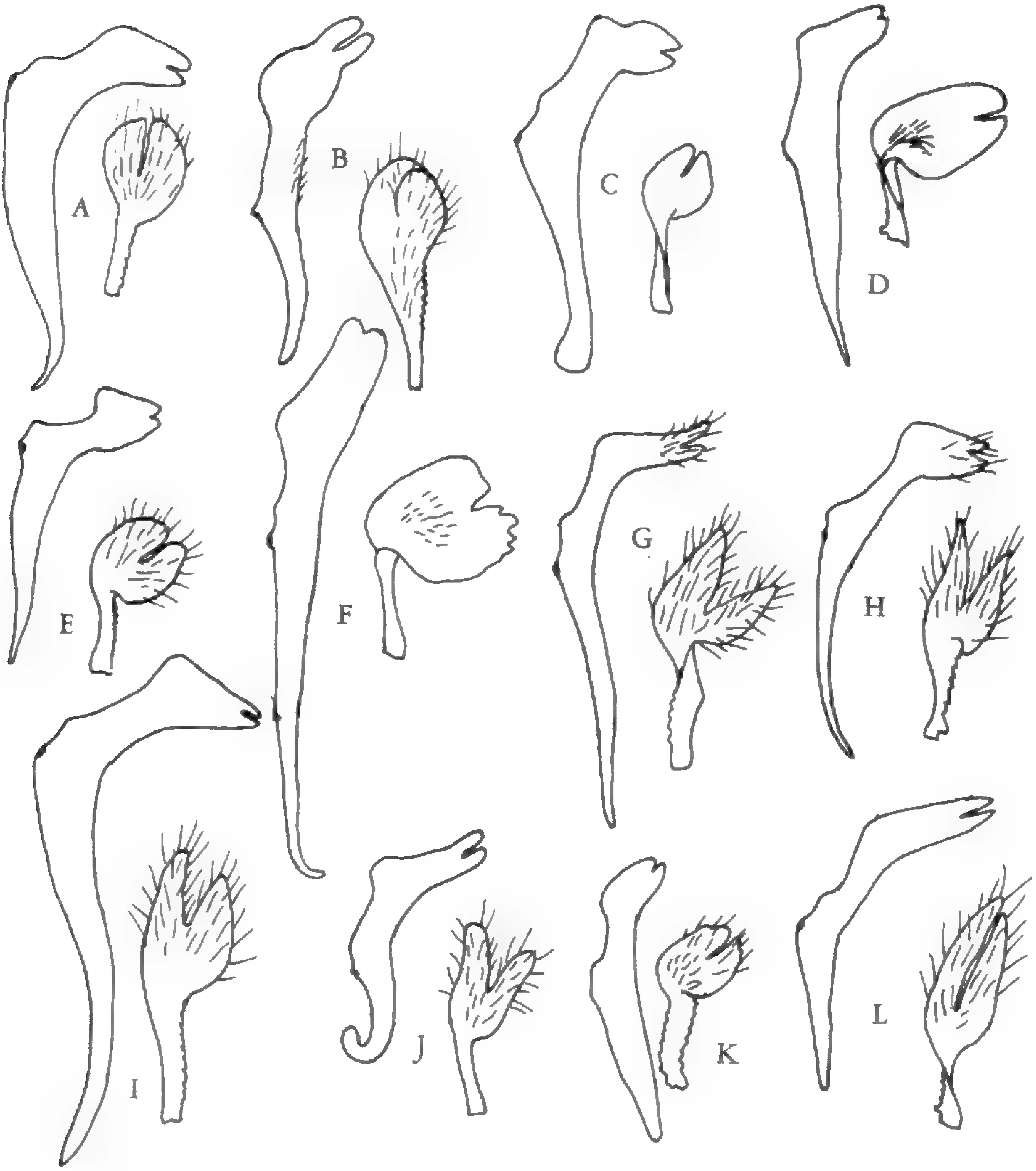

FIGURE 5. **Delphinium**, GROUP IV. Petals, the upper spurred, the lower clawed. A. *D. schmalhausenii*; upper lamina 8 mm. long, spur 15 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Hohenacker* in 1834 (BM). B. *D. semibarbatum*; upper lamina 10 mm. long, spur 8 mm.; lower lamina 5.5 mm. long, claw 5.5 mm.; drawn from *von Knorring* at Samarkand (GH). C. *D. semiclavatum*; upper lamina 8 mm. long, spur 9 mm.; lower lamina 3 mm. long, claw 4 mm.; drawn from *Lipsky* TYPE (LE). D. *D. suave*; upper lamina 8 mm. long, spur 12 mm.; lower lamina 6 mm. long, claw 4 mm.; drawn from *Aitchison 862* ISOTYPE (BM). E. *D. szowitsianum*; upper lamina 7 mm. long, spur 11 mm.; lower lamina 4 mm. long, claw 4 mm.; drawn from *Szowitz* (GH). F. *D. tetanoplectrum*; upper lamina 12 mm. long, spur 20 mm.; lower lamina 5.5 mm. long, claw 5 mm.; drawn from *Koelz 13725* TYPE (US). G. *D. tuberosum*; upper lamina 10 mm. long, spur 14 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Miss Lindsay 1288* (MO). H. *D. tuberosum*; upper lamina 8.5 mm. long, spur 11.5 mm.; lower lamina 6 mm. long, claw 4.5 mm.; drawn from *Pichler* June 20, 1882 (type material of *D. caerulescens*, WU). I. *D. turkmenum*; upper lamina 11 mm. long, spur 21 mm.; lower lamina 5 mm. long, claw 6.5 mm.; drawn from *Sintenis 1672* (MO). J. *D. uncinatum*; upper lamina

50. **Delphinium suave** Huth, Bot. Jahrb. **20**: 470. 1895. FIG. 5, D.

Delphinium penicillatum Boiss. var. *macroplectrum* Buser in Boiss. Fl. Orient. Suppl. 19. 1888. Based on *Aitchison 862.*

Delphinium saniculaefolium Boiss. var. *kurramensis* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 95. 1896. New name for *D. penicillatum* var. *macroplectrum.*

Stem or stems slender, erect, simple or few branched, terete, more or less strigulose throughout or more loosely so in the inflorescence, 1.5–4.5 dm. tall; lower leaves apparently trifid into broad cuneate segments that are somewhat toothed or lobed, the laminae 1.5–2.5 cm. broad; petioles slender, 2–5 cm. long, vaginate at base; cauline leaves remote, short petioled, the blades 2–3 cm. long, with few lobes 1–3 or more mm. wide; inflorescence simple, racemose, several flowered, bracts entire, lance-linear, 3–8 mm. long; pedicels ascending, 5–15 mm. long; bracteoles lance-linear, 1.5–2 mm. long, above the middle of the pedicel; sepals pale blue, slightly strigulose, the upper about 7 mm. by 3.5 mm., the spur 10–15 mm. long, spreading, straight, pointed; lateral sepals round-obovate, pubescent on midrib, 7 mm. long, 5 mm. wide; lower sepals 8 mm. by 6 mm.; upper petals glabrous, the blade oblique, dilute yellow or bluish, 9–11 mm. long, with terminal lobes ca. 1 mm. long, spur 12 mm. long; lower petals with an oblong or roundish-oblong, sparsely bearded, blade divided to 2.5–3.5 mm., the claw 4 mm. long; stamens 4.5–5 mm. long, glabrous; anthers dark, 1 mm. long; follicles 3, strigulose.

TYPE: Afghanistan, 2600–3600 m., Kurrum Valley or "in pratis vallis Alikel," *Aitchison 862*; holotype (LE) and isotypes (BM, GH, P, PH), seen.

DISTRIBUTION. Rocky slopes, meadows, and the like, 2600–3800 m., Afghanistan, West Pakistan.

ILLUSTRATION. BRÜHL & KING, Ann. Bot. Gard. Calc. **5**: *pl. 117, fig. 3.* 1896.

REPRESENTATIVE COLLECTIONS. **Afghanistan:** mt. above Sari Casma, *Bacon 73.* **W. Pakistan:** Chitral, *Harriss 15837.* Kohat, *Burtt & Nairn 586.* Punjab, *Ram Bahsli 14811.* Beluchistan, *R. R. Stewart 579*; *Appleton 3862.*

51. **Delphinium szowitsianum** Boiss. Fl. Orient. 1: 89. 1867. FIG. 5, E.

Delphinium hybridum Steph. ex Willd. var. *szowitsiana* Trautv. Acta Horti Petrop. II. **2**: 493. 1873.

Delphinium hybridum var. *dasyanthum* Avé Lallem. Ind. Horti Petrop. 1842, fide Huth.

Delphinium dasystachyum Boiss. & Hohen. ssp. *szowitzianum* N. Busch in Fl. Cauc. Crit. III. **3**: 58. 1903.

Delphinium tricolor Bernh. ex Steud. Nomencl. ed. 2. **1**: 489. 1840; *nomen.*

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8 mm. long, spur 5.5 mm.; lower lamina 5 mm. long, claw 4 mm.; drawn from *Stewart 12688* (NY). K. *D. ursinum*; upper lamina 7 mm. long, spur 9 mm.; lower lamina 4 mm. long, claw 4 mm.; drawn from *Rechinger 6083* ISOTYPE (US). L. *D. vanense*; upper lamina 11 mm. long, spur 11 mm.; lower lamina 8 mm. long, claw 4 mm.; drawn from *Davis 22735* (BM).

Stem simple, 3–9 dm. tall, closely strigulose or subglabrous below, densely strigulose and pubescent above, more or less angled and sulcate; leaves largely dead by anthesis, the cauline scattered, with petioles dilated at the base, short in upper leaves; blades largely 2–4 cm. in diameter, ternate, then laciniate into many strigose or pubescent linear lobes, 0.5–1(–2) mm. wide; inflorescence very dense, many flowered, to ca. 1 dm. long; lower bracts trifid, from a broad membranous base, upper mostly less than 5 mm. long, densely pubescent or strigose; pedicels generally less than 5 mm. long, the 2 lance-linear bracteoles 5–6 mm. long; sepals densely short-hairy, yellowish with greenish tips, the upper sepal ovate, 8 mm. long, spur short-hairy, suberect, 12–13 mm. long, 3–4 mm. wide at base; other sepals about 8 mm. by 4 mm.; upper petals with bluish tinge, ca. 7 mm. long, emarginate, very short-puberulent near base, the spurs ca. 11 mm. long; lower petals 7.5–8 mm. long, bearded, with rounded lobes 2 mm. long; stamens glabrous, 5–6 mm. long; anthers yellow, 1 mm. long; follicles pubescent.

TYPE: Russian Armenia near Nachitchewan, *Szowitz,* holotype (G?) not seen; isotype (K) seen, has "*Szovits 439.*"

DISTRIBUTION. At 1800 m. or thereabouts, Transcaucasia, Russian Armenia.

ILLUSTRATION. Belg. Hort. **22:** *p. 48, pl. 3.* 1872.

SPECIMENS SEEN. **Russian Armenia:** *Szovits* (GH, P, US); *Yaroshenka & Ubanove,* July 23, 1945. **Transcaucasia:** *Hohenacker,* July, 1838; *Heideman & Aliev,* July 27, 1932.

52. **Delphinium tetanoplectrum** Rech. f. Anz. Österr. Akad. Wiss. Math.-Nat. **91:** 72. 1954. FIG. 5, F.

Stem 2–5 dm. tall, strict, erect, with short, more or less deflexed-appressed, non-glandular pubescence; lower and middle leaves with petioles 3–6 cm. long, membranous-dilated at base, the blades ashy-pubescent, round-cordate in outline, palmately lobed or incised, 1–2 cm. long, the divisions relatively simple; inflorescence very lax, few flowered, the axis with short crisped, mostly eglandular hairs; bracts narrowly linear-lanceolate, 4–6 mm. long; pedicels 1–2 cm. long; bracteoles inserted in upper third of pedicel, narrowly linear, acute, 3–4 mm. long; sepals pale purplish blue, ca. 8 mm. long, to 5 mm. wide, with short scattered hairs, the upper sepal ovate, the others elliptic-obovate; spur 15–20 mm. long, ca. 2 mm. wide when pressed, straight, acute, more densely pubescent than sepals; petals palish, the upper almost straight, the laminae oblong, glabrous, emarginate, ca. 12 mm. long, the spurs slender, 15–20 mm. long; lower petals with blade 5.5 mm. long and wide, round-obovate, sparsely bearded, shallowly bilobed, the claw 5 mm. long; stamens ca. 5 mm. long, glabrous; anthers pale, oblong, 1 mm. long; carpels 3, coarsely pubescent.

TYPE: Afghanistan, Lorinj, 2460 m., Aug. 27, 1939, *W. Koelz 13725* (US). The type and the other three collections were on loan to Dr.

Rechinger, in Vienna, and I am grateful to him and Dr. Riedl for kindly sending them on to me.

COLLECTIONS SEEN. **Afghanistan:** Gurzan, 2600 m., *Koelz 14100*; Baligali Pass, 2800 m., *Koelz 13853*; Sufedsang, 3070 m., *Koelz 13986*.

The species keys out with *D. micranthum*, of Kurdistan, but has the lower petal blade much wider and less hairy.

53. **Delphinium tuberosum** Auch. ex Boiss. Ann. Sci. Nat. II. **16**: 370. 1841. FIG. 5, G, H.

Delphinium tuberosum var. *leiocalycinum* Bornm. Beih. Bot. Centr. **19**: 201. 1905. Type, *Strauss & Bornmüller*, Mt. Latétar; not seen.

Delphinium caerulescens Freyn ex Stapf, Denkschr. Akad. Wien Math. Naturw. **1886**: 25; not Paxton, 1849. Based on a type from Jalpan (Djalpan), northern Iran (WU); seen. At the University of Vienna there is a series of four sheets from Mt. Elwend, each with "Legit Th. Pichler, 1882" and also "Iter Persicum, Dris. J. E. Polak." Of these, two have an additional label "Jalpan, 6–20–1882." Some of these specimens have the upper petals glabrous, others with a few or several stiff hairs. All have the same general flower color and form and the spur gibbous at the slightly curved apex. There seems to be the same general variation as I have found in other material referred to *D. tuberosum*. I am greatly indebted to Dr. Lothar Geitler of the University of Vienna for the loan of the type material of *D. caerulescens*.

Stem erect, flexuous or almost zigzag, 3–5 dm. tall, terete, slender, few branched, closely strigulose, sometimes apparently with a zone of gland-tipped hairs near the middle; leaves often largely gone by flowering time, the lower long petioled, the petioles long-vaginate at the base, middle cauline leaves remote, short petioled; blades 2–4 cm. wide, palmately parted into numerous mostly linear lobes, 1–2.5 mm. wide, strigulose; terminal racemes to 2 dm. long, usually with not more than 15 flowers, rather lax, the lateral racemes smaller, if present; bracts linear, 3–25 mm. long; pedicels 5–15 mm. long, ascending; bracteoles 1.5–5 mm. long, placed near or above the middle of the pedicel; sepals bluish or smoke-gray; upper sepal 8–10 mm. long, 4.5 mm. wide, pointed, mostly strigulose, the spur cylindric, horizontal, almost straight, bluish, gibbous at the curved apex, 12–15 mm. long; lateral sepals oblong-elliptical, 8–10 mm. long, 4–4.5 mm. wide, obtuse, strigose on midline; lower sepals 8.5–10 mm. long by 4 mm., oblong-elliptic, rounded at apex; upper petals oblique, the blade 8.5–10 mm. long, from glabrous to having a few stiff hairs on the surface or near the shallowly 2-lobed tip; spur 12–14 mm. long; lower petals heavily long bearded, the claw 4.5–5 mm. long, serrulate on one edge, the blade 5–6 mm. long, with 2 rather divergent pointed lobes ca. 4 mm. long; stamens 5–6 mm. long, glabrous; anthers whitish to bluish, 0.8–1 mm. long; follicles 3, ashy-strigulose to subglabrous, veiny, 8–12 mm. long, the style an additional 2.5 mm. long; seeds umbilicate, 1.2–1.5 mm. long, brownish, with transverse rows of pale scales.

TYPE: Mt. Elwind, near Hamadan, northern Iran, *Aucher 79*, holotype (P), isotype (K); both seen. Upper petals glabrous to few-haired.

DISTRIBUTION. At about 2000 m., Iran.

REPRESENTATIVE SPECIMENS. *H. F. Macmillan 7, 8, 9*; *Koelz 18110a, 18144*; *Miss Lindsay 1288*; *Pichler* in 1882; *Knapp* in 1884.

54. **Delphinium turkmemum** Lipsky, Acta Horti Petrop. **18**: 2. 1901. FIG. 5, I.

Delphinium hybridum Steph. ex Willd. var. *pilosulum* Trautv. Acta Horti Petrop. **9**: 437. 1884.
Delphinium pilosulum B. Fedtsch. Fl. Tian-schan Occid. **1**: 98. 1904.

Stem or stems terete, 2.5–7 dm. tall, slender, pilose at base, glabrous in middle, more or less glandular-puberulent on pedicels and in inflorescence; lower leaves 3–6 cm. broad, subreniform in outline, 5-fid into cuneate segments with pinnate lobing into oblong parts 2–4 mm. wide, glabrous or with a few long slender hairs; lower petioles 4–10 cm. long, basally dilated; cauline leaves remote, with narrower lobes; petioles shorter; inflorescence a simple raceme or 3- or 4-branched in an open panicle of lax, several flowered racemes to 1.5 dm. long; bracts lance-linear, 2–6 mm. long; pedicels ascending, 7–10 mm. long; bracteoles 2, lanceolate, 1.5–2 mm. long, at about the middle of the pedicel; sepals pale violet-blue, the upper sepal ovate, glandular-puberulent, 8–10 mm. long, 4–5 mm. wide, the spur stout, horizontal, 16–20 mm. long, 3–4 mm. wide at the base, obtuse; lateral sepals oblong, 12 mm. by 6 mm., obtuse, glandular-puberulent on midrib; lower sepals oblong-elliptic, 12 mm. by 6 mm., rounded at apex, glandular-puberulent; upper petals oblique, yellowish, the lamina ca. 1 cm. long, the spur ca. 2 cm. long; lower petals 12–13 mm. long, the claw 6 mm., the blade bearded, lobed for about 3 mm.; stamens 5–7 mm. long; anthers yellow, 1 mm. long; follicles 3, glandular-pubescent.

TYPE: Kisil-Arwat, Turcomania, *Al. Becker 29*, Dec. 18, 1896 (LE); seen.

DISTRIBUTION. Turcomania, Transcaspia.

REPRESENTATIVE COLLECTIONS. **Turcomania:** *Litwinow 447, 448*. **Transcaspia:** *Lipsky*, May 8, 1912; *F. N. Meyer 552*; *Sintenis 1672*; *Lipsky 3070*.

55. **Delphinium uncinatum** Hook.f. & Thoms. in Hook.f. Fl. Brit. Ind. **1**: 24. 1872. FIG. 5, J.

Delphinium penicillatum Hook.f. & Thoms. Fl. Ind. 48. 1855, not Boiss., 1841.
Delphinium vestitum Boiss. Diagn. II. **1**: 13. 1853; Fl. Orient. **1**: 92. 1867, not Wall. ex Royle, 1839.
Delphinium uncinatum var. *pseudovestitum* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 94. 1896. Based on *Stocks 994*, from Beluchistan; seen.
Delphinium uncinatum var. *aitchisonii* Boiss. in Brühl & King, Ann. Gard. Calc. **5**: 94. 1896. Based on *Aitchison*, Dec., 1879 from Kurrum Valley; (CAL), seen.

Stem simple, terete, subflexuous, 1.5–9 dm. tall, subglabrous below, densely pubescent above with spreading hairs; radical leaves crowded, the petioles dilated at the base, 2–12 cm. long; laminae 3–5-sect to base, 1.5–6 cm. long, somewhat broader, subglabrous to villous, the segments narrow-cuneate at base, pinnately dissected into narrow toothed lobes commonly 1.5–8 mm. wide; cauline leaves few, somewhat reduced, the lobes narrower; inflorescence racemose or subpaniculate, 1–2.5(–4) dm. long, lax, spreading-hairy; bracts lanceolate, 3–5 mm. long; pedicels commonly 4–6 mm. long; bracteoles lance-linear, basal, ca. 2 mm. long; sepals bluish purple to pale, sparsely villous, the upper oblong-ovate, 7–8 mm. long, pointed, the spur hooked, cylindric, 7–10 mm. long; lateral sepals hairy on midline, rounded at apex, 7–8 mm. long; lower sepals oblong, rounded at tip, ca. 8 mm. long; upper petals 7–10 mm. long, short bilobed at apex, the spur 5–6 mm. long; lower petals 8–9 mm. long, the laminae oblong, 5 mm. long, bilobed for ca. 3 mm., bearded, the claw 4 mm. long; stamens ca. 5 mm. long, glabrous or nearly so; anthers 0.6 mm. long; follicles 3, glabrous or hairy.

TYPE: *Stocks 994*, among wormwood on plains, Beluchistan (K) seen. Cited by Boissier as *D. vestitum*, by Hook. f. & Thoms. for their *penicillatum*, and by Brühl and King for their var. *pseudovestitum*.

DISTRIBUTION. At 1000–2000 m., West Pakistan (Punjab, Beluchistan), Afghanistan, Kashmir.

ILLUSTRATION. BRÜHL & KING, Ann. Bot. Gard. Calc. **5**: *pl. 116, fig. 2, 3.* 1896.

REPRESENTATIVE MATERIAL. **Afghanistan:** Kurrum Valley, *Aitchison*. Dec. 1879. **Beluchistan:** *Stocks 994*; *J. H. Lace 3351, 3326*. **Punjab:** *R. R. Stewart 7002*; *G. Watt 603*; *Jacquemont 672*. **Kashmir:** *Stewart 12688, 27322*; *T. Thomson*.

P. Brühl, in Brühl & King, Ann. Bot. Gard. Calc. **5**: 94. 1896, proposed *D. uncinatum* var. *vicaryi* from the Punjab, based on *Vicary* from near Rawal Pindi. I have not seen the specimen, which seems to have been characterized largely by being glabrous. It probably is an unusually glabrous plant of *D. uncinatum*.

56. **Delphinium ursinum** Rech.f. Anz. Österr. Akad. Wiss. Math.-Nat. **88**: 225. 1951. FIG. 5, K.

Stem grayish, 5–10 dm. tall, slender, erect, 1–2-branched above, strigulose, terete, few leaved; petioles somewhat dilated at base, the lower to 15 cm. long, the upper shorter, strigulose; leaf blades rounded-cordate in outline, 6–10 cm. broad, palmatifid almost to the base into 7 cuneate-obovate divisions, these 3-laciniate to about the middle, then again 3-lobed into oblong parts 3–6 mm. wide, mucronulate and obtuse or acute at apex; uppermost leaves trifid into lanceolate segments; inflorescence of 1 or more racemes, the terminal one many flowered and to ca. 3 dm. long, rather dense above, strigulose; bracts lanceolate, entire, 5–15 mm. long;

pedicels 2–10 mm. long, appressed to axis; bracteoles lance-linear, usually below the middle of the pedicel, 2–4 mm. long; sepals white, suffused with blue, nerves greenish, somewhat strigulose; upper sepal elliptic-ovate, 9 mm. by 5 mm., obtuse, the spur 8 mm. long, straight, subcylindric, ca. 2.5 mm. wide at base, 2 mm. at the blunt tip; lateral sepals elliptic, 8 mm. by 5 mm., obtuse; lower sepals like the lateral, but more pointed; upper petals with a bluish, almost straight lamina, bidentate at the apex, 7 mm. long, the spur 9 mm.; lower laminae bearded, 4 mm. by 3 mm., deeply cleft, the claw 4 mm. long, serrulate on back edge; stamens 4.5–5 mm. long, the upper filaments and anthers bluish; anther suborbicular, 0.6 mm. long; follicles 3, hairy.

TYPE: Iran, prov. Gorgan (Asterabad), at 2400 m., on Mt. Shahvar near Hadjilang, *K. H. & F. Rechinger 6083*, holotype (W), not seen; isotypes (K, UC, US), seen.

57. **Delphinium vanense** Rech. f. Symb. Bot. Upsal. **11**(5): 8. 1952. FIG. 5, L.

Delphinium cyphoplectrum Boiss. var. *vanense* (Rech.f.) Davis, Notes Bot. Gard. Edinb. **26**: 171. 1965.

Stem zigzag below, leafy, 3–5 dm. high, striate, strigulose, subsimple or short branched in lower half, the internodes 4–6 cm. long; petioles of lower leaves broadly vaginate, to 7 cm. long, those of lower cauline leaves 3–4 cm., the blades 3.5–6 cm. long and wide, round-cordate in outline, narrowly palmate-tripinnatisect, the ultimate lobes 10–15 mm. long, 1–1.5 mm. wide, divaricate, oblong-linear, acute, minutely strigulose, while in the upper cauline leaves the ultimate lobes are linear, 1 mm. broad; racemes glabrous to hirsute and viscid, lax, strict, erect; pedicels ca. 10 mm. long, divergent, the 2 bracteoles near the base, linear, ca. 3 mm. long; sepals deep blue to violet blue, almost glabrous, the upper sepal 10–12 mm. long, 5–6 mm. wide, lance-ovate, subapiculate, spur almost straight to slightly curved, obtuse, subglabrous, 10–12 mm. long, 2.5 mm. wide; middle sepals oblong-oblanceolate, ca. 10 mm. by 3 mm., the lower oblanceolate with a broad base, 10–12 mm. long, 5–6 mm. wide, obtuse; upper petals about as long as sepals, the laminae glabrous, vertical to the spur, ca. 11 mm. long, narrow, bidentate at apex, the spur 11 mm. long; lower laminae long-hairy, 8 mm. long, lance-ovate, deeply divided into 2 lance-oblong lobes, the claw 4–5 mm. long; stamens 6–7 mm. long, glabrous; anthers yellowish-blue, round-oblong; follicles 3, subglabrous to hairy.

TYPE: Kurdistan (prov. Van, Turkey), 20 km. from Tatvan, at 1900 m., *Frödin 328* (UPS); not seen.

DISTRIBUTION. At 1900–2900 m., Turkish Kurdistan.

SPECIMENS SEEN. **Turkey:** Bitlis, *Davis 22542*; Artos Dag, *Davis 22753*.

The specimens cited have the narrow leaf segments of *D. laxiusculum*, but that species has strigose racemes.

[*To be continued*]

THE GENERA OF EUPHORBIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

GRADY L. WEBSTER

EUPHORBIACEAE A. L. de Jussieu, Gen. Pl. 384. 1789, "Euphorbiae" (SPURGE FAMILY)

Trees, shrubs, herbs, or vines; stems in some taxa succulent and often with colored or milky latex. Leaves alternate or opposite (or, rather rarely, whorled); stipules free or connate, or sometimes reduced to glandular bodies or absent; leaf blades pinnately or palmately veined, lobed, or compounded. Inflorescences basically cymose (dichasial), but often modified into apparent spikes, heads, or pseudanthia (or flowers sometimes solitary). Flowers unisexual (the plants monoecious or dioecious), basically regular; perianth showy to inconspicuous or absent, of valvate or quincuncially imbricate lobes or segments. Calyx deeply

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[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr. This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with supplementary information in brackets. References which the author has not seen are marked by an asterisk.

Part of the data recorded in this presentation have accrued from a long-term study of the reproductive morphology of the Euphorbiaceae which has been supported by several grants from the National Science Foundation (G-7148, G-18768, G-23604, GB-2801, GB-5669). I am especially indebted to Dr. Wood for his painstaking review of the manuscript and his many valuable suggestions. Special thanks are due to my wife, Barbara D. Webster, for her critical proofreading of the manuscript copy. Mrs. Gordon W. Dillon has helped greatly in checking the abbreviations for periodicals. Dr. Derek Burch supplied distributional information on certain taxa, and valuable collections of material were received from Mrs. Blanche Dean, Dr. Delzie Demaree, and Dr. John Thieret. The chromosome count of *Hippomane* was furnished through the courtesy of Dr. Jack Ellis. The illustrations were made by Arnold D. Clapman from dissections by Dr. Wood. These materials were collected for the *Generic Flora of the Southeastern United States* by Dr. Wood, Dr. F. C. Craighead, Dr. R. C. Rollins, Mr. Alan Strahler, and Dr. J. L. Thomas.

EDITOR'S NOTE. This treatment of the Euphorbiaceae, adhering to the plan of the *Flora* but much more extensive than the other papers published in this series and ranging over problems far beyond the geographical and taxonomic bounds of the *Generic Flora of the Southeastern United States*, is presented here in its entirety because of the unusual interest and difficulty of the Euphorbiaceae and the special relevance of this work to the taxonomic framework of the entire family. — C. E. WOOD, JR.

3–6-lobed or -parted in most taxa, but sometimes lobes more numerous, or reduced or absent. Corolla of mostly 3–6 separate or connivent petals (rarely more numerous or united), or often rudimentary or absent. Disc often present in flowers of one or both sexes, usually extrastaminal, of separate segments or cuplike. Stamens (1–)3–20[–400], inserted on a flat or convex receptacle; filaments free or united; anthers mostly 2-locular, dehiscing longitudinally; pollen tectate or intectate, inaperturate to polytreme (mostly tricolporate). Gynoecium of 3 or 4 united carpels [in the majority of taxa; reduced to 1 or multiplied up to 25 in others]; stigmas entire to bifid or lacerate; styles distinct to connate; ovary superior, 3- or 4-locular; placentation axile; ovules 1 or 2 per locule, anatropous or hemitropous, inserted beneath an obturator, crassinucellate, with 2 integuments, nucellus often prolonged as a beak in contact with the obturator. Fruit typically a capsular schizocarp, of 3 elastically dehiscent mericarps falling away from a persistent columella, but in some taxa drupaceous [baccate, or samaroid]. Seeds 1 or 2 per locule, or (by reduction) solitary in the fruit; seed coats thin to bony or fleshy; endosperm usually present; embryo straight or bent; cotyledons usually broader than the radicle, plane or (rarely) folded. Embryo sac normal, monosporic (Polygonum type) or in some disporic or tetrasporic. (Including Acalyphaceae Kl. & Garcke, Antidesmaceae Walp., Peraceae Kl. & Garcke, Phyllanthaceae Kl. & Garcke.) TYPE GENUS: *Euphorbia* L.

At once one of the largest and most diverse families of angiosperms, the Euphorbiaceae comprise some 7000 species in about 300 genera. Although the family is predominantly tropical, several hundred species of the tribe Euphorbieae, together with scattered species of primarily tropical genera such as *Croton*, are found in temperate regions. In the United States, 22 indigenous genera are known, 18 occurring in the southeastern United States. The 24 native and naturalized genera in the Southeast are represented by about 115 species.

The amplitude of morphological variation is so great that it is difficult to characterize the family, and, for this reason, many authors have suggested that it may be polyphyletic in origin. For the majority of genera, the family may be recognized by the unisexual flowers, the presence of a floral disc, and the trimerous gynoecium which typically ripens into a septicidally dehiscent schizocarp with three or six anatropous seeds. Vegetatively, the family is marked by having mostly alternate, stipulate leaves, often with glandular spots or appendages on the blades. Latex is present in many genera, but is far from being as ubiquitous as is implied by many textbooks.

The cymose inflorescences of many Euphorbiaceae are distinctly proterogynous, the female flowers at the lower dichotomies of the inflorescence maturing before the males; this is especially clearly seen in *Jatropha*, *Cnidoscolus*, and many cyathia of *Euphorbia*. Pollination relationships have not been studied in the vast majority of genera, but the observations of Warmke on *Hevea* and the analysis of various floral characters suggest that pollination of many tropical Euphorbiaceae is carried out mainly by small Diptera. Despite the frequent citation of the Euphorbiaceae as an example of a wind-pollinated family, only a few genera, such as *Acalypha* and *Ricinus*, seem to be truly anemophilous. Pollination by hummingbirds has been observed in *Pedilanthus* and may occur in other red-bracteate taxa of tribe Euphorbieae.

Observations on weedy species of *Euphorbia* and *Phyllanthus* suggest that self-compatibility is widespread in many herbaceous Euphorbiaceae. Embryo sac development is of the normal, monosporic type in most genera, but tetrasporic types are prevalent in *Acalypha*, and, in *Euphorbia*, both bisporic and tetrasporic types have been recorded. Apomixis was long ago demonstrated by Strasburger in the Australian *Caelebogyne ilicifolia* J. E. Sm. which produces nucellar embryos (often with polyembryony). Adventitious embryony has also been found in *Euphorbia dulcis* L., but gametophytic apomixis has not been observed in the Euphorbiaceae.

Anatomical studies have shown that there is great variation in wood anatomy (particularly in fiber thickness, parenchyma distribution, and ray configuration), but no sufficiently comprehensive systematic survey of euphorbiaceous woods has yet been made. There is tremendous diversity in trichome shapes in some tribes (particularly the Crotoneae), but very little in others (e.g., the Phyllantheae). Petiolar anatomy was studied by Dehay, whose conclusions as to family affinities seem excessively speculative; but within certain groups it may provide an excellent indication of affinity (e.g., in evaluating the supposed relationship of *Cnidoscolus* with *Jatropha*). The laticiferous organs of Euphorbiaceae have been studied intensively in such economically important genera as *Hevea* and *Manihot*, but still have not been surveyed in the manner necessary to obtain taxonomically significant data (cf. summation by Gaucher). Latex is not reported in any genus of the subfamily Phyllanthoideae, although *Bischofia* and *Uapaca* possess tanniniferous vessels which seem homologous with the "laticifers" of many Crotonoideae. The distinction between laticiferous and tanniniferous vessels is to some extent arbitrary, since the so-called laticifers in the Crotonoideae produce a great variety of compounds, including tannins, saponins, starch, resins, terpenoids, and rubber. Clearly, a study of the origin and evolution of the laticiferous systems in the Euphorbiaceae should throw a great deal of light on phylogenetic relationships within the family.

The Euphorbiaceae contain an extraordinary diversity of organic compounds, possibly more than in any other plant family. In addition to the compounds enumerated above, a variety of alkaloids has been found in both the Phyllanthoideae (especially subtribe Phyllanthinae) and Crotonoideae (mainly in *Croton*). The oily seeds of many Crotonoideae contain unusual fatty acids and also some peculiar, highly poisonous proteinaceous compounds (phytotoxins), the structures of which have not yet been elucidated. It seems clear that there is an exceedingly bright future for chemotaxonomic studies here.

Although there have been many studies on floral morphology in the Euphorbiaceae, few general surveys of the entire family have been made, other than those of Baillon and Michaelis. A disproportionate amount of effort has been expended on investigations of the cyathium of the Euphorbieae, but the results have, in many instances (e.g., Haber, Bodmann), been vitiated by the failure of authors to correlate meaningfully anatomical structure with the systematic position of the taxa studied. The use of floral characters as indicators of relationship has been complicated by the circumstance that trends of modification of floral parts have been both fluctuating and reversible. For example, the primitive euphorbiaceous flower was probably pentamerous with two whorls of stamens, to judge from morphological relationships among the primitive genera of Phyllanthoideae such as *Astrocasia*, *Heywoodia*, and *Wielandia*. During the evolution of other taxa, there has been a general overall trend towards reduction in number of parts, so that the gynoecium in the great majority of taxa is three-carpellate, and stamens are often reduced to five, or even to only one, per flower in the Euphorbieae and some Hippomaneae. On the other hand, a secondary increase in number has occurred in calyx-lobes (e.g., up to 10 or 12 in *Dalechampia*), stamens (over 100 in several species of *Croton*), and carpels (10–20 in *Hura* and *Hippomane*).

One of the most fruitful subareas of floral morphology has been the investigation of pollen structure, which was started by Erdtman and further elaborated by Köhler, Punt, and Webster. Pollen characters seem, in many instances, to be extremely valuable indicators of affinity, as Erdtman originally suggested for the taxa with *Croton*-type pollen; Punt has shown that examination of the pollen makes possible an immediate and confident assignment of many genera to the proper tribe. The greatest diversity of pollen types is found within *Phyllanthus*, where the microspores may be tectate or intectate, prolate to oblate, inaperturate to tricolporate, polycolporate, pancolporate, or porate. The causes for this variation are still obscure, but it is notable that the gamut of pollen types in *Phyllanthus* rather strikingly parallels that in *Polygonum*, which has flowers of much the same size and configuration that probably are pollinated by similar agents (largely Diptera).

Ovule and seed characters are also important in the classification of the Euphorbiaceae but have not yet received the attention they deserve. Although the ovules are prevailingly anatropous, in the tribe Phyllantheae hemitropous ovules are common and seem to characterize natural groupings of genera. Plants such as *Tetracoccus*, with anatropous ovules which develop into shiny black seeds, clearly must be removed from the tribe. The seeds furnish important systematic characters at various levels of affinity, from characterizing species to separating tribes. Caruncullate seeds are rare in the Phyllanthoideae but are quite common in the Crotonoideae, so much so that a number of uncritical writers have described the seeds of Euphorbiaceae as generally carunculate. In fact, however, the development of the caruncle is a very fluctuating character, and within single genera (e.g., *Euphorbia*) rather closely related species may be separated by the presence or absence of the caruncle.

The schizocarpous fruit of Euphorbiaceae is generally described as a tricoccous capsule, and the mericarps as cocci. There seems to be no reason to use these special names, since the fruit is essentially similar to that found in, for example, the Malvaceae. The elastic dehiscence of the fruit is characteristic, and seeds may be hurled to a considerable distance; those of *Hura* travel several yards, with a noise like a gun shot. Drupaceous fruits are found in a considerable number of Phyllanthoideae (many of these cauliflorous), and those of some tropical species of *Phyllanthus* are baccate. The carunculate seeds of various taxa are said to be dispersed by ants, but there is still insufficient field evidence to corroborate this.

Cytologically, the Euphorbiaceae are as diversified as in most other respects, but such a small proportion of the species (less than 5 per cent) has been studied that chromosome data are at present only of limited systematic usefulness. Except in some succulent species of *Euphorbia,* the chromosomes are relatively small, so cytological comparisons have to depend largely on number alone. Perry, who completed the first chromosomal survey of the family, concluded that the basic number is 8 and that annual species are more primitive than perennials. Subsequent studies, however, suggest that neither conclusion is justified. In the subfamily Phyllanthoideae it seems most likely that $x = 13$ in the more primitive taxa, while in the Crotonoideae the most widespread basic numbers are $x = 9$, 10, and 11. Even in *Euphorbia* itself 10 seems more probable than 8 as the original basic number.

Polyploidy is frequent in many taxa, and taxonomically difficult polyploid complexes are known in *Mercurialis* and *Euphorbia* subg. ESULA. Translocation heterozygosity has been reported in *Croton californicus* Muell. Arg., and may be present in *Phyllanthus Niruri* L. Studies of interspecific hybridization have been made in weedy species of *Euphorbia* subg. ESULA, and such may prove interesting in *Croton* and other groups of *Euphorbia*; but on the whole, interspecific hybridization does not seem to be very conspicuous in the family.

The infrafamilial classification of the Euphorbiaceae has been a subject for controversy since Jussieu set up the first subfamilial divisions in 1824. Baillon initiated the primary division into one-ovulate and two-ovulate taxa which is still reflected in Pax's cleavage between Phyllanthoideae and Crotonoideae. Surprisingly, this division on the basis of a single character appears to be a relatively natural one, although the Crotonoideae are much more heterogeneous than are the Phyllanthoideae. Mueller (1866) established a different primary division, separating a relatively small group of Australian taxa as a "tribal series" Stenolobeae, characterized by narrow cotyledons (all other Euphorbiaceae falling into the series "Platylobeae" because of broader cotyledons). Mueller's two tribes of biovulate taxa and five tribes of uniovulate taxa were taken over by Pax, with some modification, as the basis of the system currently in general use.

Klotzsch and Garcke, writing contemporaneously with Baillon, initiated a policy of splitting the Euphorbiaceae which has been followed by a minority of workers; they recognized six families which were roughly the equivalents of Mueller's tribes. The most recent adherent of this philosophy is Hurusawa, who has promoted the four subfamilies of Pax (two of Stenolobeae and two of Platylobeae) to separate families. This procedure has little to recommend it, since the palynological evidence suggests that the Stenolobeae are probably an artificial group which should be returned to positions within the Platylobeae. Furthermore, while there is a rather sharp gulf between the uniovulate and biovulate Euphorbiaceae, they seem unquestionably to be related, and separation into different families overrates differences at the expense of similarities.

The proposal of Erdtman to realign the tribes of Crotonoideae on the basis of pollen morphology seems reasonable and is, on the whole, borne out by the detailed studies of Punt. As noted by Erdtman, this results in an arrangement much closer to that of Bentham than to that of any other of the 19th century systematists. Although no formal, revised system of the Crotonoideae has yet been published, it appears that many of the data necessary are already at hand.

Köhler's thorough analysis of pollen morphology in the biovulate Euphorbiaceae has, in general, confirmed and extended the observations of Erdtman and Punt. His rearrangement of the genera of Phyllanthoideae and absorption of the genera of the stenolobian Poranthoideae into their proper places among the platylobian genera represents a valuable contribution to the classification of the family. A few of his innovations (e.g., placing *Poranthera* in the Antidesmeae, rather than in the Andrachneae) do not accord with evidence from other data, but, on the whole, his new arrangement is undoubtedly much closer to the lines of natural affinity than any heretofore proposed.

The most interesting proposal of Köhler is to separate the mainly Old World biovulate genera with spinulose pollen grains as a separate subfamily. Because of the strong correlation with other morphological characters, this suggestion appears warranted, and the biovulate Euphorbiaceae are herewith assigned to two subfamilies: subfam. Phyllanthoideae Pax, with alternate leaves, nonspinulose pollen, ovules often hemitropous, and seeds not carunculate; and subfam. Oldfieldioideae Köhler & Webster,[2] with leaves often opposite or whorled, mostly spinulose pollen, ovules strictly anatropous, and seeds mostly carunculate.

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[2] Köhler described several new suprageneric taxa which are invalidly published because he failed to provide Latin diagnoses. His proposed subfamily merits acceptance and is here validated: Subfam. **Oldfieldioideae** Köhler & Webster, subfam. nov. Arbores fruticesve saepe dioicae; foliis alternis, oppositis, verticellatisve, simplices vel palmatipartitis; floribus apetalis, disco plerumque nullo; staminibus liberis, granis pollinum echinulatis; ovulis in quoque loculo collateralibus. TYPUS: *Oldfieldia* Benth. et Hook. f.

Köhler's tribe Oldfieldieae was also invalidly published, but an earlier tribal name, Paivaeuseae, is validly published and available. As a consequence of Article 19 of the International Code of Botanical Nomenclature (1966), this virtually unpronounce-

By analogy with Köhler's proposal for the biovulate Euphorbiaceae, it might be possible to divide the uniovulate Euphorbiaceae (Crotonoideae and Ricinocarpoideae of Pax) into two subfamilies based on pollen morphology. Punt has shown convincingly that the genera with crotonoid pollen should be placed together in a single taxonomic grouping. However, the morphological and anatomical evidence does not show as good a correlation with palynological characters as is true for the biovulate Euphorbiaceae. For example, *Hevea* has articulated laticifers and in this and other respects seems related to *Manihot*; yet it has colporate pollen which lacks a distinct Croton-pattern. In terms of wood anatomy the uniovulate Euphorbiaceae are less diversified than the biovulate taxa, and there is no consistent difference in seed morphology. Tentatively, therefore, it seems preferable to retain all of the uniovulate Euphorbiaceae (including the stenolobian Ricinocarpoideae of Pax) in a single subfamily Crotonoideae.

The replacement of the subfamilial quartet of Pax by the present trinity does not make much difference in the classification of North American Euphorbiaceae, since the only genus of Oldfieldioideae represented is *Tetracoccus*. That small genus of xerophytic shrubs is confined to the western United States and Mexico and does not enter our area.

The extent of phylogenetic relationship between the Euphorbiaceae and other families has long been controversial. Baillon, in 1858, imagined a tetrahedral relationship, with the Euphorbiaceae on one face and the Malvales, Geraniales-Rutales, and Rhamnales on the other faces. Pax, summing up his studies in 1924, regarded the Euphorbiaceae as of polyphyletic (or at least diphyletic) origin, with part of their ancesters in the Geraniales-Sapindales complex, and part in the Malvales. Hutchinson, whose view is perhaps the most extreme, suggested an origin from at least four orders: Bixales, Tiliales, Malvales, Celastrales (and possibly also Sapindales). Croizat, in his principal consideration of the problem (1940), emphasized the affinity to the Malvales, especially the Sterculiaceae.

The existence of so many multifarious and disparate hypotheses suggests that little understanding of the problem of relationship at the family level has been achieved. Part of the confusion surrounding the affinities of the Euphorbiaceae resides in the unsatisfactory delimitation of the family. Taxa such as the Buxaceae, Dichapetalaceae, and Callitrichaceae were classified in the Euphorbiaceae by many 19th century authors, and families such as the Empetraceae were thought to be related until well into the 20th century. Until the Euphorbiaceae is purged of such aberrant groups, it will indeed be technically a "polyphyletic" family in the Hutchinsonian sense.

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able name is automatically replaced by Oldfieldieae when both subfamilies and tribes are used in the subfamilial classification. Although the result is the possibility of *two correct names* for the same taxon with precisely the same taxonomic circumscription and with no change in rank (an unfortunately unforeseen consequence of Article 19), it seems far preferable to describe a new subfamily based on *Oldfieldia* than to perpetrate a subfamilial name such as Paivaeusoideae!

While within the Euphorbiaceae the pollen grains furnish the most critical characters for delimitation of infrafamilial taxa, at the family level the ovules may be more significant. All bona fide Euphorbiaceae have pendent epitropous ovules, with the micropyle abaxial to the funicle and roofed over by an obturator. Such taxa as the Buxaceae, which have apotropous ovules, cannot be intimately related, and the derivation of the Euphorbiaceae from taxa within the apotropous Sapindales therefore appears unlikely. A relatively overlooked similarity exists between the Euphorbiaceae and the Simaroubaceae (sensu lato). In the Irvingioideae, often treated as a distinct family Irvingiaceae, gynoecia with epitropous ovules rather similar to those of the Euphorbiaceae occur. Recently, Capuron has described from Madagascar a new genus of Irvingiaceae, *Cleistanthopsis*, which, as its name indicates, has an extraordinary general similarity to *Cleistanthus*, of Euphorbiaceae subfam. Phyllanthoideae. Despite the solitary style and uniovulate locules, which preclude its being directly ancestral to the Ur-Euphorbiaceae, *Cleistanthopsis* obviously deserves consideration as at least a possible euphorbiaceous "great-uncle." Further botanical exploration in such regions as Madagascar may therefore eventually provide the solutions to some of the problems over which several generations of morphologists have quibbled in vain.

Part of the difficulty involved in tracing phylogeny within the Euphorbiaceae and in relating it to other families comes about because of the relatively poor fossil record. Kirchheimer (1957) disposed of most of the reports of fossil Euphorbiaceae from Central Europe; and in general, it would appear that records based on leaf impressions are even more unreliable than is usual in paleobotany, due to the large amplitude of foliar variation in Euphorbiaceae.[3] Recently, however, the picture has improved somewhat due to the discovery by Chandler of a considerable variety of fossil euphorbiaceous fruits from the Eocene of England, and the description of several fossil woods from India. The preservation of the English fruits and seeds is unexpectedly good, considering the dehiscent nature of the fruits and the thin seed-coats of most genera. The striking genus *Paleowetherellia* Chandl. has fruits which, in some respects, suggest the neotropical genus *Hura*, although the orientation of the ovules precludes identification with any known euphorbiaceous genus; it may possibly

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[3] For a particularly egregious example of the ill-founded identifications perpetrated by some paleobotanists, see the paper by Potbury, who described a new species of the Old World genus *Microdesmis* from some leaves in a probably Eocene deposit in California. It would be difficult to find a genus of Euphorbiaceae with more unobtrusive leaves; those of *Microdesmis* could be matched by species in various other euphorbiaceous genera and in many other families such as Celastraceae, Flacourtiaceae, Theaceae, Moraceae, etc., etc. Her disposition can most charitably be characterized as a wild guess, and the fossils she referred to *Acalypha* and *Drypetes* are scarcely more convincing. Even the fossil leaves classified as *Aleurites* are only possibly congeneric. All of these remains could at best be ascribed to form-genera such as *Euphorbiophyllum*. Other Tertiary leaf fossils *may* be correctly ascribed to Old World genera (e.g., *Mallotus riparius*), but, to the writer's knowledge, there is as yet no unequivocal record of a living gerontogean euphorbiaceous taxon as a fossil in the New World, and vice versa.

represent some extinct branch of the family. Other carpic fossils are much closer to living taxa. For example, Chandler's *Euphorbiotheca lakensis*, which she compared to *Andrachne* and *'Securinega'* (i.e., *Flueggea*), is a very close match for *Flueggea suffruticosa* (Pall.) Baill., a species widespread in Siberia and China and with a close relative in Japan.

Mädel, in a careful review of fossil euphorbiaceous woods, has shown that at least seven form-genera from the Cretaceous and Tertiary can be recognized. Unfortunately, the woods of many taxa of subfam. Phyllanthoideae are not very distinctive and can easily be confused with woods of other families, such as the Flacourtiaceae. Mädel rather convincingly compares her Upper Cretaceous *Paraphyllanthoxylon capense* with *Margaritaria discoidea* (Baill.) Webster,[4] a tree widespread in tropical Africa today. Bailey's *Paraphyllanthoxylon arizonense*, a roughly contemporaneous New World fossil, is less similar to the neotropical *Margaritaria nobilis* L. f., but may prove to be more similar to *Margaritaria* or *Phyllanthus* than to any other genera. There are now rather good records of Tertiary woods similar to those of living species of *Antidesma, Bridelia, Aleurites,* and *Hevea.* If these fossil woods can be matched with fossils of fruits and seeds (as found in the English deposits), there would appear to be a good opportunity to make much more nearly definitive identifications and thus to produce — at last — some historical documentation to prop up the rather shaky phylogenetic classification of the family.

A number of botanists over the past century have sought to resolve some of the problems of the phylogenetic position of Euphorbiaceae by excluding various extraneous elements. Baillon proposed the removal of the Buxaceae and was followed in this by Mueller, though not by Bentham. Today it appears that the resemblance of Buxaceae to Euphorbiaceae is superficial, as the boxwoods differ in a number of fundamental characters. The perianth of the Buxaceae does not appear to be strictly homologous with that of Euphorbiaceae, as it consists of four decussate tepals in the male flower and about six to twelve imbricate bractlike tepals in the female flower. The gynoecium of Buxaceae is very different in having the styles emerging laterally, not apically, on the ovary, as well as in the apotropous ovules; and at least in *Buxus* and *Pachysandra*, endosperm development is cellular, rather than nuclear. Despite the tantalizing similarity between the pollen grains of *Buxus* and *Pachysandra* with those of various Euphorbiaceae (subfam. Crotonoideae), it appears most probable that this resemblance is due to convergence and is not indicative of affinity.

Somewhat more similar to the Euphorbiaceae is the genus *Daphniphyllum*, which resembles some taxa of subfam. Phyllanthoideae in both habit and its gynoecium with paired, anatropous, epitropous ovules. However, *Daphniphyllum* diverges markedly in its exstipulate leaves, imperfectly septate ovary, ovules without an obturator, and especially in its seeds

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[4] **Margaritaria discoidea** (Baill.) Webster, comb. nov. *Cicca discoidea* Baill. Adansonia **1**: 85. 1860. *Phyllanthus discoideus* (Baill.) Muell. Arg. Linnaea **32**: 51. 1863.

with a minute embryo. The latter feature suggests Ranalian affinities for *Daphniphyllum* and makes it necessary to exclude it from the Euphorbiaceae as the only genus of a separate family Daphniphyllaceae. The wood of *Daphniphyllum*, according to Janssonius, is very different from any Euphorbiaceae and resembles that of Hammamelidaceae, thus confirming the suggestion of affinity made by Hallier. In its gynoecial conformation, *Daphniphyllum* shows some resemblance to the Buxaceae despite its differently oriented ovules; and it also resembles *Buxus* in its exstipulate leaves and cellular endosperm. It would appear, therefore, that the Daphniphyllaceae are at least much more closely related to the Buxaceae than either family is to the Euphorbiaceae; and both probably belong in the Hammamelidales-Trochodendrales complex, but with their exact positions yet to be determined.

Still other genera which have been viewed with suspicion as to their euphorbiaceous parentage include *Aextoxicon*, *Bischofia*, and *Picrodendron*. *Aextoxicon*, which somewhat resembles the euphorbiaceous genus *Pera* in habit (partly because of its lepidote indumentum), has been excluded from the Euphorbiaceae by Pax on the basis of its aberrant perianth, apotropous ovules, and ruminate endosperm. As the only representative of the family Aextoxicaceae, it would according to Pax take a position adjacent to the Icacinaceae. *Picrodendron*, a West Indian genus with compound leaves and fruits superficially like walnuts, has been variously placed in the Simaroubaceae, Euphorbiaceae, or in its own family, Picrodendraceae. The female flower of *Picrodendron* (illustrated by Fawcett and Rendle) is quite typical for the Euphorbiaceae, as the anatropous ovules are inserted below an obturator. The genus therefore may be truly euphorbiaceous, and its leaves and spinulose pollen suggest a possible affinity with genera of the subfamily Oldfieldioideae.

Bischofia presents a more difficult problem. Although the genus resembles some of the subfam. Oldfieldioideae in habit, the pollen is different, and the wood structure is not readily distinguishable from that of some taxa of subfam. Phyllanthoideae. Airy Shaw has proposed to create a separate family Bischofiaceae, to be placed near Staphyleaceae because of the resemblance between *Bischofia* and the Chinese genus *Tapiscia*. *Bischofia* differs from *Tapiscia* in so many ways (e.g., unisexual flowers, nearly free calyx segments, completely different gynoecium, and larger embryo) that a very close relationship between the two genera can scarcely be maintained. Nevertheless, *Bischofia* is so isolated in the Euphorbiaceae that its exclusion is quite possibly warranted, and Airy Shaw's suggestion of a staphyleaceous kinship deserves further investigation.

Airy Shaw has also created new unigeneric families for *Androstachys*, *Hymenocardia*, and *Uapaca*; but, although each of these taxa is certainly aberrant, they have the fundamental gynoecial characters of Euphorbiaceae, and there does not seem to be any compelling reason why they should be removed.

A rather surprising realignment of the boundaries of the Euphorbiaceae has recently been proposed by Forman, who has removed *Microdesmis* and *Galearia* to the family Pandaceae, which heretofore included only the anomalous African genus *Panda*. Forman's arguments for an affinity between the three genera seem convincing, and it must be noted that *Microdesmis* and *Galearia* have always occupied a rather anomalous position in the Euphorbiaceae; Bentham created a special tribe Galearieae, apparently because he could not place them with any other group of genera. *Microdesmis* is aberrant from most other Euphorbiaceae in its basic chromosome number of $x = 15$, in the compression of the anthers against the vestigial gynoecium or petals in the male flower bud, and in the absence of an obturator. *Galearia* shares at least some of these characters, and both genera have a wood structure unlike that of other uniovulate Euphorbiaceae. Although it is difficult to write a diagnosis for the revised family Pandaceae which will unequivocally exclude all Euphorbiaceae, the inclusion of *Panda* — with its orthotropous ovules and unusual fruit — would make the Euphorbiaceae more difficult to circumscribe. Consequently, it seems expedient to recognize the Pandaceae as an offshoot of the Euphorbiaceae and the only other family which is at all closely allied.

When the Buxaceae, Daphniphyllaceae, and Pandaceae are excluded, the question remains as to where the closest affinities of the Euphorbiaceae are to be found. Despite all the additional information which has accrued, it must be admitted that no single taxon ancestral to the Euphorbiaceae can be designated at the present time, and it is not certain that any living taxon will ever be identified as the progenitor. The relationships of the polypetalous woody dicotyledons are notoriously reticulate, and the best that can be done at present is to specify the most plausible phylogenetic groupings. The inclusion of the Euphorbiaceae within the Geraniales of Engler appears to be justified, since in wood anatomy, floral morphology, and ovule and seed structure they resemble such families as Linaceae, Oxalidaceae, and Irvingiaceae. On the other hand, with respect to certain characters there are undeniable similarities to other groups, especially the Sterculiaceae and Thymelaeaceae, which show some striking similarities in pollen and seed structure. Croizat, among others, has emphasized the sterculiaceous affinity, but it should be noted that most of the malvalian-appearing Euphorbiaceae belong to the Crotonoideae, and the presumably more primitive Phyllanthoideae show little resemblance. Perhaps the similarities of Euphorbiaceae with the malvalean families and with the Flacourtiaceae may be explained as parallelism, in the sense that all of these families represent divergent branches of a plexus that may ultimately be of rosalian origin. It is not possible to go any further than that on the basis of current botanical knowledge.

Because of their chemical diversity, the Euphorbiaceae include a rather large number of plants of economic importance. Although rubber from *Hevea* is perhaps the most valuable commodity, commercially important products are also obtained from euphorbiaceous seed oils (*Aleurites*, *Ricinus*, and, to a lesser extent, *Croton* and *Jatropha*), starchy tubers (*Manihot*), and waxes (*Aleurites*, *Sapium*, and *Euphorbia*). Still other compounds, such as the alkaloids and saponins in the Phyllanthoideae, may yet prove to be of medicinal value. Finally, a number of Euphorbiaceae are grown as ornamentals. The most important species is doubtless the poinsettia (*Euphorbia pulcherrima* Willd. ex Grah.), but especially in tropical and subtropical gardens one may encounter species of *Phyllanthus, Acalypha, Croton, Codiaeum* (the widely cultivated "Croton" of horticulturalists), *Euphorbia*, and *Pedilanthus*.

In addition to the 24 genera treated in detail below, some of these ornamental or economically important plants may be found cultivated in our area, especially in southern Florida. The Pará rubber tree, *Hevea brasiliensis* (Willd. ex A. Juss.) Muell. Arg., may be found in Key West and perhaps extreme southern Florida; it can be recognized by its long-petiolate trifoliolate leaves, paniculate inflorescences, apetalous flowers, and large fruits. Another euphorbiaceous tree planted in the Miami area, *Bischofia javanica* Blume, also has trifoliolate leaves but the leaflets are toothed (instead of entire as in *Hevea*) and the twigs produce no latex. Various species of *Antidesma* are cultivated, especially *A. Bunius* (L.) Spreng.; these are easily distinguished from other Euphorbiaceae by the combination of entire laurel-like leaves and the spicate female flowers which mature into edible drupaceous fruits. One of the most characteristic trees which may be seen in the Miami area is the sandbox tree, *Hura crepitans* L., immediately recognizable by virtue of its spiny stem, laticiferous twigs, heart-shaped leaves, bizarre flowers (the female with a dilated umbrella-like stigma), and large multicarpellate fruits which dehisce in a violent explosion. The latex and the seeds of this plant, as in many other local Euphorbiaceae of subfam. Crotonoideae, are dangerously poisonous, and plantings close to houses should be made with care.

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Key to the Genera of Euphorbiaceae

A. Ovules paired in each locule of the ovary; sap never milky; leaves not glandular; flowers axillary, solitary or in glomerules, not in spikes; pollen (in local taxa) mostly tricolporate (Subfam. Phyllanthoideae).

B. Disc in male flower extrastaminal; flowers with or without petals; fruit dehiscent, or at least with more than 1 seed.

C. Plants dioecious; petals present; rudimentary gynoecium evident in male flower.

D. Male flowers subsessile; pollen with short colpi; trees or arborescent shrubs with leathery leaves. . . . . 1. *Savia.*

D. Male flowers pedicellate; pollen with elongated colpi; subshrubs or herbs, leaves with thinner texture. . . . . 2. *Andrachne.*

C. Plants monoecious (in most species); petals absent; male flower without a rudimentary gynoecium.

E. Disc usually present in both sexes; male calyx open at anthesis, lobes not inflexed; seeds with dry coat, lacking a ventral invagination. . . . . 3. *Phyllanthus.*

E. Disc absent; male calyx turbinate, lobes connivent-inflexed; seeds with somewhat fleshy coat, ventrally invaginated. . . . . . [*Breynia.*]

B. Disc in male flower intrastaminal, at least in part; flowers apetalous; fruit indehiscent, seeds one per locule; dioecious trees or shrubs with coriaceous leaves. . . . . 4. *Drypetes.*

A. Ovules solitary in each locule of the ovary; sap often milky or colored; leaves sometimes with petiolar or laminar glands; pollen tricolporate or inaperturate (Subfam. Crotonoideae).

F. Flowers solitary, spicate, or in cymes, not in bisexual pseudanthia.

G. Inflorescence dichasial or else stamens inflexed in the bud; petals present or else calyx petaloid; pollen spheroidal, verrucose, porate or inaperturate [tricolporate in *Hevea*].

H. Stamens scarcely or not at all inflexed in the bud; trichomes simple and uniseriate, rarely stellate or lepidote; inflorescence dichasial.

I. Perianth biseriate; pollen inaperturate; stem exudate colored, not a milky latex.

J. Calyx lobes free, imbricate; fruit capsular; seeds carunculate; stipules more or less persistent. . . . . 5. *Jatropha.*

J. Calyx lobes valvate, fused into a spathe; fruit indehiscent, seeds ecarunculate; stipules caducous. . . . . 6. *Aleurites.*

I. Perianth uniseriate; pollen aperturate; stems exuding milky latex when cut.

K. Pollen tricolporate; seeds ecarunculate; leaves compound. . . . . [*Hevea.*]

- K. Pollen porate; seeds carunculate; leaves often deeply lobed but usually not compound.
  - L. Male disc intrastaminal; stamens free; male perianth usually yellowish, greenish, or purplish; stinging hairs absent. .... 7. *Manihot*.
  - L. Male disc extrastaminal; stamens connate; male perianth white; stinging hairs present ..... 8. *Cnidoscolus*.
- H. Stamens more or less inflexed in the bud; trichomes often stellate or lepidote; inflorescence racemiform or spiciform; pollen inaperturate.
  - M. Fruit a dehiscent, 3-locular schizocarp; seeds carunculate. ... . 9. *Croton*.
  - M. Fruit indehiscent, unilocular; seeds ecarunculate. .... 10. *Crotonopsis*.
- G. Inflorescence not clearly dichasial (mostly racemiform or spiciform); petals absent or, if present, then male calyx valvate; pollen various, mostly tricolporate, never verrucose.
  - N. Petals present, at least in male flower; seeds ecarunculate; calyx lobes valvate.
    - O. Rudimentary gynoecium present in male flower; trichomes simple or glandular (not malpighiaceous); leaves finely serrate, lateral veins distinctly parallel. .... 11. *Caperonia*.
    - O. Rudimentary gynoecium absent; trichomes malpighiaceous (at least in part); leaves entire or coarsely serrate, veins not distinctly parallel. .... 12. *Argythamnia*.
  - N. Petals absent in the male flower.
    - P. Male calyx valvate; sap watery; styles conspicuously papillate to laciniate (or, if not, then plants with stinging hairs).
      - Q. Stamens free or connate, not branched or fasciculate; anthers mostly less than 10 per flower; leaves pinnately veined, at most slightly lobed; stipules discrete, not united; inflorescence spiciform, racemiform, or capitulate; female flowers proximal to the male.
        - R. Styles laciniate or pinnatifid; herbs or shrubs, never twining; stinging hairs absent; seeds usually carunculate.
          - S. Leaves opposite; plants usually dioecious; bracts small; anthers not much elongated; female flower with 2 elongated staminodia; carpels usually 2. ... . 13. *Mercurialis*.
          - S. Leaves alternate; plants monoecious (in local taxa); female bracts enlarged; anthers elongated, vermiform; female flower lacking staminodia; carpels usually 3. .... 14. *Acalypha*.
        - R. Styles unlobed, at most papillate; herbs, often twining, armed with stinging hairs; seeds not carunculate. .... 15. *Tragia*.
      - Q. Stamens branched and fasciculate, anthers many (up to 1000) per flower; leaves palmately lobed; stipules fused into a circular sheath; inflorescence paniculate, normally with female flowers distal to the male; seeds carunculate. .... 16. *Ricinus*.

P. Male calyx imbricate or reduced; styles undivided, not laciniate or pinnatifid; female bracts not accrescent; sap often milky; inflorescences spiciform or racemiform.
  T. Styles not connate into a distally enlarged column; male inflorescence not fleshy and conelike; carpels 2 or 3 (except in *Hippomane*).
    U. Seeds carunculate, dry; fruit capsular.
      V. Floral bracts conspicuously biglandular at base, not displaced from rachis of inflorescence; ovary not conspicuously stipitate.
        W. Columella not 3-horned at base; male calyx lobes and stamens 3; female flowers distinctly pedicellate. . . . . 17. *Sebastiania.*
        W. Columella with a 3-horned gynobase persistent after dehiscence of fruit; male calyx lobes and stamens usually 2; female flower sessile or nearly so. . . . . 19. *Stillingia.*
      V. Floral bracts not glandular at base, adnate to lateral axes of inflorescence (and thus displaced from rachis); ovary conspicuously stipitate. . . . . 18. *Gymnanthes.*
    U. Seeds ecarunculate, either seed coat or carpel wall fleshy.
      X. Fruit thin walled, capsular; seed coat fleshy ('arillate'); ovary 3-locular; styles connate to about the middle. . . . . 20. *Sapium.*
      X. Fruit drupaceous; seed coat dry; ovary 6–10-locular; styles connate only near the base. . . 21. *Hippomane.*
  T. Female flower with umbraculiform stigmatic disc terminating a long stylar column; male flowers aggregated into a fleshy pedunculate conelike structure; carpels more than 5. . . . . [*Hura.*]

F. Flowers aggregated into a usually bisexual cyathium (pseudanthium), usually with one central female flower surrounded by 4 or 5 male monochasia; glands (nectaries) of cyathium usually conspicuous, often with petaloid appendages.
  Y. Cyathia more or less actinomorphic, at least not conspicuously spurred; styles mostly united only below the middle and stems not markedly succulent (in native taxa).
    Z. Leaves alternate or opposite, if opposite, then not inequilateral at base and with chlorenchyma-sheathed veins; main axis not aborting, branching monopodial at least below; stipules often reduced or absent. . . . . 22. *Euphorbia.*
    Z. Leaves entirely opposite, usually distinctly inequilateral at base, stipulate, with chlorenchyma-sheathed veins; main axis aborting just above the cotyledons, branching sympodial throughout. . . . . 23. *Chamaesyce.*
  Y. Cyathia zygomorphic, the glands hidden within a conspicuous spur; styles united most of their length; stems succulent. . . 24. *Pedilanthus.*

Subfam. PHYLLANTHOIDEAE Pax

Tribe PHYLLANTHEAE [Dumort.]

Subtribe **Andrachninae** Muell. Arg., "Andrachneae"

1. **Savia** Willdenow, Linn. Sp. Pl. **4**(*2*): 771. 1806.

Dioecious shrubs or small trees. Leaves alternate, entire, chartaceous to coriaceous, short-petiolate, stipulate. Flowers axillary, the male in dense glomerules, the female few or solitary. Calyx ordinarily 5-parted, lobes imbricate; petals 5, much smaller than sepals [large and conspicuous in some Malagasian taxa]. Male flower: stamens 5, free; anthers introrse, opening longitudinally; pollen subglobose, reticulate, colpi short, endocolpus with diffuse or rounded ends; rudimentary gynoecium 3-lobed. Female flower: disc annular; carpels 3; styles more or less free, bifid, branches slender; ovary glabrous or pubescent; ovules 2 in each locule, anatropous. Fruit capsular; columella persistent; seeds 1 (2) per locule, smooth, chalaza ventral; endosperm copious; embryo straight; cotyledons broad, plane, much longer than the radicle. TYPE SPECIES: *S. sessiliflora* (Sw.) Willd. (Named in honor of Gaetano Savi, 1769–1844, professor at Pisa.)

A genus of 20 to 25 species with a remarkable tricentric distribution: West Indies, southern Brazil, and Madagascar. The circumscription adopted here is approximately that of Bentham and is also near that of Pax and Hoffmann, except that their *Savia phyllanthoides* is returned to *Andrachne*.

Our single representative, *Savia bahamensis* Britton, is a common shrub of coastal and lowland thickets from the Florida Keys south and east to the Bahamas, Caicos Islands, Cuba, Cayman Islands, and Jamaica. It is very similar in appearance to the common Cuban species *S. erythroxyloides* Griseb., from which it differs in its glabrous (rather than sericeous) ovary and its more strongly reticulate leaves (the tertiary veinlets prominent beneath, whereas they are obscure in *S. erythroxyloides*). In these characters it agrees more closely with the Cuban *S. clusiifolia* Griseb., but that species differs in its more cuneate-truncate leaves and larger seeds.

In the Keys, *Savia bahamensis* has been little collected except on Big Pine Key, although records are available from Little Torch Key, No Name Key, and Key Largo. Possibly the species is often overlooked, as the flowers (which seem to appear mainly in April and May) are relatively inconspicuous. Chromosome counts of the plant would be most desirable since not a single species of *Savia* has ever been reported on cytologically.

According to the classification proposed by Urban, *Savia bahamensis* would fit into sect. HETEROSAVIA Urb., characterized by fruits with 2-seeded locules and an embryo with the radicle about half as long as the cotyledons. In this circumscription, sect. SAVIA is monotypic, containing only *S. sessiliflora,* which has capsules with 1-seeded locules (the second ovule abortive in development). This difference is not absolute, however, since the seeds in various species of sect. HETEROSAVIA are often of different sizes and in some instances are probably not viable. However, other characters (e.g., leaf texture, petal size) are correlated with this difference, and Urban's proposed distinction may well be valid.

The biseriate perianth, unspecialized pollen, and generalized vegetative characteristics of *Savia* mark it as one of the more primitive taxa of Euphorbiaceae. Although Rothdauscher reported vessels with simple perforations in *S. sessiliflora*, Solereder found scalariform perforations in other species. Our own species, *S. bahamensis*, appears to be rather highly specialized, since it has simple vessel perforations and mostly uniseriate rays. Comparisons with the Madagascar species are much needed. Köhler has noted that *Savia* is palynologically heterogeneous even after some extraneous taxa brought in by Pax are excluded. Most of the primitive taxa in subtribe Andrachninae have oblate spheroidal grains, as found in the West Indian *S. sessiliflora* and *S. andringitrana* Leandri from Madagascar. However, in *S. Danguyana* Leandri of sect. PETALODISCUS and in species of the West Indian HETEROSAVIA (e.g., *S. erythroxyloides*), the grains are prolate and have a much finer ornamentation.

Savia cannot be delimited satisfactorily until the Madagascar species are carefully studied. It is notable that these plants differ from the West Indian ones in being monoecious and having a more conspicuous disc; further study may show that they should be segregated into a separate genus, *Petalodiscus*, as was done by Pax in 1890. This would make *Savia* an entirely American group but would not affect the obvious affinity between the West Indian and Malagasian taxa. The evidence from pollen characters, in fact, seems contradictory, since it suggests two groups of affinity, each represented in both the West Indies and in Madagascar. Examination of seeds in the Madagascar taxa might possibly help to resolve the impasse. Leandri has reported exalbuminous seeds in the Madagascar species *S. Bojeriana* Baill., whereas in all West Indian plants examined copious endosperm is present. If a correlation between seed and pollen classes can be established, the circumscription of the subgeneric taxa in *Savia* can at last be fixed.

Whatever the circumscription of *Savia* may prove to be, the genus certainly belongs in the taxonomic group which includes woody Old World genera such as *Blotia* and *Wielandia*. Its only near relative in the New World (and a rather distant one at that) would appear to be *Astrocasia*, which differs strikingly in appearance due to its long-petiolate leaves and more conspicuously petaliferous flowers; the extrorsely dehiscent stamens adnate to the vestigial gynoecium in *Astrocasia* furnish an additional technical distinction. The genus *Andrachne* is difficult to distinguish from *Savia* on a world-wide basis because of the variability of both taxa, although Köhler has shown that the pollen is quite different, and at least the typical species of *Andrachne* have hemitropous ovules. The local representatives of the two genera may be easily distinguished by the larger and thicker leaves, subsessile male flowers, and solitary seeds of *Savia*.

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2. **Andrachne** Linnaeus, Sp. Pl. 2: 1014. 1753; Gen. Pl. ed. 5. 444. 1754.

Herbs or subshrubs. Leaves alternate, stipulate, petioles abbreviated to as long as the blade; blades thin, entire, often small. Plants dioecious [in our representative, most other species monoecious]; flowers in axillary clusters, the female often solitary. Flowers petaliferous, but petals often reduced or (in the female flower) rudimentary; disc usually segmented (except in our representative). Male flower: stamens 5, opposite the calyx lobes; filaments free [sometimes united]; anthers introrse or laterally dehiscent; pollen more or less prolate, 3-colporate, colpi elongate, endocolpus pointed at ends; vestigial gynoecium usually lobed or divided. Female flower: carpels 3; stigmas capitate; styles more or less free, spreading, bifid; ovary glabrous or pubescent; ovules 2 in each locule, anatropous [or transitional to hemitropous]. Fruit capsular; columella persistent. Seeds usually 2 in each mericarp, smooth or roughened; endosperm copious; embryo straight, cotyledons not folded, broader than the radicle. $2n = 24, 26$. (Including *Lepidanthus* Nutt.) LECTOTYPE SPECIES: *A. Telephioides* L.; see Small in Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 453. 1913. (Name from Greek, *andrachne*, supposedly applied to *Portulaca oleracea* L. by ancient authors.)

As here delimited in the sense of Mueller, *Andrachne* is a small but distinctly heterogeneous genus of approximately 15 species widely scattered in both temperate and tropical regions of the Old World and New World. Only four species are known in North America; a single one, *A. phyllanthoides* (Nutt.) Coulter, $2n = 26$, enters our area.

Until recently, this species was unknown east of the Mississippi, the outlying localities being in southern Missouri (Texas and Shannon counties) and central Arkansas (Garland, Saline, and Hot Springs counties). In 1963, Mrs. Blanche Dean discovered a colony along the banks of Scarum Creek in Blount County, Alabama; according to Mrs. Dean the plant here grows in deep sand among boulders in association with *Rhus radicans*, *Salix nigra*, and *Amorpha fruticosa*. In the western parts of its range (Texas and Oklahoma), *A. phyllanthoides* appears to be an obligate calciphile, usually growing in cracks in limestone; at the same time, however, it does seem to prefer creekbed localities which are periodically flooded. In central Arkansas, on the other hand, Demaree (on labels) reports finding it on steep shale or novaculite slopes.

The discovery of the Blount County station, over 300 miles east of the nearest population, adds another interesting relict to the ones already known from central and northern Alabama and recalls the extreme restriction of *Croton alabamensis* in the Warrior and Cahaba River basins. The Alabama plants seem taxonomically indistinguishable from those farther west, although they may prove to have certain minor differences (viz., possibly smaller petals) when the population is better sampled. No other species of this family in the Southeast shows such an outstanding disjunction, although the bicentric population (Texas-Florida) of *Phyllanthus abnormis* and the vicariant pair *P. polygonoides-platylepis* (Texas-Louisiana and northwestern Florida) offer somewhat analogous distribution patterns. The relatively slight morphological differentiation which has occurred in all three instances suggests that the disjunctions may date only to the Pleistocene.

Within the genus *Andrachne*, *A. phyllanthoides* appears to be quite isolated, except for its western vicariant *A. arida* (Warnock & Johnston) Webster.[5] This latter plant, which is known only from a few desert localities in trans-Pecos Texas and Coahuila, obviously resembles *A. phyllanthoides* but differs in its shrubbier habit, smaller more rigid leaves, and shorter pedicels. As Warnock and Johnston suggest, the two species appear to represent the vicarious offspring of an originally widespread and continuous population the range of which has been dissected by climatic change.

This species-pair (*A. phyllanthoides-arida*) occupies a taxonomically isolated position within *Andrachne*. The smooth, anatropous seeds and dioecious inflorescences suggest *Savia*, where, in fact, both species have been placed by most recent workers. However, Punt and Köhler have shown that the pollen grains of *A. phyllanthoides*, with elongate colpi and large, sharply defined ora, resemble those of typical species of *Andrachne* much more than they do any species of *Savia*. Furthermore, in habit and in gross flower structure both species show a much greater resemblance to the Asiatic species of *Andrachne* sect. ARACHNE Endl. than to any species of *Savia*.

Some contemporary workers (e.g., Hurusawa, Pojarkova) accept *Arachne* as a distinct genus from *Andrachne* (sensu stricto) and would presumably place *A. phyllanthoides* in *Arachne*. However, in most characteristics the latter taxon is so close to typical representatives of *Andrachne* that it would be difficult and inconvenient to recognize two genera. In tackling this problem in the future, notice should be taken of the relatively neglected feature of ovule configuration: at least some taxa of sect. ARACHNE have anatropous ovules, whereas in *A. Telephioides* (§ AN-

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[5] **Andrachne arida** (Warnock & Johnston) Webster, comb. nov. *Savia arida* Warnock & Johnston, Southw. Nat. **5**: 3. 1960. This new combination is rather embarrassing to the author, since it was at least partly on his advice that Warnock and Johnston described their plant as a *Savia* rather than as an *Andrachne*. Since then, however, accumulating evidence shows that their plant must be excluded from *Savia*, and the most conservative course is to place it in *Andrachne*, rather than in some segregate genus.

DRACHNE) they are hemitropous. However, it is not yet certain whether this difference will hold for other species assigned to *Andrachne*. For the time being, therefore, it appears that the best disposition of the two species of the United States is still that of Mueller, who placed *A. phyllanthoides* in *Andrachne* as the only representative of section PHYLLANTHOPSIS (Scheele) Muell. Arg., characterized by the undissected male disc, somewhat woody habit, and deeply divided vestigial gynoecium.

According to both Köhler and Punt, *Andrachne* is palynologically similar to the Old World genus *Actephila*; an affinity between these two genera was pointed out long ago by Baillon. However, *Actephila* differs markedly from all species of *Andrachne* in its seeds, which are solitary (by abortion) in each locule and nearly or quite without endosperm, the cotyledons more or less folded. Through sects. ARACHNE and PHYLLANTHOPSIS, *Andrachne* seems more closely related to *Savia*, of which it may be regarded as the herbaceous derivative (cf. *Savia* for generic distinctions). In another direction, *Andrachne* stands in approximately an ancestral position to various apetalous genera of subtribe Phyllanthinae. For example, *A. ovalis* of South Africa has many of the attributes of the hypothetical ancestor of both *Meineckia* and *Chascotheca*, while *A. Telephioides* and its relatives show a possible significant resemblance to some nearctic herbaceous species of *Phyllanthus* subg. ISOCLADUS. From all of these genera *Andrachne* may be distinguished by its diminutive habit, delicate petaliferous flowers, characteristic pollen grains, and paired seeds with copious endosperm.

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Subtribe **Drypetinae** Griseb., "Drypeteae"

3. **Drypetes** Vahl, Eclog. Am. 3: 49. 1810.

Dioecious trees or shrubs, usually with dense wood. Leaves alternate, short-petiolate, stipulate, blades often leathery, entire or sharply toothed, Flowers in dense axillary clusters, sometimes almost sessile. Flowers apetalous; calyx in both sexes of 4 or 5 (rarely 6 or 7) more or less deciduous imbricate sepals. Male flower: disc intrastaminal, marginal lobes sometimes projecting between stamens; stamens 3–12 (rarely up to 50), filaments free, anthers basifixed and extrorse to introrse; pollen prolate, tricolporate, tectate, with large endocolpus; rudimentary gynoecium present or absent. Female flower: disc cupuliform; ovary of 1 or 2 [very rarely 3 or 4] carpels; styles nearly obsolete, the more or less dilated stigmas nearly sessile atop the ovary; ovules 2 in each locule, anatropous. Fruit indehiscent, becoming more or less drupaceous, exocarp fleshy or leathery, endocarp crustaceous or bony; seeds usually solitary in each locule, ecarunculate, testa smooth; endosperm copious; embryo straight, cotyledons broad. (Including *Cyclostemon* and *Hemicyclia.*) TYPE SPECIES: *D. glauca* Vahl. (Name from Greek, *dryppa*, overripe olive, in allusion to the fruit of the type species.) — GUIANA PLUM, WHITE WOOD.

Perhaps 150 species of circumtropical distribution, the vast majority in the Old World. Originally founded on a West Indian species, *Drypetes* was restricted by Mueller (1866) to American taxa, while related Old World species were assigned to *Cyclostemon* and *Hemicyclia*. However, Pax and Hoffmann (1922) appear to have combined these taxa correctly into a single genus characterized by an indehiscent fruit with reduced seed number, abbreviated styles, and an intrastaminal male disc. Hurusawa (1954) has even combined *Putranjiva* and *Drypetes*, and it must be admitted that the former scarcely differs in any essential character, except its lack of an intrastaminal disc.

Approximately eight or nine species of *Drypetes* are known from the West Indies and Central America. Two, each belonging to a different section, have entered the United States. Representing sect. OLIGANDRAE Pax and Hoffm. is *D. lateriflora* (Sw.) Urb., which normally has only four stamens isomerous with a four-lobed calyx, and a two-locular ovary which develops into a thin-walled, subglobose, scarcely fleshy fruit. It is fairly common in hammocks throughout the Florida Keys and extends northward on the Atlantic coast of Florida as far as Brevard County. Since all the other species [6] of sect. OLIGANDRAE are restricted to the Old World (mainly Africa), the relationships of *D. lateriflora* provide an interesting problem. Further study may show that it should be relegated to a different section.

Section DRYPETES (§ *Hemicyclia* of Pax & Hoffmann), with 30–40 species, includes all the remaining American species of *Drypetes*, among them our other local species, *D. diversifolia* Krug & Urb. (including *D. keyensis* Krug & Urb.). This plant differs greatly from *D. lateriflora* in having a five-lobed calyx, eight to ten stamens, and a one-locular ovary which develops into an oblong drupe with thick exocarp and endocarp.

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[6] The only other American species placed in sect. OLIGANDRAE by Pax & Hoffmann is the imperfectly known Cuban *Drypetes triplinervia* Muell. Arg. (DC. Prodr. **15**(2): 456. 1866), which must be excluded from *Drypetes* because of its dehiscent fruit. It is properly classified as **Chascotheca triplinervia** (Muell. Arg.) Webster, **comb. nov.**

The species can ordinarily be easily distinguished in the vegetative state since *D. lateriflora* has thinner leaves which are abruptly pointed at the tip, whereas the leaves of *D. diversifolia* are thicker, more rigid, and mostly rounded to obtuse (or at least not abruptly narrowed) at the tip. Furthermore, *D. diversifolia* shows an interesting leaf polymorphism. Particularly on seedlings and sprout-shoots, the leaves may be conspicuously spinulose-serrate, contrasting greatly with the "normal" entire leaves; some individual branches of a mature tree with entire leaves may show the toothed kind. No such variation occurs in *D. lateriflora*, which always has entire leaves.

Longwood reports that *D. Brownii* Standl., bullhoof, of British Honduras produces strong, hard timber with some of the properties of English oak; it is used for railway ties, rafters, beams, and other heavy construction. No studies of the timber quality of the two Florida species have been reported, but it seems doubtful that they can ever be of any commercial value because of their small size in our area (trunks not over one foot in diameter). The dense wood of *Drypetes*, which makes it potentially valuable for lumber, is correlated with characteristics of considerable systematic interest. The vessels have scalariform perforations, xylem parenchyma is abundant, and fibers are thick-walled. Janssonius grouped *Drypetes* with the Old World genera *Aporosa* and *Baccaurea* on the basis of these characteristics, and Metcalfe and Chalk associated it with the "*Aporosa* type," from which it is divergent mainly in having rather narrow rays. Anatomically, *Drypetes* appears to be the most primitive of our taxa of Euphorbiaceae, and does not show any close relationship to other local genera of Phyllanthoideae except *Savia*.

Another indication of the taxonomic isolation of *Drypetes* within the Phyllanthoideae is the report by Mangenot & Mangenot of $2n = 40$ in an African species, *D. mottikoro* Leandri. Chromosome counts are unreported for any American species, but would be of unusual interest, since the one known count suggests a base number ($x = 10$) different from that in most other Phyllanthoideae, which have $x = 13$.

Palynologically, *Drypetes* appears to be heterogeneous, for Köhler has recognized two different pollen types within sect. Drypetes. The closely related genus *Putranjiva*, which Hurusawa has combined with *Drypetes*, has very similar pollen, and *Putranjiva Roxburghii* also has $2n = 40$ in agreement with the single count in *Drypetes*. Possibly connecting *Drypetes* with taxa in subtribe Andrachninae is *Lingelsheimia*, which Léonard has shown to differ from *Drypetes* by its capsular fruit. Perhaps the most interesting relationship is that of *Drypetes* with the Australian genera *Neoroepera* and *Petalostigma*, which have a similar habit but differ in their monoecious inflorescences, and especially in their pollen grains; because these are porate and echinulate, Köhler refers *Neoroepera* and *Petalostigma* to the subfamily Oldfieldioideae. Although Köhler regards their pollen as derived within the subfamily, the suggestive resemblance to *Drypetes* warrants further analysis, and it seems possible that *Drypetes* may be the closest surviving taxon to the ancestral stem of the Oldfieldioideae.

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Subtribe **Phyllanthinae** [Muell. Arg., "Phyllantheae"]

4. **Phyllanthus** Linnaeus, Sp. Pl. 2: 981. 1753; Gen. Pl. ed. 5. 422. 1754.

Trees, shrubs, or herbs; stems not succulent, often entirely glabrous; lateral axes in some taxa deciduous, subtended by scale-like leaves. Leaves alternate (spiral or distichous), stipulate, pinnately veined, entire and unlobed; petiole short. Plants monoecious or, less commonly, dioecious; inflorescences axillary, cymose, the cymes usually highly condensed and sometimes reduced to solitary flowers. Flowers apetalous; calyx synsepalous, of 4–6 imbricate or decussate lobes; disc usually evident, segmented or cupular. Male flower: disc extrastaminal, usually segmented; stamens (2)3–5[–15], filaments free or connate; anthers extrorse, dehiscing longitudinally or horizontally; pollen prolate to globose, 3- or 4-colporate [pancolporate or porate in some exotic taxa]; vestigial gynoecium absent [very rarely present]. Female flower: disc segmented or more often patelliform to cupular [rarely absent]; staminodia absent [very rarely present]; carpels usually 3 [rarely 2 or 4–12]; styles free or basally connate, more or less bifid [rarely entire], sometimes multifid; ovules 2 in each locule, hemitropous, nucellus usually exserted from exostome in contact with obturator; embryo sac normal (Polygonum) type. Fruit usually capsular, explosively dehiscent [less commonly baccate or drupaceous]; mericarps separating from a more or less persistent columella; seeds usually 2 in each locule [rarely only one maturing]; testa dry and usually thin [rarely thickened and bony], not ventrally invaginated; endosperm copious; embryo straight or slightly curved, cotyledons broader than and about as long as the radicle. (Including *Cicca* L., *Emblica* Gaertn., *Xylophylla* L.) LECTOTYPE SPECIES: *P. Niruri* L.; see Small in Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 453. 1913. (Name from

Greek, *phyllon*, leaf, and *anthos*, flower, in allusion to the production of flowers on specialized leaf-like lateral branches.)

Approximately 750 species may be assigned to this highly diversified genus which is predominantly represented in the Old World tropics. Over 200 species have been reported from America, mostly from Brazil and the West Indies. Less than a dozen attain temperate latitudes, and the genus is unknown in Europe and temperate Pacific America. In the southeastern United States, *Phyllanthus* is represented by eight native and two naturalized species belonging to five sections in three subgenera.

Subgenus ISOCLADUS Webster, which includes about 70 herbaceous species with alternate phyllotaxy and unspecialized ramification patterns, has three Southeastern species. Belonging to section PARAPHYLLANTHUS Muell. Arg. because of their spiral phyllotaxy and dissected floral disc are two closely related species, *Phyllanthus polygonoides* Nutt. ex Spreng., $2n = 16$, and *P. platylepis* Small. A mainly calciphilous plant of limestone regions in Texas and Oklahoma, *P. polygonoides* barely enters our area in prairies of western Louisiana. The very similar *P. platylepis*, which differs mainly in its more or less rhizomatous habit and larger fruits and seeds, is confined to a small region in the hammocks of northwestern Florida (Dixie and Taylor counties). It shows an even more striking resemblance to *P. Liebmannianus* Muell. Arg., of coastal swamps in Veracruz, Mexico. These three species appear to be the vicariant relicts of an ancestral population which probably had a much more nearly continuous distribution along the perimeter of the Gulf of Mexico during the late Tertiary.

The third species of subg. ISOCLADUS, *Phyllanthus caroliniensis* Walt., belongs to sect. LOXOPODIUM Webster by virtue of its distichous phyllotaxy and very short, geniculate fruiting pedicels. This, the most widespread American *Phyllanthus*, is remarkable in being one of the few Euphorbiaceae which is distributed from temperate holarctic regions, south through the tropics into temperate southern latitudes. In the Southeast it is represented by ssp. *caroliniensis*, with smooth stems and an entire or angled female disc, occurring throughout our area except in southern Florida, where it is replaced by ssp. *saxicola* (Small) Webster. The latter taxon, mainly West Indian, has established a beach-head on the mainland only in the Florida Keys and the Dade County pinelands. An extralimital taxon, ssp. *guianensis* (Kl.) Webster, has been shown to have $2n = 36$, so that at least two different basic chromosome numbers ($x = 8, 9$) appear to be present in subg. ISOCLADUS.

Subgenus KIRGANELIA (Juss.) Webster, a primarily Old World group, is represented by a single naturalized species, *Phyllanthus tenellus* Roxb., $2n = 26$. This plant native to Africa and the Mascarene Islands belongs to sect. PENTANDRA Webster,[7] which includes about ten herbaceous African

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[7] *Phyllanthus* sect. **Pentandra** Webster, sect. nov. Herbae monoicae annuae vel suffruticosae; ramificatione more sectionis *Phyllanthi*; pedicellis capillaribus; flore ♂ calycis lobis 5, disci segmentis distinctis; staminibus 5, liberis; granis pollinis

species with thin-walled capsular fruits, undilated style-branches, and three- or four-colporate pollen grains. The section is significant phylogenetically because most of its taxa have precisely the habit and appearance of species of subg. PHYLLANTHUS, from which they scarcely differ in anything more than the five-merous rather than three-merous androecium. Since *P. tenellus* is the only herbaceous diploid species with phyllanthoid branching, it and closely related taxa such as *P. capillaris* Schum. may be regarded as the nearest living equivalents of the taxa ancestral to subg. PHYLLANTHUS.

Apparently the earliest collection of *Phyllanthus tenellus* in the United States was made by Hunnewell in Orange County, Florida, in 1924. Since then, however, its spread appears to have been rapid, for it is now known from a considerable number of localities between Sumter County, South Carolina, and Key West. The plant is an aggressive greenhouse weed due to its rapid flowering and effective ballistic seed dispersal; it seems to show a decided preference for sandy soil, and hence is to be found almost ubiquitously in *Citrus* groves in parts of central Florida. Although it has often been confused with native species of subg. PHYLLANTHUS, it is easily distinguished by its five free stamens and long capillary fruiting pedicels.

Subgenus PHYLLANTHUS, which includes well over 100 species in both hemispheres, comprises herbaceous or suffruticose plants with only two or three stamens and specialized "phyllanthoid" branching; the leaves on the main stem are reduced to scales which subtend deciduous leafy floriferous branchlets. In the Southeast there are five species of this subgenus, two or three of them native. The only representative of sect. URINARIA Webster is *Phyllanthus Urinaria* L., $2n = 52$, a weed of Old World origin which has been introduced into a number of localities in the United States during the past 25 years. Although it spreads much less contagiously than *P. tenellus*, it has been found in Texas, Louisiana, and Alabama, and doubtless will be encountered in other Gulf states. While *P. Urinaria* is occasionally confused with taxa of the next section, it differs markedly in its verrucose ovary, sessile female flowers, hispidulous leaf margins, and transversely (rather than longitudinally) ribbed seeds.

Section PHYLLANTHUS includes our remaining native species of subg. PHYLLANTHUS, characterized by pedicellate flowers, smooth ovaries, and verruculose or longitudinally ribbed or striate seeds. Subsection NIRURI Webster, with stamens partially or entirely free, slender scale-leaves, and verruculose seeds, is represented in the United States only by a relict population of *Phyllanthus Niruri* L. in east-central Texas, and does not enter our area. Subsection SWARTZIANI Webster, comprising mostly annual plants with connate stamens, broader scale-leaves, and striate or ribbed seeds, includes four local species. *Phyllanthus amarus* Schum., $2n = 52$, the most abundant and widespread weed in the genus, is common in southern Florida (Dade and Monroe counties) and has been collected

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subglobosis 3- vel 4-colporatis; flore ♀ disco patelliforme, ovario loculis 3, stylis bifidis; fructo capsulare, seminibus asperulis. TYPUS: *Phyllanthus pentandrus* Schum.

as far north as Gadsden County. Because of its nearly ubiquitous distribution, it is impossible to be certain that this species is native to Florida. The closely related *P. abnormis* Baill., which is definitely native, stands extremely close to *P. amarus* morphologically, but can be distinguished by its larger seeds, four-parted male flowers, more deeply dissected female disc, and thicker, more reddish stems. Unlike *P. amarus*, it shows a distinct preference for sandy soils and has a strikingly disjunct range: the western population extends from northeastern Mexico and western Texas to near Houston, while the eastern population is confined to peninsular Florida, from Cedar Key to Dade County. At least one additional species of the subsection, *P. fraternus* Webster, has recently been discovered in Louisiana. It is also very similar in appearance to *P. amarus*, but differs in having the male and female flowers segregated at different axils (in *P. amarus* and *P. abnormis* a male flower is paired with a female at all distal axils on the flowering branchlet).

Subsection PENTAPHYLLI Webster, a West Indian taxon of about 13 or 14 species, characterized by the perennial rootstock and blackened indurate scale-leaves on the main stems, has only a single species in the Southeast: *Phyllanthus pentaphyllus* Wright ex Griseb., $2n = 52$. This is the most widespread species in the subsection, with populations extending from Florida and the Bahamas south to Guadeloupe and Curaçao. The Florida population belongs to ssp. *pentaphyllus* by virtue of its deeply lobed female disc, and it has been distinguished as var. *floridanus* Webster because of its primarily dioecious inflorescences (in contrast to the predominantly monoecious condition in var. *pentaphyllus* of the Bahamas and Cuba). The recent report of *P. pentaphyllus* from South Carolina is erroneous, as it was based on a mislabelled specimen; in the United States the species is confined to limestone areas (mainly pinelands) in Dade and Monroe counties, Florida.

Several other species of *Phyllanthus* have been reported from Florida, but these reports lack confirmation by specimens. Small cited the commonly cultivated *P. acidus* (L.) Skeels, of subg. CICCA (L.) Webster, from southern Florida, but there is thus far no evidence that it has become naturalized. Small also reported from Key West *P. epiphyllanthus* L., of subg. XYLOPHYLLA (L.) Pers. sect. XYLOPHYLLA, a taxon outstanding because of the branchlets transformed to phylloclades and with concomitant reduction of the leaves to scales. His identification was erroneous, for the specimen from Key West collected long ago by Blodgett, as well as Small's own collection made in 1921, represent *P. angustifolius* (Sw.) Sw., a species otherwise known only from Jamaica and the Cayman Islands. Since the regions closest to Key West (Cuba and the Bahamas) have only *P. epiphyllanthus*, it seems highly unlikely that *P. angustifolius* could have occurred on Key West as a native plant. Recent attempts to locate the species on Key West have been unsuccessful, and it seems most reasonable to conclude that *P. angustifolius*, which was widely planted in Caribbean gardens a century and more ago, became temporarily naturalized and then died out again.

The remarkable amplitude of variation in both vegetative and floral characteristics evident in *Phyllanthus* has led various investigators to propose over 50 segregate genera. However, it has not been demonstrated that the genus is polyphyletic as presently constituted, and there are few large groups of species within it which could be defined by clear-cut diagnostic features. Chromosomal, palynological, and gross morphological characters, although displaying a protean diversity, fail to show the sort of correlation on which segregate genera could easily be justified. For example, the periporate pollen grains of subg. XYLOPHYLLA are correlated with the specialized branching pattern, but in the American species placed in subg. BOTRYANTHUS Webster this type of pollen is associated with definitely nonphyllanthoid branching. Until additional compelling evidence is unearthed, therefore, it seems expedient to maintain the circumscription of *Phyllanthus* as established by Mueller and modified by Hooker (when he recognized *Glochidion* as a separate genus).

The subgeneric classification of *Phyllanthus* is based primarily on characters of branching pattern and pollen, in addition to the usual floral characteristics. In the vast majority of species, an unusual pattern of vegetative development occurs which has been designated as "phyllanthoid branching." In plants of this kind, the main axis produces ordinary leaves only at the first few nodes above the cotyledons; distal nodes have the leaves reduced to scale-like cataphylls subtending deciduous leafy floriferous axes. There is thus a striking division of labor among the portions of the axial system of the plant: permanent axes produce only scale-like leaves and branchlets (never flowers) and are capable of indefinite growth, whereas the lateral axes produce both the leafy and reproductive portions of the plant and are of more or less limited growth (although the terminal bud of the branchlet does not necessarily abort). In a relatively few species, including most of those of temperate regions, such as *P. polygonoides*, there is no such vegetative specialization; flowers and leaves may be produced indiscriminately on both main and lateral axes.

Pollen diversity reaches a development in *Phyllanthus* which among the angiosperms is perhaps rivalled only by that in *Polygonum*. In a rather large number of taxa, the pollen grains are of a relatively unspecialized type similar to those of more primitive genera of Phyllantheae such as *Flueggea* and *Securinega*: they are more or less prolate, reticulate, tricolporate, with a well-defined elliptical endocolpus. In a minority of species, mainly in herbaceous taxa of subgenera ISOCLADUS and PHYLLANTHUS, distinctly prolate tectate grains with either three or four colpi have evolved; such microspores somewhat resemble those found in *Antidesma* and related genera. In the woody taxa of subgenera KIRGANELIA and CICCA, on the other hand, occur small more or less globose grains with narrow marginate colpi (often confluent at the poles) and circular endocolpus. It appears that it is from this pollen type that the unusual periporate pollen grains of subg. XYLOPHYLLA have evolved.[8] It is interesting,

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[8] These microspores, designated as "synrugoidorate" by Erdtman because the pores are connected by marginate streaks (presumably homologous with the colpi

and probably significant, that the three-colporate syncolpate grains of subg. KIRGANELIA and CICCA occur in diploid species ($2n = 26$), whereas all known species with periporate grains are at the tetraploid level ($2n = 52$) or higher. Although polyploidy is not necessarily an indication of phylogenetic advancement, the correlation of chromosome number with pollen type and other morphological characters suggests that it does indicate advancement in *Phyllanthus.*

The cytological picture is not a simple and straightforward one, however, since more than one basic number occurs in the genus, and the correlation of karyotypes with morphologically definable taxa is at best imperfect. Until recently, it appeared that the taxa in subg. ISOCLADUS were very divergent from other subgenera in having basic numbers of $x = 8, 9$ instead of $x = 13$. Since these plants also had unspecialized branching patterns, in contrast to the phyllanthoid branching found in most of the other subgenera, it might seem that a rather good argument could be presented for the generic segregation of subg. ISOCLADUS, including our commonest local species, *P. caroliniensis.* This was not attempted, however, because the flowers in subg. ISOCLADUS are so typical for the genus that a segregate genus would be very difficult to characterize morphologically. Furthermore, Miller and Webster (1967) have reported $x = 9$ in *P. Niruri*, a species with typical phyllanthoid branching (and, in fact, the type species of the taxon including plants with this branching pattern). Although cytological data are still more scanty than one might wish, it now appears that in at least two unrelated lines the basic chromosome numbers of $x = 8, 9$ have been derived by reduction from the prevailing chromosome complement of $x = 13$. This bimodality of chromosome number in *Phyllanthus* appears to be partly explicable on the hypothesis that evolution of the herbaceous habit proceeds in association with a reduction in chromosome number. However, this appears to hold only for species extending into or restricted to temperate regions; tropical herbaceous weeds such as *P. amarus* and *P. Urinaria* show a precisely contrary tendency towards (euploid) polyploidy. Cytological examination of a considerably larger number of herbaceous species will be necessary (and even then possibly not sufficient) to resolve this curious and puzzling picture.

Within the tribe Phyllantheae, *Phyllanthus* is rather well characterized by its apetalous flowers (the male without a rudimentary gynoecium), a distinct floral disc, gynoecia of mostly three carpels with bifid styles, and hemitropous seeds which are not ventrally invaginated. Subgenus CICCA, which has been treated as a separate genus by a number of workers, is indeed divergent in the usually indehiscent fruit and often in lacking a floral disc. However, its species have typical phyllanthoid branching and are so similar to certain taxa of subg. KIRGANELIA that a generic segrega-

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in subg. KIRGANELIA), possibly evolved as a result of increase in number of colpi in a syncolpate type of pollen grain; mechanical considerations apparently preclude the colpi in syncolpate grains from meeting at the poles if more than three colpi are present.

tion seems neither convenient nor necessary. The closest genus to *Phyllanthus* is the Old World *Glochidion*, which technically differs in its undivided styles and ventrally invaginate seeds. Among the numerous Australian taxa of *Phyllanthus* subg. GOMPHIDIUM [9] are some of uncertain generic status, but it seems probable that additional study will make it possible to define the boundary between the two genera more sharply. It seems fairly clear that *Glochidion* and the smaller Old World genera *Breynia*, *Sauropus*, and *Synostemon* have arisen from *Phyllanthus* subg. KIRGANELIA by loss of floral disc and specialization of seeds, styles, and male perianth. All of these genera together make up the subtribe Phyllanthinae, sensu stricto.

In comparison with many other genera of Euphorbiaceae, *Phyllanthus* includes relatively few species of economic importance; no latex or seed oils, such as are known in the Crotonoideae, occur. *Phyllanthus Emblica* L., a tree with branchlets imitating those of Leguminosae with small leaflets, is an important source of tannin and vitamin C; it is cultivated in the Miami area as an ornamental. Of some potential importance, chemotaxonomically, if not economically, are the alkaloids reported from various species of *Flueggea* and *Margaritaria*, two genera rather closely related to *Phyllanthus*. At least 10 different alkaloids are known at present (Hegnauer), and investigation of the less specialized taxa of *Phyllanthus* may produce data of interest in assessing both intra- and intergeneric relationships. Saponins are known in a number of tropical species of *Phyllanthus*, and may be the active principle in the use of foliage of various species as fish-poisons; South American species of subg. CONAMI appear to be outstanding in this regard. A few species of *Phyllanthus* have some promise as ornamentals in tropical and subtropical gardens. The most popular are probably the xylophyllas, various phylloclade-bearing species of sect. XYLOPHYLLA which have some interest as botanical curiosities. The most common greenhouse xylophylla, *P.* × *elongatus* (Jacq.) Steud., is apparently a hybrid between *P. angustifolius* and *P. epiphyllanthus*. In outdoor gardens in southern Florida, on the other hand, it is the parental species which are commonly grown, and the hybrid appears to be rare.

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Subfam. EUPHORBIOIDEAE (Crotonoideae Pax)

Tribe CROTONEAE Dumort., "Crotonieae"

Subtribe **Jatrophinae** Griseb., "Jatropheae"

5. **Jatropha** Linnaeus, Sp. Pl. 2: 1006. 1753; Gen. Pl. ed. 5. 437. 1754.

Shrubs or small trees, or a few species herbaceous. Leaves alternate, stipulate (stipules often glandular), petioles short to longer than the blade, blades entire, toothed, or palmately lobed. Plants monoecious [rarely dioecious]; flowers in terminal, often long-stalked, dichasia, the lower flowers female, the distal ones male. Flowers with biseriate perianth; calyx synsepalous, 5-lobed, sepals imbricate or open in aestivation; petals 5, imbricate to contorted, free or coherent (but not truly connate). Male flower: disc [entire or] dissected; stamens 8–10, connate, anthers biverticellate; pollen globose, inaperturate, clavate; vestigial gynoecium absent. Female flower: disc cupular or pulviniform; carpels [2] 3 [rarely 4]; styles more or less connate at the base, bifid, the style-branches entire [bifid]; ovary glabrous or pubescent; ovules 1 in each locule, anatropous, nucellar beak conspicuous. Fruit capsular; mericarps crustaceous to woody; columella persistent. Seeds 1 in each locule, more or less ellipsoidal, testa crustaceous, carunculate; endosperm copious; embryo straight, cotyledons thin, broader and longer than the radicle. (Including *Adenoropium* Pohl, *Curcas* Adans., *Mozinna* Ortega.) TYPE SPECIES: *J. gossypiifolia* L.; see McVaugh, Bull. Torr. Bot. Club 71: 457. 1944. (Name from Greek, *iatros*, physician, and *phago*, to eat, in allusion to medicinal and edible properties of the seeds and roots.)

In the circumscription of Pax & Hoffmann and McVaugh, *Jatropha* includes 125–150 tropical species of very diverse habit; a majority (70–80) of these are American, but 40–50 occur in Africa. Because of the diversity within the genus and the confused concept held by Linnaeus and many subsequent workers, the literature is beset with both nomenclatural and taxonomic problems. Although *Cnidoscolus* has been retained within *Jatropha* as recently as the revision of 1910 by Pax, it is actually very distinct, as pointed out by McVaugh. Various segregate genera have been recognized by writers of local floras in the southeastern United States and elsewhere, but Miller & Webster have shown that there is no good evidence for doing so.

According to the treatment of McVaugh, the two Southeastern taxa of *Jatropha* belong to different sections. Representing sect. MACRANTHAE Pax, which is composed of species having a nonimbricate male calyx and glabrous reddish petals, is *J. multifida* L. This shrubby or arborescent species, easily recognized by its deeply divided leaves with 10 or more sharply toothed lobes, occurs from Mexico and the West Indies south to Brazil, and has been introduced into the Old World. Although no specimens have been seen, Small reported it from the Everglade Keys in Dade County, Florida, and it seems likely that the species may become extensively naturalized in extreme southern Florida, as it is very commonly cultivated there.

Our other species, *Jatropha gossypiifolia* L., has thus far been reported only from the island of Key West; but it seems probable that it, too, will become more widespread, at least in the Florida Keys, as it is extremely weedy in other areas of the Caribbean. It belongs (as type species) to sect. JATROPHA (§ *Adenorhopium* of McVaugh), a group characterized by having distinctly imbricate male calyx lobes, pubescent petals connivent into a short "tube," and seeds with prominently fimbriate caruncle. *Jatropha gossypiifolia* is easily distinguished from its local congener, *J. multifida*, by means of its broadly and more shallowly lobed leaves beset with many stalked glands. The single specimen seen of *J. gossypiifolia* from Key West would fit into var. *elegans* (Kl.) Muell. Arg. because of its glabrous leaves.

Miller and Webster have shown that five species of *Jatropha* investigated cytologically have $2n = 22$; the species are then presumably diploid, with $x = 11$. More recently, Miller & Webster have reported two additional counts, one of which (for *J. dioica* Sessé) represents a tetraploid chromosome complement ($2n = 44$). This cytological evidence strongly supports the taxonomic association of *Jatropha* with *Aleurites,* as proposed by Bentham, since the latter genus also has a base number of 11.

A number of other tropical species of *Jatropha* are cultivated in southern Florida and may be found as escapes. These include the very ornamental *J. integerrima* Jacq. (*J. hastata* Jacq., *J. pandurifolia* Andr.) with brilliant scarlet flowers; *J. Curcas* L., with yellowish-green flowers and somewhat fleshy fruits; and *J. podagrica* Hook., with succulent stems, peltate leaves, and small, red flowers.

Species of *Jatropha* are of some economic importance in the tropics, although not the basis for any major industry. The seeds of *J. Curcas* are valued for their purgative properties and for the oil which can be used in the manufacture of soap (Lanjouw, Wilbur). The seeds are dangerously poisonous when fresh, due to the presence of the alkaloid curcine; but when roasted they are edible and distinctly palatable. Other species, such as *J. multifida*, have seeds with somewhat similar properties.

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6. **Aleurites** G. Forster, Char. Gen. Pl. 111. *pl. 56*. 1776.

Deciduous [evergreen] trees; branches and leaves with indumentum of stellate and simple hairs. Leaves alternate, stipulate (but stipules caducous and mature leaves thus appearing exstipulate), long-petioled; blades entire or lobed, palmately veined, glandular at the base. Plants monoecious; flowers in terminal panicle-like cymes. Perianth biseriate: calyx calyptrate in bud, rupturing valvately into 2 or 3 lobes at anthesis; petals 5, large and showy, imbricate or contorted. Male flower: disc of 5 segments [entire]; stamens 8–10[–20], connate; anthers introrse [extrorse], dehiscing longitudinally; pollen globose, inaperturate, clavate; vestigial gynoecium absent. Female flower: disc dissected into 5 segments; carpels [2] 3–5; styles free, bifid; ovules 1 in each locule, anatropous. Fruit drupaceous, more or less tardily dehiscent. Seeds 1 in each locule, ecarunculate, testa thick and woody; endosperm copious, oily; embryo straight, cotyledons broad and palmately veined, much longer than the radicle. TYPE SPECIES: *A. triloba* G. Forst. = *A. moluccana* (L.) Willd. (Name from Greek, *aleurites*, floury, in allusion to the pale coating of pubescence on leaves and stems.) — CANDLE NUT, TUNG TREE.

A small but economically important genus of five or six species native to the Old World. The genus was widely separated from *Jatropha* in the treatment of Mueller but fairly closely associated with it by Bentham and by Pax. Evidence from cytological and palynological studies definitely favors the latter view (Erdtman, Miller & Webster).

In the southeastern United States *Aleurites Fordii* Hemsl., the tung oil tree, is extensively cultivated, and has become naturalized to a limited extent. Herbarium specimens have been seen from Florida and Louisiana, and Thorne has reported it from Georgia. The species belongs to sect. DRYANDRA (Thunb.) Muell. Arg., which comprises four eastern Asiatic species. The section is characterized by having an indumentum of bifurcate hairs, showy flowers with petals 1.5 cm. long or more, 3–5 carpels, and a more-or-less dehiscent fruit. *Aleurites Fordii*, the only deciduous species in the genus, is adapted to a more temperate climate than its congeners. It is native to forested regions in central and western China, extending as far north as Hupeh and Szechuan provinces. As grown in the United States, it is an ornamental tree in aspect somewhat resembling *Firmiana simplex* (L.) F. W. Wight (Sterculiaceae). The attractive flowers, appearing in early spring before the leaves are expanded, are white with pink veins.

Despite its great current economic importance, the tung tree was long confused with the Japanese wood-oil tree (*A. cordata* (Thunb.) R. Br. ex Steud.) and the Mu-yu tree (*A. montana* (Lour.) Wilson), of southern China and Viet Nam. Both these species, however, are evergreen trees adapted to tropical climates and have wrinkled fruits, rather than the smooth ones of *A. Fordii.*

According to Newell *et al.*, tung oil trees were first planted in the southeastern United States in 1906, and since then they have become extensively cultivated in Mississippi, Alabama, Georgia, and northern Florida. The oil, which is contained in the endosperm of the seed, is a valuable drying oil which is essential for the manufacture of the best waterproof varnishes. The seeds have drastic purgative properties similar to species of *Jatropha* and can cause severe poisoning if eaten raw; the plant may therefore have minor medicinal uses in addition to its value to the paint industry.

All of the other species of *Aleurites* can be grown in southern Florida (from Palm Beach County southward), but they are not seriously cultivated on a commercial scale. *Aleurites moluccana* (L.) Willd., candle nut or kukui nut, is cultivated all around the tropics; it can be grown as far north as Brevard County and may quite possibly become naturalized to some extent. The type (and perhaps only) species in sect. ALEURITES, it differs from the species previously discussed in having an indumentum of stellate hairs, smaller flowers (petals usually less than 1 cm. long), and indehiscent fruits of only two carpels.[10] Cytological evidence provided by Stockar shows that *A. moluccana* is a tetraploid, with $2n = 44$, whereas the four species of sect. DRYANDRA are all diploids, with $2n = 22$.

Some interesting experimental taxonomy of *Aleurites* has been accomplished (more or less inadvertently) by tung-oil breeders who have crossed *A. Fordii* with other species in an effort to obtain cultivars with improved disease resistance or a delayed flowering period (and thus less chance of frost damage). Merrill and Kilby report that crosses can be made readily between *A. Fordii* and *A. montana*, but that the F_1 hybrids are partially sterile. Unfortunately, most of their data involves the results of backcrosses, and neither they nor other workers have presented any sort of a

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[10] Airy Shaw has recently proposed (Kew Bull. **20**: 393–395. 1966) a narrow generic circumscription in which *Aleurites* would include only *A. moluccana* (and the probably synonymous *A. Remyi* Sherff), while *A. Fordii* and its relatives would be transferred to *Vernicia* Lour., and *A. trisperma* Blanco would belong to a new genus *Reutealis* Airy Shaw. If it were not for *A. trisperma,* a reasonable argument could be made for recognizing with generic status the taxonomic gap between the small-flowered, indehiscent-fruited *A. moluccana* and the larger-flowered, dehiscent-fruited species of more temperate areas. However, in flower size and indument, *A. trisperma* to some extent bridges the gap between the extremes within the genus; and all these species have in common similar leaves, calyptrate calyx, and large, ecarunculate, oily seeds. In my opinion, the propriety of these segregations must remain in doubt until the generic limits in this entire complex (including *Deutzianthus* Gagnep. et al.) are revised monographically.

summary of crossing results which would indicate the degree of reproductive incompatibility between the species.

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Subtribe **Manihotinae** Muell. Arg., "Manihoteae"

7. **Manihot** Miller, Gard. Dict. Abr. ed. 4. 1754.

Herbs or shrubs [rarely trees], often with tuberous roots, stems laticiferous. Leaves alternate, stipulate (stipules often very small), long-petioled; blades mostly palmately lobed, stipellate at the base but without distinct foliar glands. Plants monoecious; flowers in terminal, sometimes pseudo-axillary panicles, the female flowers on several lateral basal axes, the male flowers more or less racemose along the central axis. Perianth uniseriate (presumably petals missing), often petaloid; calyx lobes imbricate. Male flower: calyx synsepalous, more or less cyathiform; disc central, intrastaminal, 5-lobed, lobes more or less bifid; stamens 10, free, biseriate, the outer opposite the calyx-lobes; anthers introrse, dehiscing longitudinally; pollen globose, periporate, exine clavate; rudimentary gynoecium present or absent. Female flower: calyx synsepalous but more deeply lobed than the male; disc pulviniform, staminodia sometimes present as well; carpels 3; styles 3, connate below; stigmas dilated and lacerate or multifid; ovules 1 in each locule, anatropous. Fruit capsular, dehiscent, sometimes winged; columella dilated above, often persistent. Seeds smooth, caruncullate; seed coats thin and crustaceous; endosperm starchy; embryo with broad palmately veined cotyledons. LECTOTYPE SPECIES: *Jatropha Manihot* L. = *Manihot esculenta* Crantz; see Adanson, Fam. Pl. **2**: 356. 1763. (Name from *manioc,* aboriginal Indian word for the cassava plant.) — CASSAVA, TAPIOCA PLANT.

Over 150 species of *Manihot* are known, according to Pax and Hoffmann; the number may, however, prove to be considerably smaller than this when the genus is monographically revised. The majority of the species is native to Brazil, but a respectable concentration is present in Mexico, and two or three cross the border into the United States.

Although originally confounded with species of *Jatropha* by Linnaeus, *Manihot* is very distinct by virtue of its apetalous flowers, central male disc, and periporate pollen grains. The basic chromosome number of $n = 18$ (x probably $= 9$) rather than $x = 11$ in *Jatropha* also supports a rather wide taxonomic separation. Mueller's placement of the two genera in adjacent subtribes presents a reasonable picture of their affinity. As pointed out by Miller & Webster, the closest genus to *Manihot* appears to be *Cnidoscolus* (*q.v.*).

The tapioca plant, *Manihot esculenta* Crantz (*M. utilissima* Pohl), is cultivated in southern Florida, as elsewhere in the Caribbean area, and has been reported by Small (as *Jatropha Manihot* L.) to be naturalized in the Florida and Everglade Keys. Lakela & Craighead report it from Collier, Dade, and Monroe counties. One specimen (*Small,* Nov. 1904) from Dade County does seem to represent this species, so that the above records may well be correct. However, collections of naturalized *Manihot* north of extreme southern Florida probably do not represent the cassava plant, which is not sufficiently frost-resistant to overwinter in northern Florida. The record of *M. esculenta* cited by Thorne from Georgia is erroneous. His collection (*Thorne 5866*), as well as naturalized plants from northern Florida (e.g., *Godfrey 54844*), may tentatively be identified as *M. Grahamii* Hook. (*M. Tweedieana* Muell. Arg.), a species native to Paraguay and western Brazil.[11] The somewhat notched leaflets of these collections suggest *M. carthaginensis* (Jacq.) Muell. Arg., and at least one sheet has been so identified. However, that species has much smaller stipules, and the leaflets are distinctly lyrately lobed.

According to the classification of Pax, both of these naturalized species belong to sect. PARVIBRACTEATAE Pax, which includes about 35 to 40 mainly Brazilian species characterized by deeply lobed leaves and small, inconspicuous bracts. *Manihot Grahamii,* assigned to subsect. ELATAE Pax, may be recognized by its slender, attenuate-acuminate, laterally toothed stipules which become 1 cm. or more long, its large glabrous male

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[11] Croizat (1943) has reduced *M. Grahamii* to a synonym of *M. flabellifolia* Pohl, and he may be correct in doing so. However, the long, glabrous, toothed stipules and completely glabrous male calyx of the Georgia and Florida plants do not accord with Mueller's description of Pohl's species.

calyces (mostly 12–15 mm. long), thin leaves with (5–)7–10 abruptly acuminate lobes, and wingless capsules with relatively large seeds (7 mm. or more across). The true cassava plant, *M. esculenta,* belongs to subsect. UTILISSIMAE Pax because of its internally pubescent male calyx and deeply lobed leaves. It may be distinguished from *M. Grahamii* by its shorter stipules, smaller male calyces (less than 10 mm. long), thicker leaves with fewer (3–7) lobes which are gradually acuminate and paler beneath, and its distinctly wing-angled capsules with somewhat smaller seeds (mostly 6.5 mm. or less across).

Cytological studies on eight species of *Manihot* have demonstrated a uniform chromosome number of $2n = 36$, except that one accession of *M. esculenta* was tetraploid ($2n = 72$). Actually, the genus may be basically tetraploid, since $x = 9$, in all probability. As pointed out by Miller & Webster, the cytological evidence alone suggests that *Manihot* is more closely related to *Cnidoscolus,* which also has $x = 9$, than to *Jatropha,* in which $x = 11$. Except for *Cnidoscolus, Manihot* does not appear to have any close relatives, and these two genera would appear to be the sole members of subtribe Manihotinae.

Manihot esculenta is a plant of great economic importance as a carbohydrate source in lowland tropical areas. Although cassava is most important as a starchy food in Latin America, it is also cultivated fairly intensively in Africa and to some extent in Asia as well. Despite the importance of the crop, the taxonomy of the cassava plant and closely related species is surprisingly imperfect. Rogers has shown that there is no morphological correlation between the two major "convariants" of manioc defined on root and stem characters with the "sweet" or "sour" nature of the roots. In sweet cultivars, the hydrocyanic acid is confined to the phelloderm of the root, but in the sour cultivars it occurs in the cortex as well, and the root is consequently dangerously poisonous unless boiled and mashed or strained. Rogers notes that sweet cultivars are found mainly west of the Andes and bitter to the east, and suggests that possibly cultivation began on the eastern slopes of the Andes.

Although of little present importance, arborescent species of *Manihot* were at one time an important source of rubber (Zimmermann, Polhamus). The most valuable species appears to have been the Ceará rubber tree, *M. Glaziovii* Muell. Arg., of sect. GLAZIOVIANAE Pax, which was extensively planted in East Africa prior to World War I. *Manihot dichotoma* Ule was also planted in Africa to a considerable extent. Although plants of *Manihot* could be cultivated in drier regions than *Hevea,* greater difficulty in tapping and obtaining high yields led to its drop from favor.

Because of the low protein content in cassava starch, it is an inferior carbohydrate source and a potential cause of malnutrition in areas where it is used heavily; consequently, efforts have been made to develop cultivars with enriched roots by crossing with other species (Bolhuis). These crossing programs, although purely utilitarian, are beginning to yield interesting data with regard to species relationships within *Manihot,* as noted by Rogers. Such species as the Guianian *M. saxicola* Lanj. and *M.*

melanobasis Muell. Arg. are easily crossed with *M. esculenta*; according to Bolhuis and Jennings, they may not even be distinct species. This evidence suggests that the taxonomic arrangement of Mueller, which was followed in general by Pax, in 1910, may be quite artificial, and that the infrageneric taxa of *Manihot* may have to be drastically revised.

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8. **Cnidoscolus** Pohl, Pl. Brasil. Ic. Descr. 1: 56. 1827, nom. cons. prop.

Herbs, shrubs, or trees; stems and leaves containing milky latex and armed with stinging hairs; pith septate. Leaves palmately [or pinnately] veined or lobed [sometimes parted into segments and almost compound]; petioles usually long, glandular at junction with blade; stipules entire to laciniate [rarely obsolete]. Plants monoecious; flowers in terminal (sometimes pseudo-axillary) dichasia, the female flowers at the lower (proximal) nodes, male at the upper (distal) nodes. Flowers apetalous; calyx more or less petaloid, usually white. Male flower: calyx synsepalous; calyx lobes imbricate; disc annular; stamens 8–10[–25], the outer free and inner connate [or all connate]; pollen globose, periporate, clavate; staminal column without terminal filiform staminodia [these present in some exotic taxa]. Female flower: calyx aposepalous; sepals deciduous [synsepalous in some species]; disc annular, sometimes associated with staminodia; carpels 3 [rarely 5]; styles more or less free, several times bifid or laciniate [rarely once bifid], sometimes apically dilated; ovule 1 in each locule, anatropous. Fruit capsular [rarely drupaceous]; columella slender. Seeds 1 in each locule, carunculate; endosperm starchy; embryo straight, with broad cotyledons longer than the radicle. (*Bivonea* Raf.) LECTOTYPE SPECIES: *C. hamosus* Pohl; see Small in Britton and Brown, Illus. Fl. No. U. S. ed. 2. 2: 462. 1913. (Name most appropriately derived from Greek, *cnide*, nettle, and *skolos*, thorn, in allusion to the stinging properties of the plants.) — STINGING NETTLE, BULL-NETTLE.

This distinctive genus of about 50 American species has long been confused with *Jatropha*, due to the influence of Mueller, who so treated it. However, McVaugh (1944) pointed out its distinguishing characteristics

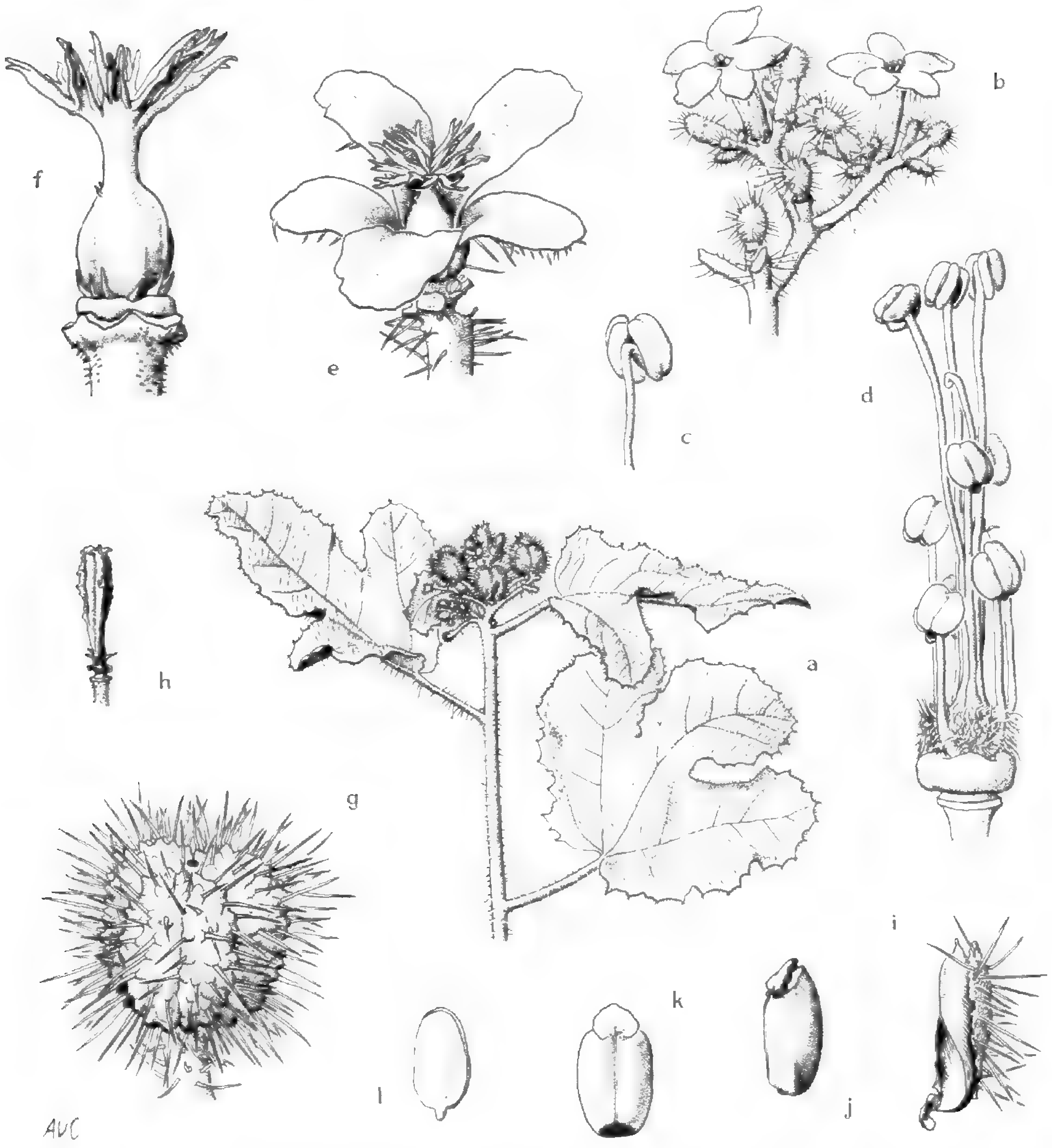

FIG. 1. **Cnidoscolus.** a–l, *C. stimulosus:* a, portion of flowering and fruiting plant, × ½; b, part of cymose inflorescence with two young fruits, two male flowers, and buds, × 1; c, stamen from unopened bud to show attachment of anther, × 6; d, androecium after anthesis, showing disc, ten stamens, and staminode, × 6; e, female flower, with adjacent male buds removed — note quincuncial aestivation, × 6; f, gynoecium with disc and staminodia, × 6; g, nearly mature fruit, × 2; h, columella after dehiscence of schizocarp, × 2; **i, one valve of schizocarp after dehiscence, showing bony endocarp,** × 2; j, k, lateral and adaxial surfaces of seed with caruncle, × 2; l, embryo, × 2.

and correctly insisted that it is very distinct from *Jatropha.* Miller & Webster subsequently showed that evidence from petiolar anatomy, pollen morphology and chromosome counts agrees and furthermore suggests that *Cnidoscolus* is much more closely related to *Manihot.* Baillon long ago noted this relationship which has been generally ignored by later workers.

Cnidoscolus clearly differs from *Jatropha* in its uniseriate perianth, stinging hairs, petiolar glands, laciniate style tips, septate pith, and other characters (McVaugh). Baillon noted that, although *Cnidoscolus* was much closer to *Manihot*, it differed in its free stamens and extrastaminal disc. The interesting South American *C. urnigerus* (Pax) Pax appears to be partly transitional between the two genera, since it has free stamens as in *Manihot* but the extrastaminal disc and stinging hairs of *Cnidoscolus*. There can now be little doubt that *Cnidoscolus* is more closely related to *Manihot* than to any other genus in the family, as is indicated in this treatment by the association of the two genera in the subtribe Manihotinae.

In our area *Cnidoscolus* is represented by two species belonging to sect. JUSSIEUIA (Houst.) Pax, which, in the circumscription proposed by McVaugh, is characterized by distinct outer filaments (but see *C. texanus*) and small multiple petiolar glands. Our representatives belong to the subsect. URENTES (Pax) Pax & Hoffm., a small group of five more or less herbaceous species which have the inner stamens united, and styles 2–3 times bifid. The only other representative of sect. JUSSIEUIA, the aberrant *C. urnigerus*, differs strongly in its completely distinct filaments and simply bifid styles, and perhaps should be referred to a different section. *Cnidoscolus stimulosus* (Michx.) Engelm. & Gray is widespread in dry, often sandy areas along the Coastal Plain from southeastern Virginia to the Florida Keys and west to Mississippi and eastern Louisiana; it is not recorded west of the Mississippi River in Louisiana. It may be recognized by its small male flowers (tube under 1 cm. long) with glabrous tube and small seeds (under 9 mm. long). Our other species, *Cnidoscolus texanus* (Muell. Arg.) Small, differs in being a much coarser and more viciously stinging plant with larger stipules, male flowers (tube 1–2 cm. or more, spinose), and seeds (mostly 12–15 mm. long). The androecium of *C. texanus* also differs in having the outer whorl of stamens connate below, so that the species does not agree with the sectional character. It is a characteristically Texan species of limestone areas, but it enters our range in southwestern Arkansas and western Louisiana. A gap of about 150 miles separates its easternmost station in Rapides Parish, Louisiana, from the westernmost known locality of *C. stimulosus* in Washington Parish. The two species are "classical" vicariants, therefore, and may represent the collateral descendants of a widespread ancestral population on the pre-Pleistocene coastal plain.

Cytological observations (Miller & Webster) indicate a chromosome number of $2n = 36$ in both local species, suggesting that they are tetraploid if $x = 9$. The same chromosome number has been reported for four Mexican species (Miller & Webster), so the genus is cytologically homogeneous so far as is known, and its karyotype appears close to that of *Manihot*.

The relationships between our two species and the other taxa of sect. JUSSIEUIA remain to be worked out. Mueller included all of the taxa of subsect. URENTES except *C. texanus* in his inclusive *Jatropha urens*.[12] As

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[12] A complicating factor in the taxonomy of the *C. urens* group is the typification of *C. urens* (L.) Arthur. Mueller (1866) correctly pointed out that the specimen in the Linnaean Herbarium is not the common weedy plant but rather a very different

noted by McVaugh, however, both *C. stimulosus* and *C. texanus* seem to be sufficiently distinct species, whatever the disposition of the Brazilian taxa of the complex.

It is perhaps not too surprising, in view of its relationship with *Hevea* and *Manihot*, that *Cnidoscolus* also includes species with a high rubber content in the latex. At least two arborescent Mexican species, *C. elasticus* Lundell and *C. tepiquensis* (Cost. & Gall.) Lundell, the "chilte rojo" and "chilte blanco" of Mexicans, yield rubber somewhat resembling that of *Hevea* (McVaugh, Lundell). During World War II these were investigated as possible emergency sources of rubber, but the latex proved to have too high a resin content, and no commercial production of any importance was sustained. Since the war, some commercial exploitation has continued, for the latex provides a useful additive to other gutta-like gums (Williams).

The characteristic stinging hairs of *Cnidoscolus* have never been intensively studied, although Solereder and Lutz mentioned their resemblance to those of *Urtica*. The mechanism may be similar, as in both genera the unicellular hairs end in a minute spherical tip which breaks off to permit injection of the poison. In *Cnidoscolus* the size of the hairs and their distribution on parts of the plant, especially the flowers, varies considerably, although the fruit is usually quite spiny, even if the perianth is not. A few tropical species, especially *C. aconitifolius* (Mill.) Johnston and *C. chayamansa* McVaugh, have nearly unarmed leaves which are used as a vegetable and may prove to be a good source of vitamin C.

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species belonging to sect. CALYPTROSOLEN (i.e., *C. Kunthianus* (Muell. Arg.) Pax & Hoffm.). This specimen is so different, however, from the illustrations of Commelin, Marcgrav, and Plukenet cited by Linnaeus that it is hardly desirable to designate it as the type. The Commelin illustration accords rather well with the plant later described by Pohl as *C. Marcgravii*, so that it may perhaps serve to typify the species. In that event, *C. urens* (*sensu stricto*) is to be interpreted as a Brazilian plant similar to *C. stimulosus*, but differing, *inter alia*, in its closely pubescent leaves and differently shaped seeds (more compressed, notched at the base, and with a smaller caruncle).

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Subtribe **Crotoninae** Benth., "Eucrotoneae"

9. **Croton** Linnaeus, Sp. Pl. 2: 1004. 1753; Gen. Pl. ed. 5. 436. 1754.

Herbs, shrubs [or trees]; stems often with colored or resinous sap but not with milky latex; indumentum at least in part of branched or lepidote trichomes. Leaves alternate, sometimes crowded and subopposite or pseudo-whorled, stipulate (stipules sometimes obsolete), pinnately or palmately veined or sometimes lobed; petioles sometimes with distinct glands at junction with blade. Plants monoecious or (in a minority of species) dioecious; flowers in usually bisexual spiciform racemes or thyrses, the female flowers solitary at lower (proximal) nodes, the male flowers 1 to several at upper nodes. Flowers with biseriate or uniseriate perianth: petals usually present in male flowers, reduced or absent in female flowers. Male flower: calyx 5-lobed (lobes rarely 4 or 6), lobes imbricate to valvate; disc entire or dissected into segments alternate with the petals; petals isomerous with calyx lobes, mostly about as long (rarely absent); stamens [3–]8–20[–400], free, filaments usually inflexed in bud; anthers extrorse in bud; pollen globose, inaperturate, clavate; vestigial gynoecium absent; receptacle often densely lanate. Female flower: calyx lobes (4) 5–7(–10), sometimes accrescent; disc annular or rarely dissected, sometimes with staminodia; carpels 3 (rarely 2); styles free or nearly so, once to several times bifid or bipartite into slender tips; ovules 1 in each locule, anatropous, nucellus elongated into a slender beak. Fruit capsular [rarely somewhat fleshy]; columella persistent, usually slender;

seeds 1 in each locule, terete to compressed, carunculate; testa smooth and dry, usually thin; endosperm copious; embryo straight, cotyledons broader than and as long as or longer than the radicle. LECTOTYPE SPECIES: *C. aromaticus* L.; chosen here.[13] (Name from Greek, *kroton*, tick, in allusion to the resemblance of the seed of *Ricinus* to the arachnid; arbitrarily applied to the present genus by Linnaeus to replace Tournefort's *Ricinoides*).

A very large genus comprising more than 600 species, according to Pax & Hoffmann, or around 1000 species, in the opinion of Croizat. It seems probable that the latter estimate will prove to be somewhat inflated when the genus is monographically revised. More than two-thirds of the species are American, and, of these, the majority are South American and West Indian; perhaps 75 or 80 species occur in mainland North America.

In the circumscription established by Mueller and followed by later workers, *Croton* is a very natural and rather isolated genus, without any close relatives other than such small satellite genera as *Crotonopsis* and *Eremocarpus*.[14] The characteristic large pollen grains with large, hexagonally arranged excrescences are much like those in other subtribes of the tribe Crotoneae. However, *Croton* is well characterized by the distinctive racemiform inflorescence and the male flowers with stamens inflexed in the bud. Furthermore, the stellate or lepidote pubescence and the non-milky sap of *Croton* permit its easy distinction from many other taxa of Crotonoideae.

The circumscription of the infrageneric taxa of *Croton* is as controversial as that of the genus is not. Bentham and various later workers sharply criticized the system of Mueller as highly artificial and unnatural; but it is most difficult to find clear-cut assemblages of species, and protracted acquaintance with the genus tends to induce greater sympathy for Mueller's adoption of an artificial arrangement. Johnston has sensibly placed the Texas species of *Croton* in informal groups, and Ferguson did not use any subgeneric designations at all. In the present treatment an attempt has been made to incorporate the results of recent anatomical and cytological investigations without introducing any more taxonomic changes than are absolutely necessary.

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[13] Small (in Britton and Brown, Illus. Fl. No. U. S. ed. 2, **2**: 454. 1913) selected *Croton Tiglium* L. as the type species, and he has been followed by recent workers. However, Klotzsch long ago removed that species as the type of a segregate genus *Tiglium*, and Baillon preserved Klotzsch's group as a section, while restricting sect. *Eucroton* to species with a valvate male calyx. The only species originally included in *Croton* by Linnaeus which have not been removed are *C. lacciferus* and *C. aromaticus*, so it would appear that one of these must be designated the lectotype. Since Geiseler combined the two species under the latter name, that one is chosen here.

[14] In agreement with the opinion of Macbride (Publ. Field Mus. Bot. **13**(3A): 57. 1951), *Croton* is here construed to include *Julocroton* Mart. (Beibl. Flora **1837**(2): 119. 1837). Despite the arguments of Croizat, *Julocroton* does not seem to be any more distinct than many other infrageneric groups of *Croton*, and it seems best treated as *Croton* sect. **Julocroton** (Mart.) Webster, comb. nov. No species of this section have as yet been reported from our area, although *C. argenteus* L. enters southern Texas and may possibly become established in peninsular Florida.

The 13 or 14 species of *Croton* in our area belong to seven sections. Section ANDRICHNIA Baill. (§ *Eluteria* Griseb.), the only section in which female flowers with well-developed petals occur, is represented by the interesting and rare *C. alabamensis* E. A. Sm. ex Chapm., which is known only from two populations occupying less than 100 acres in central Alabama (Bibb and Tuscaloosa counties). Farmer carefully studied the life history of the species, the reproductive biology of which is now the best known of any species of *Croton*. He found the Bibb County plants to be diploids ($2n = 32$), whereas the larger-leaved plants from the Warrior River area, in Tuscaloosa County, are tetraploids ($2n = 64$). The species does not appear to have any close relatives in North America, unless Croizat was correct in suggesting that *C. argyranthemus* is a depauperate member of this section.

Section CROTON, although by far the largest subgeneric group in the Muellerian sense (with over two-thirds of the species), is represented in our area by only three species. Plants of this section, which includes the "typical" crotons with smooth seeds, pubescent male receptacle, and pentamerous regular calyces, may be assigned to several subsections. Plants with stellate, rather than lepidote, indumentum and stamens relatively few in number (20 or less) belong in subsect. MEDEA (Kl.) Pax; our representatives are *C. linearis* Jacq. and *C. humilis* L., both tropical species confined to southern Florida. Subsection ARGYROCROTON Muell. Arg., including plants with lepidote indumentum, is represented by *C. argyranthemus* Michx., which occurs along the Coastal Plain from Georgia and Florida west into eastern and southern Texas.

Section ASTRAEA (Kl.) Baill. is in many ways the most distinctive group within *Croton* and has the best claims to generic status.[15] It is an entirely American group of less than 10 species, all of which except the local one, *C. lobatus* L., are confined to South America. *Croton lobatus* appears to be a newcomer to our flora, since it was first reported in 1965 by Lakela and Craighead from Dade County, Florida. It may be easily distinguished from other local species of *Croton* by its three-to-five-lobed leaves, glabrous male petals and receptacle, and cylindrical seeds. Despite the undoubted distinctiveness of *Astraea*, its species resemble some of those in the following section, and, except for the absence of oil cells mentioned by Froembling, there really seems to be no basis for excluding the group from *Croton*.

Section GEISELERIA (Kl.) Baill. (§ *Decarinium* of Mueller) is an entirely American group of about 30 species brought together by Mueller on the basis of the irregular female calyx which has two of the lobes greatly reduced. As Mueller himself admitted, the section may be unnatural; the species with lepidote leaves placed in series LAMPROCROTON Muell. Arg. should perhaps be referred to one or more other sections. Series GEISELERIA

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[15] Mueller's circumscription of sect. ASTRAEA was arbitrarily based on the single character of the male receptacle, and is consequently unnatural. However, if the two North American species (*C. humilis* and *C. panduriformis*) are excluded, the remainder of the section represents a very natural and distinctive group.

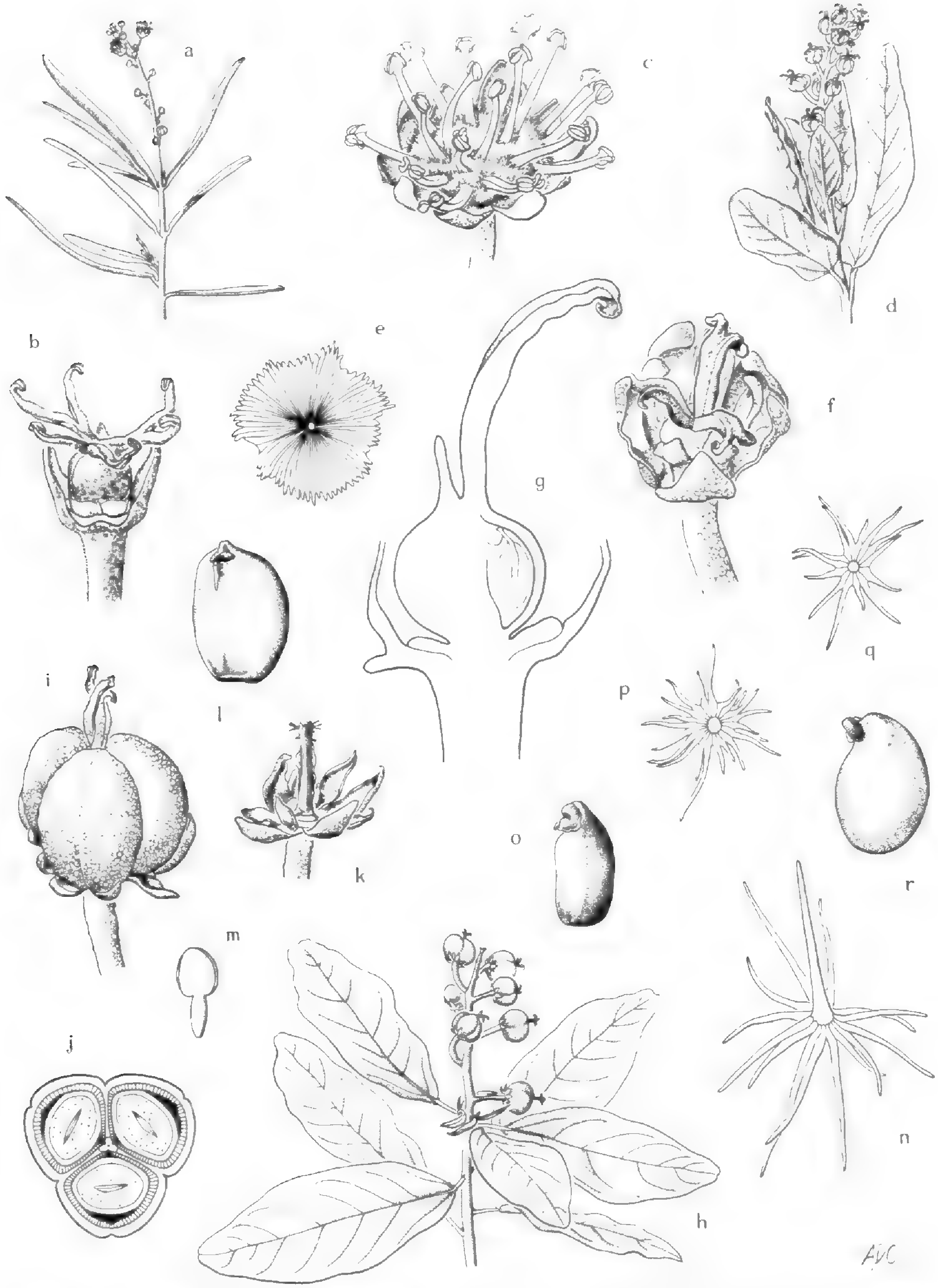

FIG. 2. **Croton.** a–b, *C. linearis:* a, branchlet of male plant, × ½; b, female flower, two sepals removed to show disc and staminodia, × 6. c–m, *C. alabamensis:* c, male flower, × 4; d, flowering branchlet of female plant, × ½; e, scale from leaf, × 50; f, female flower, × 8; g, same in diagrammatic vertical section to show disc and ovule with nucellus protruding from micropyle into obturator above ovule, × 10; h, branchlet with nearly mature fruit, × 1; i, mature schizocarp before dehiscence, × 2; j, same in diagrammatic cross section to show columella at center, seeds with embryo embedded in endosperm (stippled), and bony endocarps (hatched), × 2; k, persistent sepals, petals, and columella after dehiscence of fruit, × 2; l, seed, adaxial face, × 3; m, embryo, × 3.

(Kl.) Muell. Arg., comprising plants with stellate pubescence, is represented in our area by four taxa of controversial relationship. The commodest and best known, *C. glandulosus* L., occurs from Maryland to Iowa, south to western Texas and Florida, and beyond our limits into South America. It differs from the species so far mentioned in its sharply dentate leaves with large patelliform glands at the base of the blade, male flowers with only seven to nine stamens, and much sparser coat of stellate trichomes. In peninsular Florida occur a number of similar populations which have been recognized as separate species. Perhaps the most distinctive is *C. arenicola* Small, which includes plants with shorter and much more densely pubescent leaves; it was mistaken for the West Indian *C. betulinus* Vahl by Ferguson. *Croton floridanus* Ferg., on the other hand, is a name applied to plants with much less pubescence than usual. Further studies are needed to determine whether either of these taxa should be ranked as distinct species or whether they should take their place among the plethora of varieties of *C. glandulosus* already recognized by Mueller, Ferguson, and Croizat. A fourth species which seems to be quite distinct, *C. trinitatis* Millsp., is known in our area only from a single collection at Pensacola, but it may be expected in waste places farther south in Florida. It is easily distinguished from *C. glandulosus* by its broader, more coarsely toothed leaves.

A small, entirely North American group of four taxa, sect. HEPTALLON (Raf.) Muell. Arg., well represented in our area, differs little from sect. CROTON except for the calyx of usually six to ten lobes; otherwise, the stellate pubescence and twice bifid styles would relate it to herbaceous taxa of subsect. MEDEA. *Croton capitatus* Michx., as treated by Johnston, is a wide-ranging species with three varieties, two of which, vars. *capitatus* and *Lindheimeri* (Engelm. & Gray) Muell. Arg., occur scattered through most of our area, except southern Florida. Further study may show that these "varieties" should indeed be recognized as distinct species. *Croton Elliottii* Chapm., a seldom-collected plant of Georgia and northern Florida, is very similar but has narrower leaves and less deeply divided styles.

Section ANGELANDRA Muell. Arg. includes two annual North American species, both of which occur in our area. Mueller's "key" character of the male calyx "inaequaliter (3–) 5-partitus" was poorly chosen, since the male flowers are in fact not particularly zygomorphic. A more distinctive feature is provided by the rather highly reduced inflorescences often with a single female flower which becomes reflexed (except in an extralimital Texas population). *Croton monanthogynus* Michx., common and widespread from Maryland and Iowa, south to Georgia, Texas, and northern Mexico, was made the basis of the genus *Gynamblosis*, primarily because of its female flowers with only two carpels, one of which usually becomes abortive in fruit. However, *C. Lindheimerianus* Scheele, a closely related but coarser and more heavily pubescent species which enters our area in

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n, o, *C. glandulosus:* n, hair from leaf, × 50; o, seed, lateral view, × 5. p, q, *C. punctatus:* hairs from leaf, × 50. r, *C. argyranthemus:* seed, lateral view, × 5.

western Arkansas, has three carpels which develop into a three-seeded fruit; it thus bridges the gap between *C. monanthogynus* and more "typical" taxa of the genus. Johnston has provided detailed descriptions and distribution maps of these taxa as they occur in Texas.

Our last group, sect. DREPADENIUM (Raf.) Muell. Arg., comprises eight or nine American species, mostly of temperate North America (except for the aberrant *C. Eichleri* Muell. Arg. of Brazil). It is set apart from all the other sections by apetalous male flowers and a distinctive pale indumentum of trichomes often more or less intermediate between typical stellate hairs and scales. *Croton punctatus* Jacq. (*C. maritimus* Walt.), the most widespread species, common on sandy coastal beaches from Cape Hatteras, North Carolina, south throughout our area and beyond, differs from related taxa in its long-petioled leaves and monoecious inflorescences. *Croton texensis* (Kl.) Muell. Arg., a dioecious species with narrower, more sparsely pubescent leaves, is adventive in Alabama, according to Johnston. The chromosome number $2n = 14$, at variance with all other counts for *Croton*, has been reported from an extralimital species of this section, *C. californicus*; cytological observations on *C. punctatus* would therefore be of especial taxonomic interest.

Recent cytological studies on *Croton* suggest that the genus may prove to have a diversity of karyotype exceeded only by *Euphorbia* (Miller & Webster). Chromosome numbers are now reported from seven sections, and, although scarcely more than ten species have been sampled, it would appear that there are four base numbers represented: $x = 7$ in sect. DREPADENIUM; $x = 8$ in sects. ELEUTERIA, GEISELERIA, ANGELANDRA, and CROTON (subsect. MEDEA); $x = 9$ in sect. ASTRAEA (*C. lobatus*); and $x = 10$ in sects. CROTON (subsect. CYCLOSTIGMA), ASTRAEA, and HEPTALLON. These results suggest that additional chromosome studies, when correlated with anatomical data, will give a considerably better insight into relationships and provide the basis for a much more natural classification.

Froembling, in a rather comprehensive anatomical investigation, showed that there is a tremendous diversity within *Croton*, particularly in trichome conformation and in the distribution of secretory (oil-bearing and laticiferous) elements. Further detailed investigations of trichome types would appear warranted, since it may prove possible to correlate anatomical characters with systematic divisions better than Froembling was able to do. Especially interesting was Froembling's demonstration that many species of *Croton* lack the characteristic "latex"-bearing elements ("Ungegliederte Milchsaftröhren") and that the typical species of sect. ASTRAEA lack oil cells.

Compared with other genera of Crotoneae such as *Jatropha*, *Hevea*, and *Manihot*, there are few economically important species of *Croton*. The best known, doubtless, is the Asiatic species *C. Tiglium* L., the seeds of which furnish the well-known croton-oil, which possesses properties similar to castor oil or the seeds of *Jatropha Curcas*. At least one American species furnishes a similar substance in the stems which has been utilized under the name of Cascarilla Bark. Unfortunately, the botanical identity of the plant is uncertain due to long-standing confusion, but it appears probable that it is the West Indian *Croton Eluteria* (L.) Sw. It would not be surprising, however, if further investigation were to show that many other species of *Croton* are also valuable sources of similar substances.

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10. **Crotonopsis** Michaux, Fl. Bor.-Am. 2: 185. *pl. 46.* 1803.

Delicate annual herbs, stems and foliage with lepidote trichomes; latex absent. Leaves alternate, or subwhorled below branching-points; stipules obsolete; petioles short; blades entire and without basal glands. Plants monoecious; flowers in abbreviated spiciform racemes, bracts 1-flowered. Flowers with pentamerous calyces; calyx lobes imbricate. Male flowers: petals present, imbricate; disc dissected into 5 small segments; stamens 5, opposite the petals, free, filaments incurved in bud; pollen globose, inaperturate, clavate; gynoecium vestigial or absent. Female flower: calyx lobes 3–5, more or less unequal and some lobes often obsolete; disc inconspicuous, deeply lobed or divided; petals absent; carpel solitary; style twice or more bifid; ovary lepidote; ovule solitary, anatropous. Fruit dry, achene-like, indehiscent; seed solitary, not carunculate; seed coat smooth and thicker than carpel wall; endosperm copious; embryo straight, cotyledons broader than and about as long as the radicle. TYPE SPECIES: *C. linearis* Michx. (Name alluding to resemblance of the plant to herbaceous species of *Croton*.)

A genus of two species confined to eastern temperate North America. In branching pattern, leaves, and the characteristically reduced inflorescences, these plants somewhat resemble herbaceous species of *Croton*, especially *C. monanthogynus* Michx., of sect. ANGELANDRA. However, the indehiscent unicarpellate fruit with an ecarunculate seed is quite different from the dehiscent fruit with carunculate seeds of *C. monanthogynus*. While it would scarcely do any violence to nature to combine *Crotonopsis* with *Croton*, the group is sufficiently distinctive and well characterized to make it seem best to let it stand as an independent genus.

Although Gray and Chapman, as well as many other floristic writers, followed Pursh in construing the genus as containing but a single species, Pennell showed that there are two and gave a clear summary of their distinctions. *Crotonopsis linearis* Michx., recognizable by its narrow leaves with equal-rayed stellate hairs above, elongated 3–6-fruited spikes, and fruits with small pale scales, occurs from South Carolina, south to Florida, and west to Missouri and Texas, with a disjunct population in eastern Iowa and northwestern Illinois. *Crotonopsis elliptica* Willd., often confused with *C. linearis*, may ordinarily be distinguished by its relatively broad leaves which are more densely and coarsely hispid-stellate above (due to unequal development of one of the radii of the hairs); more abbreviated spikes with only one or two female flowers; and fruits with darker and larger scales. Furthermore, in *C. elliptica*, branching occurs closer to the base so that the plants often are lower and more spreading than the erect, more sparsely branching plants of *C. linearis*. *Crotonopsis* *elliptica* has a much broader range than its sister species, as it is known to extend from New Jersey south to northern Florida, and west to Texas, southeastern Kansas, and southern Illinois. According to reports in the literature (e.g., McVaugh; and on specimen labels) it is a characteristic species of bare sandstone or granitic outcrops, although it may occur in disturbed weedy habitats as well. In contrast, *C. linearis* is most often found in sandy soil in clearings or open woods.

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(*To be concluded*)

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THE GENERA OF EUPHORBIACEAE IN THE SOUTHEASTERN UNITED STATES *

GRADY L. WEBSTER

Tribe ACALYPHEAE Dumort.

Subtribe **Ditaxinae** Griseb., "Ditaxideae"

11. **Caperonia** St. Hilaire, Hist. Pl. Remarq. Brésil. 244. 1825.

Annual or perennial herbs, sometimes rhizomatous, often with glandular pubescence. Leaves alternate, undivided, petiolate, serrate, stipulate. Plants monoecious [rarely dioecious]; inflorescences spiciform, axillary, usually bisexual, with 1–5 basal female flowers and several distal male flowers; bracts uniflorous. Male flower: pedicel articulate; calyx usually 5-lobed, lobes valvate in the bud; petals 5, often unequal, basally adnate to the staminal column; disc absent; stamens 10, connate, anthers in 2 superposed whorls; pollen subglobose, reticulate, 6-colporate, germ pores large; vestigial gynoecium terminating the staminal column. Female flower: subsessile [rarely pedicellate]; calyx deeply 5-lobed, with 0–5 smaller supernumerary lobes; disc obsolete; carpels 3; styles 3, more or less deeply 3–7-lobed; ovary usually densely muricate; ovules solitary in each locule, anatropous, nucellus not elongated. Fruit capsular, more or less verrucose; columella slender, apically dilated. Seeds spheroidal, minutely foveolate, with narrow raphe; caruncle absent; endosperm copious; cotyledons broader than radicle. LECTOTYPE SPECIES: *C. castaneifolia* (L.) St. Hil.; see Britton and Wilson, Sci. Surv. Porto Rico **6**: 486. 1924. (Named in honor of Noël Capperon, 16th Century pharmacist of Orléans, France, the discoverer of *Fritillaria Meleagris* L.)

A genus of 35 to 40 species, about three-fourths of these native to tropical America and the remainder to Africa. Although placed near *Argythamnia* in most treatments, the plants look very different from that genus because of their serrate leaves with conspicuously parallel lateral veins and simple, often glandular, trichomes (as opposed to the bifurcate trichomes of *Argythamnia*).

A single introduced species, *Caperonia palustris* (L.) St. Hil., is now

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* Continued from volume 48, p. 361.

found in ditches and swampy areas in Texas, Louisiana, and Florida. It belongs to sect. CAPERONIA because of its annual habit, prickleless stems, and female calyx usually with one or more small supernumerary lobes. Another species, *C. castaneifolia* (L.) St. Hil., was reported from Florida by Small in 1933, apparently on the basis of misdetermined specimens of *C. palustris*. The two species are easily distinguished, as *C. palustris* has conspicuously glandular-pubescent stems, narrow lanceolate stipules, and petals about equalling the calyx in the male flower; whereas *C. castaneifolia* lacks glandular pubescence, has ovate stipules, and the male petals are exserted beyond the calyx. There are no authentic records of *C. castaneifolia* in the continental United States.

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PAX, F. Euphorbiaceae–Acalypheae–Chrozophorinae. Pflanzenreich IV. **147–VI** (Heft 57): 1–142. 1912. [*Caperonia*, 27–49.]

12. **Argythamnia** P. Browne, Civ. Nat. Hist. Jamaica 338. 1756.

Herbs or shrubs; stems and foliage with indumentum of bifurcate (malpighiaceous) hairs, tissues often stained with purplish pigment. Leaves alternate, petioles short, stipules small; blades entire or dentate, not glandular. Plants monoecious [rarely dioecious]; inflorescences short, racemiform, bisexual, with one to few basal female flowers; bracts small, uniflorous. Male flowers: calyx [3–]5-lobed, lobes valvate in the bud; petals 5, narrowed to a claw at base, more or less adnate to base of staminal column; disc dissected, segments opposite the calyx lobes; stamens 5–15, monadelphous; anthers 1–2(–3)-seriate; 1–3 filiform staminodia sometimes present atop staminal column; pollen oblate, tectate, tricolpate, bilaterally symmetrical; vestigial gynoecium absent. Female flower: calyx 5-parted, lobes imbricate; petals 5, imbricate, entire, sometimes reduced; disc more or less dissected into sometimes elongated segments; carpels 3; styles free or basally connate, bifid, style-branches more or less dilated at the tips; ovules 1 in each locule, anatropous, nucellus not elongated. Fruit capsular; columella persistent. Seeds subglobose, foveolate to reticulate, caruncle absent; endosperm present; embryo straight, cotyledons broader than the radicle. (Including *Ditaxis* Vahl.) TYPE SPECIES: *A. candicans* Sw. (Name from Greek, *argios*, white, and *thamnos*, shrub; the type species noted by Browne as having white bark.[16])

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[16] The generic name has been variously spelled *Argithamnia, Argothamnia*, and *Argyrothamnia*; but Bentham (Gen. Pl. **3**: 304) pointed out that the last name was based on Mueller's erroneous derivation from *argyros*, silver. As affirmed by Wheeler (Contr. Gray Herb. **127**: 55, 56. 1939), there seems to be no reason why the original spelling should not be followed.

An American genus of about 50 species, mostly tropical but some attaining temperate latitudes in the southern United States and in Argentina. The circumscription adopted here is approximately that of Bentham, who followed Mueller in including *Ditaxis* within *Argythamnia* but excluding *Speranskia*. Pax in 1912 adopted a radical view in which most of Mueller's sections (e.g., *Philyra, Chiropetalum*) were treated as genera. The pollen studies of Punt provide some support for Pax's view, since most of the taxa in question have easily distinguishable pollen types. *Argythamnia* is rather closely related to our other genus of Ditaxinae, *Caperonia*. However, it not only differs strikingly in its entire, triplinerved leaves, but is technically separable on the basis of its malpighiaceous hairs, male flowers without a rudimentary gynoecium, three- or four-colporate tectate pollen, and ornamented seeds.

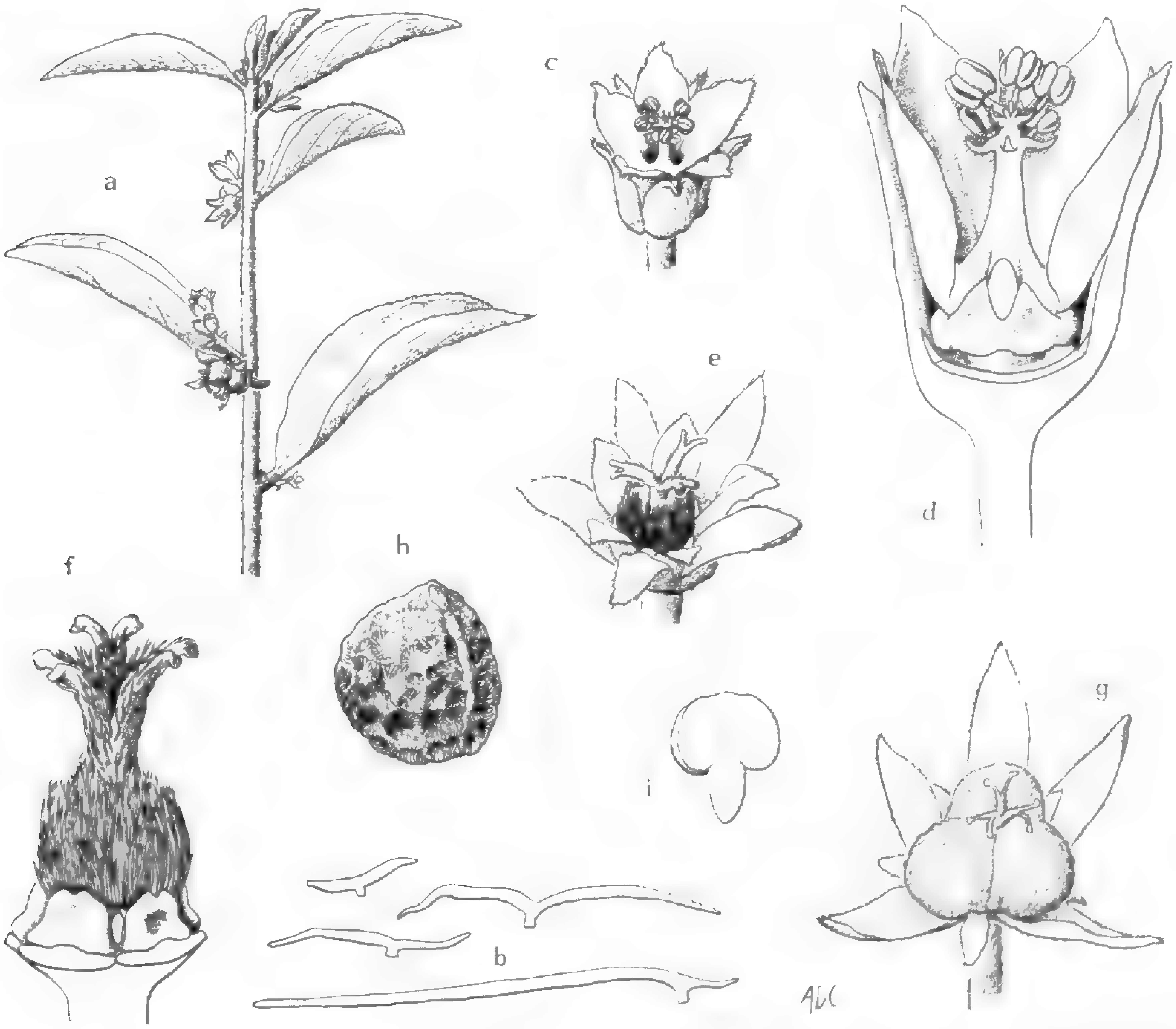

FIG. 3. **Argythamnia.** a–i, *A. Blodgettii:* a, tip of branchlet, × 1; b, malpighiaceous hairs, lateral view, detached from stem and gynoecium, × 100; c, male flower, × 6; d, same, with two sepals, one petal, and five anthers removed to show disc, insertion of petals, and arrangement of stamens in two whorls, the hairs omitted, × 12; e, female flower, × 6; f, same, with sepals and petals removed to show disc and gynoecium, × 12; g, nearly mature schizocarp, × 4; h, seed, × 8; i, embryo, × 8.

Our representatives of *Argythamnia* all belong to subg. DITAXIS (Vahl) Croizat, which includes the species with a usually biseriate androecium of approximately 10 stamens and bifid styles (the branches sometimes bilobed). Section SEROPHYTON (Benth.) Webster[17] is represented by two species which have been reported from Arkansas: *A. mercurialina* (Nutt.) Muell. Arg., with elongated inflorescences (over 5 cm. long), petals obsolete or wanting in the female flower, and large (4–5 mm.), wrinkled seeds; and *A. humilis* (Engelm. and Gray) Muell. Arg., with abbreviated inflorescences scarcely 1 cm. long, petals present in the female flower, and small (ca. 2 mm.), reticulate seeds. In Florida, sect. DITAXIS [(Vahl) Muell. Arg.] is represented by *A. Blodgettii* (Torr.) Chapm.; this species differs from members of the preceding section in having the petals adnate to the staminal column. Pax followed Mueller in assigning the Florida plants to *A. Fendleri* Muell. Arg. [= *A. argothamnoides* (Bert.) Ingram], a species otherwise known from South America. The plants involved do look much alike, but differ in various floral details (e. g., petals broader and staminodia ciliate-tipped in *A. Blodgettii*) and in the sculpturing of the seed-coat. Apparently, therefore, *A. Blodgettii* is a distinct species endemic to pine woods and hammocks on limestone in extreme southern peninsular Florida and the Florida Keys.

A single chromosome count of $n = 13$ has been recorded in *A. Brandegei* Millsp., a species of Mexico. Our local species have not yet been studied cytologically, but if they prove to have the same number, this would provide interesting evidence toward defining relationships in the subtribe Ditaxinae. So far counts in *Chrozophora* and *Caperonia* show $x = 11$, indicating a more distinct separation of *Argythamnia* than might otherwise be suspected.

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Subtribe **Mercurialinae** Pax

13. **Mercurialis** Linnaeus, Sp. Pl. 2: 1035. 1753; Gen. Pl. ed. 5. 457. 1754.

Annual [or perennial] herbs [sometimes rhizomatous]; leaves opposite, stipulate, petiolate, more or less pellucid-punctate, with crenate margins. Plants dioecious (rarely a few male flowers developed on female plants)

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[17] *Argythamnia* sect. **Serophyton** (Benth.) Webster, comb. nov. *Serophyton* Benth. Bot. Voy. Sulphur 52. 1844.

[or monoecious in some polyploid taxa]; flowers in modified thyrses, the male racemiform or spiciform, the female capituliform-pedunculate; female bracts 1-flowered, male several-flowered. Flowers apetalous. Male flower: calyx closed in bud, splitting into 3 valvate segments at anthesis; disc absent; stamens 8–15 (–20), free, filaments variously oriented in bud, anthers extrorse, anther-sacs subglobose, dehiscing transversely; pollen ellipsoidal, tectate, tricolporate, colpi narrowly operculate; vestigial gynoecium absent. Female flower: calyx lobes 3, imbricate; disc absent; 2 elongate staminodia usually present; carpels 2 (very rarely 3); styles free except at base, unlobed, conspicuously papillate; ovule 1 in each locule, anatropous, nucellus not elongated. Fruit capsular; valves echinate; columella slender. Seeds not compressed, testa rugose, caruncle present but small and delicate; endosperm present; cotyledons broader than and about equalling the radicle. LECTOTYPE SPECIES: *M. perennis* L.; see Small in Britton and Brown, Illus. Fl. No. U. S. ed. 2. **2**: 460. 1913. (Classical name used by Pliny to honor the god Mercury, the mythical discoverer of the therapeutic properties of the plant.) — MERCURY.

A small genus of seven or eight Old World species, mostly in the Mediterranean region but with one or two taxa in China, Japan, and Formosa. The genus is similar to *Acalypha* but lacks the highly specialized male flowers of that genus, and it is easily distinguished by its opposite leaves and small female bracts. In fact (cf. Pax, 1914), the closest relationships are probably with three small genera of Pax's series Mercurialiformes: *Seidelia* and *Leidesia*, from South Africa, and *Dysopsis*, from the southern Andes. The only species of *Mercurialis* naturalized in the United States is *M. annua* L., which has been reported from widely scattered localities within our area.

It is rather remarkable that a plant as undistinguished in appearance or properties (aside from a few dubious medical virtues) as *M. annua* has had such an outstanding botanical career. It was the first species experimented on by Camerarius (1691) in his demonstration of sexuality in plants; he simply isolated female plants and proved that seeds did not occur in the absence of fertilization. Actually, he may have been lucky in getting positive results, for exactly three centuries later Kerner made the claim that isolated female plants did set seed and that *M. annua* was therefore parthenogenetic. Further investigations showed that Kerner's observations were correct but his explanation wrong. Isolated female plants may indeed produce seeds, but Bitter and Malte showed that megasporogenesis and seed development is normal and that the apparent parthenogenetic fruits are actually produced as the result of fertilization by scattered reduced male flowers on otherwise strictly female plants; these small male flowers develop rapidly and are difficult to detect.

The remarkable variability in sexual expression in mercuries has attracted the interest of many investigators (e.g., Yampolsky), but for a long time no very convincing explanations could be offered. The key to the problem was found only recently, when Durand and Thomas discovered that different kinds of sexual expression were correlated with a remarkable polyploid series within *M. annua* (*sensu lato*). Durand has shown that within the Linnaean *M. annua* there are no less than seven levels of ploidy: from $2x$ ($2n = 16$) to $14x$ ($2n = 112$). Strictly dioecious plants are found only in the weedy diploid species, *M. annua* (*sensu stricto*), which is the form immigrant in the United States and elsewhere. In southern France is found a nonweedy diploid plant of dolomitic outcrops, *M. Huetii* Hanby, which may represent the ancestor of the weedy populations. Although treated by Mueller as a variety of *M. annua*, it is reproductively isolated and morphologically distinctive. Along the shores of the Mediterranean in both Europe and Africa occur a large number of polyploid populations which differ in not being perfectly dioecious. Durand has assigned the tetraploid and hexaploid races, which include both monoecious and unisexual plants, to *M. ambigua* L. f., while he has created a new name (invalid in the absence of a Latin description) for the plants at the octoploid level and higher. With these discoveries a considerable insight into population structure in the annual mercuries has been gained, and the stage is now set for a definitive taxonomic revision of the genus.

The work on *Mercurialis* has many interesting implications. Yampolsky, among others, has investigated the remarkable diversity of intersexual flowers in *Mercurialis*: curiously, completely functional hermaphroditic flowers appear to be absent or extremely rare. Thomas speculates that in *Mercurialis,* in which experiments have shown the female to be the heterogametic sex, the Y allosome for maleness functions by inhibiting production of female flowers. The conflicting results of previous investigators may then be at least partially explained by their failure to appreciate the complex interactions between genetic control of sexual expression and the lability of organogenesis as affected by environmental factors. It seems likely that *Mercurialis* may now become a classical organism for more profound studies of the genotype-phenotype relationship.

The reproductive biology of *Mercurialis* demands further study, especially in the field. Although earlier reports of parthenogenesis have been discredited, little is known of pollination in the wild, and reports are conflicting. The flowers have all the earmarks of anemophily (e.g., apetaly, long filaments, papillate styles) and are cited in many textbooks as a standard example of wind pollination. Wettstein described the remarkable mechanism for pollen dispersal, in which the entire male flower dehisces explosively and may be thrown as far as 20 cm. The process of pollen transfer might therefore be described as a combination of wind and "ballistic" pollination. On the other hand, some authors (e.g., Michaelis) have pointed out that the staminodia in the female flower function as nectaries, and the male plant gives off a distinctive odor; visits by flies, thrips, and even moths have been recorded. Weiss thought that *Mercurialis* was originally anemophilous and is in the process of becoming insect pollinated. However, in agreement with Pax & Hoffmann, it would seem that the opposite is more likely true. As in *Castanea,* the flowers of *Mercurialis* seem to have acquired many anemophilous characteristics, without however entirely losing the potentiality of a certain lesser amount of insect pollination.

Cytological studies have yielded much information of taxonomic and evolutionary interest, as already partly discussed for the *M. annua* complex. The base number in all species investigated of *Mercurialis* is definitely $x = 8$, which contrasts with the base numbers of 11 and 13 in subtribe Ditaxinae, and with $x = 10$ in *Acalypha,* which has been placed close to *Mercurialis* in many taxonomic treatments. So far no other morphologically similar genus with $x = 8$ has been detected. Gadella & Kliphuis have made a remarkable report that in *M. perennis* $2n = 64$ in the female and 66 in the male. If confirmed, this would apparently mean that the mechanism of sex inheritance is different from that found in *M. annua,* where there is no difference in number nor any morphologically detectable sex chromosomes.

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Subtribe **Acalyphinae** Griseb., "Acalypheae"

14. **Acalypha** Linnaeus, Sp. Pl. 2: 1003. 1753; Gen. Pl. ed. 5. 436. 1754.

Annual or perennial herbs or shrubs [rarely trees]; indumentum of simple hairs or glands. Leaves alternate, stipulate, petiolate, unlobed, often punctate. Plants monoecious or rarely dioecious; inflorescences spiciform [rarely paniculate], unisexual or bisexual, terminal or axillary; female flowers 1–3 per bract, bracts large and foliaceous, often lobed or parted [rarely small and entire]; male flowers several per bract, bracts very small. Flowers apetalous, disc absent. Male flowers subsessile; calyx valvate, parted into 4 segments; stamens 4–8, filaments free or connate at base; anther-sacs pendent, unilocular, more or less elongated and vermiform; pollen oblate-spheroidal, 3–5-pseudoporate, tectate, psilate; vestigial gynoecium absent. Female flowers sessile; calyx lobes 3[–5], imbricate; carpels 3 (rarely only 1 or 2); styles free or basally connate, laciniate or lacerate into filiform segments [rarely subentire]; ovary smooth, pubescent, or echinate; ovules 1 in each locule, anatropous, sometimes with a short nucellar beak; embryo sac tetrasporic. Fruit capsular, sometimes surrounded by the accrescent female bract. Seeds ovoid, carunculate, smooth to pitted or tuberculate; endosperm whitish; embryo straight, cotyledons reniform, broader than the radicle. LECTOTYPE SPECIES: *A. virginica* L.; see Small in Britton and Brown, Illus. Fl. No. U. S. ed. 2. **2:** 457. 1913. (Name from Greek, *akalos*, unattractive, and *aphe*, touch; Linnaeus's derivation obscure, as the plants he placed in the genus are not stinging.) [18]

A very natural genus of about 400 species, the majority American, and the largest concentration (about 100 species) in Mexico and Central America. The genus is isolated in the Euphorbiaceae, as the only other taxon in the subtribe Acalyphinae is the monotypic *Acalyphopsis*, based on an aberrant species from Celebes. Mueller and others have placed *Acalypha* close to *Mercurialis*, perhaps because of the similarity in habit and wind-pollinated flowers. However, the basic chromosome number and pollen grains are different in the two genera, and the resemblances may prove to be superficial. As suggested by Pax & Hoffmann, the relationship of *Acalypha* probably lies with some group within the subtribe Mercurialinae, but a more exact affinity cannot be pointed out at this time.

The infrageneric classification of *Acalypha* presented by Pax & Hoffmann was modelled closely on that of Mueller, except that the ranks of the subgeneric taxa were inflated so that no less than 40 sections were recognized in place of the two proposed by Mueller. Because of the narrow amplitude of divergence among the species of *Acalypha*, these "sections" of Pax and Hoffmann are really comparable to subsections or series in other genera of Euphorbiaceae, and they are so treated here.[19]

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[18] Pax & Hoffmann (Pflanzenreich **147-XVI**(Heft 85): 12. 1924) derive the generic name from *akalyphes*, not covering, in apparent allusion to the female bracts; but this is contradicted by Linnaeus's explicit derivation of the name (Philos. Bot. 183).

[19] It is difficult to reconcile the systems of infrageneric taxa erected by students of *Acalypha* with biological reality, on the one hand, and with the requirements of the present Code of Nomenclature on the other. Hurusawa (Jour. Fac. Sci. Univ. Tokyo Bot. **6:** 295–301. 1954) has inflated the subgeneric taxa to an even greater (and more unacceptable) extent than did Pax and Hoffmann. Mueller's division of the genus into two sections with many infrasectional taxa appears to reflect degrees of relationship better, but on the basis of his own explanation (Linnaea **34:** 2–4. 1865) his ultimate taxa designated by the sign "§" were not subsections but simply "Gruppe." Pax & Hoffmann unwarrantedly treated these groups as though Mueller had published them as sections. Technically, Mueller's names are almost all illegitimate under current rules of nomenclature, but, since his ultimate taxa appear to correspond rather closely to those currently accepted at the rank of "series," they are accepted at this rank here, and presumably are valid from the date of publication of this paper. The ten series occurring in the United States or mentioned in this discussion are then as follows:

(1) Series **Sclerolobae** Muell. Arg., ser. nov.; based on § *Sclerolobae* Muell. Arg. Linnaea **34:** 23. 1865. LECTOTYPE: *A. setosa* A. Rich.

(2) Series **Plumosae** Muell. Arg., ser. nov.; based on § *Plumosae* Muell. Arg. *loc. cit.* 49. LECTOTYPE: *A. alopecuroidea* Jacq.

(3) Series **Phleoideae** Muell. Arg., ser. nov.; based on § *Phleoideae* Muell. Arg. *loc. cit.* 46. LECTOTYPE: *A. phleoides* Cav.

(4) Series **Brachystachyae** Muell. Arg., ser. nov.; based on § *Brachystachyae* Muell. Arg. *loc. cit.* 42. LECTOTYPE: *A. brachystachya* Hornem.

Of the 17 species of *Acalypha* recorded from the United States, nine species in four series occur in our area. All of these plants belong to sect. ACALYPHA because of the sessile female flowers with large bracts: the few taxa in sect. LINOSTACHYS (Kl.) Muell. Arg., characterized by pedicellate female flowers subtended by small bracts, occur mostly in tropical America and do not reach our limits.

The basic division of the genus was made by Mueller largely on the basis of the relative position of the female and male flowers, which may be either proximal or distal on terminal or axillary unisexual or bisexual spikes. The group Pantogyne-Acrogyne of Mueller, distinguished by unisexual spikes with the female spike terminal, is represented in our area by ser. SCLEROLOBAE Muell. Arg. ex Webster, which is characterized by narrow female spikes and deeply lobed female bracts. The two local representatives are *A. ostryifolia* Ridd., with 13–17-lobed female bracts, occurring throughout our area; and *A. setosa* A. Rich., with mostly 7–8-lobed female bracts, restricted to the Coastal Plain at scattered localities from South Carolina to Florida and Louisiana. The latter, native to the West Indies and Central America, is strictly a weed in the southeastern United States and appears to have been introduced.

Mueller's group Polygynae-Acrogyne, in which the spikes are usually bisexual and terminal (often with axillary ones as well), is represented by two series, each with a single species. *Acalypha alopecuroides* Jacq., belonging to ser. PLUMOSAE Muell. Arg., and recognizable by its dense, thickly pubescent spikes, has been sparingly introduced into southern Louisiana from tropical America. *Acalypha chamaedrifolia* (Lam.) Muell. Arg., of ser. PHLEOIDEAE Muell. Arg., is a native species restricted in our area to extreme southern Florida and the Keys; its principal distribution is in the West Indies. It is easily distinguished from our other species by the perennial habit and small seeds (usually only about 1 mm. long).

Most of our local plants of *Acalypha* belong to Mueller's group Polygynae-Pleurogynae, in which the spikes are bisexual and strictly axillary. Our four or five species, the weedy members of the notorious *Acalypha virginica* complex, are all annuals referable to ser. BRACHYSTACHYAE Muell. Arg. because of their abbreviated spikes with few female bracts. Weatherby recognized 3 species in this group, one with two varieties;

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(5) Series **Boehmerioideae** Muell. Arg., ser. nov.; based on § *Boehmerioideae* Muell. Arg. DC. Prodr. **15**(2): 871. 1866. LECTOTYPE: *A. boehmerioides* Miq. [= *A. lanceolata* Willd.].

(6) Series **Repandae** Muell. Arg., ser. nov.; based on § *Repandae* Muell. Arg. DC. Prodr. **15**(2): 868. 1866. LECTOTYPE: *A. indica* L.

(7) Series **Dentatae** Muell. Arg., ser. nov.; based on § *Dentatae* Muell. Arg. Linnaea **34**: 17. 1865. LECTOTYPE: *A. mollis* HBK.

(8) Series **Monostachyae** Muell. Arg., ser. nov.; based on § *Monostachyae* Muell. Arg. *loc. cit.* 53. LECTOTYPE: *A. monostachya* Cav.

(9) Series **Palminerviae** Muell. Arg., ser. nov.; based on § *Palminervia* Muell. Arg. *loc. cit.* 9. LECTOTYPE: *A. macrostachya* HBK.

(10) Series **Caturoideae** (Pax & Hoffm.) Webster, stat. nov.; based on sect. *Caturoideae* Pax & Hoffm. Pflanzenreich **147-XVI**(Heft 85): 139. 1924. LECTOTYPE: *A. Caturus* Blume.

whereas L. Miller more recently has distinguished five species, one with two varieties. The group is taxonomically difficult, and Steyermark has described putative hybrids between three species in Missouri; but hybridization has still not been conclusively demonstrated.

Weatherby in a critical study of typification established that the name *A. virginica* L. is to be associated with the relatively narrow-leaved plant having female bracts cut mostly into 10–14 lanceolate lobes with long, spreading hairs. This species is common in Arkansas, Tennessee, and North Carolina but almost completely avoids the Coastal Plain. Far more abundant, widespread, and weedy is *A. rhomboidea* Raf., which has broader leaves and mostly 7–9-lobed female bracts that lack long hairs. It is common throughout the eastern United States and is the only species which crosses into Canada (in Ontario); in our area it is found both in the highlands and the Coastal Plain but does not enter peninsular Florida. Very similar to *A. rhomboidea* in appearance is *A. Deamii* (Weatherby) Ahles, a sibling species only recently discriminated. It has leaves and bracts much like those of *A. rhomboidea*, but differs in its two- rather than three-seeded fruit and in its larger seeds (2.2–3.2 mm. long *vs.* 1.2–2.0 mm. in *A. rhomboidea*). *Acalypha Deamii* seems to be restricted to more mesophytic sites and is known only from scattered localities in the Mississippi-Ohio River drainage, entering our area in Arkansas and Tennessee.

The most controversial populations in ser. BRACHYSTACHYAE include those to which the name *A. gracilens* Gray has been applied. These are plants with narrow leaves, the margins nearly or quite entire, and with much shallower lobing on the female bracts than is found in *A. rhomboidea* and related taxa.

A still unpublished analysis of this group made by L. Miller indicates that there are at least two major taxa involved. Throughout the Coastal Plain in our area, and in some inland localities as well, occurs ssp. *gracilens*, with leaves crenate-lanceolate and staminate spikes very short. To the west, this population is more or less replaced by an Ozarkian population which extends from central Texas into Oklahoma, Arkansas, and Missouri. Plants of this taxon, which differ in their narrower leaves, long male spikes, and, most strikingly, in having one-seeded instead of three-seeded capsules, may be designated as *A. gracilens* ssp. *monococca* (Engelm. ex Gray) Webster.[20] Lillian Miller regards this taxon as meriting specific rank, and it is possible that further investigation may substantiate her viewpoint. Field studies are needed in eastern Texas and Louisiana, where there are plants with the narrow leaves and long male spikes of ssp. *monococca* combined with the 3-seeded capsules of ssp. *gracilens*. These plants have been interpreted by Miller as an undescribed variety of *A. gracilens*, but the alternative explanation (followed here) is that this more or less intermediate population may represent a transition between the two subspecies. Additional studies of the natural populations may eventually provide a generally acceptable answer.

[20] *Acalypha gracilens* ssp. **monococca** (Engelm. ex Gray) Webster, stat. nov. *A. gracilens* var. *monococca* Engelm. ex Gray, Man. Bot. No. U.S. ed. 2. 408. 1856.

Cytological studies in *Acalypha* have so far led to conflicting results, since earlier workers such as Perry and Landes reported $x = 7$, whereas more recent reports (Kapil; Miller; Miller & Webster) suggest a base number of $x = 10$. Miller found $2n = 40$ in *A. virginica*, *A. Deamii*, and *A. monococca*, which suggests that at least the taxa of ser. BRACHYSTACHYAE are tetraploids. Miller & Webster found both tetraploid and octoploid levels among three tropical American species.

Perhaps the most interesting aspect of reproductive biology in *Acalypha* is its embryology. In contrast to most genera of Euphorbiaceae, only tetrasporic embryo sacs have been reported in *Acalypha*, and these are of several different kinds; reviews of embryo-sac diversity have been provided by Mukherjee and by Kapil, among others. According to Mukherjee the basic type of female gametophyte in *Acalypha* is the *Penaea* type, in which the mature embryo sac typically contains four egg-apparatuses (each of three cells) and four polar nuclei; this type has been reported in *A. rhomboidea* by Landes, as well as in several Asiatic species. In *A. indica* L. there are eight polar nuclei which fuse, and the four lateral groups are two-celled (Maheshwari & Johri). Finally, there is a report in *A. lanceolata* Willd. of the *Peperomia hispidula* type, in which there is one two-celled egg-apparatus and a $14n$ polar fusion-nucleus.

The taxonomic implications of this diversity are obscure, partly because of problems in identification. For example, Banerji reported the *Acalypha indica* type in *A. fallax* Muell. Arg.; that name, however, is a synonym of *A. lanceolata* Willd., of ser. BOEHMERIOIDEAE, in which Thatachar reported the *Peperomia hispidula* type. Furthermore, the results so far do not correlate well with the system of Pax & Hoffmann. In *A. malabarica* the embryo-sac is of the least specialized *Penaea* type, whereas in the closely related *A. lanceolata* the presumably most specialized *Peperomia hispidula* type has been reported. In a similar, although somewhat less disconcerting manner, *A. australis* L. and *A. indica* L. are reported to have the *Penaea* type and *A. indica* type respectively, even though they are closely related species of ser. REPANDAE. It may therefore be questioned whether the embryological results thus far throw any light on evolutionary relationships within the genus. However, further studies on a wider range of carefully identified taxa, especially on the less specialized representatives of sect. LINOSTACHYS, are needed before we can dismiss the embryological work as completely irrelevant taxonomically.

In marked contrast with most other sizeable genera of Euphorbiaceae, *Acalypha* is almost devoid of species with economic utility, although various species are cultivated as tropical ornamentals. *Acalypha Wilkesiana* Muell. Arg., a rather unattractive species of ser. PALMINERVIAE Muell. Arg., probably of Fijian origin, is grown presumably because of its variegated foliage. Much more striking is *A. hispida* Burm f., of ser. CATUROIDEAE (Pax & Hoffm.) Webster, possibly of Papuasian origin, which has attractive reddish female spikes. Both are grown in southern Florida, but there is no evidence that either has become naturalized.

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Subtribe **Plukenetiinae** Pax

15. **Tragia** Linnaeus, Sp. Pl. 2: 980. 1753; Gen. Pl. ed. 5. 421. 1754.

Perennial herbs, sometimes suffrutescent, decumbent to erect or twining; indumentum of uniseriate hairs, stalked glands, and stinging hairs. Leaves alternate, stipulate, petiolate or sessile, entire to more commonly toothed or lobed [rarely divided]. Plants monoecious; inflorescences racemiform, bisexual, opposite the leaves or terminal on lateral branches; female flowers at 1 to several proximal nodes, remaining nodes male; bracts small, subtending solitary flowers. Flowers apetalous, calyx 3–6-lobed, disc absent. Male flower: pedicel articulate; calyx lobes valvate; stamens 2–5 (–8) [–50]; filaments connate at least at base, anthers dehiscing longitudinally; pollen spheroidal, finely reticulate, tricolpate with colpi operculate, or inaperturate; rudimentary gynoecium small or absent. Female flower pedicellate; staminodia absent; carpels usually 3; styles 3, united at least at base, unlobed, often papillate; ovary hispid with stinging hairs; ovules 1 in each locule, anatropous, nucellus not beaked. Fruit capsular; columella persistent, with 3 apical interlocular points. Seeds subglobose, smooth or slightly roughened, not carunculate; endosperm whitish; cotyledons foliaceous, considerably broader than the terete radicle. LECTOTYPE SPECIES: *T. volubilis* L.; see Small in Britton and Brown, Illus. Fl. No. U.S. ed. 2. 2: 458. 1913. (Name in honor of the German herbalist Hieronymus Bock, 1498–1554, whose name was latinized as Tragius.)

A rather protean genus of more than 100 species found mostly in the tropical regions of Africa and Latin America, but with a few in warm-temperate areas. The intrageneric diversity of *Tragia* is indicated by Mueller's recognition of 12 sections, nine of which were retained by Pax & Hoffmann. Various segregates, such as *Ctenomeria*, have been recognized in the past, and the generic limits still present an interesting problem for study. Punt pointed out that the taxa in sect. BIA (Kl.) Muell. Arg. have nonaperturate pollen and suggested that this group possibly might warrant generic status. The discovery of a somewhat transitional kind of pollen in some species of the United States (Miller; Miller & Webster) favors the retention of *Bia* within *Tragia,* but the issue can still not be regarded as settled.

To some extent, the taxa of *Tragia* in the United States represent the outliers of mainly tropical groups, but there are several species which are primarily of eastern temperate North American origin. Both sections found in the United States are represented in the southeastern United States. Section TRAGIA, which includes those species with mainly 3–5 stamens and tricolpate pollen grains, is represented by 11 species in the United States. These include the weedy "nose-burns" characteristic of disturbed areas in Texas and adjacent states, which Johnston interpreted as all belonging to a single species, *T. nepetifolia* Cav. In the judgment of Miller & Webster, however, that species is restricted to Mexico and Arizona, while some of the taxa reduced to synonymy by Johnston are accepted as distinct species. Five species of sect. TRAGIA enter our area; the commonest is *T. urticifolia* Michx., found from North Carolina to Texas and Arkansas and barely entering northern Florida. It occurs mostly in the Piedmont and foothill regions and enters the Coastal Plain at only a few points. It is easily separated from related species by the long, persistent base of the staminate pedicel, which equals the bract (in other species it is much shorter); and it often has conspicuously hispidulous stems.

Two species which superficially resemble *T. urticifolia* enter our area from the west in Arkansas. *Tragia ramosa* Torr., which includes the majority of populations placed in *T. nepetifolia* by Johnston, is an extremely variable species which may, however, be generally recognized by its small female calyx lobes (shorter than the gynoecium) and its typically narrow (sometimes even linear) upper leaves. Often confused with it is *T. betonicifolia* Nutt., which has broader leaves like those of *T. urticifolia* and a larger female calyx with lobes which extend above the tips of the styles. More isolated both geographically and morphologically is *T. saxicola* Small, which has very slender, wiry stems and broad, sharply toothed leaves; the female flowers and seeds are smaller than those of *T. betonicifolia,* which it somewhat resembles. It is restricted to pine woods growing on limestone in the Florida Keys and the adjacent Florida mainland.

Occupying a rather divergent position among our species of *Tragia* is *T. cordata* Michx., a twining vine with large deeply cordate leaves and large seeds (more than 4 mm. long). Although widespread, it has a spotty distribution and seems nowhere very abundant; in our area it is known from a few localities in Arkansas and Louisiana, east to Tennessee, Georgia, and extreme northwestern Florida. It appears to be distinctly less weedy than other species and is probably restricted to relatively undisturbed tracts of deciduous forest.

Our two other species of *Tragia* constitute the section LEPTOBOTRYS (Baill.) Pax, which is nearly confined to our area. *Tragia urens* L., extending from southeastern Virginia to southern Florida and west to eastern Texas, is the most abundant representative of the genus on the Coastal Plain. Uniquely, it has terminal inflorescences (on lateral leafy twigs) and very characteristic leaves which are entire to irregularly lobed but never sharply toothed as in many congeners. The entire-leaved forms have been recognized as a distinct species *T. linearifolia* Ell., but such a separation seems unjustified. *Tragia Smallii* Shinners, although having the androecium and pollen of *T. urens*, differs strikingly in its broader, distinctly toothed leaves and in its inflorescences, which are opposite the leaves, as in all other temperate North American taxa of *Tragia*. It is primarily a species of the Gulf Coastal Plain, being found in open sandy places from central Florida west to extreme eastern Texas. In contrast with members of section TRAGIA both of these species have two stamens and pseudocolpate pollen.

Miller (1963) reported the first chromosome counts in the genus, and chromosome numbers are now known for six species. In both sect. TRAGIA and sect. LEPTOBOTRYS the basic number is apparently 11, as five species are tetraploids with $2n = 44$; an extralimital species, *Tragia amblyodonta* (Muell. Arg.) Pax & Hoffm., is apparently a decaploid, with $2n =$ ca. 110. Unfortunately, the significance of these counts cannot be evaluated at the generic level, since not a single other genus of this subtribe has been studied cytologically.

Pollinating mechanisms are still scarcely known in *Tragia*, but one curious feature of the reproductive biology has now been detected in several species. Ule long ago pointed out that some South American twining plants of *Tragia* (*T. volubilis* L. vel aff.) produce dimorphic fruits: in addition to the usual three-locular capsules there are some indehiscent one-seeded fruits which have two or three long horns. Miller found similar fruit dimorphism in the North American *T. brevispica* Engelm. & Gray; here the production of two kinds of fruit is an important taxonomic character, since it provides one of the main distinctions between that species and the very similar *T. ramosa*, which never seems to produce aberrant capsules. In *T. brevispica* the one-seeded, winged fruits develop from a three-locular ovary with normal ovules, but two of these abort and the outer part of the ovary wall develops unequally to produce the wings. Although Ule rather naively suggested that the winged fruits functioned to raise the plants' competitive ability through animal dispersal, the role the fruits actually play during the life cycle has not yet been elucidated. In a number of South American species horned or crested three-locular fruits occur, as illustrated for *T. Paxii* Lourt. & O'Don., so that a tendency to produce "aberrant" fruits appears to be widespread in the tropical American taxa of the genus.[21] The distinctive stinging hairs of *Tragia* were studied by Knoll and found to be of subepidermal origin. Their structure is unique and unlike the nettle-hairs of *Cnidoscolus* and various Urticaceae, because in *Tragia* the stinging element is a large, sharp-pointed crystal which represents one arm of a highly modified druse. Such a crystal type is found in no other family, and the other genera of Euphorbiaceae possessing it (e.g., *Cnesmosa*, *Acidoton*, and *Dalechampia*) are probably all related to *Tragia*.

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[21] Hauman, on the basis of observations in Argentina, claimed that the winged fruits observed by Ule were teratological (i.e., galls resulting from infestation by a cecidomyid larva). As far as the North American plants are concerned, however, this explanation is highly improbable, since microtome sections of a considerable number of fruits failed to disclose any evidence of insect attack, and winged fruits regularly developed on plants of *Tragia brevispica* grown in the greenhouse.

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Subtribe **Ricininae** Griseb., "Ricineae"

16. **Ricinus** Linnaeus, Sp. Pl. **2:** 1007. 1753; Gen. Pl. ed. 5. 437. 1754.

Shrub or tree (annual in temperate regions); twigs smooth, usually glaucous; sap watery. Leaves alternate; stipules fused into a caducous sheath, leaving a circumaxial scar; petiole elongated, with patelliform glands at least at base and at junction with blade; lamina peltate, palmately 7–11-lobed, lobes serrate. Plants monoecious; inflorescences paniculate, terminal (appearing opposite the leaves and axillary due to sympodial growth), proximal nodes with several-flowered male cymules, distal bisexual or female (the bisexual with female flowers central and males lateral); bracts papery, glandular at base. Flowers apetalous, disc absent. Male flower: calyx completely synsepalous in bud, valvately 3–5-partite at anthesis; anthers extremely numerous, up to 1000; filaments partially connate at base, irregularly branched; anthers introrse in the bud; pollen spheroidal, tectate (psilate), tricolporate, colpi narrow; rudimentary gynoecium absent. Female flower: calyx similar to the male, usually caducous; carpels 3; styles connate below, bifid, style-branches usually conspicuously papillate; ovary spinose-muricate; ovules 1 in each locule, anatropous, chalazal region vascularized, nucellus narrowed but not distinctly beaked. Fruit capsular, echinate (rarely smooth); columella wing-dilated above. Seeds somewhat compressed, smooth, usually mottled, carunculate; endosperm copious; embryo straight; cotyledons foliaceous, basally cordate, palmately veined, much longer and broader than the radicle. TYPE SPECIES: *R. communis* L. (Name said to come from the Latin word for tick, suggested by the appearance of the seed.) — CASTOR BEAN.

A genus of a single highly variable species native to Africa and perhaps to India. Mueller distinguished 15 "varieties" and a number of forms which are really cultivars; it is not clear (and probably never will be) whether the species ever showed geographic subspeciation. Because of the economic importance of the seeds, *Ricinus* has received considerable attention from botanists, and it has become a classical experimental plant during recent years. The seeds are valuable for their high content (50 per cent or more) of castor oil, which is a mixture of ricinoleic acid and smaller amounts of oleic, linoleic, and other fatty acids. The unique properties of ricinoleic acid, which thus far has not been isolated from any other plant, have led to the use of castor oil, not only as the familiar purgative, but in many industrial applications (e.g., in the manufacture of paints, inks, plastics, soaps, and linoleum). Almost all of the castor oil used in the United States today is imported, although the plant was grown as a crop

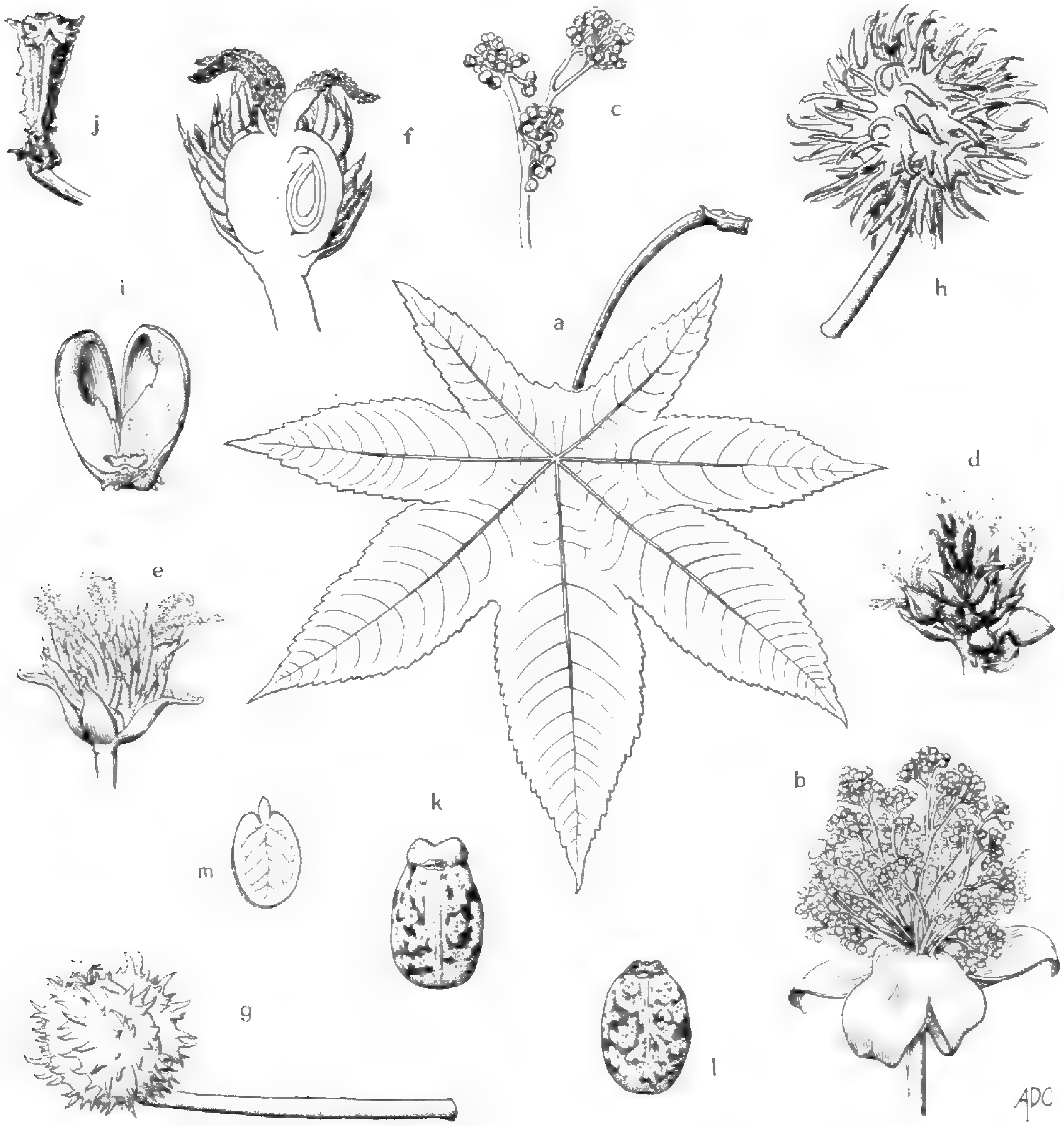

FIG. 4. **Ricinus**. a–m, *R. communis:* a, small leaf, × ½; b, male flower, × 2; c, detail of stamen fascicle, × 4; d, tip of inflorescence showing female flowers, × 1; e, female flower, × 2; f, same in semidiagrammatic vertical section — note two-integumented anatropous ovule with obturator reaching to micropyle, × 4; g, h, nearly mature fruits from two populations to show variation in fruit surface and pedicel length, × 1; i, carpel wall after dehiscence of schizocarp, × 1½; j, columella, × 1½; k, l, seed before and after drying of caruncle, × 1½; m, embryo oriented as in seed, × 1½.

in the Midwest during the 19th century, and the industry has revived to some extent at the present time. In our area, climatic conditions permit successful cultivation of *Ricinus* only in Arkansas and western Tennessee, as a serious fungal disease prevents it from being cultivated on the Gulf Coastal Plain. The plant is commonly grown as an ornamental, however, and escaped individuals may be expected throughout most of our range. In the tropical area of southern Florida the plant attains its normal wild expression and becomes a sizable tree very different in appearance from the usual garden herb.

It is well known that the seeds (specifically, the seed-coats) of *Ricinus* are extremely poisonous. This is due not to the alkaloid, *ricinine*, but rather to the phytotoxin, *ricin*, which is one of the most toxic compounds known: the minimum lethal dose by injection is only 0.001 mg. per kg. It is interesting that similar phytotoxins have been reported in the seeds of *Jatropha Curcas* and *Aleurites Fordii*, but our present inexact knowledge of the structure of these complex proteins does not permit placing much taxonomic significance on the distribution of the substances.

Various aspects of the morphology of *Ricinus* have been investigated, especially the remarkable androecium. Delpino called attention to the explosive dehiscence of the anthers, which is similar to that in some Urticaceae, and Steinbrinck and others have seen a resemblance between the *Ricinus* microsporophyll and that of pteridophytes; suggestions have even appeared that the *Ricinus* androecium is a mass of dichotomizing telomes! Such woolly speculations have been effectively discredited by Van der Pijl, but the fascicle-formation of the stamens still has not received a satisfactory explanation.

Various assertions of myrmecophily have been made for *Ricinus*, but the plant has not been sufficiently studied in the wild state, and the significance of the various observations is not clear. The extrafloral nectaries found on the leaves and bracts secrete noticeable quantities of nectar, and Reed has reported visits by ants. Gates has speculated that the caruncle on the seed is attractive to ants, but no observations of large tropical ants carrying off the seeds have been published. The flowers seem to be the most completely anemophilous of any Euphorbiaceae in our area, and, since the seeds are explosively dispersed, any role of animals in the reproductive cycle would appear to be quite hypothetical.

Considerable work has been done on the genetics of *Ricinus*, partly in the attempt to improve its characteristics as an economic plant. The tendency of the capsules to shatter, as in most other Euphorbiaceae, makes mechanical harvesting very difficult and has motivated geneticists to breed for slow-dehiscing fruits. Sex inheritance has also been worked on, although not to the same extent as in *Mercurialis*. Plants which are female in early ontogeny have been obtained, but these eventually produce male flowers, and truly dioecious strains of *Ricinus* are extremely rare, if they exist at all.

Jakob has found evidence of secondary association between two of the ten pairs of chromosomes. This might suggest that the chromosome complement was originally $x = 9$, but the cytological evidence is equivocal, and secondary association was not observed among the 10 chromosomes in haploid plants (Poole & Hadley).

Ricinus seems to be related to the Asiatic genus *Homonoia*, which was associated with it in the subtribe Ricininae by Pax & Hoffmann; *H. javensis* (Blume) Muell. Arg., in particular, has similar male and female flowers, but its habit is utterly different. The evidently wind-pollinated flowers and chromosome complement of $x = 10$ suggest a possible distant relationship to *Acalypha*. The lobed, glanduliferous leaves and large, foliaceous cotyledons might appear to suggest an affinity with *Jatropha*, but that seems negated by the differences in androecium, pollen, chromosome number, and many other characters.

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Tribe HIPPOMANEAE Bartl. ex Endl.

Subtribe **Hippomaninae** Muell. Arg.

17. **Sebastiania** Sprengel, Neue Entdeck. Pflanzenk. 2: 118. *pl. 3.* 1821.

Shrubs [or trees, rarely herbs]; twigs glabrous or with simple hairs [spinescent in some species]. Leaves alternate [very rarely opposite], stipulate; petiole short; blade undivided. Plants monoecious [rarely dioecious]; flowers in usually bisexual spikes which are terminal or (due to sympodial growth) opposite the leaves [rarely axillary]; female flowers solitary in axils of lower bracts, male flowers usually in clusters of 2 or 3 subtended by upper bracts; bracts biglandular at base. Flowers apetalous, disc absent. Male flower: calyx synsepalous, lobes usually 3 (2), subequal [sometimes distinctly unequal], imbricate; stamens [2 or] 3; filaments free or nearly so, anthers extrorse; pollen subglobose, tectate (psilate), tricolporate, 3-lobed in polar view; rudimentary gynoecium absent. Female flower subsessile; calyx 3-lobed, lobes imbricate, with minute adaxial processes at base; carpels 3 [rarely 2]; styles free or connate at base, entire; ovary smooth [sometimes muricate]; ovules 1 in each locule, anatropous. Fruit capsular; columella dilated above, usually persistent. Seeds subglobose [cylindric in some species], smooth [or roughened], carunculate; endosperm copious; embryo straight, cotyledons broader and longer than the radicle. TYPE SPECIES: *S. brasiliensis* Spreng. (Named in honor of Antonio Sebastiani, 1792–1831, Italian professor of botany.)

As circumscribed by Pax, a diversified genus of some 75 species, at least three-quarters of which are native to southern Brazil. Although Pax enumerated three species from the Old World, one of these (*S. inopinata*, from Africa) has been made the type of a segregate genus *Duvigneaudia* by Léonard, primarily on the basis of its drupaceous fruit and ecarunculate seeds. Three species from Indonesia (two described by Van Steenis) are of dubious affinity, and their possible relationship to *Duvigneaudia* needs to be examined. *Sebastiania Chamaelea* (L.) Muell. Arg., an herb found across the tropical belt from Africa to northern Australia, appears to be fairly closely related to the weedy American herb, *S. corniculata* (Vahl) Muell. Arg., and there is no reason to question its position in the genus. *Sebastiania* consequently has at least one gerontogean representative, but its remarkable paucity of development there remains unexplained.

Our only species, *Sebastiania fruticosa* (Bartr.) Fern. (*S. ligustrina* (Michx.) Muell. Arg.), is a shrub 3–4 m. high which is found in hardwood forests (often along streams) from North Carolina to Florida, west to eastern Texas. The species is the only representative of sect. STILLINGIOPSIS (Muell. Arg.) Webster,[22] which differs from sect. CNEMIDOSTACHYS (Mart.) Webster [23] in its ovoid seeds, smooth ovary, connate male sepals, and woodier habit. It is much closer to sect. SEBASTIANIA, which differs only in its reduced male calyx lobes and larger bracteal glands; the type species, *S. brasiliensis*, strongly resembles *S. fruticosa* in many respects.

A peculiarity which is shared by some other Hippomaneae is that *Sebastiania fruticosa* does not produce noticeably milky juice, even though laticifers are present (according to Herbert). The single chromosome count, $2n = 56$ (Perry), suggests that the species may be an octoploid on a base of seven. However, this report merits reinvestigation, since $x = 7$ has not been confirmed for any other genus of Hippomaneae.

Certain Mexican species of *Sebastiania* have attained a degree of botanical notoriety as the source of "Mexican jumping beans" ("semillas brincadores"). The two plants most often cited in this connection are *S. Pringlei* Wats. and *S. Palmeri* Rose; Pax (under the latter species) has reviewed the literature, which is more voluminous than the apparent triviality of the phenomenon would seem to warrant. Within a few years after Hooker provided the first botanical description in 1854, the cause of the erratic behavior of *Sebastiania* seeds was shown to be due to the activity of the larva of a microlepidopteran moth (*Laspeyresia saltitans*, Tortricidae). Similar "springenden Bohnen" have also been reported from other taxa of Hippomaneae (e.g., *Colliguaya odorifera* Mol., *Sapium biloculare* (Wats.) Pax), and in all instances (where known) the causative agent has proved to be a tortricid larva. Although little has appeared in the literature since the plethora of papers between 1890 and 1926, a number of questions remain to be resolved. The biological relationship

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[22] *Sebastiania* sect. **Stillingiopsis** (Muell. Arg.) Webster, comb. nov. *Gymnanthes* sect. *Stillingiopsis* Muell. Arg. Linnaea **32**: 96. 1863.

[23] *Sebastiania* sect. **Cnemidostachys** (Mart.) Webster, comb. nov. *Stillingia* sect. *Cnemidostachys* (Mart.) Baill. Étud. Gén. Euphorb. 515. 1858. *Cnemidostachys* Mart. Nov. Gen. Sp. **1**: 66. 1824.

between lepidopteran and plant has not been studied in sufficient detail (i.e., through entire life-cycles) and the classification of the taxa of both host and parasite is still imperfect. Mueller originally determined the infected Mexican plant as *Sebastiania Pavoniana* (Muell. Arg.) Muell. Arg., and it is possible that most of the various Mexican host plants may prove to be varieties of that species.

Generic limits in the tribe Hippomaneae have long been subject to controversy, and it is not certain that taxa such as *Sebastiania* can be maintained in their present circumscription when more data become available. Baillon, taking a broad view of generic limits, included *Sebastiania, Stillingia, Maprounea,* and *Sapium* within a very inclusive genus *Excoecaria.* Mueller separated *Excoecaria, Maprounea,* and *Sapium,* but kept *Sebastiania* united with *Gymnanthes.* Bentham, followed by Pax, separated *Gymnanthes* on the basis of its reduced perianth. There is little doubt that *Gymnanthes* and *Sebastiania* are closely related, but they can be fairly readily distinguished, so there seems to be no urgent necessity to combine them. The Old World genus *Excoecaria* is also closely related to *Sebastiania* but is sufficiently distinguishable by virtue of its axillary dioecious inflorescences and ecarunculate seeds.

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Under family references see BAILLON (1873, pp. 120–123), HERBERT, NOZERAN, PAX & HOFFMANN (1912, V: 88–153), PERRY, and THATACHAR.

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18. **Gymnanthes** Swartz, Prodr. Veg. Ind. Occ. 95. 1788.

Glabrous trees or shrubs; sap not appreciably milky. Leaves alternate, stipulate, unlobed, entire or dentate; petiole short, not glandular. Plants monoecious [rarely dioecious]; inflorescences spiciform, axillary, protected by a conspicuous bud, bisexual; female flower usually only 1 per inflorescence, long-pedicellate from the lowermost node; male flowers

[1–]3 per cymule, occupying remaining nodes; bracts more or less glandular at base. Flowers apetalous; calyx small to absent; disc absent. Male flower: calyx rudimentary, of 1 or 2 small sepals often confounded with bractlets, or absent; stamens 2 or 3 in lateral flowers of the cymule, 3–5 in the central flower; filaments free or basally connate; pollen subglobose, tectate, tricolporate, circular or 3-lobed in polar view; rudimentary gynoecium absent. Female flower: calyx minute, of 2 or 3 reduced sepals [or absent]; carpels 3; styles free or connate at base, unlobed, slender and recurved; ovary smooth, stipitate [or sessile]; ovules 1 in each locule, anatropous. Fruit capsular; columella 3-winged, persistent. Seeds subglobose, smooth, dry, carunculate; cotyledons much broader than radicle. LECTOTYPE SPECIES: *G. lucida* Sw.; typification effected by Grisebach, Fl. Brit. W. Indian Is. 50. 1859. (Name from Greek, *gymnos*, naked, and *anthos*, referring to the highly reduced perianth of the flowers.) — CRAB-WOOD.

As circumscribed by Pax, a small genus of 12 species confined to the Caribbean region, mostly in the West Indies. *Gymnanthes* is extremely difficult to separate from *Actinostemon*, on the one hand, and from *Sebastiania*, on the other, and Baillon's suggestion to merge these and some other genera under *Excoecaria* is not entirely without merit. However, until additional data, such as chromosome counts (unrecorded for any species of *Gymnanthes*), are forthcoming, the traditional circumscription is diffidently maintained here.

Our only representative, *Gymnanthes lucida* Sw., the most widespread species in the genus, has been recorded from southern Florida throughout the Bahamas and Greater Antilles to Guadeloupe, in the Lesser Antilles. In Florida it is mainly confined to hammock vegetation on limestone in the Miami area and Florida Keys, extending to Key West; the northernmost collection known is from Palm Beach County. The species is easily distinguished from all its congeners by the remarkable stipitate ovary, the gynophore attaining a centimeter in length and appearing as a prolongation of the peduncle. The solitary, long-pedicellate female flower and stiff, crenate leaves also make it readily separable from *Sebastiania fruticosa*, even though the genera on the whole may be difficult to distinguish.

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Under family references see HERBERT, NOZERAN, PAX & HOFFMANN (1912, V: 81–88), and PUNT.

SARGENT, C. S. *Gymnanthes*. Silva N. Am. **7**: 29–32. *pl. 309*. 1895.

19. **Stillingia** Garden in Linnaeus, Mant. Pl. 19. 1767.

Glabrous herbs, shrubs, or small trees; sap not evidently milky. Leaves alternate [opposite, or verticillate]; stipules small and often glandular; blade unlobed, pinnately veined, [with or] without basal glands, serrate. Plants monoecious; inflorescences terminal, spiciform; female flower 1 per bract, proximal; male flowers [1–]3 or more per bract, distal; bracts biglandular. Flowers apetalous, disc absent. Male flower: calyx 2-lobed, lobes imbricate; stamens 2, filaments connate below, anthers extrorse; pollen ellipsoid to spheroid, with [1] 3 colpi, tectate but sometimes pseudoreticulate, slightly to distinctly 3-lobed in polar view; rudimentary gynoecium absent. Female flower: sepals 3, imbricate [sometimes absent]; carpels 3 [2]; styles more or less connate, unlobed, slender; ovary smooth (not muricate); ovules 1 in each locule, anatropous. Fruit capsular; columella dilated distally, often deciduous, surrounded by 3-horned structure ("gynobase") left after dehiscence of the carpels. Seeds not or scarcely compressed, [smooth or] rugulose, the caruncle sunk in a ventral depression [absent in some taxa]; endosperm present; embryo straight, the cotyledons broader than the radicle, cordate at base. TYPE SPECIES: *S. sylvatica* Garden ex L. (Named in honor of Benjamin Stillingfleet, 1702–1771, English botanist and disciple of Linnaeus).

A well-defined genus of 26 or 27 known species with a strange distribution somewhat paralleling that of *Sebastiania*. The vast majority (23) of the species are American, but two or three occur in the Mascarene Islands and one is known only from Fiji. There seems to be no reason to question the assignment of these Old World species, which belong to the single sect. PACHYCLADAE Pax, to *Stillingia*.

The American species have been revised by Rogers, who has reaffirmed the distinctness of the genus. Rogers regards *Sapium* as the genus most closely related but differing in its united sepals, fleshy seed coat, usually elongated foliar glands, and especially in its lack of the three-horned "gynobase" which characterizes the dehiscent fruit of *Stillingia*.

The infrageneric taxa of *Stillingia* have been differently treated by the last two monographers, Pax dividing the genus into six sections, Rogers recognizing two subgenera with a total of five series. As construed here, *Stillingia* comprises four sections, two of which are represented in the United States. However, none of the southwestern representatives of sect. LEPTOSTACHYAE Pax (ser. *Treculianae* Rogers), which are characterized by reduced female calyx and ecarunculate seeds, enter our area.

Both species of *Stillingia* in the southeastern United States belong to sect. STILLINGIA by virtue of their well-developed female calyces and carunculate seeds. *Stillingia aquatica* Chapm., of ser. OPPOSITIFOLIAE Rogers, an erect shrub with lenticellate twigs, is confined to swampy areas in Florida, except for outlying stations in southwestern Georgia and Baldwin County, Alabama. Closely related, although placed in a different series, SYLVATICAE Rogers, on account of its herbaceous nonlenticellate stems from an enlarged rootstock, is *S. sylvatica*, queen's delight. This species, which is found from southeastern Virginia to Florida, westward into Kansas and New Mexico, occurs in our area mainly in dry habitats (e.g., sandy flats or pine woods) on the Coastal Plain. It is thus ecologically separated from *S. aquatica*, but Rogers has suggested that it hybridizes both with that species and, to the west, with *S. texana* I. M. Johnston.

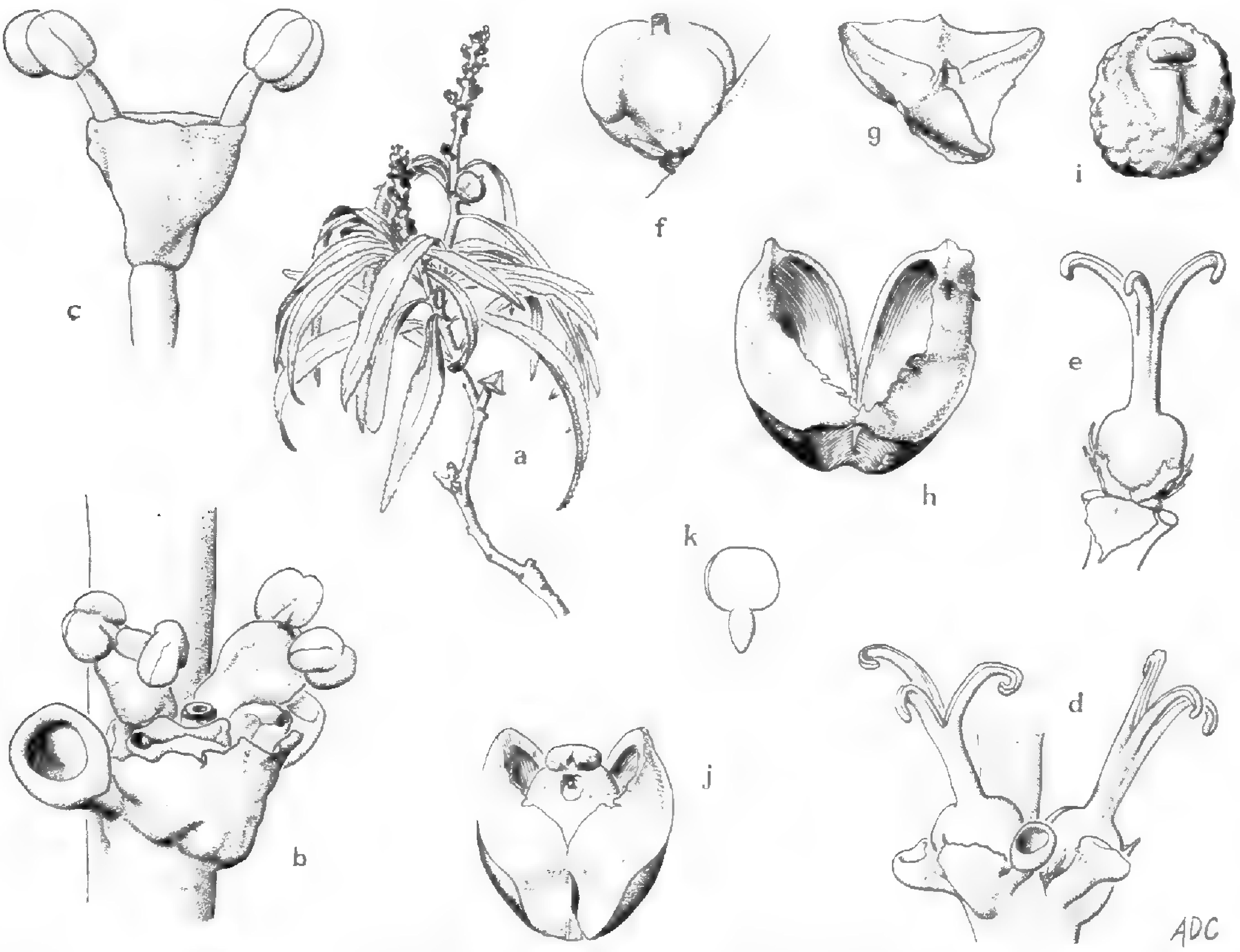

FIG. 5. **Stillingia.** a–i, *S. aquatica:* a, branchlet with male flowers and nearly mature fruit, × ½; b, male cymule, showing bract, two cup-shaped glands, pedicel of central male flower, two male flowers at anthesis, two buds, × 8; c, male flower — note synsepalous calyx, × 12; d, two female flowers from base of inflorescence, × 12; e, female flower with glands removed and bract retracted to show two perianth segments, × 6; f, nearly mature schizocarp with persistent perianth segment at base, × 2; g, persistent base of schizocarp (cf. a, f) with lower part of brittle columella, × 4; h, segment of schizocarp wall, × 4; i, seed, × 4. j, k, *S. sylvatica:* j, segment of schizocarp with seed, × 2; k, embryo, × 2.

Identification of specimens from Florida, where *S. aquatica* and *S. sylvatica* are extensively sympatric, may therefore be difficult, but in addition to the difference in habit *S. sylvatica* may be recognized by its less distinctly petiolate leaves and its smooth and larger seeds (3–7 mm. broad *vs.* 2–3 mm. in *S. aquatica*). In extreme southern Florida (Dade County) occurs the form recognized by Small as *S. tenuis* and designated by Rogers as *S. sylvatica* ssp. *tenuis* (Small) Rogers. As Rogers suggests, it may be a narrow-leaved ecotype adapted to the limestone substrate in the Miami area. However, careful field studies throughout peninsular Florida are certainly needed in order to evaluate the status of this southernmost population as well as the putative hybrid swarms between *S. aquatica* and *S. sylvatica*. The evident close relationship between all these taxa suggests that *S. aquatica* and *S. sylvatica* should probably be placed in the same series.

As in the other Hippomaneae, almost nothing is known of the reproductive biology of the species of *Stillingia*, although the pollen structure and conspicuous glandular bracts suggest that they are at least partly entomophilous. The chromosome number of *S. sylvatica* was reported to be $2n = 36$ by Perry, but Rogers was unable to confirm this and thought that Perry's count was probably too low. The only firm count for any species of *Stillingia* appears to be $2n = 60$ in *S. sanguinolenta* Muell. Arg., of ser. OPPOSITIFOLIAE. Until more taxa in this and related genera are studied, it will not be clear whether the basic number in that species is 10 or 15.

REFERENCES:

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ROGERS, D. J. A revision of *Stillingia* in the New World. Ann. Missouri Bot. Gard. **38:** 207–259. 1951.

20. **Sapium** P. Browne, Civ. Nat. Hist. Jamaica 338. 1756.

Glabrous trees or shrubs; stems usually with copious milky latex. Leaves alternate, stipulate; petiole usually biglandular at apex; blade denticulate, pinnately veined. Plants monoecious [rarely dioecious]; flowers in terminal bisexual spikes; female flowers several per spike, solitary in the axil of each proximal bract; male flowers in several-flowered clusters in the axils of distal bracts; bracts conspicuously biglandular at base. Flowers apetalous, disc absent. Male flower: calyx synsepalous, 2- or 3-lobed, lobes imbricate or open at anthesis; stamens 2 or 3, filaments free or basally connate; anthers extrorse; pollen subglobose, tectate, tricolporate, 3-lobed in polar view; rudimentary gynoecium absent. Female flower: calyx lobes [2] 3–5, small; carpels [2] 3; styles [free or] connate, unlobed, slender; ovary smooth; ovules 1 in each locule, anatropous. Fruit capsular [sometimes subdrupaceous]; valves often somewhat woody; columella slender and usually persistent. Seeds rounded (not compressed), outer seed coat fleshy and pseudoarillate, ecarunculate; cotyledons broader than radicle. (Including *Triadica* Lour.) TYPE SPECIES: *S. aucuparium* Jacq.[24] (Classical name used by Pliny for a resin-exuding species of *Pinus*; ultimately derived from Celtic, *sap*, fat, perhaps alluding to the sticky latex.) — MILK-TREE.

A pantropical genus of over 100 species, the majority American, only one native to the United States. In terms of discrimination of species,

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[24] As pointed out by Croizat (Jour. Arnold Arb. **24:** 174. 1943), the Jamaican plant on which Browne based *Sapium* was later designated as *S. aucuparium* by Jacquin. Although Jacquin subsequently applied the name to a South American species, his original disposition must be followed. Consequently, *S. aucuparium* Jacq. is the correct name for the species treated in most floristic manuals as *S. jamaicense* Sw.; the plant generally called *S. aucuparium* probably should take the name *S. salicifolium* HBK.

Sapium is one of the most difficult genera in the Euphorbiaceae. Our comprehensive ignorance of the reproductive biology and ecology of the species makes it impossible at present to pinpoint where the difficulty lies. Hemsley's work, as far as it went, appears to be sound, and his illustrations at least provide a point of departure for further studies; but Pax's monograph is extremely difficult to use, and his supraspecific taxa are probably highly unnatural.

In the southeastern United States, *Sapium* is represented only by the naturalized *S. sebiferum* (L.) Roxb. (*Triadica sebifera* (L.) Small), Chinese tallow tree, which is commonly cultivated as an ornamental. Wild trees have been found in low, often swampy, areas in South Carolina, Georgia, and Louisiana. The species belongs to sect. TRIADICA (Lour.) Muell. Arg., a group of six Asiatic species characterized by having a somewhat fleshy fruit and by the seed coat being white and adherent to the columella, rather than reddish and free from the columella as in most tropical American species.

In the United States, *Sapium sebiferum* is grown mainly as an ornamental, especially for the foliage, which turns bright red in autumn. In central and southern China, Japan, and northern India, however, the tree is cultivated for the seeds. Both waxy seed coat and endosperm are used, the former providing the "tallow" used for candle-making in China, and the latter yielding an oil with some of the properties of tung oil. Unfortunately the labor costs involved in harvesting the fruits preclude commercial exploitation of the tree in countries such as the United States.

Small recorded a second species, *Sapium glandulosum* (L.) Morong, evidently on the basis of a Curtiss collection from near Pensacola, but the plant has not been re-collected and cannot be regarded as naturalized. The only other species of *Sapium* in the United States is *S. biloculare* (Wats.) Pax, one of the Mexican jumping-bean plants, which enters southern Arizona.

Perry has reported $2n = 36$ in *Sapium sebiferum*, which is the only published chromosome number for the species. Ventura found that embryo-sac development was of the normal type in trees studied in Italy, but reported that only one seed developed per capsule; this is quite at variance with our plants, in which three seeds regularly develop in each fruit.

Although merged by Mueller with *Excoecaria*, *Sapium* has been recognized by most botanists on the basis of its monoecious inflorescence production, fleshy-coated seeds, and biglandular petioles. As pointed out by Pax, the relationship to *Stillingia* is probably closer, but Rogers has shown that *Sapium* can usually be distinguished from that genus by its fleshy seeds, elongated foliar glands, and lack of a persistent gynobase upon dehiscence of the fruit.

According to Horn and Polhamus, the rubber contained in latex of *Sapium* species is comparable in quality to the best *Hevea* rubber and, in fact, surpasses the latter in strength and elasticity. However, the trees are difficult to tap, and significant commercial production has never been established. Because of the abundance of the plants in Latin America, it would appear that further investigation of the potentialities of *Sapium* latex might be warranted.

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21. **Hippomane** Linnaeus, Sp. Pl. 2: 1191. 1753; Gen. Pl. ed. 5. 499. 1754.

Glabrous trees or shrubs; milky latex copious, poisonous. Leaves alternate, stipulate (stipules caducous); petioles elongated, with a single gland at the apex; blade pinnately veined, more or less cordate. Plants monoecious [dioecious]; inflorescence spiciform, terminal, bisexual, the rachis more or less thickened; female flowers few, solitary at proximal nodes; male flowers several to numerous in dense glomerules at each of the distal nodes; bracts conspicuously biglandular at base. Flowers apetalous, disc absent. Male flower: calyx 2- or 3-lobed, lobes imbricate; stamens 2, filaments connate; anthers extrorse; pollen subglobose, tectate, 3-colporate, 3-angled in polar view; rudimentary gynoecium absent. Female flower sessile: calyx 3-parted; carpels (5) 6–9; styles connate at base, unlobed, spreading and recurved, densely papillate; ovary smooth; ovules 1 in each locule, anatropous. Fruit drupaceous, mimicking an apple, with yellowish or reddish fleshy exocarp, bony endocarp. Seeds not compressed, smooth, ecarunculate; endosperm present; cotyledons flat, much longer and broader than the radicle. LECTOTYPE SPECIES: *H. Mancinella* L.; see Baillon, Étude Gén. Euphorb. 540. 1858. (Name from Greek, *hippos*, horse, and *mania*, fury, referring to the effect of the poisonous latex.) — MANCHINEEL.

A small tropical American genus of two or three species, well characterized by the multilocular drupaceous fruit which is so apple-like in appearance that it has been the cause of serious poisonings. Two very closely related species with smaller drupes and spinose leaves, *H. spinosa* L. and *H. horrida* Urb. & Ekm., are endemic to dry scrub on limestone in southwestern Hispaniola. Our representative is the well-known manchineel tree, *Hippomane Mancinella* L., $n = 11$,[25] which is widespread along seashores in the Caribbean area from Florida to Mexico, Colombia, and Venezuela, with outlying populations in the Galapagos and Revillagigedo Islands. In Florida, the manchineel is restricted to the Keys and the immediately adjacent mainland, where it is found in hammock vegetation behind the mangrove zone.

From the earliest days of European colonization the manchineel has had a sinister reputation, and its toxicity has been exaggerated by some writers; still, there is no doubt that the latex is extremely dangerous if taken internally, and it can produce severe irritation of the skin. The wood has, in the past, been used here and there in the West Indies for making furniture, but this has now almost ceased, as the trees have been ruthlessly extirpated from many parts of their previous range.

Despite its widespread occurrence and familiarity, the reproductive biology of the manchineel remains almost completely unknown; but in our area it flowers in April. The pollination process and embryological development have not been followed, nor has germination and seedling establishment been carefully studied. The affinities of *Hippomane* have seldom been discussed, but there seems to be no reason to dissent from Baillon's opinion that it is very close to *Sapium*. The overall habit of the manchineel certainly recalls species of that genus, and it can scarcely be distinguished generically except on the basis of its indehiscent multilocular fruit.

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[25] Previously unpublished chromosome count by Dr. Jack Ellis, based on examination of meiosis in male flower buds of shrubs growing at Auchenskeoch Beach, Tobago (*Webster et al. 9825*).

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Tribe EUPHORBIEAE [Dumort.]
Subtribe **Euphorbiinae** Hurusawa

22. **Euphorbia** Linnaeus, Sp. Pl. 1: 450. 1753; Gen. Pl. ed. 5. 208. 1754.

Herbs, shrubs, or trees of diverse habit, aërial parts sometimes succulent, latex whitish. Leaves alternate, opposite, or whorled, persistent or deciduous (or sometimes caducous and then plants appearing leafless); stipules present or absent, sometimes represented by glands; blade undivided (sometimes lobed), usually pinnately veined, eglandular. Plants monoecious or rarely dioecious; inflorescence a bisexual (rarely unisexual) pseudanthium (cyathium); cyathia borne in terminal or axillary dichasia or pleiochasia (or, by reduction, apparently solitary). Cyathium with a solitary terminal female flower subtended by (4) 5 male cymes, the bracts opposite the male cymes fused into a radially or isobilaterally symmetrical, campanulate to hemispheric involucre; tips of bracts alternating with 4 or 5 (rarely fewer) glands (nectaries); glands entire, 2-lipped, or variously lobed, sometimes with petaloid appendages; male cymes monochasial or possibly dichasial at base, each developing 1–10 or more flowers; bracteoles of male monochasia conspicuous to reduced or absent, often fringed or lacerate, sometimes partly fused into the involucral partitions. Male flowers monandrous, simulating a single stamen; perianth usually absent, very rarely developed as a small cup (more commonly represented by an articulation); anthers dehiscing longitudinally and "introrsely" (i.e., centripetally); pollen subglobose, tricolporate, reticulate to tectate (psilate), sometimes operculate, with conspicuous intine thickenings parallel to colpi. Female flower pedicellate, pedicel often reflexed; perianth of 3–6 more or less united scalelike sepals or more commonly rudimentary or absent; carpels 3 (very rarely 2 or 4); styles free or basally connate, bifid or rarely entire; ovary glabrous or pubescent, often angled or carinate; ovules 1 in each locule, anatropous, with a more or less evident nucellar beak; embryo sac normal (Polygonum type) or rarely of various aberrant tetrasporic types. Fruit capsular [rarely drupaceous]; columella more or less persistent. Seeds smooth, ridged, or variously pitted or tuberculate, with or without a caruncle; endosperm copious; cotyledons fleshy, broader

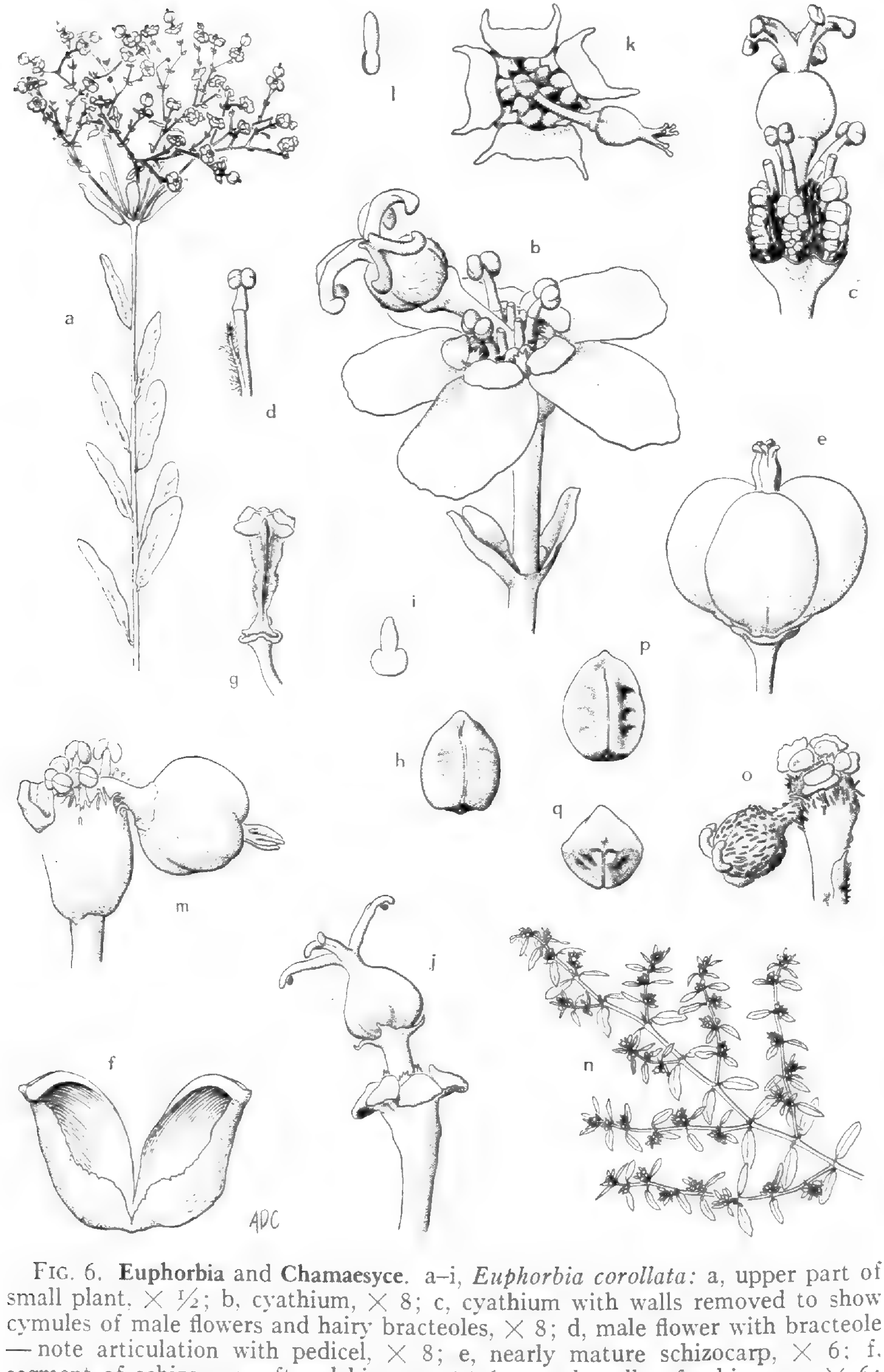

FIG. 6. **Euphorbia** and **Chamaesyce**. a–i, *Euphorbia corollata:* a, upper part of small plant, × ½; b, cyathium, × 8; c, cyathium with walls removed to show cymules of male flowers and hairy bracteoles, × 8; d, male flower with bracteole — note articulation with pedicel, × 8; e, nearly mature schizocarp, × 6; f, segment of schizocarp, after dehiscence, × 6; g, columella of schizocarp, × 6; h, seed, × 6; i, embryo oriented as in seed, × 6. j, *E. inundata:* cyathium and female flower with three-lobed perianth, × 4. k, l, *E. commutata:* k, cyathium from above, × 8; l, embryo, oriented as in seed (compare with "i"),

than the radicle. (Including *Agaloma* Raf., *Dichrophyllum* Kl. & Garcke, *Elaeophorbia* Stapf, *Galarhoeus* Haw., *Poinsettia* Graham, *Tithymalopsis* Kl. & Garcke, *Tithymalus* J. Gaertn. [nom. cons.], and *Zygophyllidium* (Boiss.) Small.) LECTOTYPE SPECIES: *E. antiquorum* L.; see Millspaugh, Field Mus. Publ. Bot. 2: 306. 1909. (Named for Euphorbus, physician to King Juba of Numidia, a contemporary of Pliny, Euphorbus having drawn attention to the properties of the succulent *E. officinarum* vel aff.) — SPURGE.

In the broad circumscription of Pax & Hoffmann, *Euphorbia*, with over 1500 species, is the largest genus in the family and one of the largest among the angiosperms. This inclusive genus is characterized by its more or less regular bisexual pseudanthium, to which the term "cyathium" has been applied by most workers. Boissier, in the first general monograph, placed the cyathium-bearing Euphorbiaceae into only four genera: *Anthostema*, *Euphorbia*, *Synadenium*, and *Pedilanthus*. Among these, *Euphorbia* included all the species in which the male flower lacks a perianth and the cyathial involucre bears four or five glands. Pax & Hoffmann admitted a number of additional genera, such as *Stenadenium* and *Monadenium*, which differ from *Euphorbia* only in relatively slight modifications of the cyathium. The least justifiable segregation would appear to be the recognition of the genus *Elaeophorbia* Stapf for certain African species with drupaceous fruits; these species should be returned to *Euphorbia* subg. EUPHORBIA, where they find a place adjacent to sect. TEKEANAE Croizat.[26]

Croizat and Dressler, in a number of articles, have severely criticized the traditional circumscription of *Euphorbia* (without, however, using most of the segregate taxa in their own publications). Some of these criticisms have considerable merit, as the current concepts of generic limits in the Euphorbieae are indeed illogical and unnatural. The African genera *Monadenium* and *Synadenium*, although generally accepted by most 20th century workers, are evidently allied to *Euphorbia* sect. TIRUCALLI and are scarcely more distinctive overall than are many of Boissier's sections which are usually retained within *Euphorbia*.

If one accepts the position that the cyathium is a tribal character of the Euphorbieae rather than diagnostic for the genus *Euphorbia*, other criteria must be sought for generic delimitation in the tribe. The tremendous diversity in habit, leaf morphology, chromosome number, and pollen configuration might at first appear to favor the dissolution of *Euphorbia* into a number of smaller genera. However, a review of the

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[26] *Euphorbia* sect. **Elaeophorbia** (Stapf) Webster, stat. nov. *Elaeophorbia* Stapf, Hooker's Ic. Pl. IX. **4**: *pl. 2823.* 1906.

× 6. m, E. *dentata:* cyathium, × 8. n–q, *Chamaesyce maculata* (*C. supina*): n, part of prostrate plant to show branching habit, arrangement of leaves, and interpetiolar stipules, × ½; o, cyathium, × 16; p, q, seed, adaxial surface and from above, × 16.

taxonomic history of the Euphorbieae is sufficient to indicate that the problem does not have an obvious solution. Variations in such features as the cyathial glands (appendaged or not), seeds (carunculate or not), and female flowers (naked or "calyculate") do not seem to show strong correlation with major phyletic groups. There is the additional practical difficulty that the numerous exceptions to such characteristics (e.g., carunculate seeds) make it extremely difficult to find good "key" characters to diagnose segregate taxa. If the various microgenera of Euphorbieae cannot be easily distinguished, there seems little reason to adopt them simply because they represent evolutionary units; it is quite as easy to discuss the evolution of these taxa if they are referred to as infrageneric components of *Euphorbia*.

The present author finds himself no more able to resolve this taxonomic impasse than have the many others who studied the situation earlier. A major difficulty appears to reside in the lack of basic morphological and cytological data. Although many papers have been published on *Euphorbia*, most have dealt either with species in subg. ESULA or with the African succulents. Chromosome numbers are available for over 80 species, but many of these require confirmation, and no counts have been reported for *any* species in 18 of the 27 sections recognized by Boissier. Although much (perhaps too much!) has been published on the morphology of the cyathium, anatomical data — even for the cyathia — are inadequate for comparisons between sections, and the nature of the spines in the succulent taxa is still controversial. In view of this present scarcity of systematically meaningful facts, and in the face of the highly contradictory opinions of experts living and dead, a compromise view on generic limits is adopted in the present treatment: *Chamaesyce* is accepted diffidently as a distinct genus, whereas all other segregate taxa, including *Poinsettia*, are relegated to subgeneric status within *Euphorbia*. This disposition is frankly one of expediency and does not claim either logical or phylogenetic justification. *Chamaesyce* happens to be a large and doubtless natural group of several hundred species which is rather easily definable. It seems more convenient, in practice, to recognize *Chamaesyce* as an independent genus than to retain it within *Euphorbia*; whereas, in my opinion, this is not true, in our present state of knowledge, for the other taxa of Euphorbieae in question.

As thus delimited, *Euphorbia, sensu stricto,* is still a large, polymorphic genus consisting of more than 1000 species distributed into about seven subgenera; in the southeastern United States it is represented by about 30 native or naturalized species belonging to four subgenera. All species of three other subgenera recognized by Wheeler (EREMOPHYTON, LYCIOPSIS, and RHIZANTHIUM) are confined to the Old World and in our area will be found only in cultivation.

Subgenus ESULA Pers. (§ *Tithymalus*, of Boissier), with over 500 species, is probably the largest and most diversified group within *Euphorbia*; it includes some of the most primitive as well as most highly specialized taxa in the genus. Despite this remarkable amplitude of diversification, the great majority of taxa of subg. ESULA have in common alternate phyllotaxy (at least below), exstipulate leaves, and bibracteate cyathia with exappendiculate glands. Boissier's treatment of this group in De Candolle's *Prodromus* is unsatisfactory as regards supraspecific categories, since he crowded over 300 species into a single one of his 27 sections. Prokhanov, in Flora URSS, has tended toward the other extreme in recognizing ten sections and a large number of subsections and series for the relatively limited diversity of taxa found in the Soviet Union. In the present circumscription, the 17 Southeastern species of subg. ESULA are referred to three sections.

Section LATHYRIS Godron (§ *Epurga* Prokh.) includes only *Euphorbia Lathyris* L., a European species occurring as a weed (perhaps partially escaped from herb gardens). The species differs sharply from other representatives of subg. ESULA in its decussate phyllotaxy; thick-walled, tardily dehiscent capsules; and large (4–5 mm. long), roughened, carunculate seeds. Although it was placed at the opposite end of subg. ESULA in Boissier's arrangement, the group closest to sect. LATHYRIS would appear to be sect. MYRSINITEAE (Boiss.) Pojero, a group of Mediterranean perennial species with similar cyathia (horns of glands dilated, male bracteoles reduced). Our remaining species, which have the leaves alternate (at least below) and less massive capsules with smaller seeds, are about equally divided between two sections (very perceptively distinguished by Roeper in 1824, although without distinguishing names).

Section ESULA [(Roeper) Koch] includes those species of subg. ESULA with truncate to crenulate or bicornate nectaries, linear to oblong cotyledons, smooth ovaries, and prevailingly entire cauline leaves. Over 200 species have been described, primarily from temperate regions of the Northern Hemisphere, but extending into tropical latitudes along high mountain ranges. The section is close to sect. TITHYMALUS and not always easily distinguishable from it, but the placement of most individual species is usually not in doubt. Perhaps the local species of most dubious relationship is *Euphorbia trichotoma* HBK., a West Indian coastal plant which occurs in southern peninsular Florida as far north as Tampa Bay. Norton appears to have been correct in transferring it from sect. TITHYMALUS, and it seems best regarded as our only representative of subsect. PARALIOIDEAE Prokh., diverging from other taxa in the section by its crenulate leaves and peculiar branching pattern. There is a rather striking resemblance between *E. trichotoma* and *E. Paralias* L., a Mediterranean plant of similar maritime habitats, and the two may perhaps be vicariants.

Subsection ESULAE Boiss., a primarily Old World group of perennials with smooth, carunculate seeds, is represented in our area only by the pernicious introduced weed *Euphorbia Cyparissias* L., $2n = 20, 40$; other related species (e.g., *E. Esula* L.) have been introduced into the northern United States and Canada and may eventually be found in mountainous areas of the Southeast.

Subsection FOVEOSPERMAE Hurusawa, comprising Holarctic annuals or short-lived perennials with pitted, usually carunculate seeds, includes the remaining five or six species in our area. Both exotic weeds, such as the ubiquitous *Euphorbia Peplus* L., and native species, such as *E. commutata* Engelm., are represented.

Section TITHYMALUS Roeper, characterized by rounded, entire cyathial glands; suborbicular cotyledons; and usually smooth seeds, includes at least 150 species, mainly of north temperate regions but with perhaps a majority in Eurasia. Our species fall into three subsections. The type species of the section, *Euphorbia Helioscopia* L., is an introduced European weed belonging to subsect. GALARRHAEI Boiss., a group of about ten species including annuals or biennials with obovate serrulate leaves and carunculate reticulately ornamented seeds. Our only native species, the rather variable *E. spathulata* Lam. (*E. dictyosperma* Fisch. & Mey.) differs from *E. Helioscopia* in having verrucose, rather than smooth, capsules.

Subsection PURPURATAE Prokh., a group of perennial rhizomatous species with generally entire leaves and roughened ovaries and seeds, is primarily Eurasian. Its only typical representative in North America is the taxonomically rather isolated *Euphorbia purpurea* (Raf.) Fern. (*E. Darlingtonii* Gray). Two additional species in our area, *E. platyphylla* L. and *E. obtusata* Pursh, are anomalous in their annual habit, and *E. obtusata* is somewhat transitional to subsect. GALARRHAEI in its serrulate leaves and slightly wrinkled seeds.

Subsection INUNDATAE Webster,[27] an entirely New World group, is represented in the Southeast by three related Coastal Plain species: *E. floridana* Chapm., *E. inundata* Torr., and *E. telephioides* Chapm. These plants resemble *E. Ipecacuanhae* in their habit and female flowers with perianth, but they differ in lacking stipules and appendages on the cyathial glands. It would appear that subsect. INUNDATAE is a group transitional in certain respects between subg. ESULA and subg. AGALOMA. Boissier included a dozen South American species in the same subsection, but further study is needed to determine whether these should be closely associated with the species of the United States.

Subgenus AGALOMA (Raf.) House, in the circumscription of Wheeler, is an American group of ten sections with approximately 100 species. Although plants of very diverse habit are included, the subgenus can be characterized by the appendiculate glands of the cyathium; the majority of species also have stipulate leaves and ecarunculate seeds. Boissier's treatment of the taxa now gathered into subg. AGALOMA is not very satisfactory, as his ten sections (II–XI) are not very well defined and are really equivalent to his subsections in sect. TITHYMALUS; doubtless they

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[27] *Euphorbia* sect. *Tithymalus* subsect. **Inundatae** Webster, subsect. nov., foliis infra sparsis, stipulis nullis, capsulis calyculatis, seminibus ecarunculatis. TYPUS: *E. inundata* Torr.

Norton (Missouri Bot. Gard. Rep. **11**: 2. 1899) pointed out that *Euphorbia Ipecacuanhae* L. must be transferred from subg. ESULA to subg. AGALOMA. Since *E. Ipecacuanhae* is by inference the type of Boissier's subsect. IPECACUANHAE, its excision necessitates renaming the residue of the taxon.

will be drastically recast in the next monographic revision. Three sections with about 10–12 species occur in the Southeast.

Section TITHYMALOPSIS (Kl. & Garcke) Boiss., typified by *Euphorbia corollata* L., is a taxonomically difficult and phylogenetically interesting group of rather uncertain limits. The typical element of the section may be referred to subsect. COROLLATAE Webster,[28] which includes perennial plants with rhizomatous or somewhat tuberous rootstocks, alternate exstipulate leaves below the inflorescence branches, five distinctly appendiculate cyathial glands, and finely or shallowly pitted seeds. Small recognized no less than ten binomials in the *E. corollata* complex, but the number of distinct species is surely less than that. *Euphorbia corollata* itself is a notoriously variable species, and some of the Smallian taxa (such as *Tithymalopsis apocynifolia* and *T. olivacea*) may prove to be tenable at subspecific rank when the variations are worked out. Species which appear distinct from *E. corollata* include *E. Mercurialina* Michx., with the lower leaves reduced to scales and an aspect resembling that of *E. Ipecacuanhae*; *E. Curtisii* Engelm., with very slender branching stems and narrow leaves; and *E. polyphylla* Engelm., with narrow revolute leaves and a habit recalling that of *E. Cyparissias.* Proposed species such as *E. discoidalis* Chapm., *Tithymalopsis exserta* Small, and *T. eriogonoides* Small, require further scrutiny before their status and relationships are clear. Extralimital species in Texas and Mexico, such as *E. Maysillesii* McVaugh, *E. sphaerorhiza* Benth., and *E. Wrightii* Torr. & Gray, appear to belong to subsect. COROLLATAE on the basis of technical characters, but have a different aspect and may eventually have to be placed in a separate subsection.

Subsection IPECACUANHAE Boiss.,[29] which, in contrast to the preceding subsection, appears to be confined strictly to the United States east of the Mississippi River, includes plants the relationships of which have long appeared problematical. Boissier placed *Euphorbia Ipecacuanhae* in a subsection of subg. ESULA because of its presumably exappendiculate glands, but he noted its resemblance to *E. corollata.* As pointed out by Norton, however, *E. Ipecacuanhae* must be expelled from subg. ESULA because of its minutely stipulate leaves and its appendiculate cyathial glands; the appendages, though very narrow, are comparable to those in subg. AGALOMA. Although the distinct female perianth (Boissier's "caly-

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[28] *Euphorbia* sect. *Tithymalopsis* subsect. **Corollatae** Webster, subsect. nov., ab subsect. IPECACUANHAE differt stipulis nullis, glandulis involucrorum 5, manifeste appendiculatis, capsulis ecalyculatis. TYPUS: *E. corollata* L.

[29] *Euphorbia* subsect. IPECACUANHAE Boiss. (DC. Prodr. **15**(2): 101. 1862), implicitly typified by *E. Ipecacuanhae* L., is here restricted to that species and its near relatives and at the same time is transferred from subg. ESULA to subg. AGALOMA. The remainder of the species in Boissier's subsection remain in subg. ESULA as subsect. INUNDATAE Webster of sect. TITHYMALUS (see previous footnote). The species of sect. TITHYMALOPSIS may therefore be referred to three subsections: COROLLATAE, IPECACUANHAE, and subsect. **Innocuae** Webster, subsect. nov.: perennis, caulibus prostratis; foliis sessilibus, inferne sparsis, superne oppositis; cyathiis solitariis, glandulis 4 appendiculatis; seminibus scrobiculatis. TYPUS: *E. innocua* L. C. Wheeler.

culus") of *E. Ipecacuanhae* does suggest affinity to *E. inundata* and related species in subg. ESULA, the preponderance of characters (particularly the cyathial appendages, the leaf morphology, and the shallowly pitted seeds) argues for inclusion of *E. Ipecacuanhae* in sect. TITHYMALOPSIS. Subsection IPECACUANHAE, as redefined, then includes *E. Ipecacuanhae*, *E. gracilior*, Cronq., and some dubious populations which have been named *E. arundelana* Bartlett and *E. marilandica* Greene. It seems probable, as suggested by Gleason (New Britt. Brown Illus. Fl. Northeast. U. S. 2: 486. 1952), that these latter taxa represent hybrid swarms between *E. corollata* and *E. Ipecacuanhae*, but the necessary field and experimental studies to substantiate this hypothesis have not yet been made.

Section ZYGOPHYLLIDIUM Boiss., evidently related to sect. TITHYMALOPSIS but differing in habit (plants annual and more highly branched) and having tuberculate rather than pitted seeds, is a small North American group of perhaps six species. Only *Euphorbia hexagona* Nutt. ex Spreng. crosses into our area in Arkansas. It differs from all our taxa of sect. TITHYMALOPSIS in its prevailingly unisexual cyathia with thickened acute glandular appendages, as well as in its completely different aspect. However, some western species of sect. TITHYMALOPSIS, notably *E. Wrightii*, show a strong resemblance to *E. hexagona*, except in having a thickened perennial root. Since Boissier's treatment, additional species more or less referable to sect. ZYGOPHYLLIDIUM have been described from Mexico, and it seems likely that the sectional boundaries will have to be redefined.

Section PETALOMA Boiss. is a North American group of three species, two of which enter our area in Arkansas and Louisiana. Plants of this section are easily recognizable by the annual root, sparingly branched stems with alternate leaves below, and conspicuously white-edged floral bracts subtending the large cyathia. *Euphorbia marginata* Pursh, the familiar snow-on-the-mountain, native to Texas, is cultivated in many southern gardens and may be found as an escape here and there, but has not yet been recorded as native to our area. Very similar, but differing in its narrower leaves and more densely pubescent capsule, is *E. bicolor* Engelm. & Gray, which enters Arkansas from Oklahoma and Texas. A third closely related species, *E. torrida* DC., is known from Mexico (San Luis Potosí, Veracruz, Campeche, and Oaxaca).

Subgenus POINSETTIA (Graham) House is an American taxon treated by Dressler as an independent genus with eleven species. The group is characterized by its reduced number of more or less cup-shaped exappendiculate glands (mostly one or two, rarely three or four), condensed dichasial or pleiochasial inflorescences, and tuberculate seeds. However, as Dressler himself pointed out, the poinsettias show a strong resemblance to taxa of subg. AGALOMA, especially species of sect. DICHILIUM Boiss. such as *Euphorbia lancifolia* Schlecht. Although the cultivated poinsettia, *E. pulcherrima* Willd. ex Kl., certainly appears to be very different from familiar representatives of subg. AGALOMA such as *E. corollata*, the genus *Poinsettia* as defined by Dressler is actually not as sharply defined as some sections within AGALOMA. Whether treated as genus or subgenus, its relationships with sect. DICHILIUM and other taxa within subg. AGALOMA need to be further evaluated.

In our area four native or naturalized species of subg. POINSETTIA have been recorded. Dressler has untangled much of the confusion surrounding these common weedy annuals, and it is apparent from his discussion that identifications in the literature are highly untrustworthy. The most widespread species in North America appears to be *Euphorbia dentata* Michx. (*Poinsettia dentata* (Michx.) Kl. & Garcke), $2n = 14, 28, 56$, which occurs over most of eastern temperate United States and extends south into Texas and Mexico. It may be recognized by its opposite, coarsely dentate leaves; floral leaves lacking basal red splotches; slender cyathium with bilabiate gland; and rounded, sharply tuberculate, usually caruncculate seeds. Also widespread in eastern temperate North America and probably occurring throughout our area is *E. cyathophora* Murr. (*P. cyathophora* (Murr.) Kl. & Garcke), $2n = 28, 56$, a highly variable species which has suffered much confusion in taxonomic treatments. It may usually be recognized by having the lower leaves alternate; floral bracts red splotched; cyathia broader, with a larger gland; and finely tuberculate seeds without a caruncle. This species has been confused in many floristic manuals with *E. heterophylla* L. (*P. heterophylla* (L.) Kl. & Garcke), but, as shown by Dressler, that name is properly applied to a species of primarily tropical distribution which within our area has been found only in Louisiana and Florida. Although superficially resembling some forms of *E. cyathophora*, with which it is sympatric in much of the Caribbean region, *E. heterophylla* differs in its floral bracts lacking basal red splotches; its more slender cyathia with a round, stipitate gland; and its angular, more coarsely tuberculate seeds.

Burch, in a brief review of the Florida taxa of subg. POINSETTIA, has upheld *Euphorbia pinetorum* (Small) Webster[30] as a species distinct from *E. cyathophora* (to which Dressler had referred it as a synonym). Although it closely resembles certain narrow-leaved forms of *E. cyathophora* in aspect, it differs in having a perennial base with thickened storage roots and cyathia mostly with three or four glands. According to Burch, *E. pinetorum* is endemic to the pinelands on limestone in extreme southern Florida (Dade and Monroe counties).

The morphological patterns in many species of subg. POINSETTIA display a remarkable amplitude of variation; this is especially true of *Euphorbia cyathophora*, in which plants with linear and with pandurate leaves may be found intermingled in the same population. Some of the variation is doubtless ecotypic, and some may be due to hybridization. Dressler has suggested that introgression occurs between *E. dentata* and *E. heterophylla*, and the Florida populations of these two species would repay closer study. Curiously, no evidence of crossing between *E. dentata* and *E. cyathophora* has been reported, although these species are sympatric over hundreds of thousands of square miles.

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[30] **Euphorbia pinetorum** (Small) Webster, comb. nov. *Poinsettia pinetorum* Small, Fl. Miami 111, 200. 1913.

Cytologically, the taxa of subg. POINSETTIA are interesting in that polyploid series ($2n = 28, 56$) occur in at least *Euphorbia cyathophora* and *E. dentata*. Dressler suggested that the basic number of *Poinsettia* may be $n = 14$, but the reports of $n = 7$ in one population of *E. dentata*, and the multivalent associations in *E. pulcherrima* described by Ewart & Walker would seem to point toward a basic number of $n = 7$. In contrast, *E. heterophylla* has proved to be uniformly tetraploid ($2n = 28$), on the basis of counts from at least seven populations. It is evident that additional field surveys of chromosome number, when correlated with analysis of morphological variation patterns, may provide a fascinating insight into the dynamics of speciation in this group.

The commonly cultivated Christmas poinsettia, *Euphorbia pulcherrima* Willd. ex Kl.[31] (*Poinsettia pulcherrima* (Willd. ex Kl.) Graham) is grown in many parts of our area and may occasionally be found escaped in southern Florida, although it shows no signs of becoming naturalized. According to Dressler, the species is native to rocky canyons along the Pacific coast of Mexico, where it occurs in the tropical deciduous forest formation. In addition to its woody habit, it differs from our local representatives in its larger cyathia and seeds and glabrous stems.

Subgenus EUPHORBIA, a large group of some 400 Old World (mainly African) succulent species, includes most of the familiar "cactiform" euphorbias.[32] A single species, *Euphorbia lactea* Haw., has been reported as escaped from hedgerows in extreme southern Florida. According to Croizat, *E. lactea* is native to Ceylon, whence it was early introduced by the Dutch into cultivation on various West Indian Islands and eventually into Florida. Apparently the plant does not flower commonly in Florida, if at all, so that its spread must be entirely vegetative. Various other succulent species of subg. EUPHORBIA are cultivated in gardens in the Miami area. Perhaps the commonest is *Euphorbia Tirucalli* L., of sect. APHYLLIS Webb & Berth. (§ *Tirucalli*, of Boissier). It is a tree with slender, green, pencil-thick twigs bearing alternate deciduous leaves (and hence often appearing leafless); the latex is resinous and said to be poisonous to the touch, causing blindness if gotten into the eyes. Possibly the most familiar of the cultivated shrubby species of *Euphorbia* is *E. Milii* Desmoul. (*E. splendens* Boj.), the crown of thorns, which has stipular spines, well-developed leaves, and conspicuous red cyathial bracts. Although placed in sect. EUPHORBIA (§ *Diacanthium*) by Boissier, it appears to belong rather in sect. GONIOSTEMA along with a number of other Madagascar species characterized by spinose or comblike stipules, long peduncles, and variously colored cyathial bracts.

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[31] Dressler deserves the commendation of horticulturalists who may prefer to recognize *Poinsettia* as a genus for salvaging the name *Poinsettia pulcherrima*; by describing a new Mexican species as *P. coccinea* Dressler, he thereby pre-empted an earlier epithet (*Pleuradena coccinea* Raf.) for the common ornamental species.

[32] In the narrowest possible generic circumscription within the Euphorbieae, the name *Euphorbia* would be restricted to a group of about 80 African and Asian succulents with ribbed stems and paired "stipular" spines (i.e., approximately to sect. DIACANTHIUM of Boissier, excluding *E. Milii* and *E. Bojeri*).

The relationships of subg. EUPHORBIA are controversial, but fortunately a resolution of the problem is beyond the scope of the present treatment. A few American species, such as *Euphorbia alata*, from Jamaica, and *E. phosphorea* Mart., from Brazil, could be referred to subg. EUPHORBIA on the basis of general habit; but it is possible, if not probable, that their resemblance to the African cactiform taxa is due to convergence, rather than consanguinity. The origin of subg. EUPHORBIA is, in any event, probably to be sought within subg. ESULA, where thick-stemmed species of sect. BALSAMIS Webb & Berth. (subsect. *Pachycladae*, of Boissier) suggest a starting point for the evolution in the direction of progressive succulence which reaches a climax in the *Cereus*-like taxa of South Africa.

Relationships within subg. EUPHORBIA are perhaps less well understood than in any other part of the genus, despite the relatively great degree of attention these succulent species have received. Boissier grouped most of the succulent and semisucculent species into five sections (XVIII–XXII) which, on the whole, are poorly defined. These fall into three main groups: (1) sects. EUPHORBIA (§ *Diacanthium*, of Boissier) and GONIOSTEMA, with spines or crests of presumably stipular origin; (2) sect. ANTHACANTHA Lem. (§ *Euphorbium*, of Boissier), with spines (where present) of peduncular origin; and (3) sect. APHYLLIS Webb & Berth. (§ *Tirucalli*, of Boissier) with well-developed leaves and spineless stems, the plants scarcely differing from subsect. PACHYCLADAE of Boissier's sect. TITHYMALUS except in the succulence of their stems. Wheeler has associated Boissier's sects. CAULANTHIUM and RHIZANTHIUM into an additional succulent subgenus RHIZANTHIUM, but the reasons for this disposition are not quite clear, since the species included have in common mainly a thickened underground rootstock, but differ otherwise in reproductive characters and geographic distribution. It is quite possible that the various taxa of succulent euphorbias have been polyphyletically derived from different nonsucculent ancestors; the neotropical and paleotropical taxa almost certainly have separate origins. Since neither a satisfactory outline of supraspecific taxa nor a plausible phylogenetic scheme has yet been proposed, it is obvious that the succulent euphorbias present an especially fascinating challenge for future studies.

Morphological studies of the Euphorbieae have suffered from an excessive preoccupation by morphologists with homologies of the cyathium, aggravated by a lack of sufficient familiarity with the taxonomic diversity. The initial basic monograph of Roeper, in which morphological data were carefully related to classification, is an inspiring model which has never been sufficiently followed up, even for any major section within the genus.

The morphology and anatomy of the cyathium have been exhaustively studied by several generations of botanists since Roeper's day, and the basic structure is now rather well understood, although this knowledge has never been very effectively related to problems of generic and subgeneric delimitation in the Euphorbieae. The original thesis of Linnaeus that the cyathium is a hermaphroditic flower was still held a century later by Baillon and Payer, but Lamarck and A. L. de Jussieu had already suggested (1788–1789) that it might be an inflorescence, and this was convincingly verified by Robert Brown, in 1818, and by Roeper, in 1824. For most of the past century the controversy with regard to the cyathium has shifted to questions of homologies between cyathial structures and the less modified reproductive organs of other Euphorbiaceae. Roeper suggested that the involucre of the cyathium represents a verticil of five connate bracts (such as may be seen in *Euphorbia Helioscopia* subtending the main rays of the umbelliform pleiochasium) and that the glands (nectaries) are duplex commisural structures of stipular origin. The glands, being formed by the fusion of adjacent glandular bracteal stipules, in this interpretation are thus homologous with the connate interpetiolar stipules of species of *Chamaesyce*. Unfortunately such a straightforward explanation has apparently seemed distasteful to many botanists with restless imaginations, and a number of alternative theories have been proposed, especially with regard to the origin of the glands. Haber, for example, after laborious scrutiny of microtome sections of cyathia, ignored the obvious evidence of gross morphology and interpreted the gland as representing "a pair of modified secondary branches of a lateral inflorescence branch, fused with which are parts of the adjacent involucral bracts." Bodmann came to somewhat similar conclusions on the basis of an analysis of teratological cyathia, and proposed that the glands are really modified staminate flowers; but Neville more recently has supported the "classical" theory on the basis of other teratological specimens. It would appear that teratological evidence is equivocal, at best, and certainly cannot offer a convincing refutation of the "stipular" theory.

There seems to be no reason to discredit the Brown-Roeper theory of cyathial structure, but this does not mean that the problems are all "solved," for a number of fascinating questions remain. There is a considerable gap between the primitive cyathium of *Anthostema* and that of the various genera of Euphorbiinae, and it is not apparent which, if any, of the cyathia of existing taxa should be regarded as most "primitive." One curious feature, for example, is that the cyathia of the more primitive genera of Euphorbieae tend to be mostly four-merous, whereas those of the Euphorbiinae are commonly five-merous. The nature of the male "bracteoles" and partitions is still not entirely clear, and the evolution of the involucral nectaries also requires considerably more study. Presumably, appendiculate nectaries have been derived from unappendaged ones, judging from the condition in *Anthostema* and those species of *Euphorbia* with an evolute female calyx; but nectary appendages can be lost and a secondarily exappendiculate condition attained (e.g., in subg. POINSETTIA and in *Chamaesyce*). In species such as *E. Ipecacuanhae*, which stands on the borderline between subg. ESULA and subg. AGALOMA, it is far from clear whether the nearly exappendiculate condition is primary or secondary.

Except for the relative development of the calyx, the female portion of the cyathium is very stereotyped in all Euphorbieae, there always being a single terminal female flower (the apparent lateral position in *An-*

thostema seemingly due to differential growth). The main exception involves species with a tendency to unisexual cyathia, in which the female flower is reduced to a vestigial structure or is even entirely absent. Roeper pointed out that the first cyathium terminating the axis (in species of subg. ESULA) is often male, whereas cyathia on ultimate branches are either hermaphroditic or female. This initial production of male cyathia followed by hermaphroditic ones may be seen in many taxa of Euphorbieae, including the succulent species of subg. EUPHORBIA and subg. POINSETTIA.

A minor and perhaps unimportant controversy has surrounded the questions of the basic structure of the male part of the cyathium. The classic explanation espoused by Wydler (1843) envisioned the male flowers as borne in five monochasia (cincinni), the "paleae" within the cyathium being the modified bracteoles of the individual male flowers. Schmidt & Haber proposed a modification in which each male partial-inflorescence is regarded as a once-branched dichasium with a pair of monochasial branches. Schoute has judiciously considered this theory and rejected it as unconvincing; and, in fact, the male cymes of *Euphorbia* are usually so highly reduced that definitive proof may be impossible, making extended discussion of the problem profitless. An interesting analysis of the male inflorescence pattern was presented by Mansfeld in his description of *E. Tessmannii* Mansf., of sect. ADENORIMA (Raf.) Webster.[33] The cyathia of this plant have a pair of conspicuous bracts subtending the two male flowers of each cyme, and thus closely approach the Australian *E. paucifolia* (§ CALYCOPEPLUS (Planch.) Boiss.), except that the latter has four-merous rather than five-merous cyathia. It seems likely that the typical euphorbian cyathium, with the involucre partially divided by five partitions at the base, may be derived from these less highly modified cyathia in sect. ADENORIMA by fusion of the major male bract-pair, together, perhaps, with some of the bracteoles associated with flowers at distal forks of the monochasia.

The floral biology of *Euphorbia* is still rather poorly known, despite a considerable number of scattered observations. Many European species of subg. ESULA are pollinated primarily by flies (especially Muscidae, Syrphidae), but visits from a variety of other insects (small bees, beetles, etc.) have also been commonly recorded. In most species hermaphroditic cyathia are distinctly proterogynous, but since the first one or few cyathia produced in the inflorescence are often entirely male (e.g., in *E. Cyparissias*, *E. Peplus*, and *E. platyphylla*), the plant as a whole may be proterandrous. Gramuglio reports that over 70 per cent of plants of *E. dendroides* examined in Sicily had both the primary terminal cyathium and the first cyathia of the branches entirely male. Autogamy has been reported for *E. Peplus* (which may account for its success as a greenhouse weed) and probably occurs in other annual species as well.

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[33] *Euphorbia* sect. **Adenorima** (Raf.) Webster, stat. nov. *Adenorima* Raf. Fl. Tellur. **4:** 112. 1838. TYPUS: *E. punicea* Sw.

In view of the relatively unspecialized pollination mechanism in *Euphorbia*, it is rather surprising that so few hybrids have been reported. Most of the recorded instances involve European species of sect. ESULA, especially *E. Cyparissias*, *E. Esula*, *E. lucida*, and *E. virgata* (Zimmermann); and it is interesting that no crosses have been reported between species in sect. TITHYMALUS and sect. ESULA. During the 20th century, some of these European weeds have been introduced into North America, and Moore has reported on the situation in Canada. Here *E. Cyparissias* occurs in two forms: a fertile tetraploid race ($2n = 40$) and a sterile diploid race ($n = 20$). According to Moore, *E. Esula*, a hexaploid species ($2n = 60$), has been introduced into temperate North America in a number of places where it has become a troublesome weed, and has occasionally crossed with the tetraploid race of *E. Cyparissias* to give rise to an infertile hybrid which resembles the European population designated as *E.* × *pseudo-Esula* Schur. The chromosomal pairing in the hybrid, with an average of nearly 20 bivalents, suggests that *E. Esula* may possibly be an allopolyploid originating from a cross between *E. Cyparissias* and some as yet unidentified diploid taxon. In our area *E. Esula* has not yet been recorded, but judging from its spread during the past 50 years, both it and the hybrid with *E. Cyparissias* may eventually be found in the Appalachian uplands.

The only group of native U. S. species in which extensive hybridization is suspected is sect. TITHYMALOPSIS: *Euphorbia Ipecacuanhae* is not only a notoriously variable species, but it is also suspected of crossing with related taxa. However, the complex has not been carefully studied, and reports in the literature are conflicting. Fernald (Gray's Manual, ed. 8, 1950) regarded *E. arundelana* Bartlett, a Maryland population differing from *E. Ipecacuanhae* in having distinctly appendaged cyathial glands, as a possible hybrid between that species and *E. marilandica* Greene. Gleason (New Britton and Brown, 1952), on the other hand, has interpreted both *E. arundelana* and *E. marilandica* as hybrids between *E. Ipecacuanhae* and *E. corollata*. Although Gleason's view seems more plausible, the southeastern taxa of sect. TITHYMALOPSIS obviously are in need of thorough monographic studies.

The great diversity in chromosome size and number within *Euphorbia* (*sensu lato*) exceeds that known in any other genus in the Euphorbiaceae (Perry). Although a considerable number of chromosome counts have been published since Perry's work, variation in subg. ESULA still appears to equal that of all of the other subgenera combined. In sect. TITHYMALUS basic numbers of 6, 7, 8, 9, and 10 have been reported, as well as higher numbers of uncertain origin; these include 11 diploid counts, 4 tetraploid, and 1 hexaploid. Section ESULA includes taxa with $x = 7, 8, 9$, and 10, based on 19 diploid counts, 7 tetraploid, 1 hexaploid, and 1 octoploid. It is difficult to draw any firm conclusions from these data, partly because of the bewildering diversity of karyotypes and partly because of conflicting reports on several species which suggest that some of the published counts may be erroneous. Contrary to the impression given by Perry, the majority of the perennial taxa reported on in sect. TITHYMALUS are diploid, whereas the annuals are about equally divided between diploids and polyploids. Most annuals have relatively small chromosomes, while some of the perennials have distinctly large ones; but the chromosomes in some perennials are small, including even those in some diploid taxa (*E. Paralias*, *E. terracina*); and one annual (*E. Lagascae*) has large chromosomes.

Perry suggested that $x = 8$ is the probable basic number, partly on the questionable assumption that annual species are primitive. In subg. ESULA, $x = 8$ is the commonest basic number in the annuals (six species), but five annual species have $x = 7$. Among the perennials, the situation is quite different; eight species have $x = 8$, but 16 have $x = 9$ or 10. On the basis of present evidence, ten seems the most probable original basic number for subg. ESULA, and perhaps for *Euphorbia* (*sensu lato*) as a whole. Before this cytological information can be of much use in either classification or construction of phylogenies, many of the old reports need to be checked and a broader range of taxa needs to be investigated. Even on the basis of the present small percentage of counts, it seems probable that subg. ESULA (*sensu* Wheeler) is more diverse than the other taxa, but additional investigations may produce some surprises. At present, and despite certain conflicting accounts, it appears that in subg. EUPHORBIA $x = 10$, while $x = 7$ in subg. AGALOMA. Extremely high polyploidy (10-ploid or more) is known only in certain species of subg. EUPHORBIA.

Embryological studies have already yielded results of considerable taxonomic interest, and these should be carried out on a more systematic basis than heretofore. Normal (Polygonum type), monosporic, eight-nucleate embryo sacs have been reported in most of the major taxa (*Euphorbia corollata*, subg. AGALOMA; *E. Milii*, subg. EUPHORBIA; *E. Lathyris*, subg. ESULA sect. LATHYRIS; *E. Helioscopia* et al., subg. ESULA sect. TITHYMALUS; *E. Peplus* et al., subg. ESULA sect. ESULA). Bisporic embryo-sac development of the Allium (Scilla) type has been reported in four species, three of these in subg. ESULA (*E. Lagascae*, in sect. TITHYMALUS, and two related species of sect. ESULA, *E. amygdaloides* and *E. Characias*) and one species in subg. EUPHORBIA (*E. mauritanica*). Tetrasporic types, in contrast, have not been encountered except in subg. ESULA. The 16-nucleate *Penaea* type has been recorded for two taxa in sect. ESULA which may be conspecific (*E. pilosa* L. and *E. procera* Bieb.), while the eight-nucleate Fritillaria type is thus far known only in *E. dulcis* L., of sect. TITHYMALUS. This last species also provides the only authenticated instance of polyembryony in *Euphorbia* (Kapil). Originally reported by Hegelmaier (1901), polyembryony in *E. dulcis* was confirmed by Carano (1926), who showed that at least in var. *purpurata* Thuill. the pollen is sterile and the embryos entirely of nucellar origin. Carano also reported tetrasporic embryo-sac development with fusion of the three chalazal nuclei into a single triploid nucleus, and Kapil (1961) has confirmed that the megagametophyte of *E. dulcis* develops according to the "classical" Fritillaria type.[34] Cesca has now shown that (at least in his Italian material) only the tetraploid biotype, with $2n = 24$, is apomictic by adventitious embryony, and that diploid plants ($2n = 12$) are regularly amphimictic. He has found that the situation is rather complex, since some tetraploid plants produce apparently good pollen even though all tetraploids examined were apomictic; in Carano's opinion this suggests the possibility of a hybrid origin for the tetraploids. So far, however, the other species involved has not been identified, and there is obviously a need for a thorough cytotaxonomic survey of all of the taxa in sect. TITHYMALUS related to *E. dulcis*.

Although the tetrasporic embryo-sac development in *Euphorbia dulcis* is associated with polyploidy and with apomixis, all other instances of aberrant gametogenesis have been reported for diploid species, and no other species of *Euphorbia* is known to be apomictic (in the strict sense, excluding vegetative reproduction). The present need appears to be for a more extensive sampling of gametogenesis in taxa of subg. EUPHORBIA and AGALOMA, where only three species out of more than 500 have been investigated, as well as critical studies of certain additional taxa in subg. ESULA (e.g., *E. Esula* and *E. Cyparissias*, in which chromosomal races are reported and some degree of apomixis is possible).

All species of *Euphorbia* appear to have laticifers which produce abundant latex, containing both rubber and resinous (terpenoid) compounds. Moyer found that the latex of different species could be distinguished by its behavior in electrophoresis (perhaps the first taxonomic study utilizing this technique). However, his results did not throw any appreciable light on intrageneric groupings of affinity, and the technique would seem to be most useful for studying rather closely related taxa within a single section or subsection (see Moyer's work on subg. POINSETTIA).

Because of its usually high resin content, *Euphorbia* latex has not often been exploited as a source of rubber. The only important exception involves *E. Intisy* Drake, of subg. EUPHORBIA sect. APHYLLIS, a shrub or small tree native to arid regions in Madagascar. It was extensively gathered from the wild by the French during the last decade of the 19th century, but has never been brought into cultivation in significant amounts. The latex of certain North African species of subg. EUPHORBIA (*E. officinarum* L., *E. resinifera* Berg) was known in antiquity for the resinous euphorbium it yielded. The resin appears to be a mixture of tetracyclic triterpenoids such as euphol and tirucallol ($C_{30}H_{50}O$) and euphorbol ($C_{31}H_{50}$), together with a variety of other compounds which remain partially unidentified. The latex of a number of species, especially succulent or shrubby ones, contains dangerous poisons which are mostly still uncharacterized chemically.

Future chemotaxonomic studies of Euphorbieae should include investi-

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[34] By right of strict priority, the Fritillaria type ought to be called the *Euphorbia dulcis* type, since Carano's was the first report of this kind of tetrasporic megagametophyte.

gations not only of latex and resins, but of waxes as well. Eglinton has shown that various species of *Euphorbia* have characteristic distribution of different alkanes (saturated paraffinic hydrocarbons) in the cuticular waxes. The results of his study are not very exactly in accord with the taxonomic system, since the alkanes in *E. balsamifera*, with a mode at 27-carbon chains, differ from such presumably closely related species as *E. Regis-Jubae*, *E. atropurpurea*, and *E. Bourgaeana*, in which the modal class includes the 31-carbon alkanes. The latter, on the other hand, are much more similar, insofar as alkane distribution is concerned, to *E. Peplus*, which would certainly not be considered closely related by any taxonomists familiar with the group. Nevertheless, the diversity of alkanes in this relatively small sample suggests that further more extensive surveys might be very rewarding. It would be interesting, for example, to compare critically the alkane composition in the Old World taxa mentioned above with the stem waxes of *E. antisiphylitica* Zucc., candelilla, of Mexico. This is the only species in the genus which currently furnishes a commercially important nonhorticultural plant product; its stem wax, which contains 50–60 per cent n-hentriacontane (a 31-carbon alkane), is the raw material for a flourishing but minor industry in drier parts of the Mexican plateau. About 2–10 million pounds of crude candelilla wax are imported yearly from Mexico into the United States, where the refined product is used mainly as an additive to carnauba wax or (as a hardener) to certain softer waxes. The harvesting methods are extremely wasteful, since entire plants are torn up, leaving no underground parts for regeneration, and only 50 pounds of wax are obtained from boiling the stems of a ton of plants. Nevertheless, due to the abundance of the species and its occurrence in many remote desert areas, its extinction appears unlikely.

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23. **Chamaesyce** S. F. Gray, Nat. Arrang. Brit. Pl. **2:** 260. 1821.

Herbs or subshrubs [rarely large shrubs or small trees], without thickened fleshy roots; main axis of stem abortive above the cotyledons, apparent main axes actually sympodia. Leaves opposite; blade entire or toothed, usually distinctly inequilateral at base, never lobed; stipules present, sometimes connate. Plants monoecious [rarely dioecious]; pseudanthia (cyathia) in pseudoaxillary cymes or solitary; bracts of cymes mostly inconspicuous. Pseudanthium nearly or quite actinomorphic; involucre cup shaped; involucral glands 4 (rarely 5), each usually with a petaloid appendage; female flower solitary; male flowers in 5 monochasia, each of 1 to several flowers. Flowers naked, perianth and disc absent. Male flower monandrous; pollen tricolporate (endocolpus usually conspicuous), perforate-tectate, intinal thickenings often small. Female flower pedicellate; carpels 3; styles free or basally connate, bifid or rarely entire; ovary glabrous or pubescent, sometimes carinate but never verrucose; ovules 1 in each locule, anatropous. Fruit capsular; columella persistent. Seeds terete to angled, testa mucilaginous, smooth to wrinkled or sulcate, ecarunculate; endosperm copious; cotyledons fleshy, broader than the radicle. TYPE SPECIES: *C. maritima* S. F. Gray, an illegitimate substitution for *Euphorbia Peplis* L. (*C. Peplis* (L.) Prokh.). (Classical name used by Dioscorides for some prostrate plant, from Greek, *chamai*, on the ground, and *sykon*, fig; applied to *E. Chamaesyce* L. by Clusius and by Bauhin).

A very natural, if rather weakly defined, genus of some 250 species. The vast majority (at least three-fourths) of the species are American, and it seems probable that the genus originated in the New World. As pointed out by various recent authors (Croizat, Dressler, Burch, Hurusawa), *Chamaesyce* is easily distinguishable from the vast majority of species in other taxa of Euphorbiinae by having the main stem abortive just above the level of the cotyledons. Roeper long ago showed that the entire aërial portion of a *Chamaesyce* plant is therefore more or less "homologous" with the inflorescence of plants in *Euphorbia* subg. ESULA. The peculiar internal leaf structure in *Chamaesyce*, with chlorophyll concentrated in the vein-sheaths, is therefore explicable on the assumption that these apparent foliage leaves are actually transformed bracts (cyathophylls). Croizat and Degener have claimed that even the shrubby and arborescent Hawaiian taxa of *Chamaesyce* display this abortion of the main axis as an ancestral "vestigial" character and that the apparent main stem is really a pseudoaxis developed from one of the flowering sympodia. Further observations on the Hawaiian and other shrubby taxa are desirable in order to test this interesting hypothesis.

Conservative American taxonomists (Fernald, Gleason, Wheeler, *et al.*) have treated *Chamaesyce* as a subgenus of *Euphorbia* (subg. CHAMAESYCE Raf.), whereas it has been adopted as a genus by Millspaugh, Small, Croizat, and such recent "extremists" as Shinners, Dressler, and Burch. However, the arguments for retaining *Chamaesyce* at subgeneric rank boil down to two: a distaste for cutting up *Euphorbia* into a number of smaller genera (with an attendant multitude of new combinations) and the difficulty in defining the segregate genus exactly. The first argument, which merely indicates the role of inertia in taxonomic practice, may be dismissed on operational grounds. For North American taxa, at least, nearly as many combinations are now available under *Chamaesyce* as under *Euphorbia*. The difficulty in writing an unequivocal generic diagnosis of *Chamaesyce* is real, but not greater in actuality than for many other euphorbiaceous genera. A few species in Texas and Mexico do seem to stand on the boundary line between *Chamaesyce* and *Euphorbia* subg. AGALOMA, but further study may result in a more positive disposition of these and a better definition of generic boundaries. Since *Chamaesyce* includes a large number of widespread species recognizable by a characteristic habit, its recognition as a distinct genus seems sufficiently expedient; but those who prefer strict logic in classification will probably prefer to retain it as a subgenus of *Euphorbia*.

The infrageneric taxa of *Chamaesyce* have never been very well defined, partly because the genus is rather homogeneous for its size and lacks obvious major groupings of related species. The seven groups named by Small are fortunately illegitimate, as their rank was left unspecified. Hurusawa has recognized three sections, which, however, are simply three Boissieran subsections inflated in rank.

In the southeastern United States about 20 species of *Chamaesyce* are known, of which a number are restricted to southern Florida. Section SCLEROPHYLLAE (Boiss.) Hurusawa, a pantropical group of about 30 insular or maritime species, is represented by *C. mesembrianthemifolia* (Jacq.) Dugand (*C. buxifolia* (Lam.) Small). This plant, which in our region is restricted to coastal areas in southern Florida and the Keys, differs from our other chamaesyces in its fleshy, cordate, entire leaves and erect, articulate stems which are somewhat woody at the base. It occurs throughout most of the Caribbean area, from the Bahamas and Greater Antilles, south to Trinidad and northern South America.

The remainder of our species may be referred to sect. CHAMAESYCE, which includes the great majority of the other taxa in the genus. Most are annual or perennial herbs (very rarely shrubs, as in the Mexican *Chamaesyce perlignea* (McVaugh) Webster),[35] with thinner, often toothed

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[35] **Chamaesyce perlignea** (McVaugh) Webster, comb. nov. *Euphorbia perlignea* McVaugh, Brittonia **13**: 185. 1961.

leaves and usually nonarticulate stems. The several hundred taxa of sect. CHAMAESYCE constitute a vast complex of both New and Old World taxa, within which it is difficult to demarcate infrasectional groupings. In the absence of any clear alternative, the system of Boissier is diffidently followed here.

One of the better-marked groups within sect. CHAMAESYCE is subsect. HYPERICIFOLIAE Boiss., which includes mostly coarse, erect, annual species with rather large, serrate leaves, involucres in stalked cymes, and smooth seeds. Burch has recently presented a review of the confused nomenclatural history in the group, and has convincingly defended the application of names made by Boissier to such species as *Chamaesyce hypericifolia* (L.) Small (*Euphorbia glomerifera* of Wheeler) and *C. nutans* (Lag.) Small (*Euphorbia maculata* of Wheeler). Most of the local taxa of the subsection are quite weedy, and the native range of several of them is now difficult to determine.

The rest of our species, with annual or perennial rootstocks, often spreading or prostrate stems, smaller often entire leaves, and prevailingly solitary cyathia, may be referred to subsect. CHAMAESYCEAE Boiss. This is a very large group of more than 200 described species, including most of the representatives of *Chamaesyce* in temperate regions. The 18 Southeastern species belonging here may be assigned to four circles of affinity, here designated as series. Series PEPLIDES Webster[36] comprises about a dozen holarctic annual species, most of them American, except for the Eurasian *C. Peplis* (L.) Prokh. and *C. humifusa* (Willd.) Prokh. Some of these species tend to prefer sandy habitats, and most of the seven in our range occur on beaches or dunes. In the Carolinas *C. polygonifolia* (L.) Small and its smaller-seeded relative *C. ammannioides* (HBK.) Small are sympatric, while in Florida and along the Gulf coast only the latter is found. One endemic species, *C. cumulicola* Small, occurs in southern Florida.

Much weedier than those in the preceding series, and common along roadsides and in fields, are the species in ser. PROSTRATAE Webster.[37] This series of more than 50 species, which includes most of the African and Eurasian species of *Chamaesyce*, is almost equally represented in the Old and New worlds. At least five have been recorded from our area, including that nearly ubiquitous weed of temperate regions, *C. maculata* (L.) Small (*Euphorbia supina* of Wheeler). Tropical weeds such as *C. thymifolia* (L.) Millsp. are, in contrast, found only in southern Florida. No endemic Southeastern species belong to this series.

Closely related to ser. PROSTRATAE is ser. ADENOPTERAE Webster,[38] a

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[36] Series **Peplides** Webster, ser. nov.; herbae glabrae saepe annuae, caulibus prostratis, foliis integris vel vix denticulatis, capsulis seminibusque laevibus. TYPUS: *Euphorbia Peplis* L.

[37] Series **Prostratae** Webster, ser. nov.; herbae annuae, caulibus prostratis, foliis saepe puberulis plusminusve denticulatis, capsulis puberulis, seminibus sulcatis. TYPUS: *Euphorbia prostrata* Ait.

[38] Series **Adenopterae** Webster, ser. nov.; herbae annuae, caulibus prostratis, foliis

small taxon of less than ten species differing mainly in the appendages of the cyathial glands, two of which are usually much larger than the other two, giving a very zygomorphic appearance to the cyathium. Species of ser. ADENOPTERAE are apparently native to both hemispheres, although the group seems probably to be of American origin.

Perhaps the most interesting group of *Chamaesyce* in the southeastern United States is the complex of perennial hirsutulous-leaved plants of southernmost Florida. As interpreted by Burch, there are four species endemic to limestone substrates in this area: *C. deltoidea* (Engelm. ex Chapm.) Small, *C. Garberi* (Engelm. ex Chapm.) Small, *C. pinetorum* Small, and *C. Porteriana* Small. Many other Floridian species proposed by Small have been reduced to subspecific rank or outright synonymy by Burch. These endemic taxa of Florida do not fit into ser. Peplides because of their hirsutulous foliage and perennial habit, and their closest relationships appear to be with endemic species in the Bahamas and other parts of the West Indies. Because of uncertainty as to the demarcation of this West Indian complex, which is also related to species of Mexico, no formal series is created for them at this time.

Considering the abundance of the weedy species of *Chamaesyce*, the genus has been surprisingly little studied cytologically. Reports have been published for only eight species, and these are somewhat contradictory. Nevertheless, these few counts show a considerable diversity in chromosome number and suggest that a thorough cytotaxonomic study might be most useful in defining infrageneric taxa. At present, no counts have been reported for any species of sect. SCLEROPHYLLAE.

In sect. CHAMAESYCE subsect. HYPERICIFOLIAE, three species have been reported on, and for each there are two conflicting reports (*Chamaesyce hirta*, $2n = 12, 20$; *C. hypericifolia*, $2n = 16, 28$; *C. nutans*, $2n = 12, 14$). It is difficult to say whether these discrepancies are due to faulty technique, misidentifications, or intraspecific aneuploidy. D'Amato regarded Perry's report of $2n = 14$ in *C. nutans* as probably incorrect; if so, this would establish $x = 6$ in two species but would still leave *C. hypericifolia* discordant.

Four species have also been reported from subsect. CHAMAESYCEAE, three of these from ser. PROSTRATAE: *Chamaesyce granulata*, $2n = 40$; *C. maculata*, $2n = 28$; *C. thymifolia*, $2n = 18$. One species from ser. PEPLIDES, *C. Peplis*, has been studied; it proves to have $2n = 12$. No reports are available for any species of ser. ADENOPTERAE. The results of cytological studies until now are baffling and unsatisfactory. Although basic numbers of 6, 7, 8, 9, and 10 can be inferred from the data, only $x = 6$ seems reasonably demonstrated; other reported numbers require further substantiation. One additional count of $2n = 86$ in *C. cristata*

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plusminusve puberulis, appendicibus manifeste inaequalibus, seminibus sulcatis. TYPUS: *Euphorbia adenoptera* Bertol. = *Chamaesyce adenoptera* (Bertol.) Small.

Chamaesyce rosea (Retz.) Webster (comb. nov., based on *Euphorbia rosea* Retz. Obs. Bot. **4**: 26. 1786), a perennial species of India, has not been accounted for in the diagnosis of the series since it may not be directly related to the other species.

(Heyne) Webster,[39] belonging to the Indian subsect. ELEGANTES Boiss., suggests that both polyploidy and amphiploidy may be important in the evolution of the genus.

Very little has been published about the reproductive biology of any species of *Chamaesyce*. Almost nothing is known of pollinating mechanisms, for example, except that Krombein has reported visits to *C. albomarginata* by small Hymenoptera and Diptera; and Von Veh has reasonably suggested that self-pollination is common in the weedy annual species. The cyathia of *Chamaesyce* tend to be proterogynous, as in *Euphorbia*, and are sometimes unisexual. A very high percentage of seed is set even in isolated plants in the greenhouse, but there is no evidence that this is due to apomixis, since only normal-type embryo-sac development has been reported in the five different species studied. As in many other Euphorbiaceae, but not in all Euphorbieae, the nucellus is elongated into a prominent beak in most species of *Chamaesyce* which have been studied. The tricolporate, reticulate pollen is shed in the three-celled condition and shows the intinal thickenings characteristic of most Euphorbieae.

The studies of Von Veh and those on the Hawaiian species by Degener & Croizat suggest that all species of *Chamaesyce* have in common a characteristic ontogeny: the main axis of the stem aborts above the first one or two pairs of leaves beyond the cotyledons, and further growth is produced by shoots axillary to the leaves (and sometimes axillary to the cotyledons as well). The apparent "stems" of *Chamaesyce* are then sympodial inflorescence axes, since each pair of leaves subtends a terminal but often apparently axillary cyathium. As discussed by several authors and illustrated by Hurusawa, the aërial portion of a *Chamaesyce* plant is then topologically equivalent to the inflorescence in plants of subg. ESULA, and the leaves in *Chamaesyce* are homologous with the bracts or "cyathophylls" of other Euphorbieae.

Although a number of shrubby species of *Chamaesyce* are known, the ontogenetic characteristic strongly suggests an herbaceous ancestry for the genus. Such taxa as the Mexican shrub *C. perlignea* and the Hawaiian taxa of subsect. GYMNADENIAE Boiss. — even including the arborescent *C. Rockii* (Forbes) Croiz. & Deg. — are therefore secondarily woody. The inflorescence-dominated vegetative structure of *Chamaesyce* is relatively highly specialized in the Euphorbieae and represents the opposite extreme, in a way, to some of the succulent species of *Euphorbia* in which the monopodial vegetative body is predominant and the inflorescences are relatively inconspicuous.

The closest relationships with *Chamaesyce* are to be found among those taxa of *Euphorbia* subg. AGALOMA which have prevailingly opposite stipulate leaves and appendiculate cyathial nectaries. Within that subgenus, sect. ZYGOPHYLLIDIUM seems especially close, since some species have ecarunculate seeds and strictly opposite leaves. Such North American species as *C. florida* (Engelm.) Millsp. and *C. revoluta* (Engelm.) Small,

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[39] **Chamaesyce cristata** (Heyne) Webster, comb. nov. *Euphorbia cristata* Heyne ex Roth, Nov. Sp. 226. 1821.

with scarcely inaequilateral leaves, look suggestively similar to *Euphorbia* (*Zygophyllidium*) *hexagona* Nutt. and *E. exstipulata* Engelm., of the same geographic region. There are a few species, including some of those placed in *Euphorbia* subsect. PLEIADENIAE of sect. ANISOPHYLLUM (i.e., *Chamaesyce*) by Boissier, which actually appear to be transitional between *Chamaesyce* and subg. AGALOMA.[40] *Euphorbia innocua* Wheeler, of sect. TITHYMALOPSIS, from coastal sands in southern Texas, is an almost textbook-model of a hypothetical intermediate. It has a growth habit very similar to prostrate species of *Chamaesyce* but differs in having its leaves alternate below and with equilateral bases. The origin of the distinctive characters of *Chamaesyce*, on the testimony of this and other species, may be a consequence of the assumption of a geophilous habit in the AGALOMA-like ancestors. Although the evolutionary history may have been very complex, a crude model of the sequential origin of *Chamaesyce* from *Euphorbia* is provided by the following sequence of species: (1) *E. inundata* (subg. ESULA); (2) *E. Ipecacuanhae* (subg. AGALOMA, sect. TITHYMALOPSIS, subsect. IPECACUANHAE); (3) *E. innocua* (subsect. INNOCUAE); (4) *C. potentilloides* (Boiss.) Croiz.; (5) *C. acuta* (Engelm.) Small; (6) *C. hypericifolia* (L.) Small.[41] A number of interesting species on the boundary line between *Chamaesyce* and *Euphorbia* remain to be investigated; only further study can show whether such puzzling species as the Brazilian *E. peperomioides* Boiss. (which has a remarkable resemblance to *E. innocua*) should be placed in *Chamaesyce*.

It should be noted that the initial species in the suggested phyletic sequence given above has exappendiculate cyathial glands and exstipulate leaves. The stipules in *Chamaesyce* are better developed than in almost any taxon in *Euphorbia*, except possibly in some succulent species. The presumed ancestral type of *Chamaesyce* would therefore be a plant combining characters of both subg. AGALOMA and subg. ESULA, so that despite the rather high degree of morphological specialization *Chamaesyce* would seem to have branched off early in the differentiation of major taxa of the subtribe Euphorbiinae. On a phyletic basis, therefore, it may be as distinctive a group as *Pedilanthus*, if not more so. Nevertheless, the degree of inflorescence divergence is much less in *Chamaesyce*, and there are enough "transitional" species to make its boundary with *Euphorbia* somewhat fuzzy. Those who wish to maintain *Euphorbia* in its traditional limits may therefore wish to treat the group in question as *Euphorbia* subg. CHAMAESYCE Raf.; but logical consistency would then seem to demand that *Pedilanthus* also be included as a subgenus of *Euphorbia*.

On the whole, plants of *Chamaesyce* are not particularly attractive;

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[40] At least one species of subsect. PLEIADENIAE, *Euphorbia macropus* (Kl. & Garcke) Boiss., must be placed in subg. AGALOMA, rather than in *Chamaesyce*, because of its 5-glandular cyathia and equilateral leaves which lack chlorophyllous vein sheaths.

[41] These species, no one of which is directly ancestral to the next, illustrate the following sequential changes: 1 → 2, from unappendaged to narrowly appendaged glands, exstipulate to stipulate leaves; 2 → 3, inconspicuously to conspicuously appendaged glands; 3 → 4, leaves alternate below to entirely opposite; 4 → 5, reduction from five glands to four; 5 → 6, perennial to annual habit.

there is no record of the intentional widespread cultivation of any species. Any possible economic importance would seem to be negative, since many species are undesirable weeds and few are both sufficiently large and abundant to serve as sources of latex. The arborescent Hawaiian species of sect. SCLEROPHYLLAE have been investigated as a possible source of rubber (McGeorge & Anderson), but the trees are limited in distribution, and the latex, with over 55 per cent resin, does not appear to be of a commercially promising quality. In common with species of *Euphorbia* (mainly subgenera ESULA and EUPHORBIA), various weedy species (e.g., *C. hypericifolia*, *C. prostrata*, *C. thymifolia*) have been shown to harbor trypanosomes of the genus *Leptomonas* in their laticifers (see Mesnil, and references under *Euphorbia*).

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24. **Pedilanthus** Poiteau, Ann. Mus. Hist. Nat. Paris **19**: 388. 1812, nom. cons.

Trees or shrubs, twigs and foliage more or less succulent, with whitish [rarely yellow] latex. Leaves alternate, distichous, deciduous or persistent, stipulate; blade entire, pinnately veined, eglandular. Plants monoecious; inflorescences bisexual pseudanthia, these borne in terminal or (by reduction) lateral dichasia. Pseudanthium (cyathium) bilaterally symmetrical, the involucral tube produced into a posterior spur containing 4 [or, by modification, 2 or 6] glands; female flower solitary in the cyathium, central; male flowers in 5 more or less bracteolate monochasia. Flowers lacking a perianth; disc undeveloped. Male flower monandrous, simulating a stamen; filament separated from pedicel by an articulation; anther dehiscing longitudinally and abaxially; pollen tricolporate, perforate-tectate, with paired intine thickenings parallel to the colpi. Female flower pedicellate; perianth perhaps represented by a disciform structure at base of ovary; carpels 3; styles connate along most of their length into a slender column much longer than the ovary; style tips bifid; ovary angled or carinate; ovules 1 in each locule, anatropous; nucellus short-beaked; embryo-sac development normal. Fruit capsular [rarely indehiscent]; columella slender, expanded distally. Seeds subterete, testa smooth or minutely tuberculate, ecarunculate; endosperm copious; embryo straight, cotyledons somewhat fleshy, broader than the radicle. (*Tithymalus* sensu Small.) LECTOTYPE SPECIES: *P. Tithymaloides* (L.) Poit.; see Millspaugh, Field Mus. Publ. Bot. 2: 353. 1913. (Name from Greek, *pedilon*, sandal, and *anthos*, flower.) — SLIPPER-SPURGE.

A very natural and well-characterized genus of 14 neotropical species, mostly concentrated in Mexico. Dressler has given the genus an exhaustive revision and provided an excellent model and stimulus for further work in the tribe Euphorbieae; the present account leans heavily on his work.

Our single native species is *Pedilanthus Tithymaloides* (L.) Poit., $2n = 34, 36(?)$, which is represented in Florida by ssp. *Smallii* (Millsp.) Dressler, a shrub up to 2 m. high with succulent, conspicuously zig-zag stems. It has been collected in pinelands and hammocks from the eastern shore of Lake Okeechobee, south to Meigs Key (Monroe County), as well as in northern Cuba, near Matanzas. Dressler regards this Floridian subspecies as closely related to ssp. *parasiticus* (Kl. & Garcke) Dressler, of Central America and the Greater Antilles, and suggests that both taxa may have invaded the West Indies from northern Central America. If his reconstruction of the migrational history is correct, this species has made a remarkable double invasion of the West Indies: once from Central America to Cuba and Florida, and once from the northern coast of South America via the Lesser Antilles to the Greater Antilles. Unfortunately, the popularity of the species as a hedge-plant has led to its cultivation and escape in many areas, so that the provenance of many older collections may be doubtful. In the Miami area ssp. *Tithymaloides* (and perhaps other subspecies) is cultivated and may possibly be found escaped to some extent; it may usually be distinguished from ssp. *Smallii* by its straight, rather than zig-zag, stems, but identification of the variegated-leaved cultivars is often difficult.

Pollination of the slipper-like cyathia by hummingbirds has been reported for two species by Dressler, doubtless to the relief of the ethologists who had dubbed *Pedilanthus* a "humming-bird flower" on the basis of circumstantial (i.e., purely morphological) evidence. Additional observations, including studies in Florida, are much needed. Dressler has not unreasonably speculated that the unusual bilaterally symmetrical conformation of the *Pedilanthus* cyathium represents an "adaptive peak" attained as a result of pollinator selection from an ancestral type of regular involucre.[42]

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[42] Croizat has recently (1962) launched a violent attack on Dressler's "ornithogenetic" model of the origin of the cyathium of *Pedilanthus*. It is true that this hypothesis is speculative and largely circumstantial, particularly with regard to estimations of geological time. I hope, however, that Croizat does not expect that taxonomists will resign themselves merely to turning out compendia of data, thereby eschewing attempts to synthesize a unified picture of the phenomena they are investigating. Croizat's own "explanation" of the cyathium of *Pedilanthus* is not especially illuminating, perhaps because he has been overly influenced by Bodmann's misleading work on *Euphorbia*. To the extent that morphologists have neglected developmental considerations and attempted to draw mechanical one-to-one homologies between organs such as the parts of the cyathium, some of Croziat's comments are

According to Dressler, *Pedilanthus* is related to and has been derived from *Euphorbia* subg. AGALOMA, with which it corresponds in many respects, differing mainly in its zygomorphic cyathia. As clearly shown in Dressler's diagrams, the projecting anterior "beak" of the *Pedilanthus* cyathium is formed mainly from a pair of involucral bracts, whereas the posterior spur has been derived mainly from the remaining three bracts and the four adjacent partially connate (and highly modified) gland appendages. The closest surviving species to the putative "ancestral type" is perhaps the familiar Mexican species *Euphorbia fulgens* Karw., of sect. TRICHEROSTIGMA (Kl. & Garcke) Boiss., which has alternate leaves and brilliant-red petaloid appendages; a plant of this kind might be considered "pre-adapted," in the Dresslerian sense, to enter on the road of ornithophilous evolution. At least two other taxa of *Euphorbia* have followed a convergent path of adaptation to red-colored cyathia with modified nectaries, but Dressler appears to be correct in regarding these as unrelated to *Pedilanthus*. *Euphorbia* subg. POINSETTIA appears to have had a different source within subg. AGALOMA (i.e., a taxon such as sect. DICHILIUM with a tendency toward opposite leaves and reduction in number and appendages of cyathial glands). The West Indian genus *Cubanthus* (Boiss.) Millsp., which was included in *Pedilanthus* as sect. CUBANTHUS by Boissier and treated as a genus by Dressler and Millspaugh, differs strongly from *Pedilanthus* in its basically actinomorphic cyathia with exappendiculate glands. As pointed out by Dressler, it stands quite apart from both *Pedilanthus* and subg. POINSETTIA, and appears to have been derived from sect. ADENORIMA of subg. ESULA. Comparative studies of pollinating agents in these three groups, although necessitating field work in some difficult areas, would be of great evolutionary interest and might help elucidate certain aspects of cyathial evolution in the more primitive neotropical Euphorbieae.

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apropos. However, in my opinion, he goes too far in adopting a counsel of despair which assumes that "glands, lobes, etc." of the *Pedilanthus* cyathium are morphologically indefinable. While it may not be worth much time or effort to quibble over whether, for example, the cyathial glands are stipular in nature, careful comparative studies of systematically well-understood taxa certainly ought to bring workers closer to a unanimity of opinion on controversial interpretations. In point of fact, there seems to be no reason to doubt that the cyathial glands in both *Euphorbia* and *Pedilanthus* are essentially homologous with the bracteal glands in the Hippomaneae and that they do *not* represent metamorphosed flowers. On the other hand the homologies of the glands of primitive Euphorbieae such as *Neoguillauminia* remain dubious, and further study of the cyathia of that remarkable plant is indicated.

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ADDENDA

(1) Beguiled by long usage of and excessive familiarity with the subfamily name Crotonoideae Pax, the author [and editor] failed to notice that since it includes the type genus of the family (*Euphorbia*), the subfamily must under the current rules of nomenclature take the name Euphorbioideae. Consequently, the reader should substitute Euphorbioideae for Crotonoideae wherever it occurs in the earlier part of the text.

(2) The following reference was omitted from the general bibliography (Jour. Arnold Arb. **48:** 315):

CHANDLER, M. E. J. The Lower Tertiary floras of southern England. I. Palaeocene floras. London Clay flora (supplement). xi + 354 pp. Atlas, *34 pls.* (separately bound). Brit. Mus. (Nat. Hist.), London. 1961 [Euphorbiaceae, 203–211]; II. Flora of the pipe-clay series of Dorset (Lower Bagshot). xi + 176 pp. *29 pls.* Brit. Mus. (Nat. Hist.), London. 1962 [Euphorbiaceae, 80–90].

(3) In the generic key (Jour. Arnold Arb. **48:** 322), the final part of the second lead A should read: pollen colporate, porate, or inaperturate (Subfam. Euphorbioideae).

(4) The generic descriptions of *Manihot* and *Cnidoscolus* are excessively reticent with regard to the calyx; it is pentamerous in both genera.

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FREEMAN AND CUSTIS' ACCOUNT OF THE RED RIVER EXPEDITION OF 1806, AN OVERLOOKED PUBLICATION OF BOTANICAL INTEREST

C. V. Morton

My attention was drawn some twenty-five years ago by the late Dr. John Swanton, of the United States Bureau of American Ethnology, to a small book in the library of the U. S. Geological Survey that was of interest to him for its information on certain Indian tribes. This anonymous book is entitled "An Account of the Red River in Louisiana, drawn up from the returns of Messrs. Freeman and Custis, to the War Office of the United States, who explored the same in the year 1806."[1]

Swanton mentioned this book and quoted extensively from it, in connection with the Caddo Indians, in his book "Source Materials for the History and Ethnology of the Caddo Indians" (U. S. Bur. Am. Ethnol. Bull. 132. 1942). The work is mentioned briefly and with scant regard by William H. Goetzmann in his fascinating and wonderfully documented book "Army Exploration in the American West 1803–1863" on pages 34–36 (Yale University Press). This Freeman and Custis work is of historical and ethnological interest, but in addition it contains lists of plants (including some novelties), animals, birds, insects, amphibians, and so forth, and the plants, at least, have been completely overlooked by subsequent botanists up until the present day. There is, for instance, no mention of this publication at all in Mrs. Susan Delano McKelvey's monumental book "Botanical Exploration of the Trans-Mississippi West, 1790–1850." The botanical part of this narrative is quite interesting, being the first published information concerning the native plants of Louisiana after the Louisiana Purchase, and it includes perhaps the first mention of some important plants, such as the Osage Orange.

HISTORICAL ACCOUNT OF THE EXPEDITION AND THE PUBLICATION

The historical background of the expedition to the Red River is briefly as follows: While the English were colonizing the eastern seaboard of the United States, the French were in control of Canada and Louisiana, which included all the territory on the western side of the Mississippi River, including the present states of Louisiana, Arkansas, Kansas, Missouri, Nebraska, Iowa, North and South Dakota, Minnesota, and Montana. At

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[1] Octavo, 63 pp., 2 folded tables. Without place of publication, without date. The Library of Congress card and Swanton give the date as 1806, but Goetzmann gives it as 1807, and that the latter is probably correct is indicated below (see p. 437).

the end of the French and Indian War, in which the French were disastrously defeated, all of Louisiana was ceded to Spain by the Treaty of Paris, February 10, 1783. However, for reasons best known to Spain and Napoleon, Louisiana was ceded back to France by the secret Treaty of San Ildefonso in 1800. Alarmed by this evidently not so secret treaty, President Jefferson sent James Monroe to Paris to negotiate for the sale of New Orleans, which was needed as a seaport by the settlers in Tennessee, Kentucky, and elsewhere in the Middle West. Surprisingly, Napoleon, at the time in firm control of France as First Consul of the Republic, agreed not only to sell New Orleans but all of Louisiana for $15,000,000, surely the greatest bargain in history since the sale of Manhattan Island to the Dutch by the Indians. The sale was agreed to with alacrity by Jefferson and ratified by the United States Senate in 1803.

Jefferson's first concern was to ascertain the boundaries of the new territory. An expedition to explore the upper part of the Purchase was immediately organized, the Lewis and Clark Expedition of 1803–1806, which was brilliantly successful and justly acclaimed. The Red River, a tributary of the Mississippi River running northwest from about the middle of the present state of Louisiana, was supposed to be the southwestern boundary between Louisiana and the Spanish possessions in Texas and the west. Two expeditions were authorized. One, authorized by Henry Dearborn, Secretary of War, March 30, 1804, was for an expedition under the command of William Dunbar and George Hunter.[2] This expedition got under way October 16, 1804, from St. Catherine's Landing, on the Mississippi River below Natchez. It proceeded up the Red River only about 26 miles, and then turned north on the tributary Black River (now the Ouachita River) and went up into present-day Arkansas. Hunter returned to St. Catherine's Landing on January 31, 1805. The journal of this expedition was in family hands until very recently, but it has now been published as "The Western Journals of Dr. George Hunter, 1796–1805" edited by John Francis McDermott, in the Transactions of the American Philosophical Society (new series, vol. 53, part 4, 1963).

At almost the same time as the Dunbar and Hunter expedition, another expedition to explore the Red River was authorized April 14, 1804, under the command of Thomas Freeman, an expedition doomed to failure and consequently known today only to historians. The expedition was delayed for almost two years by the opposition of the Spanish and also by the Osage Indians, but it finally started April 19, 1806, perhaps using some of the supplies left behind for its use by Hunter after his return the previous year. The party consisted of "Mr. Thomas Freeman, Surveyor,

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[2] Dunbar's account of this expedition has been published from a manuscript in the library of the American Philosophical Society, "Journal of a Voyage Commencing at St. Catherines landing, on the East bank of the Mississippi, proceeding downwards to the mouth of the Red river, and from thence ascending that river, the Black river and the Washita river as high as the Hot-Springs in the proximity of the last mentioned river," in "Documents relating to the Purchase and Exploration of Louisiana." Houghton, Mifflin & Company, 1–189. 1904.

who was furnished with the requisite instruments, for determining geographical positions by astronomical observations; Dr. Peter Custis, whose attention was directed to botany, and natural history; Captain Sparks, and Lieutenant Humphreys, two non-commissioned officers, seventeen private soldiers, and a black servant." The connection, if any, between the Dunbar-Hunter Expedition and the Freeman-Custis Expedition is not at all clear. In Jefferson's letters to Dunbar, quoted by McDermott, there is no mention of Thomas Freeman or Peter Custis.

The party entered the Red River from the Mississippi May 3, expecting to be able to ascend in their boats to the country of the Pawnee Indians. Their orders were [3] to purchase horses from these Indians and to ascend to the top of the mountains, the distance being supposed to be about 300 miles. It is evident that the distance was vastly underestimated. As a matter of fact, the real source of the Red River was unknown and unexplored until the famous Marcy Expedition of 1852, almost 50 years later.[4]

The expedition proceeded upstream through country inhabited by friendly Indians until July 28, when a point was reached that was held by a force of perhaps 300 Spanish cavalrymen under the command of Captain Don Francisco Viana. It is said that by his strategy and diplomacy Mr. Freeman saved the party from destruction. However, from the published account it seems that the Spanish commander was civil and not unfriendly but firm in his purpose not to allow the expedition to proceed. Since the Americans were far outnumbered, there was no alternative but to turn back, which the party did on July 30, arriving back in Natchitoches on August 23. Since the expedition did not reach its destination it was evidently considered a failure, even though it did provide some information on the course of the river, the countryside, the climate, the Indian inhabitants, and the flora and fauna.

The farthest point reached by the expedition, that where it was stopped by the Spanish, has been a matter of conjecture. Sabin [5] summarizes the information as follows:

> "Map makers and later writers are far from agreement as to where on the Red River Freeman was halted by Captain Viana. Thwaites, editor of the James-Long expedition (Early Western Travels, Vol. XVIII) is clearly wrong in stating that the halt occurred where the Little River joins the Red. This is fifteen miles or so east of the Texas-Louisiana north-south boundary and thirty miles or so east of the western boundary of Arkansas.[6] The long note in Wagner-Camp to the 1810 Pike is delightfully indefinite on this point, as is Thomas M. Marshall

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[3] The original orders are in the manuscript division of the Library of Congress.

[4] Marcy, Randolph B. Exploration of the Red River of Louisiana in the year 1852, pp. i–xv, 1–286. 1854. Botany of the Marcy Expedition by John Torrey, *op. cit.* pp. 245–272, *pl. I–XX*. The botanist-collector of the Marcy Expedition was Dr. G. C. Shumard.

[5] Sabin, Joseph. Bibliotheca Americana, A dictionary of books relating to America from its discovery to the present time. **7**: 15. 1875.

[6] Sabin is right; it is obvious from the published account that the expedition proceeded much farther than this point.

FIGURE 1. Photograph of left half of the original "Map of the Red River in Louisiana" of Freeman and Custis.

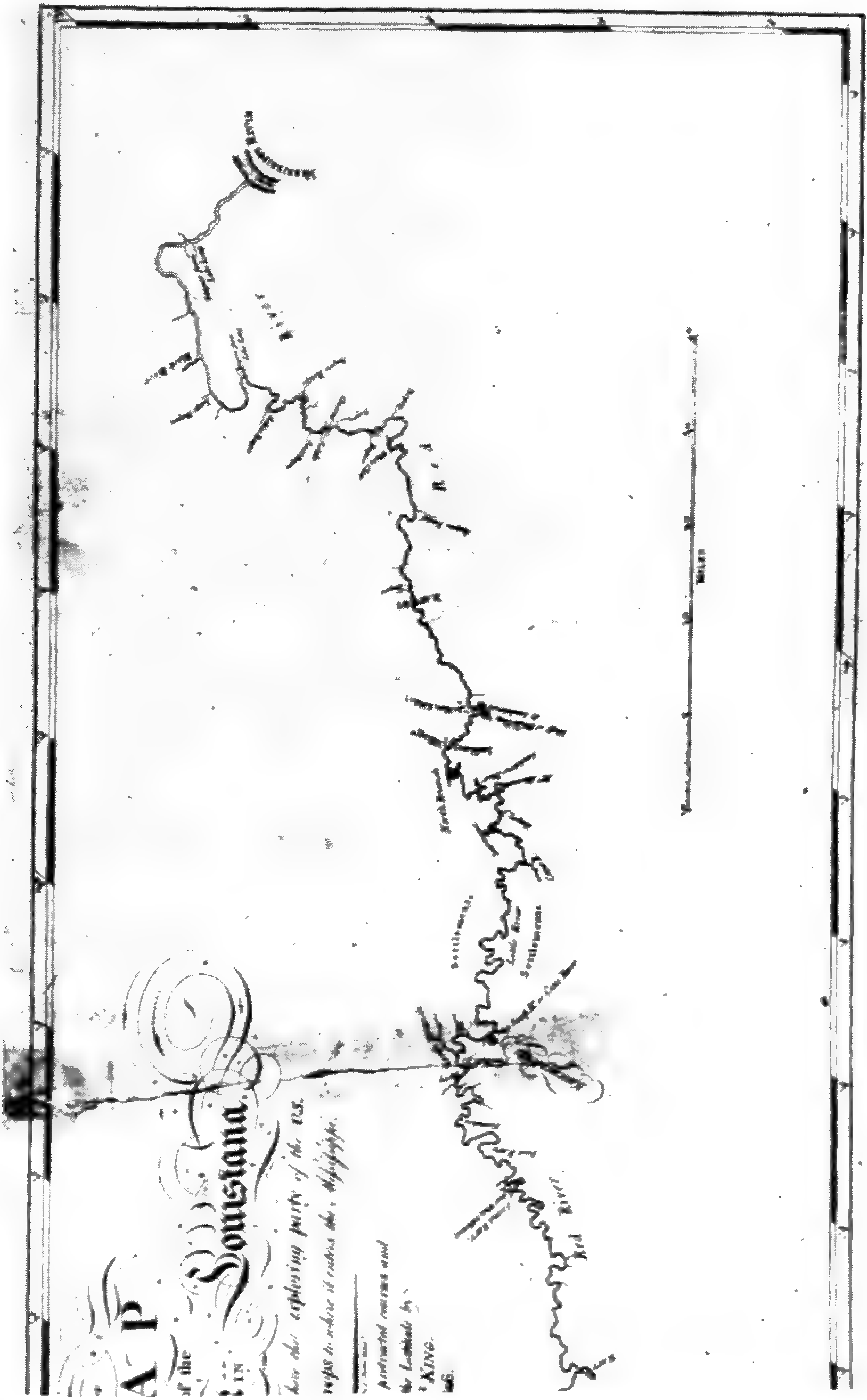

FIGURE 2. Photograph of right half of the original "Map of the Red River in Louisiana" of Freeman and Custis.

in his *History of the Western Boundary of the Louisiana Purchase.* My guess is that the Freeman party was halted near the little Texas village of River View on the Red River about thirty miles or so west of the north-south Texas-Louisiana boundary. This may be the 'handsome bluff' mentioned in the Freeman account. This would fairly well agree with the location for the halt given in the famous Robinson Map of Mexico, Louisiana. . . Philadelphia, 1819 (No. 1073),[7] which places it twenty-five miles or so west of the present Texas-Louisiana line. The map in the Philadelphia, 1810, Pike (No. 1047), 'The First Part of Captn. Pike's Chart of the Internal Part of Louisiana' is invaluable for following the route of the Freeman expedition up the Red River, but its legend for 'the exploring Party stopped here' seems to be too far west by at least a degree of longitude; and Map No. 55, showing Arkansas Territory, in P. M. G. Van der Maelen's *Atlas Universel,* Bruxelles, 1827 (No. 1095), is almost certainly in error in the legend it has at the confluence in Oklahoma of the Red River and Boggy Creek (about 80 miles west of the Texas-Louisiana line), 'La R. rouge a été reconnue jusqu'ici par Th. Freeman.' "

Sabin and the writers mentioned by Sabin seem to have been unaware that the original map of Freeman and Custis was in existence. It is still preserved in the National Archives (Map M33–1); it is reproduced in this paper as FIGURES 1 and 2. This map shows that Sabin was right, that the stop was at or near the present River View, Red River County, Texas, a point very near the Texas-Oklahoma-Arkansas meeting point. The expedition was, therefore, mostly confined to present-day Louisiana, but did traverse the southwestern part of Arkansas, and a short distance along the boundary between Texas and Oklahoma.

The published account of the Red River expedition is a small book of 63 pages, probably always very rare. Copies are in the Library of Congress; U. S. Geological Survey; Bancroft Library, University of California, Berkeley; Howard-Tilton Memorial Library, Tulane University; Boston Athenaeum; Clements Library, University of Michigan; Harvard University; Streeter's Collection, Morristown, New Jersey; and the Maryland Historical Society, Baltimore. The book does not have any place or date of publication. The place was undoubtedly Washington, D.C., as given on the Library of Congress card, which gives the date as "1806?", and Swanton (U. S. Bur. Am. Ethnol. Bull. 132. 1942) gives the date as 1806 without a question mark. However, Custis' final report is dated at Fort Adams, October 1, 1806. For this report to reach Washington (probably requiring several weeks overland by stage coach), and for it to be combined with the previous report and with Freeman's reports, would seem to require too much time to have the account published before the end of 1806. I am indebted to my friend, Mr. A. DeWeese, chief of the Information Desk, New York Public Library, for looking into the matter. He has found a reference establishing the probable date as 1807, which is the date to be expected. Item no. 1040 in Thomas W. Streeter's *Bibliography of Texas* is devoted to this book of Freeman and Custis, and the third paragraph discusses the date of publication as follows:

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[7] These numbers refer to the appropriate entries in Sabin's *Bibliotheca.*

"The 1807 date given here to the Freeman pamphlet was suggested by the late Wilberforce Eames, on what was for me a memorable occasion when, not long before his death, Mr. Eames, accompanied by Lathrop Harper, spent the day with me in Morristown. He pointed out that as the copies of the Freeman pamphlet and the undated *Account of a Voyage up the Mississippi River . . . in the Years 1805 and 1806. Compiled from Mr. Pike's Journal* had come to the Library of Congress and to the Bancroft Library sewn together and as in his copy of the *Account* there was laid in a letter of presentation signed by General Dearborn, the Secretary of War, and dated, 'War Department, March 9, 1807,' there was a strong presumption that the Freeman pamphlet was published early in 1807. Edwin James in his *Account of An Expedition from Pittsburgh to the Rocky Mountains*, Philadelphia, 1823, says he had access to the Freeman journal, now lost, and at pages 306–314 of Volume III gives an account of the expedition which, in places, supplements the Account entered here. There is an interesting article on Freeman in the *Dictionary of American Biography*. That article gives the place where Freeman was halted as 'near where the present boundaries of Arkansas, Oklahoma and Texas meet.' "

Thomas Freeman, who led the expedition, was born in Ireland[8] and emigrated to the United States in 1784. On March 25, 1794, he was appointed to survey a part of the newly created District of Columbia, a survey completed June 25, 1795. After planting the stones for the boundary, he commenced the first topographical survey of the District, but resigned July 7, 1796, to accept an appointment as U. S. surveyor to determine the boundary between the United States and Spain, which at that time held Louisiana in control. After the Red River Expedition, he mapped a part of the boundary between Alabama and Tennessee in 1807. In 1811 he was appointed U. S. Surveyor of Public Lands south of Tennessee, a position he held until his sudden death at Huntsville, Alabama, November 8, 1821.

I have been unable to find out anything definitely about the ancestry of Peter Custis, the botanist who accompanied the expedition, perhaps as a substitute for George Hunter, who, it appears, did not wish to return to the Red River for personal reasons. In spite of its prominence in connection with George Washington and with Robert E. Lee, both of whom had connections through marriage, there is no published genealogy of the Custis family. Peter Custis was the son of one Robinson Custis, of Accomac County, Virginia, in whose will of 1797, he was left a part of the estate for "a Latin education and to be brought up in one of the learned professions."[9] Peter Custis is also mentioned in R. T. Whitelaw's "Virginia Eastern Shore,"[10] where he is said to be a doctor. He did receive the degree M.D. from the University of Pennsylvania in 1807, that is, after he returned from the Red River Expedition. Since he is mentioned in the published account of the expedition as "Dr. Peter Custis" this may indicate that he obtained the degree early in 1807 before

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[8] Dictionary of American Biography. 7: 13. 1931.

[9] This information was kindly supplied by a member of the staff of the New York Public Library who has Custis family connections.

[10] Vol. 2, p. 968.

the account was published or that he was given the title "Dr." in anticipation of his receiving the degree shortly.

The other two leaders of the expedition are not of especial interest in this connection. Richard Sparks was appointed First Lieutenant of the U. S. Infantry in 1791, a Captain in 1792, a Major in 1806 (presumably after his return from the Red River Expedition), a Lt. Colonel in 1807, and a Colonel in 1812. He died in 1815. Enoch Humphreys was appointed Lieutenant, First Artillery and Engineers in 1801, a Captain in 1809, and later a Major. He died in 1825.

Although the Account of the Red River is anonymous, it must be attributed to Freeman and Custis, as it is by the Library of Congress, by Streeter in the work mentioned above, and by Sabin.[11] The work was compiled from one or more reports by Freeman to the Secretary of War and from two reports by Custis, obviously by someone fairly incompetent because of the numerous misspelled words, inconsistencies in punctuation, and especially by the many misspelled scientific names. The original manuscript reports by Custis are still in existence, in the National Archives in Washington, available on microfilm.[12] Custis' handwriting is exceptionally clear but even so the published work has numerous errors of transcription. All the data regarding the natural history of the region and the meteorological data come from Custis, the general remarks regarding the progress of the expedition and the encounter with the Spanish evidently come from a report by Freeman, the manuscript of which is apparently lost. Dr. Custis' second letter, enclosing the final lists, follows.

"Fort Adams
Oct. 1, 1806

"Sir:

"Inclosed I have the honor to forward my last communications, consisting of Lists of such vegetables & animals as you have not already had an account of, together with one of all the trees of Red River & my meteorological observations. — I have to lament that a more complete opportunity had not occurred, that I might have been enabled the better to perform the duties alloted me, but it is a thing well known that a person subject to the movements of another has little, or I might add, no time to make botanical excursions. — With respect to the country it will be unnecessary to say anything, as it is similar to that of which you have before had accounts. I could however report what I mentioned in my last letter that in point of beauty, fertility and salubrity there is not its equal in America, nay in the world. — The water of Red River above Coashatta Village is so strongly impregnated with salt as to render it unfit to drink. When this water is low we find the sand beaches rendered white with salt.

"I have to return my most sincere thanks for the appointment with which you have honored me, & to regret the failure of the expedition. — Permit me, Sir, to tender you my best wishes.

Yrs.
Peter Custis

"The Honble.
Henry Dearborn
Secretary of War."

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[11] Sabin, *op. cit.* 16.

[12] Letters Received by the Secretary of War 1806, M221, Roll 4, C140, C207.

Perhaps the very first list of the trees of the lower Mississippi River region was that given in *The Journal of Andrew Ellicott* (first edition, Philadelphia, 1803, republished by Quadrangle Books, Inc., Chicago, Illinois, 1962). Ellicott's Journal is concerned mostly with political and military matters, but on pages 285 to 289 of the republished edition he gives a list of some of the common trees and other plants. Although he professes himself an indifferent botanist it appears that he did know a good deal, and many of his names are more correct than those supplied later by Custis. Although Ellicott was never on the Red River, many of the same plants occur along the banks of the Mississippi also, and, therefore, it is not surprising that Ellicott should mention many of the same species as those commented on by Custis. There is no indication that Custis ever saw this list of Ellicott; if he had, he might very well have made some changes in his nomenclature.

A list entitled "Common Names of some of the Trees, Plants, Shrubs etc. growing in the Country adjacent to the Ouachita" was prepared by the Dunbar and Hunter Expedition of 1804, probably by William Dunbar. This list is in the Hunter Papers in the library of the American Philosophical Society but was never published until by McDermott in *The Western Journals of George Hunter, 1796–1805*, in 1963 (pp. 120, 121). It consists of common names only; the plants listed are in part the same as those listed by Custis, but they can not be at all definitely determined. Another shorter "List of Vegetables (perhaps non-descripts) from the River Washita" was also prepared, and this also was published by McDermott (pp. 121, 122). This list contains extensive notes on a few plants considered to be of especial interest, among them being the "Bois d'arc" or Osage Orange. There is no reason to believe that Custis saw these lists either.

Peter Custis wrote a letter from Natchitoches, dated June 1, 1806, to his teacher, Benjamin Smith Barton, and signed it "your sincere and ever-devoted Friend and Pupil." This letter contained a brief account of the trip up to that date, and included, of course, a number of the same observations that were published later in the full account. Barton lost no time in publishing this letter, in his "The Philadelphia Medical and Physical Journal, collected and arranged by Benjamin Smith Barton, M. D., Professor of Materia Medica, Natural History, and Botany, in the University of Pennsylvania," vol. 2, part 2, pp. 43–48, Sept. 26, 1806. This is the first published record of the natural history of the expedition, but it also has been completely overlooked. A good many of the trees noted in the later account are also recorded here, including the first mention of *Juglans petiolata* Custis.

Custis presumably did not take along equipment for preparing herbarium specimens which was probably not considered necessary, since this was not primarily a scientific expedition for studying the natural history of the region. Moreover, there would probably not have been room for much equipment in his small boats. His botanical observations were of course based on living material, but he did manage to collect 26 numbers of herbarium specimens, which he enumerated (see below, p. 455) but did not name. These probably represented species that he could not name from the books at hand, and it may be conjectured that most of them were undescribed at the time.

These herbarium specimens were never formally identified and reported on, apparently. They were given to Custis' teacher, Benjamin Smith Barton who, in 1791, had been appointed the first Professor of Natural History and Botany in the United States, according to Francis W. Pennell (The Elder Barton — His Plant-Collection and the Mystery of his Floras, Bartonia **9**: 17–34. 1926). Among the contents of Barton's herbarium Pennell mentions (*op. cit.* p. 21) "Peter Custis specimens from Virginia and '450 miles up the Red River.'" Frederick Pursh was employed in 1806 and 1807 as a collector by Barton and apparently also as a herbarium assistant, since most of the specimens in the Barton herbarium bear determinations in Pursh's hand. It is likely that he saw and may have identified the Custis Red River collections, and it may be that some of these formed the basis of some records in Pursh's later *Flora Americae Septentrionalis* (1814), which was prepared after Pursh went to England. That the Custis specimens have remained unknown is the result of the general neglect of the Barton Herbarium, which, after Barton's death in 1815, was presented to the American Philosophical Society. It was kept but remained essentially unknown and unused until it was turned over to the Academy of Natural Sciences some 80 years or more later. Of course, the Barton Herbarium is historically and botanically very important because it contains more than 800 of the collections of Frederick Pursh. Since the Custis collections do not even bear generic names, except for three indicated as *Mimosa*, *Lonicera*, and *Polypodium*, and they have not been cited in the botanical literature, they can not be otherwise identified.

As may be seen from a perusal of the lists and my commentaries, which follow, Custis' identifications of the plants observed leave much to be desired, but in extenuation one must consider the circumstances. It is hard for us now to realize the paucity of literature existing on the plants of the southern United States in 1806 and particularly on those of the western part, in Louisiana. Michaux's *Flora Boreali-Americana* had appeared in 1803, but it is evident that Custis had not yet seen it, for he mentions none of Michaux's species. He was familiar with Marshall's *Arbustum Americanum* (1785) and Walter's *Flora Caroliniana* (1788), for Marshall and Walter are mentioned, but it is doubtful that he had these works along on the expedition. Professor Ewan suggests that he was probably also familiar with Bartram's *Travels* and with Thomas Jefferson's *Notes on Virginia*, which is certainly likely, but he would not have had these works along with him either, and they would not have been very helpful in any case. What is certain is that he did have and use Linnaeus' *Systema Vegetabilium*, ed. Murray (either ed. 14, 1784, or ed. 15, 1797, which are very similar in format and content), because all the names used are found in this work and many of them are not in any American works available at that time.

The identifications came from Linnaeus' *Systema*, a work in which all of the known plants of the world were crammed into one volume. The treatment is the ultimate in condensation, consisting only of diagnoses of from six to ten words, and sometimes a citation or two. All the descriptions of the *Species Plantarum* (ed. 3) are omitted, and also all mention of geographic distribution. I can picture Custis sitting in the open flat boat while it was proceeding up the river at a snail's pace trying to match up his specimens with these brief Linnaean diagnoses, throwing up his hands at the impossibility, and finally tossing a coin as to which name to enter in the list. This explains why he reports from Louisiana so many species known only from Europe, Africa, Asia, Australia, and tropical America. I had much the same experience when I was a student at the University of California. Dr. Harvey M. Hall asked Tom Howell and me to identify the plants for a local wildflower show in Berkeley. We were unexpectedly deluged with specimens, many not at all local but from the Sierras and distant Coast Ranges, and many belonging to difficult genera like *Lupinus, Gilia, Phacelia,* and *Arctostaphylos.* As the time for the opening of the show grew close we, in desperation, just put down species names almost at random, in order for the plants to have some designation for the public, confident that no one was likely to question the names, except perhaps our teacher, Professor Jepson, who was unlikely to make an appearance. Similarly, Custis must have felt that in order to uphold his position as a botanist and to earn his pay he must supply names for the plants. He could be fairly confident that no one in the office of the Secretary of War was going to question them, and he was right. It is only now after 150 years that the names are coming to light. It is well for botanical nomenclature that he was chary of assigning new Latin names, because many of the plants that he saw really were undescribed species, which is why he could not find their diagnoses in Linnaeus' work. He actually created only three new botanical names, which are discussed below, and these all prove to be synonyms at the present time.

The next list of plants of the Red River Valley was not published until Torrey's list of 1854, in the Marcy report mentioned previously. A comparison with Torrey's list gives some clues to the identity of the plants recorded by Custis.

ACKNOWLEDGMENTS

This account, first written some twenty years ago and recently revised, has been read by my colleagues Drs. Mason E. Hale, David B. Lellinger, Harold Robinson, Velva Rudd, Lyman B. Smith, and William Stern, to whom I am grateful for many valuable suggestions. I am especially grateful to Professor Joseph Ewan of Tulane University, who, from his

vast knowledge of botanical history, was able to draw my attention to several references I would otherwise have overlooked; and to Dr. Clair A. Brown, of Louisiana State University, who was able, from his wide knowledge of the native flora of Louisiana, to suggest the identification of several of the plants mentioned that were doubtful to me.

EXTRACTS FROM THE NARRATIVE

Some extracts from the narrative in which the vegetation is particularly mentioned are given below, with my commentaries in footnotes, and following them are the complete plant lists, again with my commentaries. In the quoted parts the old spellings (and misspellings) of the original are reproduced.

"Left Fort Adams, on the Mississippi, April 19, 1806 . . . (p. 5) For two or three miles [from the confluence with the Mississippi] this river [the Red River] is beautifully bordered with willow trees,[13] which extend back from its margin nearly half a mile to the second rise in the land or bank, about six feet higher than that which borders the river. The trees of this second bank or plane are various. The Pecan is the most abundant; this is a species of *Juglans,* which bears the much admired Illinois nut. In its habits the Pecan is so very different from the *Juglans alba,*[14] as not to be mistaken for it, by the most (p. 6) careless, yet the only difference which can be pointed out, is in the leaf: both have pinnate leaves; the *Alba* has an odd leaflet sessile, the Pecan has odd leaflet petiolate. *Juglans petiolata*[15] would be an appropriate name for this species. The cotton tree, which of late has excited so much attention, is found here; although considered a populus, and by some termed Lombardy poplar, there is no other resemblance than the leaf.[16]

"The other trees are oaks, (*Quercus rubra, alba* and *phellos.*)[17] Persimmon (*Diosphyros Virginiana*),[18] Hagberry (*Prunus padus*),[19] Syca-

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[13] *Salix nigra* Marsh. and *S. interior* Rowlee.

[14] Presumably the Mockernut Hickory, *Carya tomentosa* Nutt., which should perhaps be known as *C. alba* (L.) Nutt. It is doubtful if *Juglans alba* L. should be rejected as a *nomen ambiguum,* as it was by Rehder, who has been followed more recently by Little.

[15] *Juglans petiolata* Custis, a name overlooked in the botanical literature, was validly published in the preceding year in Phila. Med. & Physic. Jour. **2**(2): 45. Sept. 25, 1806. Fortunately, no change in the accepted name of the species need be made, for the pecan had been described, unknown to Custis, three times previously — as *Juglans pecan* Marsh. (1785), *J. illinoensis* Wangenh. (1787), and *J. oliviformis* Michx. (1803). The name currently accepted as correct is *Carya illinoensis* (Wangenh.) K. Koch.

[16] It is the Eastern Cottonwood, *Populus deltoides* Bartr., common and of large size on the river-banks in the area traversed.

[17] *Quercus phellos* L., the distinctive Willow Oak, was surely identified correctly, but *Q. alba* L. and *Q. rubra* L. were probably applied to any of the White and Red Oaks respectively, most of which had not been distinguished in the time of Custis.

[18] Properly *Diospyros.*

[19] *Prunus padus* L. is the European Bird Cherry. Presumably the plant referred

more, or the American Plane tree (*Plantanus Occidentalis*) [20] and the *Crataegus aria.*[21] After passing three miles up the river, no trees but the willow and Pecan are seen from it, until approaching the Black River, where the Cyprus (*Cupressus disticha*) [22] is noticed. The Pecan is covered with Misleto.

"The bank of Black river on the right side is high, the soil very rich and light, and occasionally flooded, and besides all the trees above enumerated, except the Sycamore and Cotton trees, which disappear shortly after entering the river, it produces the Red Gum (*Liquid amber styraciflua*) [23] of a very large size, and the Ironwood (*Lyder axylon mite.*) [24] . . . (p. 7) The banks of the river are from 18 to 25 feet higher than the water at this season, and the land generally declines from them, for about one fourth of a mile to Cypress swamsp.

"At the Avoyell's settlement, about 35 miles higher than Black river, the *Plantanus Occidentalis*, and Cotton trees begin to make their appearance, with the *Cornus Sericea* [25] and Cypress; the Pecan and Persimmon are most abundant, the first of which generally grows to the height of 100 feet. Nine miles above the settlement is a beautiful bluff, nearly a mile in length, and fifty feet in height, formed of a reddish yellow sandy clay; here is first seen the *Quercus Nigra* or Black Oak, the *Myrica Cerifera* or Candle berry bush, and Maple (*Acer Pennsylvanicum.*) [26]

"Six miles above this bluff, a stratum of large trees and leaves, thirty feet below the surface of the ground, and covered by 10 or 12 feet of hard marle or clay, was exposed to view in the bank of the river. The Pine (*Pinus Sylvestris,*) [27] Dogwood (*Cornus Florida,*) Sassafras (*Laurus Sassafras,*) [28] Chesnut Oak (*Quercus Esculus,*) [29] Holly (*Ilex aqui-*

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to is the Black Cherry, *Prunus serotina* Ehrh., which was formerly called hagberry or hackberry.

[20] In mss. correctly *Platanus.*

[21] *Crataegus aria* L. is a European species. There are several native species of *Crataegus* along the Red River, and the one referred to can not be determined.

[22] In mss. correctly cypress. *Cupressus disticha* is now correctly *Taxodium distichum* (L.) L. C. Rich.

[23] In mss. correctly *Liquidambar.*

[24] A compiler's error. In mss. correctly *Sideroxylon*; however, this was a misidentification by Custis, for *S. mite* L. is an African plant, and the genus *Sideroxylon* does not occur at all in Louisiana. Probably the plant so named was *Bumelia lanuginosa* (Michx.) Pers. or *B. smallii* Clark.

[25] The plant referred to is probably the Rough Dogwood, *Cornus drummondii* C. A. Meyer, because *C. sericea* L. does not occur in Louisiana. The latter, as typified by Fosberg (Bull. Torrey Bot. Club **69**: 583–589. 1942) and Dandy (Watsonia **4**: 47. 1957) is the proper name for the northern red osier usually known as *C. stolonifera* Michaux.

[26] The Striped Maple, *Acer pensylvanicum* L., does not occur in the region explored; very likely the plant so identified was Drummond's Red Maple, *Acer rubrum* var. *drummondii* (Hook. & Arn.) Sargent, which is common in the area.

[27] *Pinus sylvestris* L., the Scotch Pine, is a European species; presumably the plant so identified was the Shortleaf Pine, *P. echinata* Mill., which is common along the Red River.

[28] Now properly *Sassafras albidum* (Nutt.) Nees.

[29] This is a misidentification, for *Q. esculus* L. is a European species, reported to be

folium,)[30] Hickory (*Juglans alba,*) Spice Wood (*Laurus Benzoin,*)[31] and Buckeye (*Esculus parviflora* of Walter,)[32] make their appearance at this place; the Benzoin being the only undergrowth to be found for a considerable extent.

"A shrub is found in great abundance every (p. 8) where along the river, growing to a height of from 10 to 20 feet, bearing a drupe resembling the Olive, but not so large, which, when ripe, is of a reddish purple color. The season of its flowering being passed, the species could not be ascertained, but Dr. Custis supposes it to be the *Elaegus* of Linnaeus. The putamen is of a woody fibrous texture, easily separated by the fingers; the Peduncles are rameous, and sub-apposite, each bearing from 10 to 15 drupes, the leaves eliptic.[33] . . . The banks of the river here [above the second fall] are high; the land very rich, somewhat broken and well adapted to the growth of cotton, and not (p. 9) subject to be overflowed. Most of the Red river lands are either of a clayey or marley soil, apparently not desirable for cultivation; the fact however is otherwise; they are found to be more productive than the best Mississippi lands, and the cotton raised on them always commands a higher price than that of the Mississippi. At the foot of the falls, and on the left bank of the river, is Rapide Court House;[34] and its vicinity is a considerable settlement. Here the Chequapin (*Fagus pumila*)[35] grows to a very large size; some of them 30 feet high and seven in diameter. The *Myrica Cerifera* is very abundant. . . .

"Twenty-three miles higher up the river than the falls, on a bluff about 50 feet higher than the surface of the water, is an Indian village, called the Appalaches. . . . A few miles above this village, on the left hand, there is a sand stone rock, which projects into the river. . . . (p. 10) here the Tooth Ache tree (*Zanthoxylum Clava Hercules*)[36] is first met with, and a little higher the Prickley Ash (*Zanthoxylum fraxinifolium*).[37] Almost im-

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a synonym of *Q. cerris* L. The commonest Chestnut Oak of the Louisiana region is the Swamp Chestnut Oak, *Q. michauxii* Nutt.

[30] *Ilex aquifolium* L., the English Holly, is a European species; the plant referred to is certainly the American Holly, *I. opaca* Aiton.

[31] Now generally *Lindera benzoin* (L.) Blume.

[32] *Aesculus parviflora* Walt. is a plant confined to the southeastern seaboard; the only Buckeye in the region under consideration is *A. pavia* L. In flower this species is quite distinct from the true *A. parviflora* Walt.

[33] Properly *Elaeagnus,* but this was a poor guess, for this genus does not occur in the Red River Valley, at least not in the lower region where Custis was observing. The description of the branched, opposite peduncles and olive-like fruits indicate that the plants observed were the Swamp Privet, *Forestiera acuminata* (Michx.) Poir., an identification suggested by Dr. Clair A. Brown.

[34] The small town of Rapide is still in existence.

[35] The Chinquapin is now properly *Castanea pumila* Mill.

[36] In mss. correctly *Zanthoxylum clava herculis.*

[37] *Zanthoxylum fraxinifolium* Marshall (non Walter) is considered a synonym of the common Prickly Ash, *Z. americanum* Mill.; the occurrence of this species in the Red River region is doubtful, for it is slightly outside the present known range.

mediately above these Indian villages, Red River divides into two branches; that to the right is about one third of the whole width of the river, retains the name of Red river, but is impassable, on account of the rafts of lumber which are lodged in it. [The clearing of this so-called "Great Raft" was begun in 1837 by Captain Shreve but was not finished until after the Civil War.] It separates from the other branch of the river, called Old river or Cane river . . . (from the *Arundo donax* [38] with which its banks abound) . . . (p. 11) The banks of Little river [a branch of Cane River] are in many places low, not more than eight feet high, but the water does not flow over them; the current in the river is very rapid. The timber is like what has been described, with the addition of Ash and Elm (*Fraxinus,* and *Ulmus Americana,*) which are most abundant. The Pecan continues in plenty, one of which near the mouth of Little river was measured and found to be 10 feet in circumference, at the height of five feet from the ground.

"(p. 12) The timber [about 9.2 miles above Natchitoches] is White Gum, Cotton Wood, very large Pecan, Ash, Hickory, Mulberry, and Locust . . . (p. 13) The Cotton Wood tree grows to a great size in this neighborhood; one standing in a cornfield was found to be five feet in diameter and 141 and a half feet high . . . (p. 14) The timber continues the same as below, with Cane on one, or both banks all the way . . . The trees are so covered with vines and creeping plants, as to present an impermeable mass of vegetation, while the low banks of the river are edged with willows . . . (p. 16) After passing up the bayou, about five miles against the current, running at a rapid rate of three miles an hour, they entered a lake called by the Indians, Big Broth, from the vast quantity of Froth which collects in, and floats along it, during the time of high water.[39] On the margin of the lake there is a growth of Willows and low bushy Cypress, for about 80 yards, beyond which the land is of good quality, rises to a height of forty feet, and is cloathed with White and Black Oak, Hickory, and Dogwood. The left or west side of the lake is low, and covered with large Cypress trees and bushes for about two miles. This beautiful lake is said to extend seventy miles, in a northerly direction, and is about two miles wide, agreeably variegated.

(p. 22) "In addition to the trees noticed in ascending to Natchitoches, they here meet with the Sour Gum (*Nissa integrifolia,*) [40] Lime Tree (*Tilia Americana,*) Locusts (*Robinia Pseudacacia,*) [41] this was only seen

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[38] *Arundo donax* L. is an Old World species, now somewhat introduced into the United States but surely not the abundant wild cane mentioned by Custis, which was certainly the native Giant Cane, *Arundinaria gigantea* (Walt.) Muhl.

[39] Big Broth Lake is called Lake Bistino by Custis in the plant lists, a corruption of Bistineau, which is the present name of the lake.

[40] *Nyssa integrifolia* Aiton is a synonym of *N. sylvatica* Marshall, which is common in the area in various forms.

[41] Probably not *Robinia* but the Honey Locust, *Gleditsia triacanthos* L. or the Water Locust, *Gleditsia aquatica* Marsh.

on Bayou Badtka [now Bodeau], *Cephalantus Occidentalis,*[42] or Button Wood, which is abundant all along the river. Haw (*Viburnum Prunifolium,*)[43] Red Cedar (*Juniperus Virginiana,*) the first makes its appearance about 20 miles below the Cooshutta village, Wild Cherry, (*Prunus Virginiana,*)[44] two kinds of plum, both of which are small, round, and red, the one ripens about the middle of June, the other in August; the latter is too sour to be eaten.[45] There are an abundance of grapes: the Fox Grape, the Wine, and a small blue one, which ripens about the first of June.[46] Oaks, (*Quercus rubra,*[47] *alba,* and *nigra,*) and the Hickory, (*Juglans Alba,*) are the most abundant, except on the margin of the river, where the Cotton tree and *Plantanus Occidentalis* abound.

"Cat Fish were taken at the camp near the village, of from 15 to 70 pounds weight, equal in taste and flavor to any caught within the U. States . . . (p. 43) Above the mouth of the Upper Little river, Red river is said to preserve nearly the same width for three or four hundred miles. The valley opens into a level, rich, and almost continued prairies, where range immense herds of buffaloe, upon which the Indians almost entirely subsist, moving their camps, as the animals migrate with the season, from north to south and back again. The Panis nation are possessed of fire arms, having smooth bored guns and ammunition, which they reserve for war, but never use them in hunting. They are the character of a peaceable and friendly people.

"The extensive prairies which are found in this rich and level country, appear to be owing to the custom which these nations of hunters have, of burning the grass at certain season. It destroys the bushes and underwood, and in some instances the timber, preventing the future growth where once the timber is destroyed. The small spots of wood with which these prairies are interspersed, are found in the poorest spots, and on the margins of the water courses, where the undergrowth is less luxuriant, or the water stops the progress of the flames. It is observed, that where these prairies are enclosed, or otherwise protected from fire, they soon become covered with bushes and timber trees, a circumstance which proves, that neither the nature of the soil, nor any other natural cause, gives rise to these extensive and rich pastures, with which Western America abounds."

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[42] In mss. correctly *Cephalanthus.*

[43] *Viburnum prunifolium* L., the Black Haw, does not quite reach the Red River region, where its place is taken by the related species *V. rufidulum* Raf.

[44] *Prunus virginiana* L., the Common Chokecherry, does not quite reach the Red River Valley, and so this was doubtless the Black Cherry, *Prunus serotina* Ehrh.

[45] Presumably the plum ripening in June was the Chickasaw Plum, *Prunus angustifolia* Marshall or possibly the Wildgoose Plum, *P. munsoniana* Wight & Hedr., and the one ripening in August the Mexican Plum, *P. mexicana* S. Wats.

[46] The Fox Grape is *Vitis labrusca* L.; it is uncertain which species is intended by the Wine Grape, but presumably not the true European Wine Grape, *V. vinifera*; the small blue grape ripening about the first of June may have been the June Grape, *V. riparia* var. *praecox* Engelm., which is perhaps not definitely known from the region being explored but which may occur there.

[47] Probably not Red Oak, *Q. rubra,* but Black Oak (*Q. velutina* Lam.).

(p. 44)

"A LIST

of the trees and shrubs, observed to grow on
the margin of Red River, or in its vicinity.

"1. Cotton Tree, a species of *Populus*; grows on the borders of the river from its mouth to the Spanish Camp. [*Populus deltoides* Bartr.; see above p. 442.] [48]

2. Pecan, (*Juglans Petiola.*) abundant as high as Natchitoches, after which it is very rare for 500 miles, when it is said to be again in plenty. [Correctly *petiolata* in mss.; see above p. 442; = *Carya illinoensis* (Wangenh.) K. Koch.]

3. Plane Tree, (*Platanus Occidentalis,*) plentiful on the borders of the river to the Spanish Camp.

4. Hagberry, (*Prunus padus.*) abundant. [Presumably a misidentification of *P. serotina* Ehrh.; see above p. 442.]

5. Persimmon, (*Dyosphyros Virginiana,*) every where to be met with. [As *Dyospyros* in mss.]

6. Honey Locusts, (*Gleditsia triacanthos* and *monosperma*) very abundant. [*Gleditsia monosperma* Walt. is a synonym of *G. aquatica* Marshall, the Water Locust.]

7. Oaks. (*Quercus, rubra, alba, phellos, nigra, and esculus.*) [See above pp. 442, 443; *Q. esculus* is probably a misidentification of *Q. michauxii* Nutt.]

8. Box Elder. [i.e. *Acer negundo* L.]

9. Sweet Gum, (*Liquidambar Styraciflua*) frequent.

10. Pines, (*Pinus Sylvestris, and Foeda,*) the *Foeda* is in great abundance, and of a very large size. [*P. sylvestris* is probably a misidentification of *P. echinata* Mill. (see above p. 443); "*Foeda*" is correctly *taeda* in the mss., the Loblolly Pine.]

11. Cypress, (*Cypressus disticha,* and *Thyoides.*) The *disticha* is met with as high as the party ascended the river, the other was only noticed below Natchitoches. [*Cupressus disticha,* the Bald Cypress, is now *Taxodium distichum* (L.) L. C. Rich.; *C. thyoides* is now correctly *Chamaecyparis thyoides* (L.) Britt., Sterns, & Poggenb., the Southern White Cedar. It was probably correctly identified, although this tree is apparently not known today in the Red River region, according to Dr. Clair A. Brown.]

12. *Celtis Occidentalis.*

13. Ash, (*Fraxinus Americana* and *excelsior*). [*F. excelsior* L., the European Ash, does not occur wild in the United States; the plant so identified was probably the Water Ash, *F. caroliniana* Mill.]

14. Sour Gum, (*Nyssa integrifolia*). [Now *N. sylvatica* Marshall; see above p. 445.]

15. Elm, *Ulmus Americana.*

16. Sassafrass, (*Laurus Sassafras*) every where met with. [Now *Sassafras albidum* (Nutt.) Nees; see above p. 443.]

17. Hickory, (*Juglans alba*) very abundant. [Presumably *Carya tomentosa* Nutt.; see above p. 442.]

18. Maple, (*Acer Pennsylvanicum,* and *Saccharinum.*) [*A. pensylvanicum* was probably a misidentification of the Red Maple, *Acer rubrum* var. *drummondii* (Hook. & Arn.) Sargent; see above p. 443.]

19. Mulberry, *Morus Nigra.* [Since the Black Mulberry is not native in the United States, presumably the plant so identified was the Red Mulberry, *Morus rubra* L., which is widely distributed in Louisiana.]

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[48] My identifications and notes are in square brackets. C.V.M.

20. *Sideroxylon mite.* [Probably *Bumelia lanuginosa* (Michx.) Pers. or *B. smallii* Clark; see above p. 443.]

21. Red Bud, *Cercis Siliquastrum.* [*C. siliquastrum* L. is the European Redbud; the plant observed was surely the American Redbud, *C. canadensis* L., which is common in Louisiana.]

22. Dogwood, *Cornus florida* and *Sericea.* [*C. sericea*, see above p. 443.]

23. Walnut, (*Juglans Nigra*) This tree becomes more abundant as you ascend the river, and high up it is found of a very large size.

24. Papaw, (*Anno Galbra*) every where abundant. [The cryptic "*Anno Galbra*" is a misinterpretation of the mss. by the compiler; the mss. "*Anno. glabra*" was an abbreviation of *Annona glabra* L., which however was a wild identification, for this species, the Pond Apple, is a tropical species native in southern Florida and the West Indies. The Papaw is, of course, *Annona triloba* L., now *Asimina triloba* (L.) Dunal.]

25. Chinquepin, (*Fagus pumila*) abundant all through the country as high as the first Little River, and probably much higher. [Now *Castanea pumila* Mill.; see above p. 444.]

26. *Hamamelis Virginica.* [The Witch Hazel.]

27. *Halesia Telrapetra.* [A misspelling by the compiler of *H. tetraptera* Ellis, now generally *H. carolina* L., the Carolina Silverbell; however, this species apparently does not occur in the Red River region, where its place is taken by *H. diptera* Ellis.]

28. Lime Tree, *Tilia Americana.*

29. Locust, (*Robinia Pseudacia.*) [A misprint or abbreviation of *pseudacacia.*]

30. Red Cedar, (*Juniperus Virginiana*;) it becomes more abundant as you ascend above the Coashatta Village. In many places this is the principal tree found on the borders of the river.

31. *Magnolia Tripetala.* [The presence of this species, the rather distinctive Umbrella Tree, on the list is an indication that the party did reach into present-day Oklahoma, for it is known from southeastern Oklahoma but not from Louisiana, although it is possible that it may have occurred there in 1806 and now be extinct.]

32. Tooth Ache Tree, (*Zanthozylon Clava Herculis*, and *fraxinifolia* of Marshall.) [The last-named is now *Z. americanum* Mill.; see above p. 444.]

33. Beech, (*Fagus Sylvatica.*) [*F. sylvatica* L. is the European Beech; the plant observed was surely the American Beech, *F. grandifolia* var. *caroliniana* Fern. & Rehd.]

34. Holly, (*Ilex Aquifolium.*) [Surely *I. opaca* Aiton; see above p. 444.]

35. Wild Cherry, (*Prunus Virginiana.*) [Identification a little doubtful; see above p. 446.]

36. *Prunus Lauro-cerassus.* [In mss. correctly *lauro-cerasus.*]

37. A tree growing on the banks of the bayous between the Coashalla Village and Natchitoches, and is probably new. It resembles in its size and manner of putting forth its leaves, the *Bignonia Catalpa.* The leaves are very large and three lobed; lobes entire, acute. Until more is known of it we will call it *Bignonia Triloba.* [*Bignonia triloba* Custis is one of the new species that have been overlooked and not indexed. The plant that is mentioned in comparison, *B. catalpa* L., is the Common Catalpa, now properly *Catalpa bignonioides* Walt. Evidently Custis' species is not really distinct but is only a form of *C. bignonioides* with three-lobed leaves; although I have not seen any specimens myself, there is good authority for the occurrence of such trilobed forms.]

38. *Cephalanthus Occidentalis.*

39. *Viburnum Prunifolium.* [Presumably not *V. prunifolium* L. but the related *V. rufidulum* Raf.; see above p. 446.]

40. *Crataegus Aria.* [See above p. 443.]

41. Spice Wood, (Laurus Benzoin) very abundant. [Now *Lindera benzoin* (L.) Blume.]

42. Candle Berry, (*Myrica cerifera*) in great abundance all through the country as high as the first Little River, and probably much higher.

43. *Prinos verticillatus.* [*P. verticillatus* L., the Winterberry, now generally *Ilex verticillatus* (L.) A. Gray; perhaps not definitely known from the Red River region, although it may occur there; some of the other species of *Ilex* are common there.]

44. Bois d'arc. This is probably a new genus; as it was not in blossom Mr. Custis could not determine whether it was so or not. It is said first to make its appearance about the Second or Upper Little River, and is very abundant in a creek called "Bois d'arc." The tree which the exploring party saw was within a mile of Natchitoches, and probably was a transplanted one. It was about 30 feet high; its trunk 7 or 8 feet in circumference, and from 6 to 7 feet to where it begins to ramify. Its general appearance that of an apple tree. The fruit about the size of large sour oranges, and of a greenish yellow colour. [Custis was right that this was a new genus, for the plant described is obviously the Osage Orange, one of the most outstanding endemic genera of the southern United States. The Osage Orange had been known previously in New Orleans, and was described in the unpublished list of Dunbar and Hunter (see p. 439), but no botanist assigned a name until Rafinesque called it *Ioxylon* in 1817, changed it to *Toxylon* in 1818 (a generic name later often accepted), and to *Joxylon* in 1819; but both the two last named can be considered orthographic errors. A year later, in 1818, Nuttall described the genus as *Maclura*, and because of his prestige over Rafinesque, Nuttall's name was generally accepted; it is now on the list of *nomina generica conservanda*, the correct name of the species at present being *Maclura pomifera* (Raf.) C. Schneider. Custis adds in the mss. letter: "The fruit I have preserved in whiskey in order to forward. — You will also receive some of the branches & leaves."]

(p. 47)

"A CATALOGUE

of vegetables seen on the banks of, and in the
vicinity of Red River, with the time of their flowering.

"NOTE. Where no mention is made of the place where they are found, it is to be understood that they are confined to no particular situation.

1806

May 2nd. *Amorpha fruticosa*, in flower.

3rd. *Oxalis acetosella*, out of flower. [The Red River region is somewhat outside the range of the Common Wood Sorrel, *Oxalis acetosella* L.; since the plants were out of flower it is likely that some other species of *Oxalis* was mistaken for it.]

Aquilicia Sambucina, in flower. [*A. sambucina* L., now generally called *Leea sambucina* (L.) Willd., is an Asiatic species of the grape family, with bipinnate leaves and a bushy rather than vine-like habit. The only plant of the Red River region with such characters is *Ampelopsis arborea* (L.) Koehne.]

5th. *Atropa Physaloides*, in flower. [*A. physalodes* L., now generally called *Nicandra physalodes* (L.) Gaertn., is a native of South America, at present somewhat naturalized in the southern United States but rather unlikely to have been naturalized so early as 1806. Doubtless some native species of *Physalis* was mistaken for it.]

Clematis Cirrhosa, do. [*C. cirrhosa* L. is a species of southern Europe; mistaken for it was very likely one of the native Leather Flowers, possibly *Clematis glaucophylla* Small.]

Convolvulus Arvensis, do. [The presence of this European plant, which was doubtless correctly identified, shows that some weeds had already been introduced into this region by 1806, as is shown also by the presence of *Portulaca oleracea*, *Verbascum thapsus*, *Arctium*, *Plantago major*, and *Taraxacum officinale*; these were probably mostly near French settlements. Professor Ewan tells me that a Dr. Prat was receiving seeds from France as early as 1725, and these doubtless included their complement of unwanted weed seeds.]

Ranulculus bulbosa, out of flower. [In mss. correctly *Ranunculus*; the European Buttercup, *R. bulbosus* L., is now commonly introduced, but probably Custis mistook one of the native species for it.]

6th. *Rhus Toxicodendron*, in flower.

Mimosa Punctata, in flower. This plant is first seen a mile above the mouth of the river, and from thence to Natchitoches is found in great abundance. In many places it completely covers the banks from low to high water mark. Like other species of the same genus, it moves from the touch. [*M. punctata* L. is a synonym of the tropical American *Neptunia plena* (L.) Benth.; there is a native *Neptunia*, *N. lutea* (Leavenw.) Benth., with sensitive leaves, but the plant observed was almost surely the native *Mimosa strigillosa* Torr. & Gray, which is common on river banks in Louisiana.]

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May 7th. *Arum triphyllum* out of flower. [Now *Arisaema triphylla* (L.) Schott.]

Echinops Sphaerocephalus, in flower. [This is the common European Globe Thistle. No plant really similar in inflorescence grows in the United States, but some of the native species of *Cirsium* have leaves that are very similar, and these may have been mistaken for *Echinops*.]

Hypericum quadrangulare, in flower. [*H. quadrangulare* J. E. Smith is a European species. The species native in the Red River region that has the stems most conspicuously quadrangular is *H. drummondii* (Hook. & Grev.) Torr. & Gray.]

——— *kalmianum*, do. [*H. kalmianum* L. is a northern species, of the Great Lakes region; the plant so identified by Custis can not be guessed at, for there are several native species of *Hypericum* in the area.]

Orobus tuberosus, do. [*O. tuberosus* is a synonym of the European *Lathyrus montanus* Bernh.; the only native species likely to have been mistaken for it is *L. venosus* Muhl.]

9th. *Mimosa tennifolia*, beginning to drop its flower. [In mss. correctly *tenuifolia*. However, *M. tenuifolia* L. is some tropical species of *Acacia*. I would guess that the native plant most likely to have been so misinterpreted would be the Sensitive Briar, *Schrankia nuttallii* (DC.) Standl.]

Hydrocotyle Vulgaris, in flower. [*H. vulgaris* L. is the European Pennywort; the very similar American plant with peltate leaves that would have been so identified is *Hydrocotyle umbellata* L.]

Malva Caroliniana, in seed. [Now *Modiola caroliniana* (L.) G. Don.]

Alcea rosea, in flower. [Now *Althaea rosea* (L.) Cav.; it would seem that Custis would know this, the common Hollyhock, and so it is likely that this was a plant cultivated by one of the settlers.]

Rudbeckia hirta, in flower.

Erythrina herbacea, seen at Rapide only and in flower.

Spigelia Marylandica, in flower.

Indigofera hirenta, in flower. [In mss. correctly *hirsuta*; *I. hirsuta* L. is an Old World species. The only species of *Indigofera* in the Red River region is *I. leptosepala* Nutt., with which the diagnosis of *I. hirsuta* in Linnaeus' *Systema*, which Custis was undoubtedly using for his identification, does not agree at all I think it likely that this was a wild determination of the native plant *Tephrosia virginiana* (L.) Pers., from the mention of the hirsute character of the spikes and the lanate pods.]

Symphitum officinale, *Solanum pamculatum* in flower. [*Symphytum officinale* L., the European Comfrey, must have been a misidentification of some native species of Boraginaceae (*Onosmodium*?); in mss. correctly *paniculatum*, but *Solanum paniculatum* L. is a Brazilian species; so identified must have been one of the native prickly solanums, almost surely the Horse Nettle, *S. carolinense* L.]

Aristolochia serpentaria.

Rosa eglanteria. [*R. eglanteria* L., the English Sweet Briar or Eglantine, must have been a misidentification of some native wild rose, unless it was a cultivated plant.]

Rubus fruticosus and *Caesius*, fruit ripe. [These two species of *Rubus* are European, evident misidentifications of native American species of blackberries and dewberries respectively.

11th. *Phytolacca decandra*, in flower. [Now properly *P. americana* L.]

Sambucus nigra, in flower. [*S. nigra*, the Black Elder, of Europe, was surely a misidentification for the American Elder, *S. canadensis* L.]

Oenothera longiflora, in flower. This is a Solar plant. It folds up its flower as soon as the sun rises, and expands at sun-set. [*O. longiflora* L., a South American species, must have been a misidentification of a native species of *Oenothera*.]

Portulaca oleracea in seed.

Oxalis purpurea, in seed. [*O. purpurea* L., a South African species is, of course, a misidentification, perhaps of the Violet Wood Sorrel, *O. violacea* L. In fact, Custis' "*purpurea*" was probably merely a slip of the pen or memory for "*violacea*."]

Passiflora, every where in the greatest abundance, and in flower. [This would be *P. incarnata* L.]

Verbascum thapsus, in flower. [Introduced weed, surely identified correctly.]

Rhus coppallinum, and *Cotinus*, in flower. [i.e. *Rhus copallina* L. and *Rhus cotinus* L.; the American relative of the latter is *Cotinus obovatus* Raf.]

Physalis pubescens, in flower.

Viola palmata, out of flower.

Mercurialis annica, about the first raft, in flower. [In mss. correctly *annua*; *M. annua* L. is European, but weedy and possibly already introduced into Louisiana in the time of Custis.]

Sida Occidentalis, in flower. [*S. occidentalis* L. is a tropical American plant; the plant so named by Custis is doubtful, perhaps not a *Sida* at all.]

Rhus coriaria, and *radicans*. [*R. coriaria* L. is European; the plant so named may have been the Smooth Sumac, *R. glabra* L.]

Smilax china, and *Sarsaparilla*. [*S. china* L. is Asiatic, and so the plant so named was probably *S. tamnoides* L., the China-root; *S. sarsaparilla* L. is tropical American, and the plant so named by Custis, with quadrangular stems, was surely *S. bona-nox* L., which was probably eliminated from consideration by Custis because it was described by Linnaeus as having aculeate leaves, but these are not always or even usually aculeate in this species.]

8th. *Rudbeckia purperea*, in flower. [In mss. correctly *purpurea*. Now *Echinacea purpurea* (L.) Moench.]

Podophyllum peltatum, every where abundant.

Nymphaea nelumbo, and *alba*. These cover the lakes. The leaves of the *Nelumbo* are of a very large size. Some of them measure nine feet in circumference. In flower. [*N. nelumbo* L. is the Old World Lotus; the plant intended, the American Lotus, is *Nelumbo lutea* (Willd.) Pers.; *N. alba* L. is the European White Waterlily; the related American species is *N. odorata* Aiton.]

10th. *Jussicua repens*, in flower. [In mss. more correctly *Jussieua*.]

Aretium Lappa. [In mss. correctly *Arctium*. All the Burdocks are introduced weeds; the plant seen *may* have been correctly named as the Great Burdock, *A. lappa* L., but more likely it was the Common Burdock, *A. minus* (Hill) Bernh., which was not distinguished in Linnaeus' *Systema*. According to Clair Brown, burdock is not at present found in Louisiana or, at least, not commonly.

Solanum Virginianum, on Lake Bistino. [In spite of its misleading specific name, *S. virginianum* L. is an African species; the plant of the Red River region more or less agreeing with the diagnosis of *S. virginianum* is *Solanum carolinense*.]

Hypericum proliferum, in flower. [Intended was *H. prolificum* L.]

Tradiscantia Virginica, everywhere abundant, and nearly out of flower. [In mss. correctly *Tradescantia*.]

Allium odorum, in flower. [*A. odorum* L. is an Asiatic species; this may have been the cultivated garlic, *A. sativum* L., or the weedy Field Garlic, *A. vineale* L., or most likely the native Wild Garlic *A. canadense* L.]

16th. *Leontodon taraxacum*, in flower. [Now *Taraxacum officinale* Weber; the dandelion must be one of the first weeds to be introduced into a new temperate region, along with *Plantago major.*]

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Physalis angulata, in flower.

17th. *Datura Stramonium*, in flower. This plant is very abundant at Natchitoches. [Where it may have been introduced; this was a favorite plant of the American Indians for religious(?) ceremonies.]

Marubium Vulgare, and *Mentha Lativa*. [In mss. correctly spelled *Marrubium* and *sativa*; these European plants, horehound and mint, which were collected by Custis in Natchitoches, were undoubtedly cultivated by the French settlers there. The horehound may very well have come in first as a weed.]

19th. *Cactus Opuntia*, very plentiful at Natchitoches, and in flower. [Surely the present *Opuntia humifusa* Raf.]

Tillandsia usneoides, found on almost all the trees in this country; in flower.

27th. *Spigelia Anthelmia*, near Natchitoches, in flower. [*S. anthelmia* L. is known in the United States only from Florida, and therefore this must be a wrong determination. Presumably it was *Spigelia marilandica.*]

Sonicera Sempervivum, in flower. [In mss. correctly *Lonicera sempervirens.*]

Podophyllum Peltatum, in flower.

June 4th. *Bignonia radicans*, in flower. [Correct name still uncertain, but mostly called now *Campsis radicans* (L.) Seem., the Trumpet Vine.]

6th. *Hibiscus fraternus*, in abundance on the borders of the river. [*H. fraternus* L. is South American; presumably the plant so identified was the Rose Mallow, *H. militaris* Cav.]

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Cassia chamaescrista, begins to put forth its flowers on the 5th June. This plant was first seen at Campte, and becomes more abundant as you ascend the river. It abounds in the prairies, and even throughout the woods, extending quite to the river's side. In Virginia this plant is thought very advantageous to poor lands, and known by the name of Magotty Bay bean, because first discovered in that place. Dr. James Greenway of Virginia, has given an account of it in the philosophical transactions. There is also a paper on its properties as a manure in one of the numbers of the Medical Repository. [An early reference to the value of legumes as a cover crop.]

Myrica cerifera, in abundance on Lake Bistino.

13th. *Polygonum Capathifolium*, in flower. [In mss. correctly *lapathifolium.*]

Erythrina herbacea, which is mentioned as having been only met with at Rapide, is very abundant on the prairies.

Fragaria vesca, abundant on the prairies. [The strawberry was surely *F. virginiana* Duchesne rather than the European *F. vesca* L.]

18th. *Passiflora minima*, abundant and in flower. [*P. minima* L. is tropical; the species intended was surely *P. lutea* var. *glabriflora* Fernald.]

Silphium laciniatum, in flower in the prairies.

Saturica Capitata. [In mss. correctly *Satureia.* However, *S. capitata* L., i.e. *Thymus capitatus* (L.) Hoffm. & Link, is European; several American mints might have been so misidentified.]

Asclepias lactifera. [An exotic species; the plant intended is doubtful; it could have been any of several species of *Asclepias, Asclepiodora,* or *Acerates.*]

——— *filiformis.* [*A. filiformis* L. is an exotic species; the only native species of Milkweed that could be said to have filiform leaves is *A. verticillata L.*]

——— *incarnata.*

Ascyrum Hypericoides, in flower.

Achillea Santolina. [*A. santolina* L. is an Old World plant, not to be expected either in cultivation or naturalized at this early date; the plant intended is doubtful.]

Plantago major. [The "White Man's Footsteps!"]

Periploca Secamore. [In mss. correctly *secamone*; *Periploca secamone* L. is an Old World species; the plant intended may have been a species of *Gonolobus.*]

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Coreopsis lanceolata, in flower.

Crotalarea latifolia. [In mss. correctly *Crotalaria.* However, *C. latifolia* L. is tropical; the plant intended was possibly *C. incana* L.]

Astragalus Carolinianus. [Perhaps *A. canadensis* L.]

Ecconymus Americanus, on the banks of the river. [In mss. correctly *Euonymus.*]

16th. *Drosera cuneifolia*, in flower. [*D. cuneifolia* Thunb. is South African; the plant observed was probably *D. brevifolia* Pursh, according to Dr. C. E. Wood, Jr.]

22nd. *Tricosanthes cucumerina*, near the upper end of the great raft. In flower. [*Trichosanthes cucumerinus* L. is an Old World species. Professor Ewan suggests that the plant intended was the Balsam Apple, *Momordica charantia* L., which was known in cultivation in the Ohio Valley in the 1750's. It seems likely though that Custis would have known *Momordica*, and so the plant seen may have been the native Bur Cucumber, *Sicyos angulatus* L.]

22nd. *Polygonum scandens*, in flower.

Palmetto (. . . .). The root is used by the natives in the cure of Lues Venerea. They use it in the form of decoction. [The palmetto of this area is *Sabal minor* (Jacq.) Pers.]

Arbutus Uva Ursi, on Bayou Badtka. [Now *Arctostaphylos uva-ursi* (L.) Spreng., the Bearberry; the inclusion of this species is perplexing, for it is rather distinctive and not easily confused with other plants, yet it is not today known from the Red River region. Dr. Clair Brown conjectures that the plant in question may have been the tree huckleberry, *Vaccinium arboreum* Marsh., which is common in this region.]

Cassia marylandica, on Bayou Badtka.

Sagittaria lancifolia, in a lake near the upper end of the raft. [*S. lancifolia* of authors not L. is *S. falcata* Pursh.]

Hedera quinquefolia. [Now *Parthenocissus quinquefolia* (L.) Planch., the Virginia Creeper.]

Cammelina Vaginata, in flower, and everywhere abundant. [In mss. correctly *Commelina*; *C. vaginata* L. is *Aneilema vaginatum* (L.) R. Brown, an Old World plant. Presumably the plant intended was *C. virginica* L., the Common Dayflower.]

24th. *Morea vegeta*, in flower. [*Morea* (properly *Moraea*) *vegeta* L. is a South African plant; intended was some native member of the Iridaceae, perhaps *Nemastylis acuta* (Bartr.) Herb.]

Sison ammi, near the upper end of the raft. [*S. ammi* L. perhaps referred to *Apium leptophyllum* (Pers.) F. Muell.]

Helianthus strumosus, in flower. [Custis' identifications in a large and difficult genus like *Helianthus* can not be taken to mean much.]

26th. *Aristolochia pistolochia*, in flower. [*A. pistolochia* L. is European; the plant so identified here is doubtful.]

Ranunculus hederaceus, in little prairie. [*R. hederaceus* L. does not occur in "prairies" in the Red River region, and so it is likely that another buttercup was mistaken for it.]

Arum pentaphyllum near the Coashatta village. [*A. pentaphyllum* L., now *Arisaema pentaphylla* (L.) Schott, is an Old World plant; it would seem that the only native species that could have been so identified is *A. quinatum* (Nutt.) Schott.]

Delphinium Staphisagria, do. [*D. staphisagria* L. is European; the local species intended was doubtless *D. carolinianum* Walt.]

Jatropha Urens, (Stinging Cassava) in flower on the 12th — very abundant. [*J. urens* L. is tropical American; the local plant intended was surely *Cnidoscolus texanus* (Muell. Arg.) Small, the Spurge Nettle.]

Ilex cassine, near the Coashatta Village. [Perhaps Yaupon, *Ilex vomitoria* Ait.]

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Polypodium, every where in plenty. [*Polypodium* in the time of Custis included, of course, not only the true Polypodiums but also all the species now referred to *Dryopteris*, *Thelypteris*, *Athyrium*, *Polystichum*, and some other genera.]

Fungi, abundant.

27th. *Carduus Verginicus*, in flower. [In mss. *virginicus*, but intended was *virginianum*, now *Cirsium virginianum* (L.) Michx.; however, this species as currently delimited does not occur in the Red River region, where its place is taken by the Yellow Thistle, *C. horridulum* Michx.]

No. 1, 2, & 4, at the Coashatta.[49]

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[49] These numbers refer to plants actually collected, presumably those that Custis was unable to identify with any in his books. (See my note above, p. 440, regarding

No. 3. In prairies. No. 5, every where in plenty. The Coashatta Indians make a decoction with this which they drink at their *green corn dance*, previous to taking the black drink. It pukes them violently immediately after drinking it. Whether it is the emetic property of the plant, or the great quantity of warm water which they drink that causes it to operate so soon is doubtful.[50]

No. 6. Very plentiful, particularly on the declivities of the hills.

No. 7. The poor people are said to use the root as a substitute for soap. The leaves are what the people of Campeachy make their cordage of.

No. 8. Abundant in the prairies. The root is a Caddo remedy for the convulsions of children. If at all useful it is most probably in cases arising from worms, by its anthelmintic properties.

No. 9. Is at the Coashatta.

No. 10. A species of *Mimosa* abundant on the prairies.

No. 11. Abundant in the prairies.

No. 12. A climber.

No. 13. On the banks of the river. The leaves feathered with an odd one.

No. 14. Abundant in prairies.

No. 15. At the Coashatta Village.

No. 16. On lake Badtka.

No. 17, 18. In the prairies.

No. 19. Polypodium every where abundant.

(p. 53)

No. 20. One of the most abundant vegetables in the country, found in every situation.

No. 21. Plentiful in the prairies.

No. 22. A small shrub growing near the head of the great raft.

No. 23. Found in the prairies.

No. 24. Supposed to be a species of *Lonicera*. It grows near the Coashatta Village.

No. 25. Very abundant.

No. 26. At the Coashatta Village.

Note. The above numbers refer to specimens of the plants.

July 11th. *Digitalis flava*, in flower, found above the Coashatta village. [There is a *D. flava* Georgi (1800) from Russia, but Custis hardly would have heard of it. Perhaps the "*flava*" was a slip for *D. lutea* L., or alternatively "*Digitalis*" was a slip for *Gerardia flava* L. The plant intended was surely one of the native False Foxgloves, *Gerardia flava*, *G. virginica*, or *G. grandiflora*.]

15th. *Spomaea Solifolia*, in flower. [In mss. correctly *Ipomoea*. Since *I. solanifolia* L. is a tropical species, the plant intended was one of our native Morning Glories, perhaps *I. pandurata* (L.) G. F. W. Meyer.]

17th. *Jussiena erecta*, on the banks of the river, in flower. [In mss. *Jussieua*, but more properly it should be *Jussiaea*, although the

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the disposition of these specimens.) It is perhaps fortunate for the stability of nomenclature that Custis did not assign any names to them.

[50] No. 5 is doubtless *Ilex vomitoria* Ait., which was used as an emetic, as the specific name implies.

matter is perhaps debatable, for Linnaeus used both spellings. Since *J. erecta* L. is a tropical American species, the plant intended was one of the native species, such as *J. decurrens* (Walt.) DC.]

Portulaca oleracea, abundant on all the sand beaches.

19th. *Hibiscus hirtus*. [This, *H. hirtus* L., an Old World plant, was surely a misidentification; one could guess that the plant intended was *H. lasiocarpos* Cav.]

Typha angustifolia.

Polygonum Pennsylvanicum.

These covered a prairie near the old Caddo village. [This note is on the three last-mentioned species, which are bracketed.]

24th. *Helianthus multiflorus*, above the second little river. [This might have been correctly named, although it is likely that some allied species was observed, for *H. multiflorus* L. is now considered a synonym of *H. decapetalus* L., which apparently does not quite reach the Red River region.]

Origanum Vulgare, in flower. [It is possible that this was a cultivated plant, brought along by the earliest French settlers as a condiment.]

Datisca hirta, at the old Cado village. [The plant so identified must remain entirely unknown; the original *D. hirta* L. is considered to be a teratological state of *Rhus typhina* L.]

26th. A species of *Hibiscus*, found above the Upper Little River, is probably new. Its stem is erect and smooth; leaves obliquely egg-lanced, sawed; flowers axillary, peduncles as if jointed, larger above the apparent joint; exterior calyx from 12 to 15 awled rays; in flower. [This description could apply to *H. lasiocarpos* Cav.]

(p. 54)

Aug. 2nd. *Clitoria ternatea*, in flower. [Probably this was the native *C. mariana* L., rather than the tropical *C. ternatea* L.]

Polygala Vulgaris. [One of the numerous native species of *Polygala* was surely misidentified as the European *P. vulgaris* L.]

8th. *Lobelia Cardinalis*, in flower.

——— *Syphililica*, in flower. [In mss. correctly *syphilitica.*]

9th. *Agaue Virginica*, in flower. [In mss. correctly *Agave.*]

Sagittaria Sagittifolia, abundant on all the bayous. [Presumably *S. latifolia* Willd., which used to be considered only a variety of the European *S. sagittifolia* L.]

Elephantopus scaber, every where abundant. [Probably the native *E. carolinianus* Willd. was the plant observed, rather than the tropical *E. scaber* L.]

Bignonia sempervirens. [Now *Gelsemium sempervirens* (L.) Aiton, the Yellow Jessamine.]

——— *Unguis*. [The plant intended was surely *B. capreolata* L., the Cross Vine, rather than the tropical *B. unguis* L.]

Cassia Chamaechrista, mentioned before, was found to overspread the whole country as they ascended, continuing to blossom from the 5th June until September. [See above, p. 453.]

25th. *Cassia occidentalis*. [This species is now naturalized in the Red

River region, and it may have been already introduced in 1806.]

Cassia Marylandica.

These are found in the greatest abundance above Natchitoches. [This note applies to the two species last mentioned, which are bracketed.]

Cassia Tora, also met with. This plant infests the whole country about Fort Adams and Natchez. [From the use of the word "infests," it would appear that this plant was considered a weed.]

28th. *Prenanthes alba*, in flower. [This was probably a misidentification of some related species, for *P. alba* L. apparently does not grow in Louisiana today.]

Chenopodium anthelminticum, abundant in the vicinity of Natchitoches. [An introduced weed, doubtless correctly named.]

Sept. 1st. *Solidago altissima*, in flower

Tillandsia usneoides, seen as high as 50 miles above the first Little River.

Borassus flabelliformis, in plenty." [Very likely the native Dwarf Palmetto, *Sabal minor* (Jacq.) Pers. was misidentified as the Old World palm *Borassus flabelliformis* L.]

"The description found on a sand beach below the Upper Little river.

Class Didynamia. Order Angeospermia.

"CALYX. Perianth double; the exterior two leaved, leaflets lance awled nearly the length of (p. 55) the tube of the corol; the interior one leaved five parted. divisions sub-equal, the length of the exterior perianth.

"COROL. One petal'd, grinning; tube rather longer than calyx, contracted above the germ; borders two liped; upper lip two cleft, obtusish, reflected; under lip three cleft, more deeply divided, more acute, with a groove in the middle of each division as if they had been doubled length-wise, reflected.

"STAMINA. Fil. four, awled, of which the two inferior are longer, shorter than the style, inserted into the bottom of the tube. Anthers roundish, pendulous.

"PIST. Germ. oblong; style thread form extended along the upper part of the corol to the division of the upper lip. Stigma cleft forming when expanded a flat orbicular surface with a small oblong incision in the middle.

"PER. Capsule oblong two-valved.

"SEEDS. Very numerous, small.

"Its stem is erect, shooting up about seven inches above the ground, entirely beset with flowers, furnished with Bractes; destitute of leaves.

"This plant is most probably a new genus, if so and there is not already a *Bartonia*, M. Custis calls it '*Bartonia Bracteata*.' There were two of these growing near each other, and the only ones of the kind that were seen." [*Bartonia* was intended to honor Custis' teacher, Benjamin Smith Barton. It is possible that because of the doubt expressed by the word "probably" that this new genus *Bartonia* should be considered as a *nomen provisorium*, and thus invalidly published, although many other authors have expressed similar doubts regarding the ultimate disposition of some of their novelties. In any case, Custis' fears that there might already be a *Bartonia* were well founded, for Muhlenberg had already proposed a *Bartonia* in 1801 for a peculiar genus of Gentianaceae. Furthermore, from the good and complete description of Custis there is no doubt that his plant is none other than the Broom-rape, *Orobanche* L. It was a new species in 1806 but the specific epithet *bracteata* can not now be transferred to *Orobanche* because there is an *Orobanche bracteata* Viviani (1830). The plant of Custis is evidently identical with the later described *Orobanche ludoviciana* Nutt. (1818).]

(p. 56) List of Animals [including the description of a new species of *Mus*, without a specific name, and on p. 57 a new species of squirrel, *Sciurus ludovicianus* Custis, which had already been validly described in Phila. Med. & Physic. Jour. 2(2): 47. Sept. 26, 1806. The epithet *ludovicianus* has been picked up and accepted by mammalogists as a valid subspecies of *Sciurus niger*.]
(p. 58) List of Birds.
(p. 60) List of Amphibians [including a brief description of a new species *Syren Quadrupeda*.]
(p. 61) List of Fishes and List of Insects.
(p. 62, 63) List of Minerals.
Finally, two folded tables of meteorological data.

When I first saw this little book of Freeman and Custis I feared that it might be filled with binomials that would upset current nomenclature, but such has not proved to be true. Many of the plants seen by Custis were actually new species, but it is evident that Custis felt a reluctance to describe them, understandably, since the reference material he had with him was so inadequate. The genus that Custis thought new and which really was new was the Osage Orange, but Custis did not assign a name, because he saw only the fruits, and according to the Linnaean system then in use flowers were necessary for a description. The only new names actually proposed are the following, which should be indexed, even though all are synonyms:

Juglans petiolata Custis, Phila. Med. & Physic. Jour. 2(2): 45, Sept. 26. 1806; Freeman & Custis, Account Red River 6. 1807 [= **Carya illinoensis** (Wangenh.) K. Koch].

Bignonia triloba Custis, in Freeman & Custis, Account Red River 46. 1807 [= **Catalpa bignonioides** Walt. forma, probably].

Bartonia Custis, in Freeman & Custis, Account Red River 55. 1807, non Muhl. 1801 [= **Orobanche** L. 1753].

Bartonia bracteata Custis, in Freeman & Custis, Account Red River 55. 1807 [non *Orobanche bracteata* Viv., 1830] [= **Orobanche ludoviciana** Nutt. 1818].

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A REVISION OF THE GENUS LUNASIA (RUTACEAE) *

THOMAS G. HARTLEY

THE GENUS *Lunasia* Blanco, with the exception of its occurrence in the Cape York Peninsula of Australia, is entirely Malesian, ranging from the Philippines and Borneo south to Java and east through New Guinea (see MAP 1). It is readily distinguishable from other genera of the Rutaceae in that area by its having trimerous flowers arranged in small, head-like clusters. The uniqueness of these floral features is indicated in Engler's treatments of the family (1896 & 1931) where they provide the basis for the placement of *Lunasia* in a separate subtribe, the Lunasiinae, of the tribe Xanthoxyleae, subfamily Rutoideae.

While the nearly apocarpous gynoecium and pellucid oil dots clearly place *Lunasia* in the Rutaceae, the small, trimerous flowers, swollen petiole apices and croton-like trichomes give it a superficial resemblance to some of the Euphorbiaceae. This is reflected in Blanco's original placement of the genus between the genera *Stilago* (*Antidesma*) and *Excoecaria* in the "Dioecia Triandra." *Mytilococcus* Zoll. and *Androcephalium* Warb., now considered to be synonyms of *Lunasia*, were also initially placed in the Euphorbiaceae.

I was able to study and collect *Lunasia* in New Guinea while employed as a botanist for the Australian Commonwealth Scientific and Industrial Research Organization, Phytochemical Survey of New Guinea, 1961–1965. This study is otherwise based on herbarium specimens. The contributing herbaria are listed below, with abbreviations from Lanjouw and Stafleu's *Index Herbariorum*, Part I. ed. 5 (Regnum Vegetabile. 31. 1964).

A	Arnold Arboretum of Harvard University, Cambridge
GH	Gray Herbarium of Harvard University, Cambridge
K	Royal Botanic Gardens, Kew
L	Rijksherbarium, Leiden
MICH	University Herbarium, University of Michigan, Ann Arbor
NY	New York Botanical Garden, New York
US	U.S. National Museum (Department of Botany), Smithsonian Institution, Washington

I wish to thank the directors and curators of these herbaria for making specimens in their care available to me.

Lunasia Blanco, Fl. Filip. ed. 1. 783. 1837. Type species: *Lunasia amara* Blanco.

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* This is the second of a series of studies on the Rutaceae of Malesia.

Rabelaisia Planch. London Jour. Bot. **4:** 519. 1845. Type species: *Rabelaisia philippinensis* Planch.

Mytilococcus Zoll. Natuurk. Tijd. Ned. Ind. **14:** 173. 1857. Type species: *Mytilococcus quercifolius* Zoll.

Androcephalium Warb. Bot. Jahrb. **18:** 196. 1893. Type species: *Androcephalium quercifolium* Warb.

Erect shrubs or small trees; dioecious; evergreen. Branchlets, leaves, inflorescences and fruits with gray to reddish brown, scale-like and/or stellate trichomes. Pellucid oil dots scattered in the leaves, perianths, and cotyledons. Leaves alternate, simple; petioles swollen apically; leaf blades pinnately veined. Inflorescences axillary, paniculate, the flowers in small, head-like clusters. Flowers unisexual; sepals and petals 3, valvate; stamens 3, rudimentary in carpellate flowers, opposite the sepals, with 2-celled, dorsifixed anthers; gynoecium 3-carpellate, rudimentary in staminate flowers, carpels connate basally, 1-locular, each with a single, pendulous ovule, placentation upper axile, styles 3, stigmas 3. Fruits 1–3 1-seeded, 2-valved follicles; follicles dehiscent along the apical and adaxial edges, in 3's, 2's or single with 0, 1 or 2 persistent, undeveloped carpels, respectively; pericarp dry at maturity, the endocarp cartilaginous and discharged from the follicle with the seed. Seeds with fleshy, oily cotyledons; endosperm absent.

It has been with considerable hesitation that I have decided on the conservative treatment presented here. *Lunasia* is extremely variable in certain vegetative features, and specimens such as the types of *L. parvifolia, L. quercifolia, L. mollis,* and *L. obtusifolia* certainly look distinct from the neotype of *L. amara.* I have found, however, that the variations represented by these and other specimens are repeated, in varying degrees of similarity, in scattered patterns of distribution that, without the correlation of specialized habitats, can hardly be considered those of natural populations. Although the ecological data I have are far from complete, there is no sound evidence of such ecologic specialization. The genus is apparently confined entirely to lowlands and grows in habitats ranging from well-drained rain forests to garden regrowth and rather dry thickets. Similar ecologic amplitude may be found in a number of well-marked Malesian species.

Trichomes in the genus vary from flat, scale-like structures composed of as many as 60 connate, radiating cells to stellate structures composed of as few as 2 separate, ascending cells. The range of variation in these structures is illustrated in FIG. 1. With the exception of the large, relatively simple trichome illustrated as TYPE VI, a clinal gradation exists in the genus from scale-like (TYPE I) to stellate (TYPE V). To some extent this gradation may be found in single specimens, the tendency being for the least dissected trichomes to occur on the lower midrib and petiole and the more stellate trichomes to occur, progressively, on the lower surface of the leaf blade, the inflorescence branches, and the flowers and fruits.

While the leaves are exceptionally variable in size, texture, number of

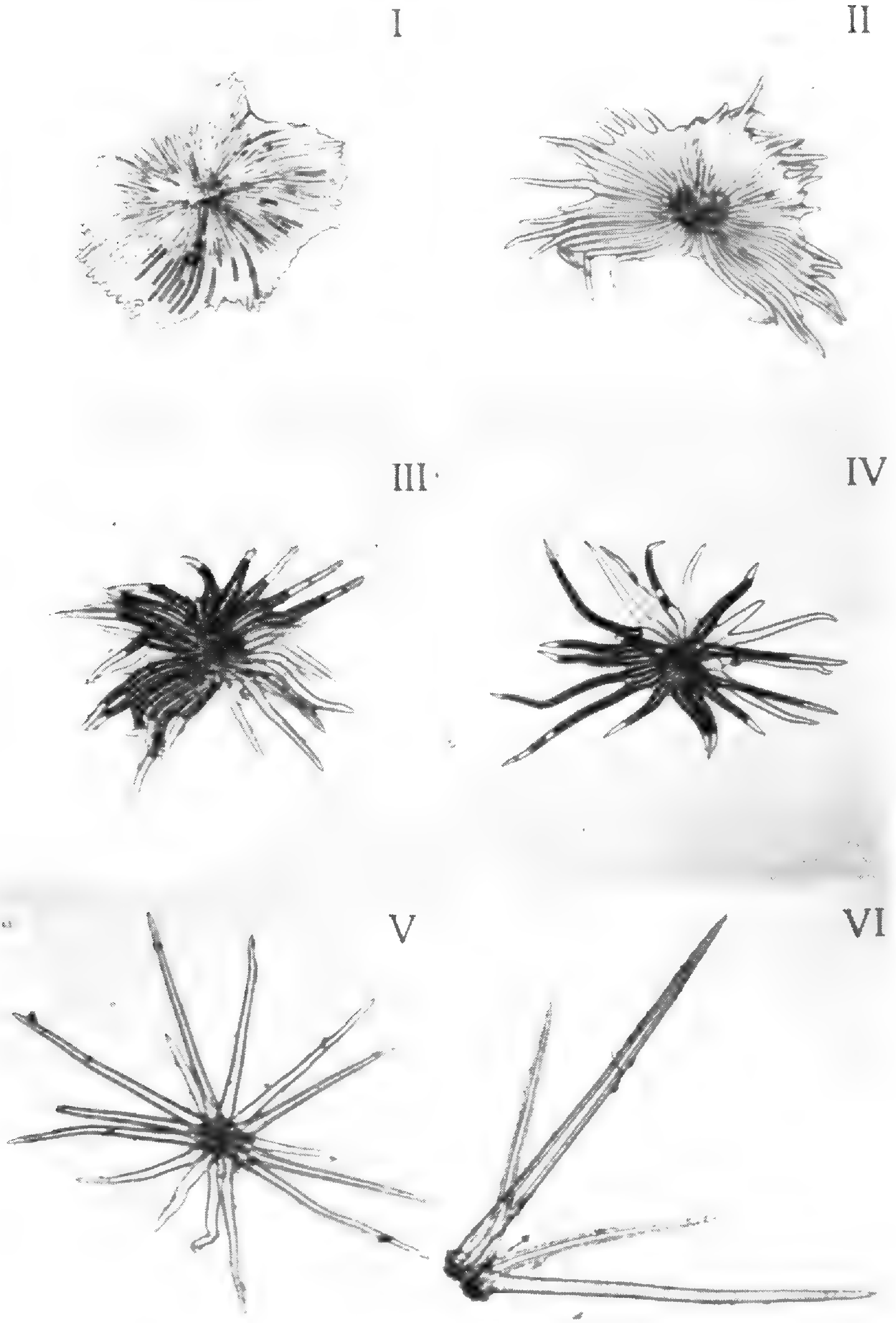


FIG. 1. Range of variation of trichomes in *Lunasia*. TYPES I–V, × 120. TYPE VI, × 67.

lateral veins and irregularities of the margins, they are nevertheless very distinctive. Apparently without exception the petioles are conspicuously swollen just below the insertion of the blade. Usually 5–10 mm. long and about one-half as wide (in dried specimens), this swelling tends to be thickest on the abaxial side of the petiole, resulting in an upward bending at that point. With only occasional exceptions the leaf blades are broadest well above the middle, tapering rather abruptly to the apex and gradually to a narrow base. The margins are seldom entire and the irregularities, ranging from undulations to sinuses, tend to become increasingly prominent toward the blade apex.

In dried condition the lateral faces of the follicles are generally marked with rather conspicuous, transverse ribs. In two collections from the Babuyan Islands, northern Philippines, the follicles are covered with twisted, simple or 2–3-branched processes which originate from the main vascular bundles (the above-mentioned ribs) of the pericarp. Other than this variation in the follicle and some variation in size of parts, the reproductive structures of *Lunasia* are remarkably uniform. The flowers, especially, vary only slightly throughout the genus.

Lunasia is well known in native medicine of the Philippines and Indonesia and reportedly has a number of uses including treatment of snake bite, skin diseases, swollen limbs and inflamed eyes. It is also reported to be taken in the treatment of digestive disorders, apparently in very dilute solution since small amounts are reputed to cause vomiting and cramps.

There are several reports of a substance from the bark being used for arrow poison. In tests on laboratory animals (Wirth, Jour. Am. Pharm. Assoc. **20**: 1254. 1931) it has been established that injections of two of the alkaloids from the bark, lunasin and lunacrin, result in decrease in responsiveness of isolated voluntary and smooth muscle, constriction of blood vessels and diminution of contractions of the heart. The lethal effect, in Wirth's tests, proved to be simultaneous stoppage of circulation and respiration.

The alkaloids have long been of interest to phytochemists and reports of their occurrence are found in the literature as far back as the late 1800's. In a recent paper dealing with the distribution of alkaloids in the Rutaceae (Price, 1963) a total of fourteen are listed for *Lunasia*. Ten of these, hydroxylunacridine, hydroxylunacrine, hydroxylunidine, hydroxylunine, kokusaginine, lunacridine, lunacrine, lunine, skimmianine and lunasine belong to a structural category of alkaloids known as furoquinolines and four, lunamarine, 4-methoxy-2- (3′, 4′ -methylenedioxyphenyl) -quinoline, eduleine and 4-methoxy-2-phenylquinoline belong to a category known as quinolines. The author points out that both these types of compounds are of wide occurrence in the Rutaceae and that they are rarely found (only one or two instances in the case of the simple quinoline derivatives) outside the family.

The following comments concern the citation of collections:

1. The collections are cited in the same geographic sequence followed in the initial paper (1966) of this series of studies.
2. The sex of each collection is indicated by the appropriate symbol fol-

lowing the collection number, or, in instances where two or more specimens of a collection from two or more herbaria are of different sex, by the appropriate symbol in parentheses following each herbarium citation. Herbarium sheets with male and female specimens of one collection are indicated by "♂ & ♀." Specimens for which I do not give an indication of sex are either sterile or at a stage where the determination could not be made.

3. Where applicable, the abbreviations listed in my previous paper of this series (1966, 175) are used for collections numbered in series. The following are additions:

BRUN	State Forest Office, Brunei
SAN	Forestry Department, Sandakan, Sabah (British North Borneo)

1. **Lunasia amara** Blanco, Fl. Filip. ed. 1. 783. 1837. Neotype: *Escritor BS 20776* (*Merrill Species Blancoanae 5*), Philippines, Luzon Island.

The synonyms are listed with the varieties.

KEY TO THE VARIETIES

1. Follicles transversely ribbed (the ribs sometimes obscured by trichomes) on the lateral surfaces, otherwise smooth .... 1a. var. *amara*.
1. Follicles densely covered with twisted, stellately pubescent processes to 8 mm. long .... 1b. var. *babuyanica*.

1a. **Lunasia amara** Blanco var. **amara**

Pilocarpus amara (Blanco) Blanco, Fl. Filip. ed. 2. 540. 1845.

Rabelaisia parvifolia Planch. London Jour. Bot. **4:** 519. 1845. Type: *Webb*, Celebes, Boeton Island.

Rabelaisia philippinensis Planch. *Ibid.* Syntypes: *Cuming 501, 1501* (not seen) and *1512*, Philippines.

Mytilococcus quercifolius Zoll. Natuurk. Tijd. Ned. Ind. **14:** 173. 1857. Type: *Zollinger 2687*, Java (not seen).

Mytilicoccus costulatus Miq. Fl. Ind. Bat. **1**(2): 388. 1859. Type: *Zollinger 2687*, Java? (not seen).

Mytilicoccus grandifolius Miq. *Ibid.* Type: *Zollinger 2687 bijvoegsel*, Lesser Sunda Islands, Sumbawa (not seen).

Lunasia grandifolia (Miq.) Miq. Ann. Mus. Lugd.-Bat. **3:** 89. 1867.

Lunasia costulata (Miq.) Miq. *Ibid.*

Lunasia parvifolia (Planch.) Miq. *Ibid.*

Lunasia philippinensis (Planch.) F.-Vill. Novis App. 35. 1880.

Androcephalium quercifolium Warb. Bot. Jahrb. **18:** 197. 1893. Type: *Hellwig 131*, Territory of New Guinea.

Lunasia quercifolia (Warb.) Laut. & K. Sch. Fl. Deutsche Schutzgebiete Sudsee 376. 1901.

Lunasia repanda Laut. & K. Sch. *Ibid.* Type: *Lauterbach 2805*, Territory of New Guinea (not seen).

Lunasia amara Blanco var. *costulata* (Miq.) Hochreutiner, Bull. Inst. Bot. Buitenzorg **19:** 54. 1904.

Lunasia reticulata Elmer, Leafl. Philip. Bot. **4:** 1511. 1912. Type: *Elmer 12119*, Philippines, Sibuyan Island.

Lunasia mollis Merr. Philip. Jour. Sci. Bot. **9:** 299. 1914. Type: *Ramos BS 11026*, Philippines, Cebu Island.

Lunasia macrophylla Merr. *Ibid.* 300. Type: *Whitford & Hutchinson FB 9299*, Philippines, Mindanao Island (not seen).

Lunasia obtusifolia Merr. *Ibid.* 300. Type: *McGregor BS 1273*, Philippines, Bohol Island.

Lunasia nigropunctata Merr. *Ibid.* 301. Type: *Escritor BS 21188*, Philippines, Luzon Island.

Lunasia amara Blanco var. *repanda* Merr. *Ibid.* 302. Type: *Fénix BS 15842*, Philippines, Mindanao Island.

Lunasia amara Blanco var. *repanda* (Laut. & K. Sch.) Laut. Bot. Jahrb. **55:** 247. 1918 (nomen illegit.).

Lunasia gigantifolia Merr. Philip. Jour. Sci. Bot. **21:** 519. 1922. Type: *Agama BS 582*, British North Borneo.

Lunasia pubifolia Merr. *Ibid.* **29:** 481. 1926. Type: *Ramos BS 43358*, Philippines, Bohol Island.

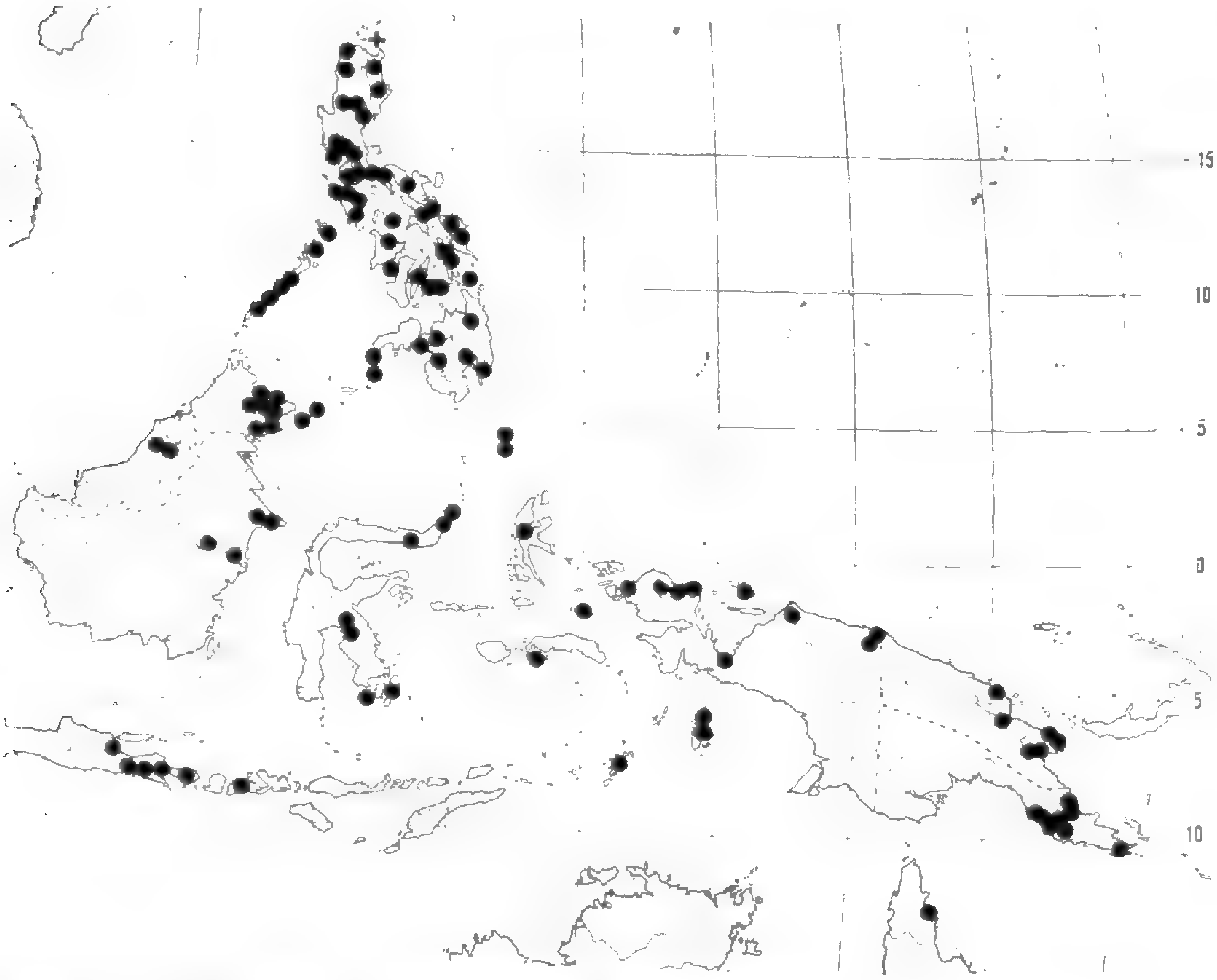
Lunasia quercifolia (Warb.) Laut. & K. Sch. var. *lanceolata* C. T. White, Jour. Arnold Arb. **7:** 232. 1926. Type: *Brass 761*, Papua.

Lunasia truncata Elmer, Leafl. Philip. Bot. **10:** 3782. 1939. Type: *Elmer 15140*, Philippines, Luzon Island (nomen illegit.).

Erect, sparsely branched shrubs or small trees to 12 m. Branchlets, leaves, inflorescences, and fruits with scale-like and/or stellate trichomes. Leaves crowded toward the tips of branchlets. Petioles 1.5–15 cm. long, ⅛ to ⅓ the length of the blade. Leaf blades chartaceous to coriaceous, dark green above, pale green below, generally oblanceolate but occasionally grading to obovate, elliptic or lanceolate, 5.5–60 cm. long; base cuneate to narrowly rounded or cordate, to 4 cm. wide; main veins 9–35 (?45) on each side of the midrib; margins subentire to sinuate with sinuses to 1.5 cm. deep; apex rounded to acuminate, the acumen to 3 cm. long. Staminate inflorescences to 28 cm. long and 8 cm. wide, the head-like clusters of flowers 3–5 mm. in diameter; sepals ovate, free to the base, about 0.5 mm. long; petals greenish yellow to white, obovate, free to the base, about 1 mm. long, with a median, longitudinal ridge on the adaxial surface, apex acuminate, the acumen inflexed in bud; stamens about 1 mm. long, anther cells longitudinally two-lobed, in bud each cell of one anther fitting into adjacent halves of two petals; rudimentary gynoecium pulvinate. Carpellate inflorescences to 25 cm. long and 2 cm. wide, the head-like clusters of flowers 3–6 mm. in diameter; sepals free to the base, broadly ovate, 1–1.5 mm. long; petals greenish yellow to white, ovate, free to the base, 2–2.3 mm. long, the apex acuminate (or erose when torn due to connation in bud); staminodes 3, about 1 mm. long, well differentiated but without pollen; gynoecium about 0.6 mm. high and 0.9 mm. wide, styles coherent basally, about 0.3 mm. long, stigmas broadly flattened, about 0.5 mm. long, spreading over the tops of each of the three carpels. Follicles obovate-truncate, somewhat flattened laterally, transversely ribbed on the lateral surfaces, otherwise smooth.

6–15 mm. high, 5–10 mm. wide, generally beaked at the abaxial apical angle, the beak to 5 mm. long. Seeds obovoid, the testa dark brown to reddish brown, sublustrous, papery.

Java. EASTERN JAVA. Surabaja Residency, Patjet, *Altman 421* ♂ (A). Besuki Residency: Near Puger, G. Watangan, *Backer 36482* ♂&♀ (L), *Jacobs 4715* ♂ (L); Puger, *Koorders 21584β* ♀ (K, L), *21585β* ♀ (K, L). Banjuwangi, *Anonymous* ♀ (L). KANGEAN ISLAND. Terrein N van Ardjasa, *Backer 26883* ♀ (L). **Lesser Sunda Islands etc.** BALI. *Anonymous* ♀ (L). SUMBAWA. Mt. Batulanteh, *Kostermans 18686* ♂ (A, L). TANIMBAR ISLANDS. Jamdena Island: central part near Ranarmoje River, near Norkesi, *Borssum Waalkes 3239* ♂ (K, L); Weri Ranarmoje, ca. 28 km. E of the coast, *Buwalda 4717* [A, K(♀), L]; Makatian, *NIFS bb 24406* (A, L). **Borneo.** EAST BORNEO. Koetai: G. Kombeng, *Endert 5120* ♀ (K, L); 15 km. upstream from Samarinda, *Kostermans 4816* ♂ (K, L); Sg. Susuk region (NE of Sangkulirang Bay), *Kostermans 5603* ♀ (L); Sangkulirang District, Mt. Medadam, N of Sangkulirang, *Kostermans 13446* ♀ (L). BRITISH NORTH BORNEO (SABAH). Tawau, *Elmer 20849* ♀ (A, GH, L, NY); Semporna, Segarong Forest Reserve, *Symington & Agama North Borneo Forestry Dept. 9257* ♀ (A, K, L); Lamag District, Sopiloring Hill, *Ampuria SAN 35283* (K); Lahad Datu District, Mt. Silam, *Hujin SAN 37830* (L); Sukau, *Meijer SAN 26594* (L); Port Myburgh, *Creagh*, ca. 1895 (K); Sandakan, *Agama BS 582* [A(♂), K(♀)] — isotypes of *Lunasia gigantifolia* Merr.; Gomantong Hill Forest Reserve, *Wing SAN 38106* ♀ (K, L); Gomantong Caves Hill, E edge of Libing payu hole, *Wood SAN A4628* ♀ (L). SARAWAK. Baram District: Ulu



MAP 1. Distribution of *Lunasia amara* Blanco var. *amara* (dots) and var. *babuyanica* (Merr.) Hartley (plus sign).

Melinau, *Ashton BRUN 3206* [K(♀), L]; Melinau Gorge, Lat 4° 10′ N., Long. 114° 55′ E., *Chew Wee-Lek 485* ♀ (K); G. Api, *Wilford SAR 4269* ♀ (K). **Philippines.** Palawan Island. Malinao Mt., *Ebalo 628* ♂ (A); Mt. Mantalingajan, *Edaño BS 77576* ♂ (NY); Mt. Pulgar, near Puerto Princesa, *Elmer 13022* ♀ (GH, L, NY, US); Quezon, Lipuum Point, *Gutierrez & Espiritu PNH 80798* ♂ (L); E-wi-ig River, *Merrill 743* ♀ (GH, NY, US); Victoria Mts., between Panacan and Aborlan, *Sulit PNH 12353* ♂&♀ (A); Maitiaguit, *Vidal 1205* ♀ (L); without definite locality, *Agama FB 21597* ♀ (A, US), *Bermejos BS 247* ♀ (NY, US). Calamian Group. Coron Island, *Ramos BS 41156* ♀ (A). Mindoro Island. Puerto Galera vicinity, *Bartlett 13504* ♀ (A), *13515* ♀ (A), *Santos 5161* ♀ (L, US); Mansalay vicinity incl. Mt. Yagaw, *Conklin PNH 18588* ♀ (A, L, US), *PNH 39202* ♀ (A, L), *Sulit PNH 17049* ♀ (A, L), *Sulit & Conklin PNH 16907* ♀ (A, L); Paluan, *Ramos BS 39751* ♀ (A); Pinamalayan, *Ramos BS 41047* ♂ (A). Luzon Island. Ilocos Norte Province, Mt. Quebrada, *Edaño PNH 17871* ♂ (L). Cagayan Province, Penablanca vicinity, *Adduru 111* two sheets, one ♂ and one ♀ (A), *240* (A, US). Abra Province, Mt. Portoc, *Alcasid et al. PNH 1601* ♂ (L). Isabela Province: Sierra Madre Mts., San Mariano, *Gutierrez PNH 78065* ♀ (A, L); without definite locality, *Velasco FB 28124* ♂ (A). Benguet Subprovince, *Curran & Merritt FB 15825* ♂ (K, US). Nueva Vizcaya Province: Dupax vicinity, *McGregor BS 11184* ♀ (L), *BS 11264* ♂ (US); without definite locality, *Cenabre FB 28496* ♀ (A). Aurora Province, Baler, *Escritor BS 21188* ♀ (US — isotype of *Lunasia nigropunctata* Merr.), *Merrill 1104* ♀ (NY, US), *Quisumbing PNH 2409* ♀ (A). Pampanga Province, Arayat, *Merrill 1357*, ♀ (GH, K, NY, US). Bulacan Province, Angat, *Ramos BS 21751* ♀ (US). Rizal Province: Manila, Laguna de Bay, *Andersson*, January, 1853 (NY); Montalban, *Loher 219* [K, NY, US(♀)], *220* [K(♂&♀), US(♂)], *5712* ♀ (US), *5723* ♂ (US), *5742* ♂ (K, US); Antipolo, Morong, *Loher 221* ♀ (US); Morong, Tanay, *Merrill 2339* ♂ (US); Antipolo, *Vidal 135 bis* ♂ (A); San Mateo, *Vidal 136* ♂&♀ (A); without definite locality, *Ahern's collector FB 2462* ♀ (K, NY, US), *FB 3106* ♂ (K, NY, US), *Ramos BS 38* ♀ (US), *BS 1830* [GH (♂), US], *BS 22688* ♀ (A). Bataan Province: Mt. Mariveles, *Elmer 6664* ♀ (NY); Mt. Mariveles, Lamao River, *Ahern's collector FB 1436* ♂ (NY, US), *Borden FB 745* ♀ (K, NY, US), *Merrill 3161* ♀ (NY, US), *Meyer FB 2261* ♀ (K, NY, US), *Whitford 5* ♀ (K, NY, US), *508* ♂ (NY, US), *Williams 34* [GH (♀), NY (♀), US], *518* ♂ (NY, US); Lamao, *Barnes FB 180* ♀ (A, NY, US); between Bagac and Moron, *Vidal 135* [A, (♀), K (♂), L (♀)]; without definite locality, *Williams*, 1905 ♀ (A). Laguna Province: Mt. Makiling, *Agra PNH 35334* ♀ (L), *Forestry Guard PNH 4311* ♀ (A), *Orden PNH 33478* ♀ (L, US); Los Baños, *Elmer 8115* (K, NY), *8119* ♂ (K), *Tamesis FB 11908* ♀ (L); without definite locality, *Cuming 501* ♀ (L, NY) — isosyntypes of *Rabelaisia philippinensis* Planch. Batangas Province, *Cuming 1512* ♂ (GH, L, NY) — isosyntypes of *Rabelaisia philippinensis* Planch. Quezon Province: Guinayangan, *Escritor BS 20776* (*Merrill Species Blancoanae 5*) ♀ (A — neotype of *Lunasia amara* Blanco, GH, L, NY, US), *Oro FB 30904* (NY); Tayabas, Laguimanoc, *Merrill 2126* ♀ (US). Camarines Sur Province, Isarog, *Vidal 682* ♀ (L). Sorsogon Province, Irosin, Mt. Bulusan, *Elmer 15140* ♀ (A, GH, K, L, NY, US) — isotypes of *Lunasia truncata* Elmer. Without definite locality, *Loher 218* (NY, US), *223* ♀ (US). Sibuyan Island. Capiz Province, Magallanes (Magdiwang), Mt. Giting-Giting, *Elmer 12119* [A (♂), K (♂), L (♂), NY (♂&♀), US (♂)] — isotypes of *Lunasia reticulata* Elmer. Ticao Island. *Clark FB 1083* ♀ (NY, US). Samar Island. Mt. Sarawag, *Edaño PNH 15331* ♂&♀ (A); Mt. Purog, Baniz, *Gachalian PNH 15463* ♀ (A); without definite locality, *Ramos BS 17509* [L (♀), US (♂)]. LEYTE. Mt. Abucayan, *Edaño BS 41677* ♀ (A, US); Leyte Province, Palo, *Elmer 7093* ♀ (A, K, NY); without definite locality, *Wenzel 1515* ♂ (A, GH, NY). BOHOL ISLAND. Kalingohan, *Ramos BS 43358* ♀ (A, K, US) — isotypes of *Lunasia pubifolia* Merr.; without definite locality, *Catalan FB 25108* (GH), *FB 25110* (A, US), *McGregor BS 1273* ♂ (NY, US) — isotypes of *Lunasia obtusifolia* Merr., *Ramos BS 42705* ♂ (A, US). CEBU ISLAND. Limusan, *Ramos BS 11026* (K, US) — isotypes of *Lunasia mollis* Merr. PANAY ISLAND. Capiz Province, *Edaño BS 46237* ♀ (L); Mt. Salibongbong, *Martelino & Edaño BS 35616* ♂ (A, L). GUIMARAS ISLAND. Bo. Tubod, Buenairsta, *Sulit PNH 11730* ♀ (A, L). SULU ISLANDS. Sibutu Island, *Herre 1228* ♀ (A), *1238* ♀ (A, NY, US); Tawitawi Island, *Ramos & Edaño BS 44031* ♀ (L), *BS 44306* ♀ (NY); without definite locality, *Kondo & Edaño PNH 38853* (A). BASILAN ISLAND. *Miranda FB 20080* ♀ (L). MINDANAO ISLAND. Zamboanga Province: Zamboanga, *Ahern*, 1901 ♀ (US), *559* ♀ (NY, US); Tetuan, *Quadras 369* (US). Lanao Province, Malabang Mt., *Ebalo 1097* ♂ (US). Bukidnon Province, Tanculan vicinity, *Fénix BS 26059* ♀ (A, US). Cotabato Province, Nutol, *Ramos & Edaño BS 84944* ♂ (A); Cotabato vicinity, *Whitford FB 11791* (US). Agusan Province, Asiga River, *Ramos & Convocar BS 83696* ♂ (A). Davao Province, Mt. Mansamuga, *Edaño PNH 11141* ♀ (A, L); Quinonoan River, *Edaño PNH 11452* ♂ (A, L); Davao District, *Fénix BS 15842* ♂ (K, US) — isotypes of *Lunasia amara* Blanco var. *repanda* Merr.; Mati, *Ramos & Edaño BS 49223* ♂ (L). SIARGAO ISLAND. *Ramos & Pascasio BS 34973* ♂ (A, L). **Celebes and neighboring islands.** CELEBES. North Peninsula: Minahassa Province, *Koorders 16946β* ♀ (L), *16948β* ♂ (L), *16953β* ♂ (L); prope Tanairanto (probably Tanahwangko, Minahassa Province), *Reinwardt 15016* ♀ (L). Gorontalo, *Riedel* ♀ (K). Central Celebes, Ond. Malili, Kawata, *NIFS bb V-271* (L), *NIFS bb V-276* ♂ (A, L). Without definite locality, *Reinwardt*, September, 1821 (L), *de Vriese & Teysmann*, 1859–1860 ♀ (L). KABAENA ISLAND. *Elbert 3238* (A, L). BOETON ISLAND: *Webb* (K — holotype of *Rabelaisia parvifolia* Planch.), *Zippelius* $\frac{31}{6}$ ♂ (L). **Moluccas.** TALAUD ISLANDS. Karakeland Island: E of Beo, *Lam 2661* ♂ (A, L); summit of G. Piapi, *Lam 3291* (A, K, L); E slope of G. Piapi, *Lam 3305* ♂ (L). Kaburuang Island, N of Mangarang, *Lam 3181* ♂ (L). HALMAHEIRA ISLAND: het fortje Dodinga Gilolo (Djailolo); *Forsten*; July 1841 (L); Lebengon Djiko djira; *Nedi 307* (L): AMBON ISLAND. *Zippelius* $\frac{69}{c}$ ♀ (L). **West New Guinea (West Irian) and neighboring islands.** SCHOUTEN ISLANDS. Biak, *Aet & Idjan 860* ♂ (A, K, L). MISOÖL ISLAND. near Waima, *Pleyte 1048* ♂ (A, K, L). AROE ISLANDS. P. Wokam, Dosinamalaoe, *Buwalda 4937* ♂ (A, GH, K, L); P. Wokam, Selibatabata, *Buwalda 5232* [A, K, L (♂)]; Soengey Waskai, *Jensen 253* ♂ (A, L). VOGELKOP PENINSULA. Sorong, near Remoe, *Main 564* ♀ (K, L); Kebar Valley, ca. 100 km. W of Manokwari, *van Royen 5073* ♂ (K, L); Sidai, ca. 65 km. W of Manokwari, *Koster BW 6803* ♂ (L); Manokwari, Tafelberg, *van Royen & Sleumer 6685* ♂ (L). GEELVING BAY. Nabire, *Kanehira & Hatusima 11527* (A). NORTHERN WEST NEW GUINEA. Mamberamo, Otken River, *Docters van Leeuwen 11382* ♂ (A, K, L); Sawia, *Gjellerup 621* ♂ (L); SE Depapre; near Cp: Maribu; *Lam 7803* [L (two sheets; one ♂ and one ♀)]. WITHOUT DEFINITE LOCALITY. *Zippelius* $\frac{192}{c}$ ♀ (L). **Papua.** CENTRAL DISTRICT. Kanosia, *Carr 11358* ♀ (A, K, L, NY), *11171* [A, (♂), K (♀), L (♂), NY (♂)]; Kairuku Subdistrict, Rubberlands Estate, head of Galley Reach, *Pullen 3505* ♂ (L); Yule Island, *White 705* ♂ (A); Sapphire Creek, *White 819* ♀ (A); Port Moresby vicinity, 6 miles N of Bootless Inlet, *Pullen 3099* ♂ (L); 2 miles E of Karema, Brown River, *Schodde 2564* ♀ (L); Laloki River, *Brass 1646* ♂ (A); tributary of Laloki River 2 miles E of Rouna, *Hartley 10641* [L (♂), A (♂&♀)]; Astrolabe Range, Sogeri Plateau, *Womersley NGF 14047* ♀ (L), *NGF 19121* ♂ (L); Budatobara, *Brass 761* ♀ (A — isotype of *Lunasia quercifolia* (Warb.) Laut. & K. Sch. var. *lanceolata* C. T. White); headwaters of U-uma River, *Brass 1459* ♂ (A). NORTHERN DISTRICT, ca. 5 km. N of Divinikoari Village, *Hoogland 3687* ♀ (A, K, L, US); Yodda Valley, ca. 10 km. from Kokoda along Wairopi Road, *Hoogland 3930* ♀ (A, L). MILNE BAY DISTRICT. Sagarai Valley, inland from Mullins Harbour, *Womersley NGF 19280* ♂ (L), *NGF 19282* ♂&♀ (L). **Territory of New Guinea.** SEPIK DISTRICT. Aitape Subdistrict, near Romei Village, *Darbyshire & Hoogland 8043* ♀ (L). MADANG DISTRICT. Hatzfeldthafen, *Hollrung 373* ♂ (K); Gurumbu, Lat. 5° 50′ S., Long. 145° 50′ E., *Henty & Sayers NGF 20537* ♂ (L), *NGF 20555* ♂ (L). MOROBE DISTRICT. Kajabit (Kaiapit) Mission vicinity, *Clemens 10641* ♂ (A, MICH), *10684* ♀ (A, MICH); Sankwep River, ca. 15 miles N of Lae, *Hartley 11330* ♂ (A, L); Bupu River, near Lae, *Henty NGF 10524* ♂ (K, L); Busu River, near Lae, *Millar NGF 12229* ♀ (A); Kelana, *Hellwig 131* ♂ (K — isotype of *Androcephalium quercifolium* Warb.); Sattelberg, *Clemens 883* (L). **Australia.** QUEENSLAND. Cape York Peninsula, Iron Range, *Brass 19317* ♂ (A), *19655* ♂ (A). **Cultivated.** JAVA. Bot. Gard. Bogor, *Hochreutiner 112* (L, NY), *113* (L, NY), *Rastini 101* (L), *Warburg 1548* ♂ (A, NY), *Woejantoro 34* ♀ (L).

DISTRIBUTION. Eastern Java, Borneo and the Philippines east to extreme southeastern New Guinea and Cape York, Queensland; well-drained rain forests, moist to rather dry thickets, gallery forests, and garden regrowth; from sea level to 900 m. elevation. See MAP 1.

ILLUSTRATIONS. PLANCHON, J. E., London Jour. Bot. **4**: *t. XVII* and *XVIII*. 1845, as *Rabelaisia philippinensis*. VIDAL Y SOLER, Flora Forestal del Archipielago Filipino, Atlas, *t. 24*. 1883. LAUTERBACH, C., Bot. Jahrb. **55**: *t. 4*. 1918, as *Lunasia amara* var. *repanda* (*A–D*), and *L. quercifolia* (*E–L*). ENGLER, A., Nat. Pflanzenfam. ed. 2. **19a**: *t. 99*. 1931, from LAUTERBACH, *loc. cit.*

Rabelaisia parvifolia Planch. [*Lunasia parvifolia* (Planch.) Miq.] was based on a collection from Boeton Island, Celebes, with unusually small leaves 6–12 cm. long and 2–4 cm. wide. Similar small-leaved plants occur sporadically, however, in Java, Borneo, the Philippines (Luzon and Mindoro islands) and Papua, and it appears that this feature is merely a response to dryer, more open conditions than the plant normally grows in.

Rabelaisia philippinensis Planch. [*Lunasia philippinensis* (Planch.) F.-Vill.] was reduced to synonymy under *Lunasia amara* by Merrill, Enum. Philip. Fl. Pl. **2**: *332*. 1923. The two syntypes examined, *Cuming 501* and *1512*, are almost identical with the neotype of *L. amara*.

I have not seen the type of *Mytilococcus quercifolius* Zoll., the type species of the genus *Mytilococcus*, but judging from the description (". . . flores glomerulati, glomerulis brevissime pedicellatis densifloris. Fructus 3-coccus, cocci profunde separati obverse mytiliformes extus ab apice dehiscentes.") it is almost certainly a *Lunasia.* Miquel apparently did not consider Zollinger's publication of the genus valid (presumably because of Zollinger's expressed hesitancy about describing it as new) and redescribed it, citing it, with a slightly different spelling, as "*Mytilicoccus* Zolling. mss." He then described two species, *M. costulatus* and *M. grandifolius*, on the basis of Zollinger's original collection number. Later (Ann. Mus. Bot. Lugd.-Bat. 3: 89. 1867) Miquel reduced *Mytilicoccus* to *Lunasia* and listed *Mytilococcus quercifolius* Zoll. as a synonym, in part, under both *Lunasia costulata* and *L. grandifolia.* Thus it seems that he considered Zollinger's species to be based on a mixed collection. Although this problem cannot be fully clarified without examination of the Zollinger collections in question, it seems reasonable to include the names here as synonyms. None of them antedate *L. amara* and, judging from the descriptions, the collections they represent would fall within the range of variation of that species. In support of this last point is the fact that *L. costulata* was reduced to a variety of *L. amara* by Hochreutiner and that later Engler (1931, p. 236) listed both *L. costulata* and *L. grandifolia* as synonyms of *L. amara.*

Whereas the neotype of *Lunasia amara* var. *amara* and the majority of specimens from almost throughout the range of the genus have scale-like trichomes (TYPES I–III) on the lower surface of the leaf blades grading to stellate trichomes (TYPES III–V) on the inflorescence and fruit, the type collections of *L. mollis* Merr., from Cebu Island, Philippines, and *L. pubifolia* Merr., from Bohol Island, Philippines, and a number of other specimens from scattered localities including Luzon Island, Sarawak, East Borneo, Celebes, and New Guinea represent an extreme in which the plants have exclusively stellate trichomes (TYPE V). Other specimens, including the type of *Androcephalium quercifolium* Warb. and a number of other scattered collections from New Guinea, Cape York Peninsula, and the Philippines (Luzon and Palawan Islands), have a mixture of scale-like and stellate trichomes (TYPES I–V) on the lower surface of the leaf blades. There are also several collections, from scattered localities, with leaves that are glabrous at maturity except for a few scale-like trichomes on the lower midrib, and a single collection from Celebes Island, *NIFS bb V-276*, has mature leaves that are densely lepidote below with overlapping scale-like trichomes. One of the functions of trichomes is to regulate water loss, and it seems that these variations probably reflect necessary adaptations in that regard. The genetic differences involved appear to be slight, since there do not seem to be any consistent correlating features.

I have not seen the type of *Lunasia repanda* Laut. & K. Sch., from New Guinea, but I did see a collection (*Gjellerup 621*) cited by Lauterbach in a later paper in which he reduced the species to *L. amara* var. *repanda* — a name invalidated by the earlier *L. amara* var. *repanda* Merr., from the Philippines. The leaves of the *Gjellerup* collection and the type of Merrill's variety are similar, each with 5–8 blunt lobes along each margin.

Approximately one-fourth of the specimens treated here as *L. amara* var. *amara* have similarly repand leaves and there are numerous gradations to the shallowly undulate (as in the neotype of *L. amara*) and subentire types of leaves. Furthermore, in a number of collections, especially from New Guinea where the repand leaves are predominant, subentire, shallowly undulate, and lobed leaves all may be found on a single branchlet.

Lunasia reticulata Elmer, from Sibuyan Island, Philippines, was based on a single collection with rather pronounced tertiary veins in the dried leaves. This is a minor variation and the venation pattern of these leaves is the same as in typical *L. amara*. Similar reticulate leaves were also noted in collections from Luzon Island and Celebes Island. *L. reticulata* was previously listed as a synonym of *L. amara* by Merrill, Enum. Philip. Fl. Pl. 2: 332. 1923, and by Engler (1931).

I have not seen the type collection of *Lunasia macrophylla* Merr., from Mindanao Island, Philippines, and I suspect that there were no isotypes distributed from Manila. Merrill described it as differing from *L. amara* in the following features: leaf blades to 45 cm. long, coriaceous, subentire, main veins to 45 pairs, petiole about 10 cm. long. Open flowers and fruits were not seen. With the exception of the high number of veins, the specimen described would fall within the range of variation I have outlined for *L. amara* var. *amara*. A number of specimens from throughout the range of that taxon have leaves similar in size and texture. The largest number of veins I have encountered, however, is 35, in a collection (*Ahern*, 1901) from the same district of Mindanao as Merrill's type. Similar specimens, with more than 30 pairs of veins, were encountered in collections from a number of other scattered localities including Borneo, Luzon Island, Celebes Island, West New Guinea, and Territory of New Guinea. Since Merrill, in the English portion of his description, stated, "Lateral nerves of larger leaves up to 45 on each side," I think it is probable that some of the leaves had considerably fewer veins and were sufficiently close, in that respect, to warrant inclusion of *L. macrophylla* with *L. amara* var. *amara*. Furthermore, in his Enumeration of Philippine Flowering Plants 2: 332. 1923, Merrill cited another Mindanao collection, *Ahern 559*, as *L. macrophylla*, the leaves of which, at least in two duplicates I have examined, have about 29 pairs of veins.

Lunasia gigantifolia Merr., from British North Borneo, was also based on a large-leaved specimen which, Merrill noted, is allied to *L. macrophylla* but ". . . easily distinguished by its membranaceous, much fewer-nerved leaves and much longer petioles." It is surprising that Merrill considered this a distinct species. The petiole lengths in his two descriptions overlap (9–15 cm. for *L. gigantifolia* and about 10 cm. for *L. macrophylla*) and leaf textures vary considerably in much of the Philippine material he identified as *L. amara*. Also, the number of lateral veins he described for *L. gigantifolia* (". . . . about 26 on each side of the midrib") is very close to that of the *Ahern* collection, mentioned above, that he later determined as *L. macrophylla*.

Lunasia obtusifolia Merr. was based on a collection from Bohol Island, Philippines, with obovate leaves that are obtuse to rounded at the apex and cordate at the base. Although the majority of specimens examined have leaves that are oblanceolate with acuminate apices and narrowly rounded or subcordate bases, a few, from scattered localities, have leaves almost identical with the type of *L. obtusifolia*. Also, there are a number of specimens, including ones from Java, Sumbawa, Borneo, the Philippines, Celebes, the Moluccas, West New Guinea, and Papua that are variously intermediate. It seems probable that shortening and widening of the leaf blade is a response to environment. The type of *L. obtusifolia* was collected on beach cliffs and similar specimens, especially from Papua, are from similarly dry, exposed habitats.

The type collection of *Lunasia nigropunctata* Merr., from Luzon Island, Philippines, has leaves with scattered oil dots that appear black. In transmitted light, however, they are pellucid and not at all different in appearance from those in the other specimens of *Lunasia* examined. Varying degrees of similar blackish dots were noted in several other collections from scattered localities, and I am satisfied the character is of no taxonomic value.

Lunasia quercifolia (Warb.) Laut. & K. Sch. var. *lanceolata* C. T. White was based on a collection from Papua with subentire, lanceolate leaves. In his original description, White stated that he had hesitated a long time before applying a varietal name since there were intermediates with the type of *L. quercifolia*. The existence of such intermediates is even more evident today, with many more New Guinea collections available, and some of the specimens even have "*quercifolia*" and "var. *lanceolata*" leaves on a single branchlet. Also, lanceolate leaves almost identical with those of White's variety have turned up in scattered collections from the Philippines.

The name *Lunasia truncata* Elmer is illegitimate since no Latin description was included in the original publication. The type collection, from Luzon Island, Philippines, differs only slightly from the neotype of *L. amara* in having very short-beaked follicles. This is a variable character and follicles with more or less obsolete beaks as well as ones with beaks to 5 mm. long occur sporadically almost throughout the range of *L. amara*. The epithet *truncata* refers to the apex of the short-beaked follicle.

Trichomes such as those illustrated in FIG. 1 as TYPE VI were noted on the leaves and/or fruits of six collections from the following localities: Kangean Island, Halmaheira Island, Ambon Island, the Vogelkop Peninsula in West New Guinea, and the Sepik and Morobe Districts of the Territory of New Guinea. In each of the specimens they are sparsely distributed on the plant and are mixed in with a predominance of the usual scale-like to stellate trichomes. Although these unusually large trichomes do not seem to grade into the other types, they nevertheless seem to represent a rather minor variation. Certainly, in view of their discontinuous geographic occurrence, they cannot be used as a taxonomic character.

1b. **Lunasia amara** var. **babuyanica** (Merr.) Hartley, stat. nov.

Lunasia babuyanica Merr. Philip. Jour. Sci. Bot. 3: 411. 1908. Type: *Fénix BS 4050*, Philippines, Babuyan Islands, Camiguin Island.

Shrub 2 m. Branchlets, petioles, lower leaf blade and inflorescences with stellate (TYPES IV & V) trichomes. Petioles 8–12 cm. long. Leaf blades chartaceous, narrowly obovate, 23–47 cm. long, 10–18 cm. wide; base obtuse to rounded, to 2 cm. wide; main veins 21–22 on each side of the midrib; margins repand toward the apex; apex obtuse to bluntly short acuminate. Follicles densely covered with twisted, simple or 2–3-branched, stellately pubescent processes to 8 mm. long.

Philippines. BABUYAN ISLANDS. Camiguin Island: Cagayan Province, Camiguin Volcano, forest slopes at 1200 ft., *Edaño BS 79141* ♀ (NY); in thickets near the seashore, *Fénix BS 4050* ♂ & ♀ (K, US) — isotypes.

It is difficult to say what taxonomic rank, if any, should be assigned to this material. While the follicles appear very different from those of var. *amara*, there are no other distinguishing features and it is impossible to identify staminate or sterile specimens. I am reasonably certain that the follicular processes, which are vascularized outgrowths from the main vascular strands of the pericarp, are the result of normal growth and not such as might result from an insect sting; the fruits contain normal seeds and the two collections were made at different localities some years apart (Fénix's in 1907 and Edaño's in 1930).

2. Collection of uncertain identity: *Wood SAN A4170* ♂ & ♀ (A, L). British North Borneo (Sabah), Lahad Datu District, NE ridge of Mt. Silam, 12 miles WSW of Lahad Datu.

The two sheets of this collection each have two staminate branchlets and a single, unattached fruit. The staminate specimens are in bud only, but match vegetatively other large-leaved specimens of var. *amara* from Borneo and the adjacent Philippines. The follicles are slightly larger, however (1.5 cm. high and 1.2 cm. wide), and the seeds differ in having trichomes sparsely scattered over the surface of the testa (which was glabrous in all other material of *Lunasia* examined). Although these seed trichomes are scale-like they are otherwise atypical for *Lunasia* in that they are 3 or 4 cells thick in the central area. Since there is a possibility that the unattached fruits of these specimens were gathered from the ground or from a different plant and do not belong with the branchlets, taxonomic designation will have to be delayed until complete material can be examined.

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———. Rutaceae. Nat. Pflanzenfam. ed. 2. **19a:** 187–358. 1931.

HARTLEY, T. G. A revision of the Malesian species of Zanthoxylum (Rutaceae). Jour. Arnold Arb. **47:** 171–221. 1966.

PRICE, J. R. The distribution of alkaloids in the Rutaceae. *In*: Chemical Plant Taxonomy, T. Swain, Editor. 429–452. Academic Press, London and New York. 1963.

INDEX TO EXSICCATAE

All of the collections listed below, with three exceptions that are indicated otherwise, are *Lunasia amara* var. *amara.*

Adduru *111, 240*
Aet & Idjan *860*
Agama *BS 582, FB 21597*
Agra *PNH 35334*
Ahern *559*
Ahern's Collector *FB 1436, FB 2462, FB 3106*
Alcasid et al. *PNH 1601*
Altmann *421*
Ampuria *SAN 35283*
Ashton *BRUN 3206*
Backer *26883, 36482*
Barnes *FB 180*
Bartlett *13504, 13515*
Bermejos *BS 247*
Borden *FB 745*
Borssum Waalkes *3239*
Brass *761, 1459, 1646, 19317, 19655*
Buwalda *4717, 4937, 5232*
Carr *11171, 11358*
Catalan *FB 25108, FB 25110*
Cenabre *FB 28496*
Chew *485*
Clark *FB 1083*
Clemens *883, 10641, 10684*
Conklin *PNH 18588, PNH 39202*
Cuming *501, 1512*
Curran & Merritt *FB 15825*
Darbyshire & Hoogland *8043*
Docters van Leeuwen *11382*
Ebalo *628, 1097*
Edaño *PNH 11141, PNH 11452, PNH 15331, PNH 17871, BS 41677, BS 46237, BS 77576, BS 79141* (*Lunasia amara* var. *babuyanica*)
Elbert *3238*
Elmer *6664, 7093, 8115, 8119, 12119, 13022, 15140, 20849*
Endert *5120*
Escritor *BS 20776, BS 21188*
Fénix *BS 4050* (*Lunasia amara* var. *babuyanica*), *BS 15842, BS 26059*
Forestry Guard *PNH 4311*
Gachalian *PNH 15463*
Gjellerup *621*
Gutierrez *PNH 78065*
Gutierrez & Espiritu *PNH 80798*
Hartley *10641, 11330*
Hellwig *131*
Henty *NGF 10524*
Henty & Sayers *NGF 20537, NGF 20555*
Herre *1228, 1238*
Hochreutiner *112, 113*
Hollrung *373*
Hoogland *3687, 3930*
Hujin *SAN 37830*
Jacobs *4715*
Jensen *253*
Kanehira & Hatusima *11527*
Kondo & Edaño *PNH 38853*
Koorders *16946β, 16948β, 16953β, 21584β, 21585β*
Koster *BW 6803*
Kostermans *4816, 5603, 13446, 18686*
Lam *2661, 3181, 3291, 3305, 7803*
Loher *218, 219, 220, 221, 223, 5712, 5723, 5742*
Main *564*
Martelino & Edaño *BS 35616*
McGregor *BS 1273, BS 11184, BS 11264*
Meijer *SAN 26594*
Merrill *Species Blancoanae 5, 743, 1104, 1357, 2126, 2339, 3161*
Meyer *FB 2261*
Millar *NGF 12229*
Miranda *FB 20080*
Nedi *307*
Netherlands Indies Forest Service (NIFS), the following by anonymous collectors: *bb V-271, bb V-276, bb 24406*
Orden *PNH 33478*

Oro *FB 30904*
Pleyte *1048*
Pullen *3099*, *3505*
Quadras *369*
Quisumbing *PNH 2409*
Ramos *BS 38*, *BS 1830*, *BS 11026*, *BS 17509*, *BS 21751*, *BS 22688*, *BS 39751*, *BS 41047*, *BS 41156*, *BS 42705*, *BS 43358*
Ramos & Convocar *BS 83696*
Ramos & Edaño *BS 44031*, *BS 44306*, *BS 49223*, *BS 84944*
Ramos & Pascasio *BS 34973*
Rastini *101*
Reinwardt *15016*
van Royen *5073*
van Royen & Sleumer *6685*
Santos *5161*
Schodde *2564*
Sulit *PNH 11730*, *PNH 12353*, *PNH 17049*
Sulit & Conklin *PNH 16970*
Symington & Agama *North Borneo Forestry Dept. 9257*
Tamesis *FB 11908*
Velasco *FB 28124*
Vidal *135*, *135 bis*, *136*, *682*, *1205*
Warburg *1548*
Wenzel *1515*
White *705*, *819*
Whitford, *5*, *508*, *FB 11791*
Wilford *SAR 4269*
Williams *34*, *518*
Wing *SAN 38106*
Woerjantoro *34*
Womersley *NGF 14047*, *NGF 19121*, *NGF 19280*, *NGF 19282*
Wood *SAN A4170* (identity uncertain); *SAN A4628*
Zippelius $\frac{31}{6}$, $\frac{69}{c}$, $\frac{192}{c}$

A SYNOPSIS OF THE ASIAN SPECIES OF DELPHINIUM. SENSU STRICTO *

PHILIP A. MUNZ

GROUP V

Perennial, from a woody rhizome. Plants hairy, rather low. Leaf blades rounded, not much dissected. Flowers large, the sepals often 20–35 mm. long, sometimes not more than 16 mm., more or less persistent after anthesis and becoming papery in texture, veiny. Spur thick, often 5–8 mm. wide at base in pressed specimens. Largely from central Asia, Himalayan region and surroundings.

Not closely coinciding with any of Huth's sections of the genus.

KEY TO SPECIES

1. Spur from almost equaling to exceeding the sepals in length.
  2. Flowers one to few; stem often less than 2 dm. tall.
    3. Upper sepal ca. 18 mm. long; lamina of upper petal narrow, ca. 2 mm. wide.
      4. Spur 16–18 mm. long. Caucasus. . . . . 61. *D. caucasicum.*
      4. Spur 8–14 mm. long. Nepal. . . . . 70. *D. nepalense.*
    3. Upper sepal over 20 mm. long; lamina of upper petal wider.
      5. Flowers mostly 1–2 on a stem; upper petal more or less setose at tip. Tibet. . . . . 78. *D. wardii.*
      5. Flowers 2–4 (–8) on a stem; upper petal glabrous at tip.
        6. Flowers greenish blue to pale violet; upper petal bilobulate at apex. . . . . 75. *D. tsarongense.*
        6. Flowers deep purplish blue; upper petal shallowly emarginate at apex. (Treated in Group VI). . . . . 114. *D. pylzowii.*
  2. Flowers several on a stem; stem usually more than 2 dm. tall.
    7. Stem glabrous below, often glaucous.
      8. The stem villous upward and in the inflorescence; sepals blue violet, 13–15 mm. long. West of Peking. . . . . . . 73. *D. siwanense.*
      8. The stem glandular-pubescent above; sepals blue, 20–30 mm. long. Asia Media. . . . . 72. *D. propinquum.*
    7. Stem with some hairs.
      9. Sepals hairy on both surfaces.
        10. Petals glabrous; upper sepal 18–25 mm. long. Yunnan. . . . . 67. *D. mairei.*
        10. Petals hairy; upper sepal 16–17 mm. long. Himalaya. . . . . 77. *D. viscosum.*

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* Continued from volume 48, p. 302.

9. Sepals glabrous on inner surface.
11. Lamina of lower petal subglabrous on surface. Western China and Tibet. . . . . 74. *D. trichophorum.*
11. Lamina of lower petal hairy on the surface.
12. Flowers few, in lax corymbs or racemes.
13. Spur 10–20 mm. long; upper petal bidentate and sparsely hairy at the tip. Himalaya. . . . . 77. *D. viscosum.*
13. Spur longer; upper petal emarginate, glabrous. Tibet. (Treated in Group VI). . . 83. *D. batangense.*
12. Flowers in racemes 1–3 dm. long; upper petal glabrous.
14. Spur ca. 10 mm. long; upper petal bidentate. Himalaya. . . . . 76. *D. vestitum.*
14. Spur 15–24 mm. long; upper petal entire. China. . . . . 74. *D. trichophorum.*
1. Spur much shorter than upper sepal.
15. Inflorescence crowded, subcapitate to elongate.
16. Upper sepal 16–17 mm. long, the spur 8–10 mm. long. Yunnan. . . . . 67. *D. mairei.*
16. Upper sepal 20–22 mm. long, the spur 6–8 mm. long.
17. Flowers purplish blue; petals dark violet; carpels 5. Afghanistan. . . . . 68. *D. minjanense.*
17. Flowers gray-blue; petals almost black; carpels 3. Kumaon. . . . . 62. *D. densiflorum.*
15. Inflorescence lax, either racemose or corymbose, or 1-flowered.
18. Upper sepal mostly 15–20 mm. long.
19. Flowers 1–2, the plant 4–10 cm. tall; sepals glabrous on inner surface. Pakistan. . . . . 66. *D. lacostei.*
19. Flowers several, the plant 15–100 cm. tall; sepals hairy within and without.
20. Spur 3–4 mm. thick at base.
21. Lower petioles to ca. 12 cm. long; stem 1–4 dm. tall. Turkestan, Pamir. . . . . 61. *D. dasyanthum.*
21. Lower petioles to ca. 25 cm. long; stem 4–10 dm. tall. Himalaya. . . . . 76. *D. vestitum.*
20. Spur 5–8 mm. thick at base.
22. Lamina of lower petal 10 mm. long; follicles 3, pubescent. Himalaya. . . . . 70. *D. nepalense.*
22. Lamina of lower petal 7–8 mm. long; follicles 5, glabrous. Pamir Range. . . . . 69. *D. molle.*
18. Upper sepal 20–30 mm. long.
23. Inflorescence racemose, at least that on the central stem.
24. Upper petals ciliate on laminae.
25. Anthers ciliate; carpels 5, glabrous. Pamir. . . . . 69. *D. molle.*
25. Anthers glabrous; carpels pubescent.
26. Carpels 5; lamina of upper petal bilobulate. Chitral. . . . . 71. *D. nordhagenii.*
26. Carpels 3; lamina of upper petal entire. Bhutan. (Treated in Group VI). . . . . 107. *D. muscosum.*
24. Upper petals glabrous on lamina; anthers glabrous.
27. Inflorescence glandular; upper sepal 20 mm. long;

spur 8 mm. long. Transcaucasia. . . 64. *D. foetidum.*
27. Inflorescence not glandular.
  28. Upper sepal 15–20 mm. long; spur 8–12 mm. long, Turkestan. (See Group IX). . . . . 223. *D. poltaratzkii.*
  28. Upper sepal 25 mm. long; spur 10 mm. long. Sinkiang. . . . . 58. *D. aconitioides.*
23. Inflorescence corymbose or with 1 to very few flowers.
  29. Leaves deeply divided into many narrow lobes mostly 1.5–2 mm. wide; upper petal bilobulate into pointed narrow lobules, hairy. Eastern Himalaya. . . . 65. *D. glaciale.*
  29. Leaves not so finely divided.
    30. Plants glandular, especially in upper parts. Himalaya. . . . . 59. *D. brunonianum.*
    30. Plants not glandular in upper parts.
      31. Lobes of petal laminae broad, not sharply pointed. Himalaya. . . . . 60. *D. cashmerianum.*
      31. Lobes of petal laminae lanceolate, sharp-pointed. Yunnan. 79. *D. wrightii.*

58. **Delphinium aconitioides** Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) **1**: 164. 1948.

Root long, thickish; stem 4–5 dm. tall, simple, very pilose; lower leaves long petioled, the blades 7 cm. long, 10 cm. wide, broadly cuneate, deeply 2-parted with cuneate lobes 2–3-fid, then coarsely crenulate incised, sparsely pilose on both sides; upper leaves 2–5 cm. long; raceme 14 cm. long, densely 30-flowered; bracts 2–2.5 cm. long, lance-oblong, bifid apically, ciliate; pedicels erect, the lower 1 cm. long, yellowish green; bracteoles 1–1.3 cm. long, lance-linear, pilose and ciliate; flowers semierect, greenish purple; sepals ovate, the upper sepal 2.5 cm. long, the lateral pair 1.5 cm. long, membranaceous, strongly veined, pilose, lower pair 1.4 cm. long, sparsely pilose, ciliate; spur 1 cm. long, 4 mm. wide at base, acute at apex, yellow-hairy; upper petals 2 cm. long, broad-linear, emarginate, dark violet; lower petals 1.3 cm. long, the laminae ovate, glabrous, violet-black; stamens 6 mm. long; anthers oblong, 1 mm. long; carpels 3, densely yellow-hirsute.

TYPE: *T. T. Yü 12827*, Aug. 21, 1937, from Taucheng Hsien, southern Sinkiang at 3800 m. (PE); not seen. No known material seen. Plant said to be aconite-like in appearance.

59. **Delphinium brunonianum** Royle, Illustr. Bot. Himal. 56. 1834.
FIG. 6, A.

Delphinium moschatum Munro ex Hook.f. & Thoms. Fl. Ind. 53. 1855. Based on *Munro*, Kanawer; seen (K).

Delphinium jacquemontianum Camb. in Jacquem. Voy. Bot. 8. *pl. 7.* 1844. Based on *Jacquemont 668* and *2025* (the latter labeled type at P, where seen and also at K).

Delphinium brunonianum var. *jacquemontianum* (Camb.) Huth, Bot. Jahrb. **20**: 392. 1895.

Delphinium brunonianum var. *schlagintweitii* Huth, *loc. cit.*

Delphinium brunonianum var. *aitchisonii* Huth, *loc. cit.* These last two varieties were proposed without designating types, although under the species as a whole both Schlagintweit and Aitchison collections were cited, and I have seen samples of both.

From a slender rootstock; plant with a musky odor when fresh, the stem erect, glabrous to soft-pubescent below, glandular-pubescent above, 1–10 dm. tall, simple at least below, leafy; lower petioles to 15 cm. long, vaginate at base, the upper much shorter; leaf blades somewhat reniform in outline, 3–8 cm. broad, more or less pilose especially beneath along the veins, 5-fid to the middle, the segments crenate or dentate incised into ovate subobtuse teeth or short lobes; upper leaves becoming leafy bracts several cm. long, the uppermost simple or usually toothed; inflorescence mostly corymbose, sometimes racemose, few flowered; pedicels erect, coarse, to 15 cm. long; bracteoles hairy, lance-ovate and entire or ovate and trilobed or toothed, rather near the flower, 5–15 mm. long; sepals royal blue to pale blue, veiny, persistent, soft-pubescent with white hairs; upper sepal round-ovate, 20–30 mm. long, almost as wide, obtuse, the spur almost straight, saccate, ca. 8 mm. wide at base, 12–14 mm. long, rapidly narrowed to a conical blunt tip; lateral sepals broadly ovate, 25–35 mm. long, obtuse; lower sepals round-ovate, 25–30 mm. long, 18–22 mm. wide; petals black, the upper with the blade 14–16 mm. long, oblique above, with a rounded erose, sometimes ciliate apex or the tip with 2 lanceolate lobules; spur 11–12 mm. long; lower petals strongly oblique, the rounded blade 6–7 mm. by 4 mm., bearded at base, ciliate, the claw 6–7 mm. long; stamens 7–8 mm. long, strongly expanded, glabrous, the dark anthers 1.2 mm. long; follicles pubescent, 4–5(–7), ca. 12 mm. long; seeds over 1 mm. long, winged on angles.

TYPE: Kunawur, Kongno Pass, *R. Inglis*; not seen.

DISTRIBUTION. Apparently abundant at about 3500 to 6000 m., Himalayan region.

ILLUSTRATION. Bot. Mag. *pl. 5461.* 1864.

REPRESENTATIVE COLLECTIONS. **Kashmir:** *Ludlow 838; Koelz 2508f, 2804, 2835a; Duthie 5301; R. R. Stewart 20176; Polunin 6250; Schlagintweit 1711, 1985, 6306.* **Afghanistan:** *Aitchison 957.* **Chitral:** *Stainton 2846, 3234; Bowes Lyon 1083.* **Tibet:** *Hanbury-Tracy 143; Ludlow & Sherriff 9010, 9925, 1995, 8930; Strachey & Winterbottom 8.* **Punjab:** *Koelz 7006, 1233, 1000A, 6703, 10112; Drummond 4348, 4346, 4341.* **Kumaon:** *Koelz 21110; Duthie 5301, 745; Wallich 1832; Schlagintweit 9004;* **Nepal:** *Lowndes 1283; Swann R8; Sharma E295.*

This is a group with considerable variation, in such characters as the presence of white and yellow pubescence especially about the sepals, in size and lobing of bracteoles, in tips of upper petals which may be entire and glabrous, bilobulate and glabrous, entire and bearded, and bilobulate

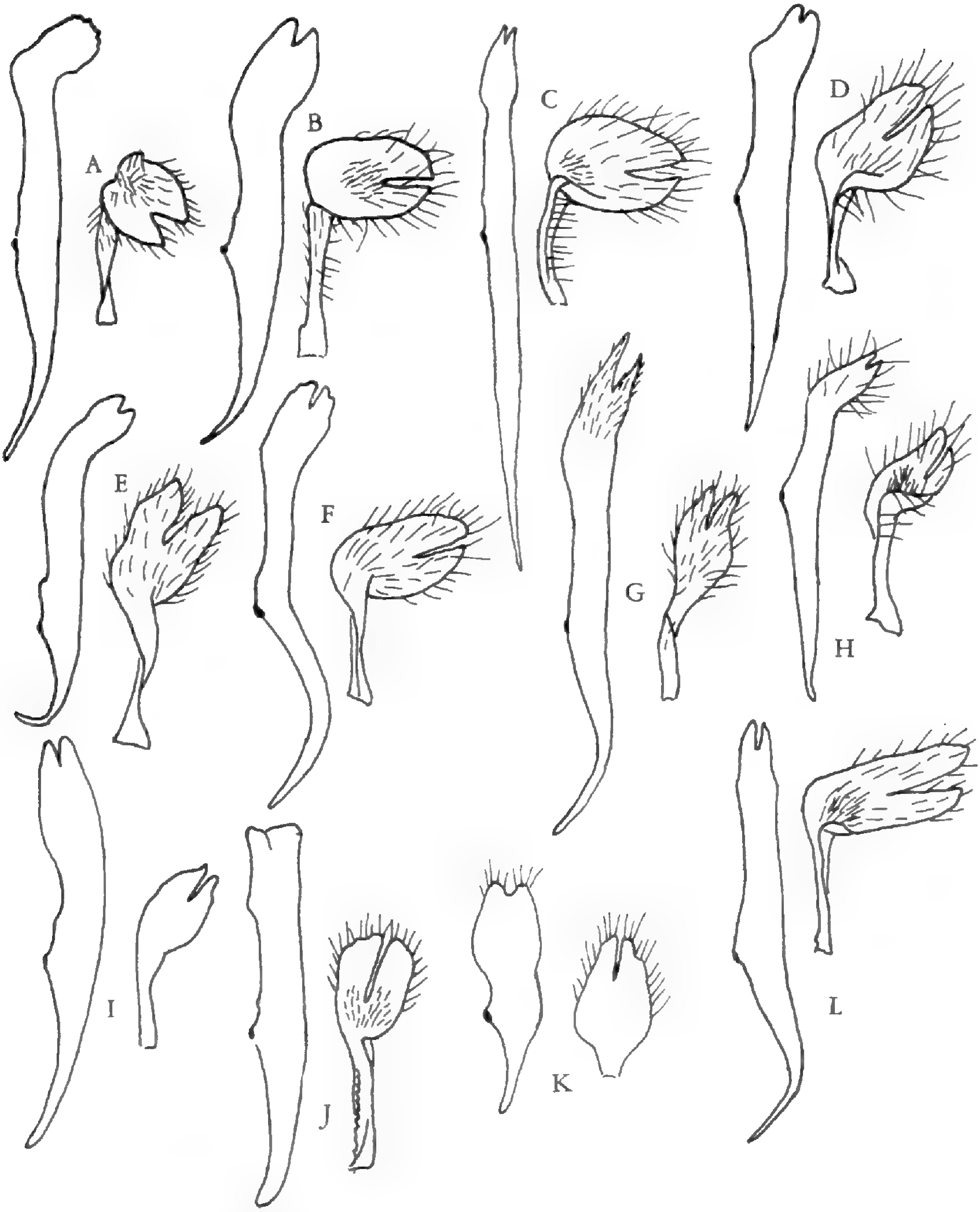

Figure 6. **Delphinium,** Group V. Petals, the upper spurred, the lower clawed. A. *D. brunonianum*; blade of upper petal 14 mm. long, spur 11 mm., blade of lower petal 6 mm. long, claw 6.5 mm.; drawn from *Koelz 7006* (GH). B. *D. cashmerianum*; blade of upper petal 13 mm. long, spur 11 mm., blade of lower petal 8 mm. long, claw 8 mm.; drawn from *Vaid* in 1946 (US). C. *D. caucasicum*; blade of upper petal 12 mm. long, spur 17 mm., blade of lower petal 6 mm. long, claw 7 mm.; drawn from TYPE (LE). D. *D. dasyanthum*; blade of upper petal 11 mm. long, spur 12 mm., blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Gontchezov* in 1928 (GH). E. *D. densiflorum*; blade of upper petal 14 mm. long, spur 6 mm., blade of lower petal 7 mm., claw 9 mm.; drawn from *Chand 881* (MICH). F. *D. foetidum*; blade of upper petal 12.5 mm. long, spur 12 mm., blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Karjagin & Isoev* in 1933 (GH). G. *D. glaciale*; blade of upper petal 15 mm. long, spur 13 mm., blade of lower petal 7 mm. long, claw 7 mm.; drawn from *J. D. Hooker* (GH). H. *D. lacostei*; blade of upper petal 10 mm. long, spur 12 mm., blade of lower petal

and bearded. In fact, there may be more than one taxon involved, or possible hybridity. One of the characteristics mentioned in the literature, and often on the collection labels, is the musky odor.

60. **Delphinium cashmerianum** Royle, Illustr. Bot. Himal. 55. 1834. FIG. 6, B.

Delphinium aitchisonii Huth, Bot. Jahrb. **20:** 395. 1895. Based on *Aitchison* in 1877, from Perfun (LE); seen.

Perennial, from slender woody rootstock; stems 1–5 dm. tall, slender, mostly strigose, sometimes with spreading hairs especially above, but nonglandular, simple or frequently branched above, scattered-leafy; lower petioles to 15 cm. long, slender, somewhat dilated at base, upper petioles much shorter; leaf blades reniform-pentagonal in outline, 2–10 cm. broad, mostly somewhat strigulose, palmately 5–7-lobed about halfway to the base, the divisions rather few toothed or lobed into ovate or lance-ovate, obtuse to acuminate teeth or lobules; inflorescence a few-flowered corymb or open corymbose panicle; lower bracts often foliose and divided, the upper entire and ovate to lanceolate; pedicels slender, 1–8 cm. long, strigose or spreading pubescent; bracteoles linear and setaceous to broadly lanceolate, 4–10 mm. long, mostly remote from the flower; sepals bluish purple, rarely pinkish, more or less concavo-convex, persistent, pubescent without and often within, reticulate veined, the upper sepal 20–30 mm. long, 12–15 mm. broad, obtusish, the spur mostly straight, conical, 12–15 mm. long, 5–12 mm. wide at the base, tapering rapidly to the mostly blunt apex; lateral sepals 15–25 mm. long, 6–12 mm. wide, obtuse; lower pair rhombic-obovate, 15–25 mm. by 6–16 mm.; petals dark purple to light blue, the upper pair slightly oblique, the laminae 13 mm. long, glabrous, erose or bidentate, the spur 8–11 mm. long; lower laminae very oblique, oblong-ovate, long-bearded and ciliate, ca. 8 mm. by 5 mm., cleft almost half way, the claw 7–8 mm. long; stamens 6–7 mm. long, well dilated in lower half, glabrous, the dark anthers 1.2 mm. long; follicles 3–7, hairy, 13–15 mm. long, 4 mm. wide, the styles an additional 2–3 mm.; seeds covered with horizontal rows of scales.

TYPE: from the Garden of Shalimer, Kashmir; not seen.

DISTRIBUTION. At roughly 3000 to 5000 m., Himalaya.

ILLUSTRATIONS. ROYLE, Illustr. Bot. Himal. *pl. 12.* 1833. Bot. Mag. *pl. 6189.* 1875, and *pl. 6830.* 1885, the latter as var. *walkeri* Hook. f.

REPRESENTATIVE COLLECTIONS. **Kashmir:** *Jacquemont 1005*; *R. R. Stewart*

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5 mm. long, claw 6 mm.; drawn from *Polunin 6208* (F). I. *D. mairei*; blade of upper petal 11 mm. long, spur 11 mm., blade of lower petal 5 mm. long, claw 5 mm.; drawn from *Schneider 2430* (US). J. *D. minjanense*; blade of upper petal 12 mm. long, spur 8.5 mm., blade of lower petal 6 mm. long, claw 7 mm.; drawn from *Koelz 12713* (US). K. *D. molle*; blade of upper petal 6 mm. long, spur 5 mm., blade of lower petal 5 mm. long, claw 2.5 mm.; drawn from *Lacoste 11* (P). L. *D. nepalense*; blade of upper petal 13 mm. long, spur 11 mm., blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Dhwoj 225* (E).

3485, 3759, 6325, 9881, 22179; *Koelz 5803, 6026, 2787, 2973*; *Falconer 65*; *Dickason 370, 367*; *Duthie 11560*; *Ludlow & Sherriff 7914.* **Punjab:** *Cooper 5309*; *Koelz 1313, 6927, 10028, 10041.* **Kumaon:** *Strachey & Winterbottom 5, 6*; *Duthie 744.* **Garwhal:** *Schlagintweit 9007.* **Tibet:** *Kingdon Ward 12367, 12317a*; *Schlagintweit 5484*; *Ludlow & Sherriff 2881, 2814.*

61. **Delphinium caucasicum** C. A. Mey. Verzeichnis Pflanzen Caucasus, 200. 1831. FIG. 6, C.

Delphinium speciosum var. *caucasicum* (C. A. Mey.) Huth, Bot. Jahrb. **20:** 416. 1895.

Stems pubescent, scarcely taller than the leaves, 1–2.5(–4) dm.; petioles scarcely dilated at the base, 4–10 cm. long; leaves coriaceous, cordate-orbicular, 2–6 cm. broad, tripartite to near the base, the segments broadly obovate, subglabrous except for minute ciliation, incised one-fourth to one-half way into 3 short broad lobes, these entire or few toothed, the teeth oblong-ovate, ca. 5–8 mm. wide; flowers 1–few, subcorymbose, the bracts reduced leaves; pedicels retrorse-hairy, erect, 4–6 cm. long; bracteoles near the middle of the pedicels, petiolulate, oblanceolate, 6–12 mm. long, 1.5–2.5 mm. wide; sepals blue, loosely white-hairy on both sides, quite persistent; upper sepal 18 by 10 mm., attenuate, the spur decurved, 16–18 mm. long, 4 mm. wide at base; lateral sepals ca. 18 mm. by 8 mm., prolonged at apex; lower sepals 20 mm. by 8 mm., attenuate; petals black, the upper lamina almost straight, ca. 12 mm. long, bidentate and glabrous at apex, the spur ca. 16 mm. long; lower laminae oblong-ovate, 6 mm. by 4 mm., bearded and ciliate, bifid almost halfway into approximate lobes; claw bearded, 7 mm. long; stamens 6–7 mm. long; anthers yellow; follicles 3, hairy, 13–15 mm. by 4 mm.; seeds brown, angled, 2 mm. long, inconspicuously squamate.

TYPE: Caucasus, western alps "ad torrentem Malka and in alpibus Kasbek" (LE), seen; rocky places, *Meyer*?

ILLUSTRATIONS. Semaine Hort. 478. 1898 and Stschukin in Karsten, Veg.-Bild. **20:** *pl. 18.* 1929, according to Index Londinensis. Not seen by me.

SPECIMENS SEEN. Caucasus prope trajectum Mamisson, prov. Terek, *Desulavi* (K); Caucasus, *C. A. Meyer 1727* (P); near Shtuch Pass, *E. & N. Busch* (K).

62. **Delphinium dasyanthum** Kar. & Kir. Bull. Soc. Nat. Mosc. **25:** 138. 1842. FIG. 6, D.

Delphinium caucasicum var. *hirsutum* Regel & Herder, Enum. 20. 1864. Type from Santash-Pass in Tussend-Thian; not seen.

Delphinium vestitum var. *hirsutum* Osten-Sacken & Ruprecht, Sert. Tiansch. 38.

Delphinium dasyanthum vars. *undulatum* and *angustisectum* Huth, Bot. Jahrb. **20:** 396. 1895. Described as having upper petals bearded and leaf-laciniae narrow, respectively. No specimens cited.

Stem simple, erect, 1.5–4.5 dm. tall, subglabrous to pilose below, with white spreading and some glandular hairs above, scattered leafy to the inflorescence; lower petioles to ca. 12 cm. long, vaginate at the base, the upper shorter; leaf blades rounded in outline, cordate at base, 2–8 cm. broad, glabrous or finely pubescent on both sides especially along the veins, 3-parted halfway or more, the lateral segments often bifid so as to make 5, these broad, cuneate-obovate, coarsely toothed or shallowly laciniate, the teeth broad, subovate, mucronulate; uppermost leaves passing into divided bracts; inflorescence an elongate often crowded raceme, pubescent, the upper bracts lanceolate, to ca. 1 cm. long, hairy; pedicels somewhat divaricate, 1–3 cm. long; bracteoles at base of flower, erect, lanceolate, 4–5 mm. long; sepals deep blue, villous within and without; upper sepal ovate, obtuse, ca. 16 mm. by 10 mm., the spur somewhat decurved, 10–12 mm. long, 4 mm. wide at base, slightly narrowed to the blunt tip; lateral sepals round-obovate, ca. 16 mm. by 16 mm.; lower sepals obovate, ca. 17 mm. by 11 mm., with an apiculate acute apex; petals black, the upper with a slightly oblique lamina 10–11 mm. long, usually almost or quite glabrous, rounded truncate at the emarginate apex, the spur about 12 mm. long; lower petals strongly oblique, the oblong-ovate lamina 7 mm. by 4 mm., cleft ca. 3 mm., with hairs to 2 mm. long; claw 6 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.5 mm. long, oblong; follicles 3, hairy, erect, 1 cm. long; styles an additional 3–4 mm.; seeds transversely lamellate, the scales almost continuous.

TYPE: "Hab. in lapidosis summarum alpium Alatau ad fluviam Sarchan et Baskan," *Karelin & Kiriloff 1169*, in 1841 (LE); isotypes also seen (K, BM, P).

DISTRIBUTION. At elevations of about 3000–5000 m., Turkestan; in ranges like the Pamir, Tien Shan, Alatau, etc.

ILLUSTRATIONS. REGEL, Gartenfl. *pl. 1027*. 1880. POPOV, Manual Fl. Tashkent, fasc. 1–2. *fig. 172*. 1923–24, according to Index Londinensis.

REPRESENTATIVE SPECIMENS. **Turkestan:** *Emme 451*; *Regel* in 1878 and 1882; *Korolkov 76*; *Rajkova 129*.

63. **Delphinium densiflorum** Duthie ex Huth, Bot. Jahrb. **20**: 393. 1895. FIG. 6, E.

Delphinium densiflorum var. *platycentrum* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 103. 1896. Based on 3 collections from Kumaon: Ralem Pass, *Duthie* (I have seen *Duthie 2677*); Lebung Pass, *Duthie* (I have seen *Duthie 5303*); and Tangut region near Amdo, *Maximowicz* (not seen).

? *Delphinium brunonianum* Royle var. *densum* Maxim. Fl. Tangutica. 24. 1889. Placed here by Huth. I have seen no material.

? *Delphinium densiflorum* var. *stenocentrum* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 103. 1896. Based on a collection from Bashahr by *Watt*. I have not seen it, but have seen other material from the same locality.

Perennial from a subcylindric rhizome; stem erect, strict, mostly simple, 3–5 dm. tall, fistulose, retrorse-strigose or almost spreading-villous, more or less glandular, leafy throughout; lower petioles rather fleshy, vaginate at base, somewhat hairy, 5–18 cm. long, the upper shorter; blades reniform to almost round in outline, 5–10 cm. broad, hairy, mostly 5-parted, the segments cuneate-obovate, trifid above, the lobes or teeth mostly rather blunt to almost rounded; uppermost leaves becoming trifid bracts of the very dense racemose inflorescence and with lanceolate lobes and teeth; pedicels appressed to the axis, 1.5–5 cm. long, the bracteoles 2, at middle of pedicel or above, adpressed, linear-lanceolate, 10–18 mm. long, villous; sepals gray-blue to deep blue, often with blue nerves, long white-hairy; upper sepal ovate, ca. 22 mm. by 14 mm., obtuse, the spur subsaccate, 6–8 mm. long, ca. 6 mm. wide at base; lateral sepals oblong-elliptic, 20 mm. by 10 mm., rounded-obtuse; lower sepals rhombic-ovate, asymmetric, 22 mm. by 15 mm., obtuse; petals almost black, the upper with a somewhat oblique, bidentate, glabrous, narrow blade 14 mm. long, the spur 6 mm. long; lower petals somewhat oblique, the bearded lamina oblong-ovate, 7 mm. by 4 mm., cleft for almost 3 mm., the claw 8–9 mm. long; stamens 8–9 mm. long, glabrous; anthers dark, almost 2 mm. long; follicles 3, villous, 5–6 mm. long; seeds brown, 2 mm. long, winged on angles with loose testa.

TYPE: Kumaon, "in parte occid. faucium Lebung, 5300–5600 m.", *Duthie 2677* (G?); isotypes (BM, E, K), seen.

DISTRIBUTION. At about 4000 to 6000 m., Himalaya.

EXAMPLES. **Kumaon:** *Chand 881*; *Koelz 21082*; *Strachey & Winterbottom 4*; *Duthie 530.* **Nepal:** *Stainton, Sykes & Williams 3707; O. Polunin 1440, 1247.* **Garwhal:** *Huggins 39*; *Schlagintweit 9180, 9552.*

64. **Delphinium foetidum** Lomak, Act. Hort. Tiflis **2**: 285. 1897. FIG. 6, F.

Delphinium speciosum M. Bieb. var. *brevicalcaratum* Huth, Bot. Jahrb. **20**: 416. 1895. Characters given and area from which specimens are cited suggest that Huth's variety may belong here.

Perennial from a creeping rhizome, the stem erect, fleshy, leafy to the top, 2–4 dm. tall, simple, yellowish-pubescent with the spreading hairs enlarged at their base; leaves rounded in outline, 2–5 cm. broad, strigulose above, viscid-pubescent beneath, 2–3-fid, then incisely lobed into obtuse apiculate lobules 3–5 mm. broad; lower petioles to 10 cm. long, dilated at base, upper very short; inflorescence racemose, densely so when young, more lax in fruit; lower bracts foliose, divided; pedicels 1–8 cm. long, erect, glandular-villous; bracteoles oblong-lanceolate, to ca. 12 mm. long, 5 mm. wide, placed near the middle of the pedicel; sepals deep blue, white-hairy on both surfaces; upper sepal ovate, ca. 20 mm. by 15 mm., acute, the spur saccate, slightly curved, ca. 8 mm. long, 5 mm. wide at the base, only gradually narrowed to the obtuse apex; lateral sepals and lower more or less ovate, 20 mm. by 15 mm., rounded at apex; petals dark, the upper with lamina almost straight, 12.5 mm. long, rounded-bidentate at apex, glabrous, the spur 12 mm. long; lower petal very oblique, ovate-oblong, long-bearded and -ciliate, 7 mm. by 4 mm., cleft 1/3 its length, the claw 6 mm. long; stamens 7–8 mm. long, the filaments much widened below, glabrous; anthers dark, over 1 mm. long; follicles glandular-hairy, 12 mm. by 5 mm., the styles an additional 3 mm.; seeds brown, slender, 4 mm. long, with many transverse rows of scales.

TYPE: Caucasus: Karabach in Peri-tshingil, 10000 ft., *Medwedew*, 1884 not seen; *Lomakin*, 1895 (LE) seen. I propose the latter as lectotype.

EXAMPLES SEEN. **Elisabethpol:** Mts. Murov-dagh, *Schelkownikow 65* (K); **Transcaucasia:** jugum Zangezur, *Karjagin & Jsoev*, in 1933 (BM, GH, K, NY). **Iraq:** MRO, Qendil, 3000 m., *Rawi & Serhang 20208* (K).

Very near to *D. brunonianum* but, of course, more western and with a racemose rather than a corymbose inflorescence.

65. **Delphinium glaciale** Hook f. & Thoms. Fl. Ind. 53. 1855.

FIG. 6, G.

Perennial from a slender woody root, the plant with a musky smell; stem softly glandular-hairy to strigulose, 6–15 cm. tall, simple, leafy; leaves reniform in outline, 2–5 cm. in diameter, soft-hairy, the blades tripartite to the base, the segments cuneate, deeply divided into many linear-oblong lobes, acute, mostly 1.5–2 mm. wide; petioles to 5 cm. long, sheathing at the base; flowers inflated-subglobose, few in a corymb; bracts multifid, to ca. 2 cm. long, the petioles broad, with vaginate base; pedicels stout, erect, 2–6 cm. long; bracteoles 3 or more, multifid, 10–15 mm. long, scattered along the pedicel; sepals pale blue, membranous, veined, loosely pilose without; upper sepal obovate, ca. 30 mm. long, almost as wide, subobtuse, the spur slightly curved, saccate, ca. 15 mm. long, 8 mm. wide at the base, narrowed rapidly to a broad tip; lateral sepals almost straight on upper edge, semicircular on lower, 25 mm. by 13 mm., obtuse; lower sepals round-rhombic, ca. 30 mm. long and wide; petals black, the upper almost straight, the lamina ca. 15 mm. long, bearded, sharply 2-lobulate, spur 13 mm. long; lower petals scarcely oblique, the lamina ca. 7 mm. by 3 mm., long bearded and ciliate, cleft to near middle into lance-oblong lobes, the claw broad, 6 mm. long; stamens 8–9 mm. long, ciliate and much widened at base; anthers dark, 2 mm. long; follicles 5, subglabrous, 11–13 mm. long; seeds 1.5 mm. long, winged along the 3 angles.

TYPE: Eastern Himalaya, Sikkim, *J. D. Hooker* at 16–18000 ft. Specimen at Kew has Sept., 1845, Donkia Pass (holotype). Isotypes also seen (BM, E, GH, NY).

DISTRIBUTION. Among boulders, in forest glades, dry scree, etc., 5000–6500 m., Nepal, Sikkim, Bhutan.

ILLUSTRATIONS. HOOKER, Icon. Pl. 13: *pl. 1224*. 1877.

REPRESENTATIVE COLLECTIONS. **Nepal:** *K. N. Sharma E 482*; *Stainton 1025*; *O. Polunin 1790*. **Bhutan:** *Ludlow & Sherriff 16786, 17128, 19724*; *Gould 1412*. **Sikkim:** *Ribu & Rhomoo 5234*.

66. **Delphinium lacostei** Danguy, Jour. Bot. Morot **21**: 50. 1908. FIG. 6, H.

Perennial from a slender rootstock; stem 4–10 cm. tall, glabrous or with retrorse-spreading hairs, leafless, 2-flowered at apex; radical leaves several, the petioles 2–8 cm. long, pubescent, vaginate at base; leaf blades round-reniform in outline, 2–5 cm. broad, sparsely pubescent at least beneath, 3–5-parted to about 5–10 mm. from the base; the segments broadly cuneate-obovate, shallowly 3-lobed, then with few round-ovate mucronate teeth; bracts foliose, short- and broad-petioled, trilobed, hairy, or lacking; pedicel ca. 1 cm. long; bracteoles oblong-linear, 5–7 mm. long, subtending the flower; sepals blue, hairy and glandular without; upper sepal ovate, 16 mm. by 10 mm., obtuse, the spur straight, 10–11 mm. long, 5–7 mm. wide at base, obtuse; lateral sepals subelliptic, 14 mm. by 6 mm., obtuse, pubescent along central part, ciliate; lower sepals somewhat asymmetric, ca. 15 mm. by 6 mm., obtuse; petals dark, the upper lamina oblique, bidentate at the long-ciliate apex and 10 mm. long, the spur 12 mm. long; lower petals somewhat oblique, the lamina oblong, 5 mm. by 2 mm., yellow-bearded at the base, white-ciliate and scattered bearded, claw 6 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, 1.2 mm. long; follicles 4–5, glabrous or hairy.

TYPE: Slopes west of Sasser-La, Pamir, West Pakistan, 4950 m., Sept. 7, 1906, *Lacoste* (P); seen.

DISTRIBUTION. At about 4000 to 5500 m., apparently mostly in West Pakistan.

REPRESENTATIVE SPECIMENS. Khagan, *J. L. Stewart* in part; Karakoram, 13 mi. east of Nagar, *O. Polunin 6208*; Pangi, Chamba State, *Lace 2094*.

67. **Delphinium mairei** Ulbrich, Bot. Jahrb. **48**: 614. 1913. FIG. 6, I.

Delphinium viride Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) **1**: 165. 1948. Type, northwest Yunnan at Atuntze, Yangtze Snow Range, 4100 m., *T. T. Yü 9670* (PE); photo. (E) seen.

D. mairei Ulbr. var. *viride* (Chen) W. T. Wang, Acta Bot. Sinica **10**: 73. 1962.

? *Delphinium fengii* W. T. Wang, Acta Phytotax. Sinica **6**: 362. 1957. Based on *K. M. Feng 2207* from Chung-tien, Yunnan (PE); not seen.

Perennial from a woody rhizome; stem mostly 3–4 dm. tall, simple or nearly so, striate, with somewhat spreading to retrorsely appressed hairs to over 1 mm. long, rather few leaved; lower petioles 5–18 cm. long, with same pubescence as on the stems, dilated-vaginate at base; cauline petioles shorter; leaf blades round-reniform, short-hairy above and below, 2–7 cm. long, 3–10 cm. broad, 3–5-fid to within a cm. or so from the base, the segments broad cuneate-obovate, 3-lobed or -toothed, the lobes then often again toothed, the teeth oblong to ovate, rounded at apex; inflorescence mostly a single subcapitate raceme; bracts leafy, trifid into oblong divisions, hairy, 1.5–2 cm. long; pedicels ascending, hairy, to ca. 1.5 cm.

long; bracteoles densely hairy, ca. 1 cm. long; oblong-linear to elliptic, ca. 1 cm. below the flower or subtending it; sepals dark blue-violet, densely clothed with long whitish or yellowish hairs; upper sepal oblong-ovate, 16–17 mm. long, 14 mm. wide, more or less cucullate, the spur saccate, 8–10 mm. long, 5–6 mm. wide at the base; lateral sepals obovate, asymmetrical, 20 mm. by 14 mm., obtuse, hairy on outer surface; lower sepals 20 mm. by 10 mm., acute; petals blue, the upper almost straight, 11 mm. long, bidentate at apex, glabrous, the spur 11 mm. long; lower petals somewhat oblique, the subelliptic blade apparently not bearded, 5 mm. by 2.5 mm., the margin ciliate to glabrous, 2-lobed ca. 1/3 its length, the claw 5 mm. long; stamens 6–7 mm. long, broad at base, glabrous; anthers dark, ca. 1 mm. long; follicles 3, glabrous or pubescent.

TYPE: Yunnan, Io-chan, 3700 m., *Bonati* distrib. ser. B, no. *2669*, coll. *E. Maire*, Aug., 1910; isotype (UC), seen.

Apparently from Yunnan, at 3500–5000 m., as evidenced by *C. Schneider 2430* (GH, K, US) from near Lichiang, and *C. W. Wang 71576* (A) from Yunnan.

68. **Delphinium minjanense** Rech. f. Anz. Österr. Akad. Wiss. Math.-Nat. **91**: 73. 1954. FIG. 6, J.

Perennial from a woody root; stems in clumps, 1.5–5 dm. tall, fistulose, scattered glandular-pilose below, densely so above, leafy; lower petioles 5–15 cm. long, glandular-pilose; blades rounded in outline, 2–4 cm. long, 4–6 cm. wide, palmately 5-fid to two-thirds or more of their length, glandular-pilose, the segments shallowly incised into broadly round, mucronulate teeth; inflorescence a rather few-flowered raceme, sometimes with 1 or 2 supplementary branches below; lower bracts foliose, divided, ca. 1 cm. long, upper gradually less toothed to entire and lanceolate, glandular-hairy; pedicels glandular-pilose, ascending, 2–4 cm. long; bracteoles 2, lanceolate, 10–14 mm. long, just below or near the middle of the pedicel; flowers fragrant; sepals purplish blue, membranous and veiny in age, rather densely villous; upper sepal broadly ovate, ca. 20 mm. by 14 mm., rounded-truncate, the spur subsaccate, 6–7 mm. long, 5 mm. wide at the base; lateral sepals rhombic-elliptic, 18 mm. by 10 mm., rounded at apex; lower sepals broadly rhombic-ovate, 20 mm. by 15 mm., rounded-obtuse; upper petals dark violet below, paler above, quite straight, the lamina 11–12 mm. long, subtruncate and shallowly 2-lobed at the glabrous apex, spur 8.5 mm. long; lower petals almost straight, bluish, the lamina oblong-obovate, 6 mm. by 4 mm., bearded near the base, ciliate, the claw 7 mm. long; stamens 6–7 mm. long, filaments quite broad at base, ciliate; anther dark, 0.7 mm. long; follicles 5, hairy; immature seeds apparently winged on angles.

TYPE: Afghanistan: Minjan Pass, 12000 feet, July 26, 1937, *Koelz 12713*; isotype seen (US).

Another collection is "Iter Pamiricum, val. Togus-bulak," Aug. 3, 1931, *Lipschitz 718* (K).

69. **Delphinium molle** Danguy, Jour. Bot. Morot **21**: 51. 1908. FIG. 6, K.

Stem subglabrous below, with spreading soft white hairs in inflorescence, erect, 2.5–3 dm. tall, scattered leafy; petioles vaginate at base, 1–2 dm. long; leaf blades suborbicular, 5–8 cm. broad, cordate at base, glabrous except for some white hairs along veins on lower surface, almost 5-lobed, the lobes cuneate, variously and obtusely lobulate with shallow, broad, round-ovate, apiculate teeth 3–6 mm. deep and 3–8 mm. broad; flowers few in a lax corymbose raceme; bracts 3-lobed or entire, to 3 cm. long; pedicels arcuate and divaricate, white-pubescent, 4–5 cm. long; bracteoles opposite, well below the calyx, linear-oblong, 12–16 mm. long, 1.5 mm. broad; flowers blue, villous; upper sepal arched, 15 mm. or more long, the spur 5–6 mm. long, 5 mm. wide at base; lateral and lower sepals ovate, 12 mm. by 7 mm., pointed; upper petals bifid at apex, ciliate, the lamina straight, 6 mm. long, spur 4–5 mm. long; lower petals oblong-ovate, lobed to below the middle, ciliate on margin, not bearded near the base; claw scarcely evident; filaments dilated at base, glabrous; anthers oblong, ciliate; follicles 5, glabrous.

TYPE: Borders of River Beik, at 4150 m., July 23, 1906, Pamir Range, Central Asia, *Lacoste 11* (P); seen. This was the only specimen seen; it had quite immature flowers.

70. **Delphinium nepalense** Kitamura & Tamura, Acta Phytotax. & Geobot. Kyoto **15**: 129. 1954. FIG. 6, L.

Perennial from an elongate root; stem 1–3.5 dm. long, villous with soft white retrorse hairs, not at all glandular, simple or few branched above; basal leaves rounded in outline, 2–7 cm. in diameter, more or less strigulose on both surfaces and more pubescent beneath, palmatifid into cuneate obovate parts which are mostly 3-lobed in outer portion, then coarsely and broadly toothed with pointed or rounded almost lobelike teeth; lower petioles 3–15 cm. long, somewhat villous, dilated at base; cauline leaves few, gradually reduced above to foliose bracts with dilated petioles and 1–2 cm. long; flowers 2 to several in a subcorymbose arrangement, the sepals blue to purplish, papery, mostly villous without and somewhat so within, very veiny; pedicels ascending to erect, 2.5–8 cm. long, loosely strigose to villous; bracteoles largely opposite, lance-oblong, pubescent, 1–2 cm. long, 3–4 mm. wide, placed at middle of pedicel or above; upper sepal more or less hooded, 1.5–2 cm. long, 1.2–1.8 cm. wide, broadly ovate, obtuse, the spur curved at end, 8–14 mm. long, 6–7 mm. wide at base, obtuse; lateral sepals almost round, 1.6–1.8 cm. across, rounded-obtuse at apex; lower sepals ovate, 1.7–2 cm. by 1.1–1.4 cm., obtuse; petals dark, the upper almost straight, narrow, the limb 13 mm. by 2 mm., with 2 oblong lobes 1.5–2 mm. long, spur 10–12 mm. long; lower petals strongly oblique, the limb oblong, ca. 10 mm. by 4 mm., bearded, cleft to about the middle into subparallel oblong lobes, claw narrow, 7 mm. long; stamens

6–7 mm. long, glabrous; anthers dark, 1.2 mm. long; follicles 3, pubescent, 13 mm. by 4 mm., the style an additional 2.5 mm.

TYPE: Chulu, Nepal, at 6200 m., *Nakao 675* (KYO). I have not been able to see material.

DISTRIBUTION. Growing on gravelly grassy slopes and scree, 4000–5500 m., Nepal and Bhutan.

REPRESENTATIVE COLLECTIONS. **Bhutan:** Thampe Ka, *Ludlow & Sherriff 17128, 19724.* **Nepal:** Khangar, *Lowndes 1505*; Kanjitoba, *Polunin, Sykes & Williams 3533*; Chalika Pahar, *Stainton, Sykes & Williams 3769, 4602*; Mustang, *Stainton, Sykes & Williams 2278*; without exact locality, *Capt. Lall Dhevoj 225.*

71. **Delphinium nordhagenii** Wendelbo, Nytt Mag. Bot. 3: 227. 1954. FIG. 7, A.

Perennial from a woody rhizome, 1.5–3 dm. tall, erect, somewhat strigose below, glandular-pubescent with spreading hairs in the inflorescence, leafy; lower petioles mostly 4–10 cm. long, somewhat dilated at the base, the blades 3–4.5 cm. broad, subreniform, thickish, somewhat pubescent especially beneath, incised to middle with 3–5 lobes variously divided but with broad rounded teeth; inflorescence simple or compound, several flowered; pedicels 2–6 cm. long, glandular-pubescent; lower bracts foliose, trifid into broad lobes with few coarse teeth, the petioles broad, upper bracts mostly 3-lobed, to ca. 1 cm. long; bracteoles opposite, bluish, hairy, 6–14 mm. long, 3 mm. wide, situated somewhat below the flower; sepals deep purplish blue, hairy without, the upper sepals oblong-ovate, 2.2 cm. long, 1.7 cm. wide, obtuse, the spur somewhat decurved, 10 mm. long, 4 mm. wide at base; lateral sepals elliptic with an apiculate tip, ca. 2 cm. long, 1 cm. wide; lower sepals broadly ovate, 2 cm. long, 1.4 cm. wide, apiculate; upper petals almost straight, the lamina 13 mm. long, narrow, the rounded apex more or less pilose, 2-lobed, the spur dark, 12 mm. long; lower petals almost straight, the lamina oblong, 8 mm. by 4 mm., with 2 lance-oblong lobes, 3–5 mm. long, hairy; stamens 8–9 mm. long, sparsely hairy; anthers dark, 1 mm. long; carpels 4–5, bearded, 10–12 mm. long, the style an additional 1.5–2 mm. long.

TYPE: N. W. Pakistan, Chitral, Barum Gol, 4500 m., *Wendelbo* (O): not seen.

Another specimen, from N. E. Chitral and annotated by Wendelbo as *nordhagenii* is Darkot Pass, 4400 m., Aug. 22, 1939, *D. F. Sanders* (BM).

72. **Delphinium propinquum** Nevski in Komarov, Fl. U.S.S.R. 7: 124. 722. 1937. FIG. 7, B.

Stem 1.5–4 dm. tall, glabrous below, short-pubescent, densely glandular-pubescent above; petioles ca. 1 dm. long, pilose, dilated at base; leaf blades 4–6 cm. broad, short pilose on both surfaces, trifid almost to the base, the middle segment obcordate, divided into 3 lobes, each with 3–5 oblong to

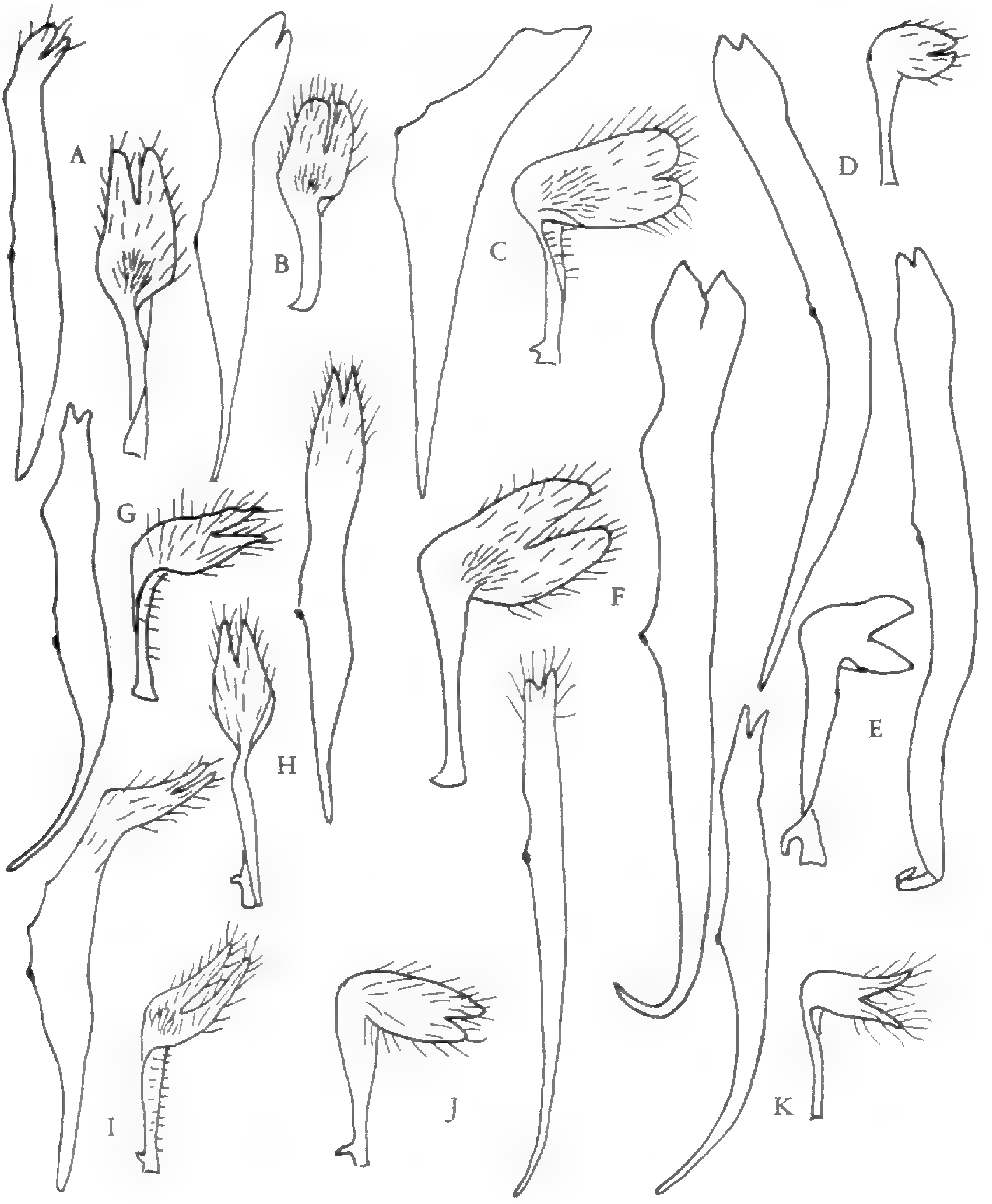

FIGURE 7. **Delphinium,** GROUP V. Petals, the upper spurred, the lower clawed. A. *D. nordhagenii*; blade of upper petal 13 mm. long, spur 12 mm., blade of lower petal 8 mm. long, claw 7 mm.; drawn from *Sanders* in 1939 (BM). B. *D. propinquum*; blade of upper petal 12 mm. long, spur 13 mm., blade of lower petal 5 mm. long, claw 6 mm.; drawn from *Lipsky 1922* (LE). C. *D. siwanense*; blade of upper petal 12 mm. long, spur 20 mm., blade of lower petal 7 mm. long, claw 7 mm.; drawn from *David* TYPE (P). D. *D. trichophorum*; blade of upper petal 17 mm. long, spur 23 mm., blade of lower petal 4 mm. long, claw 7 mm.; drawn from *Mussot* in 1897 (UC). E. *D. trichophorum*; blade of upper petal 17 mm. long, spur 20 mm., blade of lower petal 5.5 mm. long, claw 10 mm.; drawn from *Rock 18237* (GH). F. *D. tsarongense*; blade of upper petal 22 mm. long, spur 22 mm., blade of lower petal 11 mm. long, claw 12 mm., drawn from *Harry Smith 11285* (MO). G. *D. vestitum*; blade of upper petal 13 mm. long, spur 13 mm., blade of lower petal 7 mm. long, claw 7 mm.; drawn from *Nath 437* (US). H. *D. viscosum*; blade of upper petal 14 mm. long, spur 11.5 mm.,

subovate teeth, the lateral segments divided into lobes like those of the middle segment; raceme few flowered, glandular-pubscent; bracts (at least the lower) foliose, divided; pedicels 2–4.5 cm. long, densely short-pubescent and with longer soft hairs; bracteoles linear-lanceolate, obtusely acuminate, 7–15 mm. long, 2–3 mm. wide, pilose; flowers large, blue; sepals 2–3 cm. long, 1.3–1.8 cm. wide, broadly obovate, obtuse, membranaceous, covered with long flexuous hairs; spur thick-cylindric, 1.4–1.7 cm. long, obtusely acuminate, recurved distally, ca. 4 mm. wide at base; petals black, the upper lamina almost straight, 13 mm. by 3 mm., glabrous, bidentate, the spur ca. 13 mm. long; lower laminae somewhat oblique, 5 mm. by 3 mm., oblong-ovate, white-hairy and -ciliate, the claw 6 mm. long; stamens 7–8 mm. long, glabrous; anthers dark; follicles 3, pilose.

TYPE: Asia Media, "m. Karategin, ad marginem glacei Dibarar," Aug. 10, 1896, *Lipsky no. 1922* (LE); seen.

Delphinium brunonianum, D. nordhagenii and *D. propinquum* are closely related, if distinct. I have had abundant material of the first, very little of the other two. *D. propinquum* seems to have the sepal spur much longer in proportion to the blade than do the others. *D. nordhagenii* has a racemose inflorescence and a narrower lamina on the lower petal, while *D. brunonianum* tends to have a corymbose inflorescence and a broader lamina. But I doubt very much that *D. nordhagenii,* at least, is separable from *D. brunonianum.*

73. **Delphinium siwanense** Franchet, Bull. Soc. Philom. Paris, VIII. 5: 162. 1893. FIG. 7, C.

Delphinium cheilanthum Franchet, Pl. David. 1: 22. 1884; not Fisch. in DC., 1817.

Perennial, several dm. tall, the stem glabrous below, glaucous, with short branches, stiff, equably foliose; cauline petioles not dilated at the base, scattered, white-hairy, 3–5 cm. long; blades strigulose, bicolored, 3–5 cm. wide, parted almost to the base into lanceolate segments, these entire or bifid, then with about 3 salient lanceolate lobules or teeth 3–10 mm. long and 2–5 mm. wide; inflorescence and flowers retrorse-pubescent or with few long spreading white hairs; flowers solitary or in small crowded clusters at ends of branches; bracts trifoliate to linear, ca. 1 cm. long; bracteoles linear or subulate, near middle of pedicel, ca. 6 mm. long; sepals blue violet, pubescent, the upper sepal ovate, acute, 13–15 mm. long, the spur straight, somewhat subulate, 18–20 mm. long, ca. 3 mm. wide at

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blade of lower petal 6.5 mm. long, claw 8 mm.; drawn from *Brühl* illustration. I. *D. viscosum*; blade of upper petal 17 mm. long, spur 12 mm., blade of lower petal 7 mm. long, claw 7 mm.; drawn from *R. E. Cooper 802* (E). J. *D. wardii*; blade of upper petal 11 mm. long, spur 20 mm., blade of lower petal 6 mm. long, claw 9 mm.; drawn from *Kingdon Ward 6193* (BM). K. *D. wrightii*; upper blade 13 mm., spur 15 mm. long, blade of lower petal 6 mm. long, claw 5.5 mm.; drawn from *Kingdon Ward 4786* (E).

base; other sepals 14–15 mm. long, abruptly narrowed into a subacuminate tip; petals dark, the upper laminae oblique, 12 mm. long, pointed, glabrous, the spur 18–20 mm. long; lower petals with appendiculate pubescent claw 6–7 mm. long, the limb oblique-obovate, 7 mm. long, with 2 short lobules, long-ciliate, yellow bearded on inner surface; follicles ca. 13 mm. long, very hairy or glabrous, surrounded by sepals until maturity, the styles ca. 3 mm. long; seeds small, ovoid, black, transversely cristate.

TYPE: China, Siwan west of Peking, Sept., 1862, *David* (P); seen. In the type the flowers are solitary and the carpels hairy.

Another specimen apparently referable here is *Licent*, Aug. 1, 1919, on tang-L'Obo, plain of Toumet, no. *5655* (P), with flowers grouped and carpels glabrous.

74. **Delphinium trichophorum** Franchet, Bull. Soc. Philom. Paris, VIII. **5**: 166. 1893. FIG. 7, D, E.

Delphinium trichophorum var. *platycentrum* W. T. Wang, Acta Bot. Sinica **10**: 75. 1962. Based on *S. K. Wu 3381*, from Muli, Szechwan; not seen.

Delphinium trichophorum var. *subglaberrimum* Hand.-Mazz. Acta Horti Gothob. **13**: 48. 1939. Based on *Harry Smith 11689*, from Taofo, Szechwan; isotypes (A, MO); seen.

? *Delphinium trichophorum* var. *tibeticum* Lévl. Pl. Seu-Tchouen, 149. 1918. Spur said to be shorter than sepals; no specimens cited.

Delphinium pellucidum Busch, Bull. Jard. Bot. Pétersb. **5**: 134. 1905. Type, E. Tibet, River Nomu-Czu, *Ladygin*, Oct., 1900 (LE); seen.

Delphinium purdomii Craib, Kew Bull. **1912**: 380. 1912. Type, Kansu, Michu, 2400 m., *Purdom 142*, cult. Hort. Veitch (K); seen.

Delphinium forrestii Diels, Notes Bot. Gard. Edinb. **5**: 265. 1912. Type, Yunnan, e. flank of Likiang Range, 3800–4200 m., Sept., 1906, *G. Forrest 3030* (E); seen.

Perennial, from a woody root, the stem robust, erect, simple, 3–6 dm. tall, hirsute (to almost glabrous below); leaves mostly basal, reniform-rounded, 3–10 cm. broad, rather shallowly divided into broad, subcuneate, crenate-dentate, obtuse lobules, more or less hairy on both surfaces, the petioles 5–10(–20) cm. long, dilated at base; stem leaves few, much reduced, passing into leafy bracts; inflorescence racemose, usually dense, many flowered, 1–3 dm. long, somewhat peduncled, hirsute; upper bracts entire, lanceolate-oblong, 5–20 mm. long; pedicels erect, 1–5 cm. long; bracteoles lance-oblong, ca. 1 cm. long; sepals ashy blue to dull grayish red or violet purple, densely long-hairy, with white and yellow hairs, persistent in fruit; upper sepal 15–30 mm. long, 8–20 mm. wide, obtuse, the spur 15–24 mm. long, 5–10 mm. wide at base, very hairy, narrowing to a blunt often recurved tip; lateral sepals oblong, 14–17 mm. by 7–9 mm., hairy on whole outer surface; lower sepals 12–17 mm. by 7–9 mm., subacute; petals almost black, the upper often exserted, with a straight bidentate to entire lamina, glabrous, 13–17 mm. long, the spur ca. 20 mm. long; lower petals with an oblong blade 5.5–7 mm. by 3–4 mm., cleft and gaping almost halfway, the lobes ciliate or glabrous, claw 7–10 mm. long;

stamens 7–10 mm. long, glabrous; anther dark, 1.5–2 mm. long; carpels 3, hairy, 10–15 mm. long, the styles an additional 2 mm.; seeds 1.5 mm. long, dark, winged on the angles.

TYPE: Szechwan, Tizou and Tongolo, near Ta-Tsien-lou, Sept., 1891, *Soulié 23* holotype (P), seen; photo. (E) and isotype (K), seen.

DISTRIBUTION. Between 3700 and 5200 m., eastern Tibet and western China.

REPRESENTATIVE MATERIAL. **E. Tibet:** Batang, *Soulié 3909, 3038.* **Western China:** *E. H. Wilson 3103, 3106, 3107.* **Szechwan:** *Soulié 2384, 64, 2386*; *H. Smith 4421, 11704, 11568, 11574, 12484*; *E. H. Wilson 2004, 4688, 2044*; *Rock 18237, 16824.* **Kansu:** *Rock 13740*; *Farrer & Purdom 803, 800, 798.* **Yunnan:** *Forrest 22347, 22603, 6683, 16923, 15194, 17064*; *Yü 14642*; *Maire 2692*; *Rock 10860, 11696, 7786, 11458, 10979, 24938, 23090, 23444.*

As here treated, rather a variable species, with dense inflorescence, of high western China and adjacent Tibet.

75. **Delphinium tsarongense** Hand.-Mazz. Anz. Akad. Wiss. Wien. Math.-Nat. **59**: 245. 1922. FIG. 7, F.

Delphinium tsarongense var. *patentipilum* Wang, Acta Bot. Sinica **10**: 76. 1962. With spreading hairs.

Perennial, from a slender running rootstock; stem 2–10 cm. long, leafy, somewhat purplish, spreading-pubescent, especially upwards; leaves few, the petioles 2–7 cm. long, pubescent, purplish, dilated at the base; blades reniform-oval in outline, 2–6 cm. broad, not so long, somewhat pubescent, mostly 5-lobed to near base, the lobes cuneate-obovate, rounded at apex, 1–2.5 cm. wide, rather shallowly divided into 2–3 broad, rounded-oblong parts, each with 2 or 3 broad, blunt, mucronate teeth; flowers mostly 2–4 on a stem, each in an upper axil of a reduced lobed leaf; pedicels stout, 2–7 cm. long, with a pair of oblong bracteoles ca. 1 cm. long and 2.5 mm. wide, situated ca. 1 cm. below the flower; flower large, greenish blue to pale violet with darker veins, the sepals more or less yellowish-pubescent; upper sepal 2.5–3 cm. long, as wide or wider, obtuse, the spur 1.8–2 cm. long, to almost 1 cm. wide at base, gradually tapered into a broad, sometimes recurved tip; lateral sepals 2–2.5 cm. long, broadly ovate, rounded, pubescent over back surface; lower sepals about the same; upper petals dark, the limb almost straight, 22 mm. long, shallowly bilobed at apex, the spur 22 mm. long; lower petals dark, the blade bearded, oblong, ca. 11 mm. long, divided almost halfway, the claw 12 mm. long; stamens 1 cm. long, lower half of filaments 1.5 mm. wide; anther dark, 1.3 mm. long; carpels 3, bearded.

TYPE: Southeastern Tibet, Tsarong, Doker-la, 4600 m., *Handel-Mazzetti 7934*, Sept. 17, 1915 (holotype (W), not seen; isotypes (E, K, P), seen).

DISTRIBUTION. Tibet and adjacent China at 4000–5000 m.

REPRESENTATIVE MATERIAL. **Tibet:** *G. Forrest 14665.* **Szechwan:** Tachienlu, *Harry Smith 11285, 11321, 11459.* **Yunnan:** *Forrest 18962, 20979.*

76. **Delphinium vestitum** Wall. Cat. n. 4715. 1830, *nomen*; Royle, Illustr. Bot. Himalaya. 55. 1834. FIG. 7, G.

Delphinium rectivenium Royle, Illustr. Bot. Himalaya. 56. 1834. Based on "N. W. India, Hb. Royle," isotype (K); seen.

Delphinium vestitum var. *sphenolobum* Brühl ex Huth, Bot. Jahrb. **20:** 415. 1895.

? *Delphinium vestitum* var. *pumilum* Huth, *loc. cit.* A Turkish specimen by *Regel* in 1877 cited. Out of normal range of *D. vestitum*, hence puzzling.

Perennial from a slender rootstock, the stem simple or branched from below or above, 4–10 dm. tall, rather slender, often reddish, clothed with spreading to retrorse-spreading hairs 1–2 mm. long; leaves mostly basal, with hairy petioles to 2.5 dm. long, dilated at base, the 2 or 3 cauline leaves with much shorter petioles; leaf blades somewhat cordate at base, 5–12 cm. broad, reniform in outline, stiff-hairy on both surfaces, palmately 5–7-lobed to near the middle or less, the lobes broadly cuneate-obovate to rounded, coarsely incised-dentate, the teeth sharp pointed; uppermost leaves smaller, 3–5-lobed; inflorescence of elongate, few- to many-flowered racemes, peduncled, to 2–3 dm. long, spreading-hairy; bracts entire, lanceolate (or the lower lobed), 1–2 cm. long, hairy; pedicels erect, hairy, 1–7 cm. long; bracteoles 2, well above the middle of the pedicel or almost subtending the flower, lanceolate, hairy, ca. 1 cm. long; sepals purplish blue, to dull violet or pale blue, hairy without, sometimes within; upper sepal ovate, 15–20 mm. long, 8–12 mm. wide at base, rapidly narrowed to rather a blunt tip; lateral sepals almost round, ca. 15 mm. by 8 mm., pointed; lower sepals narrower, pointed, about as long; petals black, the upper with an almost straight lamina 13–14 mm. long, bidentate, glabrous, the spur 13–14 mm. long; lower petals with strongly oblique lamina ca. 7 mm. long, 3 mm. wide, cleft almost halfway into pointed lanceolate lobes, hairy on both sides but especially exteriorly, claw 7 mm. long; stamens 8 mm. long, glabrous; anthers dark, 1.5 mm. long; follicles 3, hairy, 8–15 mm. long, 3.5–4 mm. thick, the beak 2 mm. long; seeds narrowly winged, not at all squamate.

TYPE: Wallich Cat. *4715*; isotypes seen (BM, E, NY).

DISTRIBUTION. Open grassy slopes and meadows, 2500–4000 m., much of Himalaya.

ILLUSTRATION. BLATTER, Beautiful Fls. Kashmir **1:** *pl. 4.* 1927.

REPRESENTATIVE COLLECTIONS. **Kashmir:** *Steane 60*; *Metz 52*; *Duthie 19119*; *Drummond 4349, 6285.* **Punjab:** *Jacquemont 2134*; *Nath 387, 437*; *Koelz 3077, 21952*; *Falconer 64*; *Strachey & Winterbottom 1.* **Kumaun:** *Duthie 5304*; *Strachey & Winterbottom 7.* **Nepal:** *Lall Dhevoj 128, 92*; *Polunin, Sykes & Williams 5441*; *Stainton, Sykes & Williams 7729, 7733, 8007, 3724, 8586, 8585, 8485, 4401.*

77. **Delphinium viscosum** Hook. f. & Thoms. Fl. Ind. 52. 1855. FIG. 7, H, I.

Delphinium viscosum var. *ciliata* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 104. 1896. Based in part on material from Sikkim, without collection numbers, *King's collectors* (CAL), seen.

Delphinium viscosum var. *chrysotrichum* Brühl ex Huth, Bot. Jahrb. **20**: 401. 1895; and in Brühl & King, Ann. Bot. Gard. Calc. **5**: 104. 1896. Also from Sikkim, *King's collectors*, (CAL), seen.

Delphinium viscosum var. *gigantobracteum* Brühl ex Huth, Bot. Jahrb. **20**: 401. 1895 and in Brühl & King, Ann. Bot. Gard. Calc. **5**: 104. 1896. From Sikkim, Zeylapla, *King* (CAL), seen, and from Chumbi, near Kung-bur, *King's collector* (CAL), seen.

Delphinium viscosum var. *connectens* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 104. 1896. From Sikkim, Sebu Valley, *Gammie*, (CAL), seen.

Delphinium trilobatum Huth, Bull. Herb. Boiss. **1**: 330. 1893. Based on a collection from Sikkim, 4000–5000 m., *Anderson*, 1863 (BE); not seen.

Delphinium conocentrum Chatterjee, Kew Bull. **1948**: 57. 1948. Type, Sikkim, Jongri to Alotong, 4500 to 5000 m., Oct. 9, 1862, *T. Anderson 345* (K); seen.

Delphinium aureopilosum Chowdhury ex Mukerjee, Bull. Bot. Survey India **2**: 293. 1960, *nomen.*

Perennial from a slender rootstock, the stem erect or ascending, 3–8 dm. tall, with short yellow spreading glandular hairs, sometimes subglabrous below, paniculately branched from base, scattered leafy; petioles dilated at base, pubescent, the lower 4–12 cm. long, upper much shorter; blades somewhat round-reniform, 3–10 cm. in diameter, appressed-pubescent to subglabrous on both surfaces, palmately 5–7 (or more)-lobed to near the middle, the lobes coarsely crenate-dentate into broad round-ovate teeth that are glandular apiculate at the tips; upper leaves 3–5 cm. broad, 3-lobed or -parted; inflorescence of a series of few-flowered lax corymbs or racemes; bracts foliose and lobed to membranous or entire, the larger with a broad dilated base, the others ovate to lance-ovate, 1–4 cm. long; pedicels 2–10 cm. long, glandular-pubescent, ascending; bracteoles like the bracts, ca. 1–2 cm. long, near to or remote from the flower; sepals violet-blue to purplish blue, more or less yellowish villous to hirsute without; upper sepal broadly ovate, 1.8–2.5 cm. long, subacute, the spur incurved, shorter than to equaling the blade, ca. 4–5 mm. wide at the base, tapering to a blunt apex; lateral sepals oblong-elliptic, ca. 18–20 mm. by 12–15 mm., obtuse; lower sepals more pointed and narrower; petals dark purple, the upper with a suberect bidentate, sparsely hairy apex, the lamina 12–13 mm. long, the spur 10–17 mm. long; lower petals with lamina somewhat oblique, oblong-ovate, 7 mm. by 3 mm., bearded, cleft about one third its length, the claw 8 mm. long; stamens 6–7 mm. long, glabrous, somewhat dilated below, the dark anthers 1 mm. long; follicles 3, 10–12 mm. long, glabrous except for the ciliate sutures or, in some forms, hairy; seeds winged on angles, 1–1.3 mm. long.

TYPE: Sikkim, 15–16000 ft., *J. D. Hooker* in Hooker f. & Thomson collection. At Kew there are two sheets in the type folder, Kinchin-jhow, 16000′, Sept. 12, 1849, and Phutwong near Tunga, Oct., 15000′.

DISTRIBUTION. Open grassy hillsides or bushy slopes, 3000–5200 m., Nepal to Assam.

ILLUSTRATION. Ann. Bot. Gard. Calc. **5**: *pl. 123.* 1896.

REPRESENTATIVE COLLECTIONS. **S. Tibet:** *Ludlow & Sherriff 2096, 9958, 2721, 10069, 2563.* **Sikkim:** *R. E. Cooper 605, 1003*; *G. H. Cave 177*; *W. W. Smith 4128.* **Nepal:** *Stainton, Sykes & Williams 8058, 4689, 7956, 4689*; *Sharma 54, 140.* **Bhutan:** *Ludlow & Sherriff 21057*; *Cooper 2204, 4911.* **Assam:** *Kingdon Ward 14329.*

78. **Delphinium wardii** Marquand & Airy-Shaw, Jour. Linn. Soc. Bot. **48**: 157. 1929. FIG. 7, J.

Perennial, the caudex slender, bearing up to 3 flowering stems, these erect, pubescent, to 15 cm. long, leafless or with one small leaf; basal leaves reniform, 5-fid, sparsely pilose on both sides, 4–5 cm. in diameter, the lobes obtuse, trilobulate; petioles pubescent, 2–5 cm. long, dilated at base; bracts spatulate, 1–1.5 cm. long, the 3 lobes 2–3 mm. wide; flowers 1–2, terminal, violet, the sepals silky pilose; upper sepal shortly and broadly apiculate, 25–28 mm. long, 16 mm. wide, the spur slightly decurved, 17–20 mm. long, 3–4 mm. wide; lateral sepals broadly ovate, obtusely acuminate, 20 mm. long, 15–17 mm. wide; lower sepals ovate, acute, 25 by 18 mm.; upper petals linear, the lamina straight, 13 mm. long, unequally bifid and few haired at the narrowed apex, the spur 21 mm. long; lower petals 16 mm. long, the claw ca. 1 mm. wide, appendaged near the base, bearded, lamina 6 mm. long, bearded, unequally bifid at apex, strongly oblique; stamens 5–7 mm. long, dilated below; anthers dark brown, 1.5 mm. long; follicles 3, pilose on suture.

TYPE: On alpine turf slopes, Tang La, southeastern Tibet, 4200 m., Sept. 20, 1924, *F. Kingdon Ward 6193* (K), seen; isotypes (BM, E), seen.

OTHER MATERIAL SEEN. **Southeastern Tibet:** Pa-sum-kye La, 5000–5600 m., *Kingdon Ward 6124*; Bhutan-Tibet border at Phari, 4600 m., *Gould 1598*; Tsarung, Solo-la at 4500 m., *Rock 22267.*

79. **Delphinium wrightii** Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) **1**: 166. 1948. FIG. 7, K.

Perennial from a woody rootstock, the stem erect, simple, 3–4 dm. tall, with dense spreading white pubescence throughout; leaves mostly basal, reniform, the petioles 4–10 cm. long, densely white-villous, slightly vaginate at base; the blade with a broad deep sinus, wider (4–7 cm.) than long (2–5 cm.), white-hairy on both sides, palmately several-sect to ca. 1 cm., the broad subtruncate segments shallowly round-toothed at the outer edge; cauline leaves 1–2, reduced; inflorescence a more or less secund raceme with ca. 7–11 flowers, densely white-villous; lower bracts trifid, others lance-ovate, 5–10 mm. long, ciliate; pedicels erect, 1–2.5 cm. long, pilose; bracteoles subtending the flower, lanceolate, 5–7 mm. long, villous; flower horizontal, blue-violet to dull slate-purple, villous; upper sepal ovate, 18–20 mm. long, 10–12 mm. wide, obtuse, the spur 18–20 mm. long, 4–5 mm. thick at the base, strongly decurved; lateral sepals ovate, ca. 15 mm. by 8 mm., obtuse; the lower subacute, ca. 18 mm. by 8 mm.; petals very dark, the upper almost straight, the lamina 13 mm. by 2 mm., with 2 sharply lanceolate lobes at apex, glabrous, the spur ca. 15 mm. long; lower petals strongly oblique, the blade oblong, 6 mm. by 4 mm., split about halfway into 2 strongly divergent lanceolate lobes, claw 5.5 mm. long; stamens glabrous, 6–7 mm. long; anthers dark, 1 mm. long; carpels 3, densely pilose, 15 mm. by 4 mm., the style an additional 3 mm.; seeds brown, winged, almost 2 mm. long.

TYPE: Szechwan, South Sikang, Muli, Shao-siang-liang-tse, 3400 m., *T. T. Yü 7797* (isotype (A); photo. of holotype seen (E)).

DISTRIBUTION. Grassy slopes and among shrubs, 2800 m. to 4200 m., southwestern Szechwan and western Yunnan.

COLLECTIONS SEEN. **Yunnan:** Chiao-kia Hsien, *H. T. Tsai 52020*. **Szechwan:** Muli, *Kingdon Ward 4786*; mts. between Wa-Erh-Dje and Muli Gomba, *Rock 16930*.

GROUP VI

Plants perennial from woody, not tuberous, roots. Stems well developed; leaves both basal and cauline, dissected into ultimate linear, more or less oblong segments mostly 1–3 mm. broad. Sepals not markedly veiny or papery, caducous, mostly less than 2 cm. long, the spur narrow, largely 2–3 mm. wide at base.

Not corresponding exactly to any of the sections or other taxonomic subdivisions of the genus that have been proposed.

KEY TO SPECIES

1. Spur 1.5–2 times as long as the upper sepal.
    2. Plant 1–3 dm. tall.
        3. Petals almost black; stem with soft spreading hairs.
            4. Bracteoles well below the flower; upper petal bilobulate; lower petal with pointed lanceolate lobes. Szechwan. .... 102. *D. malacophyllum.*
            4. Bracteoles against the flower; upper petal entire; lower petal with broad rounded lobes. Yunnan, Tibet. ...... 112. *D. pulcherrimum.*
        3. Petals not darker than the sepals.
            5. Upper sepal 15–22 mm. long; stem strigulose or more loosely pubescent, somewhat succulent. Kansu to Tibet. .... 114. *D. pylzowii.*
            5. Upper sepal mostly 12–15 mm. long, if longer, the stem loosely pubescent; stems not fleshy.
                6. Stem strigulose; lower petal obovate. Himalaya and southern Tibet. .... 86. *D. caeruleum.*

6. Stem with looser, often spreading hairs.

7. Upper petal entire; lower petal narrow-oblong. Yunnan. . . . . 120. *D. tenii.*

7. Upper petal emarginate; lower petal obovate to round.

8. Lower leaf blades 7–14 mm. long; stem 10–16 cm. tall; sepals 12–14 mm. long. Szechwan. . . 113. *D. pumilum.*

8. Lower leaf blades ca. 33 mm. long; stem ca. 35 cm. tall; sepals 16–17 mm. long. Kansu. 104. *D. mollipilum.*

2. Plant 3–8 or more dm. tall; stem often strigulose.

9. Sepals 7 mm. long; leaf segments 3–4 mm. wide. Central Yunnan. . . . . 119. *D. tatsienense.*

9. Sepals longer.

10. Upper leaves with 3–5 entire lanceolate segments 3–5 cm. long and ca. 5 mm. wide.

11. Pedicels mostly glabrous; bracteoles 2–5 mm. long; spur 20–22 mm. long. Yunnan. . . . . 128. *D. yunnanense.*

11. Pedicels spreading-puberulent; bracteoles 4–9 mm. long; spur 16–18 mm. long. Kantze. . . . . 99. *D. kantzeense.*

10. Upper leaves not as above.

12. Stems glabrous, at least above, or with some spreading hairs.

13. The pedicels with some spreading hairs. Szechwan.

14. Flowers deep blue, upper sepal 13–20 mm. long; lateral sepals 16–20 mm. . . . . 111. *D. pseudograndiflorum.*

14. Flowers pale sordid-blue, upper sepal 11–12 mm. long; lateral sepals 9–10 mm. . . . . 117. *D. sordidecaerulescens.*

13. The pedicels lacking spreading hairs.

15. Pedicels glabrous.

16. Stems glabrous, branched above; lower petal rounded at apex. Yunnan. . . . . 120. *D. tenii.*

16. Stems white hirsute below, simple; lower petal emarginate. Szechwan. . . . . 94. *D. dolichocentroides.*

15. Pedicels loosely strigose. Hupeh. 126. D. *wilsonii.*

12. Stems strigulose.

17. Laminae of lower petals as broad as long, entire or obscurely emarginate; ultimate leaf segments 1–2 cm. long. . . . . 95. *D. grandiflorum.*

17. Laminae of lower petals longer than broad, bilobed or deeply emarginate; ultimate leaf segments mostly shorter.

18. Spur ca. 30 mm. long. Szechwan, Yunnan, Tibet. . . . . 119. *D. tatsienense.*

18. Spur 15–25 mm. long. Kansu.

19. Leaf lobes 2–3.5 mm. wide. . . . . 103. *D. maximowiczii.*

19. Leaf lobes 1.5–1.8 mm. wide. . . . . 110. *D. pseudo-caeruleum.*

1. Spur not markedly longer than sepals.

20. Upper petals dark, almost black.

21\. The upper petals with a few bristly hairs at summit, the sepals 20–25 mm. long.

22\. Spur 20 mm. long; sepals deep blue. Mongolia. . . . . 109. *D. przewalskii.*

22\. Spur 12–17 mm. long.

23\. Sepals dilute blue; spur 16–17 mm. long. Mongolia. . . . . 93. *D. dissectum.*

23\. Sepals purplish; spur 12–15 mm. long.

24\. The sepals purplish black, the upper 22 mm. long. Mongolia, Dahuria. . . . . 123. *D. triste.*

24\. The sepals purplish blue, the upper 17–18 mm. long. Nepal. (Treated in Group IX). . . . . 207. *D. himalayae.*

21\. The upper petals glabrous at the tip.

25\. Upper sepals 12–15 mm. long.

26\. Spur 22–23 mm. long; flowers sordid-bluish. Szechwan. . . . . 117. *D. sordidecaerulescens.*

26\. Spur 12–14 mm. long; flowers light blue.

27\. Inflorescence with some glandular hairs. Transcaucasus.

28\. Sepals blue, variegated with white; bracteoles ca. 2 mm. long, near the flower. (Treated in Group IX). . . . . 202. *D. elisabethae.*

28\. Sepals blue, not variegated with white; bracteoles 10–12 mm. long, just above the middle of the pedicel. (Treated in Group IX). . . . . 224. *D. pyramidatum.*

27\. Inflorescence strigose, not glandular.

29\. Inflorescence an open panicle, the central axis densely many flowered. Transcaucasus to Turkey. . . . . 91. *D. crispulum.*

29\. Inflorescence racemose or few branched, each branch few flowered. Nepal. . . 97. *D. incisum.*

25\. Upper sepals 16–25 mm. long.

30\. The upper sepal ca. 25 mm. long.

31\. Lower petal lamina bifid almost to base into lanceolate lobes. Tibet. . . . . 108. *D. nortonii.*

31\. Lower petal lamina bifid halfway into broad lobes. Kansu, Szechwan. . . . . 114. *D. pylzowii.*

30\. The upper sepal 15–20 mm. long.

32\. Sepals slaty to pale blue, 18–20 mm. long, the spur 15–25 mm. long; lower petal with broad lobes. Kansu. . . . . 81. *D. albocoeruleum.*

32\. Sepals darker.

33\. Bracteoles well below the flower.

34\. Lower petal lamina oblong, ca. 8 mm. long. Sikang. . . . . 116. *D. smithianum.*

34\. Lower petal lamina elliptic-ovate. Kansu to Tibet. . . . . 114. *D. pylzowii.*

33\. Bracteoles very near the flower; lower petal lamina broadly elliptic.

35. Flowers 1 to few in a subumbellate group; upper petal emarginate at tip. Western China. . . . . 96. *D. henryi.*
35. Flowers more numerous.
  36. Inflorescence open-paniculate; upper petal entire. Eastern Tibet. . . . . 115. *D. rockii.*
  36. Inflorescence racemose; upper petal emarginate. Honan. 122. *D. trisectum.*

20. Upper petals bluish to whitish, not darker than the sepals.
  37. Flowers several in an inflorescence; sepals largely 8–15 mm. long.
    38. Stem glabrous, even up into the inflorescence.
      39. Upper petal notched; lower petal lamina ovate.
        40. Sepals intense blue to violet, glabrous, the upper one 12–15 mm. long, the spur 15–18 mm. long. Northern Iran. . . . . 101. *D. lanigerum.*
        40. Sepals violet-blue, pubescent, the upper sepal 11 mm. long, the spur 13–18 mm. long. Western China. . . . . 118. *D. sutchuense.*
      39. Upper petal entire; lower petal lamina more or less obovate. Western China.
        41. Bracts mostly 3-parted; upper sepal 12–15 mm. long; lamina of upper petal 9 mm. long. . . . . 103. *D. maximowiczii.*
        41. Bracts entire; upper sepal 20 mm. long; lamina of upper petals 12–13 mm. long. . . . . 82. *D. autumnale.*
    38. Stem with some hairs, at least in the inflorescence.
      42. Inflorescence with some yellow glandular hairs.
        43. Bracts 2.5–5 mm. long; bracteoles 2 mm. long. Afghanistan. . . . . 121. *D. tenuipes.*
        43. Bracts 5–15 mm. long; bracteoles 6–10 mm. long.
          44. Stems 8–10 dm. tall; sepals 8–11 mm. long. Songoria. . . . . 80. *D. aemulans.*
          44. Stems to 1.5 dm. tall; sepals 13–16 mm. long. Tibet. . . . . 114. *D. pylzowii.*
      42. Inflorescence with neither yellow nor glandular hairs.
        45. Upper petals blue, the blade 12–16 mm. long; bracts leaflike.
          46. Blade of lower petal mostly entire, glabrous except for the basal patch of hair; carpels densely pubescent. Siberia. . . . . 89. *D. cheilanthum.*
          46. Blade of lower petal usually more or less cleft, bearded almost throughout; carpels subglabrous. Yunnan. . . . . 127. *D. yuanum.*
        45. Upper petals pale, the blade 8–10 mm. long; bracts mostly not leaflike, but linear to setaceous.
          47. Blade of lower petal almost round, 8–10 mm. in diameter, entire to emarginate. Eastern Siberia, through Mongolia to western China. . . . . 95. *D. grandiflorum.*
          47. Blade of lower petal deeply cleft, 4–5 mm. wide.
            48. Pedicels mostly 1–2 cm. long, with a some-

what recurved tip; bracteoles 2–3 mm. long, placed below the middle of the pedicel.

49. Inflorescence spicate; sepals 13–15 mm. long; spur 15–16 mm. long. Kashmir. (Treated in Group IV). 45. *D. roylei.*

49. Inflorescence corymbose.

50. Sepals 10 mm. long; spur 13 mm. long. Punjab. . . . 100. *D. koelzii.*

50. Sepals 13–17 mm. long; spur 15–17 mm. long. Bhutan. . . . . 85. *D. bhutanicum.*

48. Pedicels 1–4 cm. long; bracteoles 2–4 mm. long, placed near the middle of the pedicel; sepals 12–15 mm. long. Himalaya. . . . . 92. *D. denudatum.*

37. Flowers mostly 1 to a stem; sepals 15–25 mm. long.

51. Plant quite glabrous on stems and axes.

52. Spur decurved or almost hamate, 20–25 mm. long; bracteoles placed below the middle of the pedicel, 4–10 mm. long. Szechwan. (Treated in Group X). . . . . 240. *D. potaninii.*

52. Spur straight or slightly curved; bracteoles above the middle of the pedicel.

53. Spur 15 mm. long; flowers deep blue. Kumaun. . . . . . 98. *D. kamaonense.*

53. Spur 18–21 mm. long; flowers dull white. Nepal. . . . . . 125. *D. williamsii.*

51. Plant strigose to hirsute on stems and/or axes of inflorescence.

54. Blade of upper petal emarginate at apex.

55. Spur 10–15 mm. long; plant 7–10 dm. high, short-hirsute. Tibet. . . . . 108. *D. nortonii.*

55. Spur 20–25 mm. long.

56. Upper petal yellowish at apex; flowers more or less racemose. Shantung. . . . 88. *D. chefoense.*

56. Upper petal violet or blue at apex; flowers mostly 1–2 on a stem.

57. Sepals sordid-brown or purple-brown, pale on margins; upper petals setose. Tibet. . . . . . . 87. *D. candelabrum.*

57. Sepals blue; upper petals glabrous.

58. Follicles 5; bracteoles at middle of pedicel. Lichiang Range, Yunnan. . . . . . . 84. *D. beesianum.*

58. Follicles 3; bracteoles below the middle of the pedicel. Tibet. . . . . 83. *D. batangense.*

54. Blade of upper petal entire at apex.

59. Upper sepal 13–18 mm. long.

60. Spur about 20 mm. long; limb of upper petal 8 mm. long. Yunnan. . . . . . . 106. *D. mosoynense.*

60. Spur 15–19 mm. long; limb of upper petal 6–7 mm. long. Tibet, Kansu. . . . . 124. *D. tsoongii.*

59. Upper sepal 20–25 mm. long.

61. Spur 14 mm. long; lamina of upper petal 8 mm. long; blade of lower petal entire, ovate, pointed. Bhutan. .... 107. *D. muscosum.*

61. Spur 20–30 mm. long; lamina of upper petal 10–12 mm. long.

62. Lamina of lower petal oblong, rounded at tip, much longer than wide; stem 1.5–5 dm. tall.

63. The lamina of lower petal not cleft; petiole bases not conspicuously inflated. Lichiang Range, Yunnan. .... 84. *D. beesianum.*

63. Lamina of lower petal bifid; petiole bases very conspicuously inflated. Yunnan. .... 90. *D. coleopodum.*

62. Lamina of lower petal almost round, more or less cleft.

64. Stem to 1.5 dm. tall, subglabrous; flowers solitary. Kansu, Yunnan. .... 105. *D. monanthum.*

64. Stem 5–8 dm. tall, densely retrorse-strigulose; flowers laxly racemose. Shansi. .... 88. *D. chefoense.*

80. **Delphinium aemulans** Nevski in Komarov, Fl. U.S.S.R. 7: 161, 725. 1937. FIG. 8, A.

Stems 8–10 dm. tall, to 8 mm. thick at the base, lightly ribbed, with retrorse white hairs below and violet-tinged, densely glandular pubescent under and in the inflorescence, leafy; leaves glabrous, round-reniform, to 1 dm. in diameter, truncate or slightly cuneate at the base, palmatisect almost to base, the segments pinnatifid into lance-linear lobes 2–3 mm. wide, 5–25 mm. long; petioles scarcely enlarged at base, 10–12 cm. long, or the lowermost longer; raceme branched below, dense, many flowered, the axis densely glandular pubescent; bracts linear, 5–15 mm. long; pedicels erect-spreading, 1–2 cm. long, glandular; bracteoles linear-filiform, glandular-pubescent, 6–10 mm. long, 0.5 mm. wide, placed in the upper part of the pedicel; sepals deep blue, ovate, obtuse, glandular pilose; upper sepal ovate, 10 mm. by 6 mm., prolonged into a narrow point; spur 12–13 mm. long, 1.5–1.8 mm. thick, obtusely acuminate and incurved at apex; lateral sepals 11 mm. by 8 mm., ovate, obtuse; lower sepals obovate, 9 mm. by 6 mm., obtuse; petals bluish, the upper laminae somewhat oblique, pale, ca. 8 mm. long, entire, glabrous, the spur 13 mm. long; lower petals strongly oblique, the blade oblong-ovate, 4.5 by 3 mm., bearded and ciliate, bifid more than halfway; claw 4 mm. long; stamens 5.5–6 mm. long, the anthers dark; follicles 3, densely glandular pubescent.

TYPE: Dzungaria, in Monrak Mts. near Zaissan, July 22, 1930, *Gontscharov & Borissova* (LE); seen. Nevski speaks of this species as near

D. dyctiocarpum, but differing in its glandular pubescence. I have, however, placed that species in Group IX.

81. **Delphinium albocoeruleum** Maxim. Bull. Acad. Pétersb. 23: 307. 1877; Fl. Tangut. 1: 23. *pl. 4.* 1889. FIG. 8, B.

Delphinium albocoeruleum var. *pumilum* Huth, Bot. Jahrb. 20: 409. 1895. Described as 10–15 cm. high and from Tibet. The only Tibet specimen cited is *Przewalski* in 1884, which I have not seen. But I have seen several other collections from there.

Stem erect, 1–12 dm. tall, more or less angulate, often purplish, sparsely retrorse-strigulose, leafy, simple or subcorymbosely branched above; basal petioles to 10 cm. long, somewhat dilated at base, upper much shorter; leaf blades cordate at base, 5–8 cm. broad, strigulose above, more loosely pubescent or even silky beneath, 3–5-parted almost to base, somewhat less so in basal leaves, the subrhombic divisions deeply 2–3-fid and incised into lance-oblong, subacuminate teeth or lobules; inflorescence branched, the branches few flowered; bracts trifid or multifid, ca. 2 cm. long; pedicels to ca. 5 cm. long, gray-strigose; bracteoles near summit of pedicel, trifid to simple and lanceolate, 4–8 mm. long; sepals slate purple to pale blue, sometimes pubescent; upper sepal broadly oblong-ovate, 18–25 mm. by 13–14 mm., obtuse to truncate, the spur straight or somewhat decurved, 15–25 mm. long, 3–3.5 mm. wide at base; lateral sepals oblong-obovate, 18–25 mm. by ca. 18 mm., rounded-truncate at apex; lower sepals rhombic-ovate, 18 mm. by 13 mm., with an obtuse apiculation; petals very dark, almost glabrous, the upper laminae slightly oblique, 10–13 mm. long, bidentate at apex, the spur 16–19 mm. long; lower petals strongly oblique, the blade slightly bearded, oblong, 8–20 mm. long, cleft into 2 rather lance-ovate lobes, claw 7 mm. long; stamens 6–7 mm. long, ciliate on filaments; anthers dark, linear, 1.5 mm. long; follicles 3, hairy, 13–14 mm. long, the styles an additional 2 mm.; seeds 1.5 mm. long, triquetrous, with horizontal rows of fused scales.

TYPE: Kansu, "in regione Tangut prope l'Amdo, *Przewalski* 1872" (LE) seen; isotype (K) seen.

DISTRIBUTION. At 3000 to 5000 m., eastern Tibet and southwestern Kansu.

ILLUSTRATION. MAXIMOWICZ, Fl. Tangut. 1: *pl. 4.* 1889.

REPRESENTATIVE COLLECTIONS. **Tibet:** *Ludlow & Sherriff 523, 6899*; *Ludlow, Sherriff & Taylor 6921*; *Rock 14467, 14459, 14501, 14505*; *Kingdon Ward 6123, 12244, 12224.* **Kansu:** *Farrer & Purdom 242, 243, 686* in part; *Rock 13194.*

82. **Delphinium autumnale** Hand.-Mazz. Symb. Sinicae 7: 276. *pl. 5, fig. 5.* 1931. FIG. 8, C.

Stem slender, 2.5–4.5 dm. tall, rigid or flexuose, striate, glabrous or with a few spreading hairs and short retrorse-strigulose ones below, equally few-leaved above, often branched; leaves orbicular, 3–9 cm. in diameter, trifid

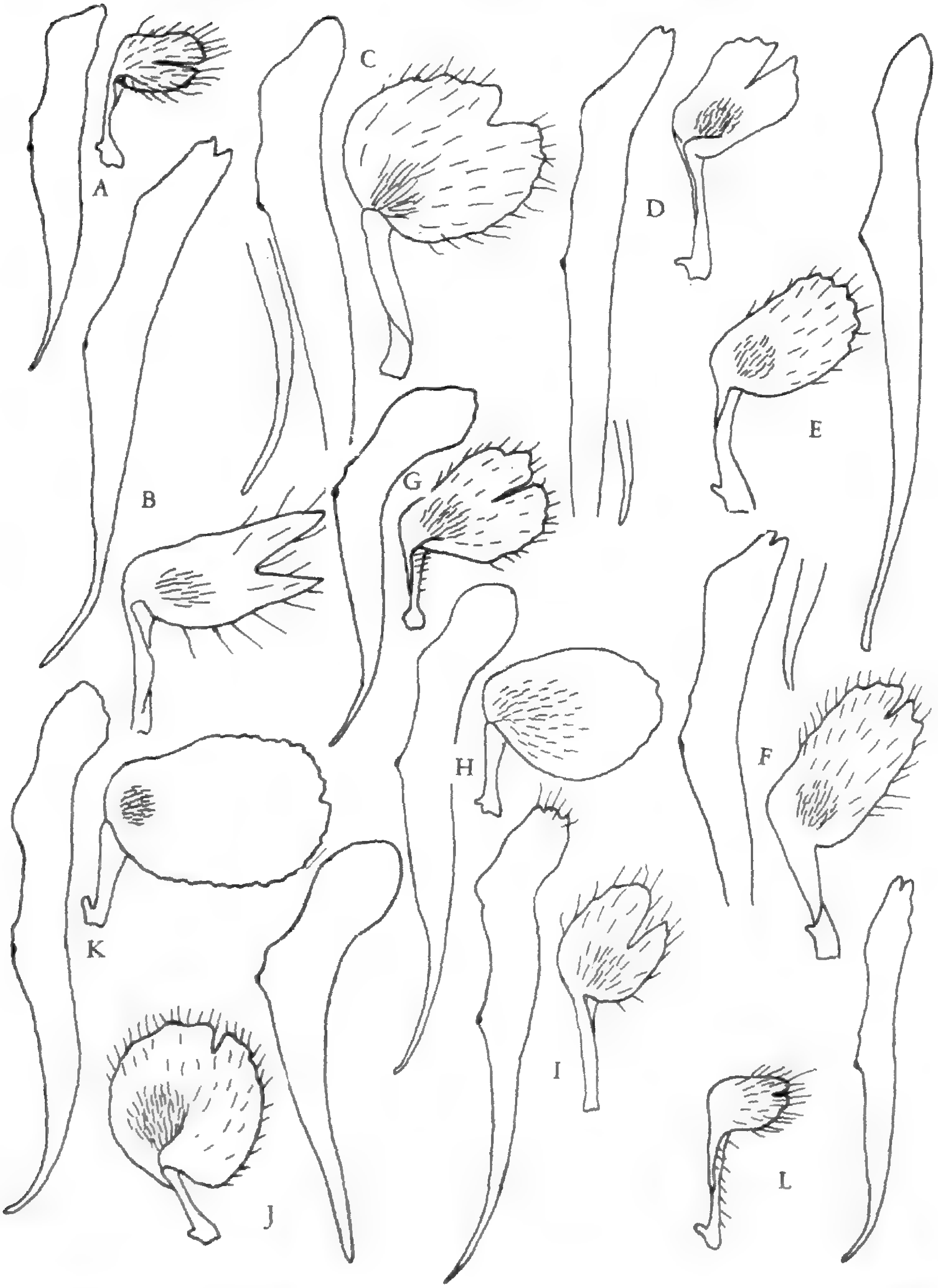

FIGURE 8. **Delphinium,** GROUP VI. Petals, the upper spurred, the lower clawed. A. *D. aemulans*; blade of upper petal 8 mm. long, spur 13 mm., blade of lower petal 4.5 mm. long, claw 4 mm.; drawn from TYPE (LE). B. *D. albocoeruleum*; blade of upper petal 13 mm. long, spur 19 mm.; blade of lower petal 10 mm. long, claw 7 mm.; drawn from *Rock 14467* (GH). C. *D. autumnale*; blade of upper petal 12 mm. long, spur 25 mm.; blade of lower petal 11 mm. long, claw 8 mm.; drawn from *Handel-Mazzetti 5495* (E). D. *D. batangense*; blade of upper petal 14 mm. long, spur 21 mm.; blade of lower petal 7 mm. long, claw 8 mm.; drawn from *Soulié 3042 bis* (P). E. *D. beesianum*; blade of upper petal 12 mm. long, spur 24 mm.; blade of lower petal 9 mm. long, claw

to base, the lateral segments bifid or trifid, all parts irregularly and distantly divided subpinnately, the ultimate divisions elongate-linear, spreading, 1.5–2.5 mm. wide, acute, thickish, strigulose above and on the revolute margins, with few longer hairs beneath; petioles of lower leaves ca. half as long as the stem, the upper shorter, short-sheathing at base, bearded-ciliate, strigulose above; racemes terminal on stems and branches, to 5-flowered, short, subcorymbose; bracts subulate-linear, to 15 mm. long, ciliate; pedicels equaling spurs or shorter, 1–2.5 cm. long, subglabrous except for some more or less retrorse hairs above; bracteoles near the middle of the pedicels, but often above or below, subulate, ciliate, 4–10 mm. long; flowers blue, horizontal; sepals broadly elliptic, ca. 20 mm. by 10–12 mm., the upper and 2 lower mucronate-thickened at apex, the 2 lateral broadly rounded, more or less erose; spur 25 mm. long, obtuse, 4.5 mm. thick at base, somewhat decurved to the slender tip; upper petals ca. two-thirds the length of the sepals, the blade slightly oblique, pale, 13 mm. by 4 mm., rounded and entire at the apex, glabrous, the spur slender, ca. 25 mm. long; lower petals with an exappendiculate claw 7 mm. long and an oblique limb, roundish or short obcordate, 11 mm. by 8 mm., erose, the surface and margin white-hairy, the base yellow-hairy; stamens 5 mm. long, ciliate; anthers blue, oblong, 1.5 mm. long; follicles 3, hirsute-villous.

TYPE: Sikang province, China; on the Hwang-liangdse, between Yenyuen and Kwapi; growing on limestone at 3600–3900 m., Oct. 5, 1914, *Handel-Mazzetti 5495*, holotype (probably W), not seen; isotype (E), seen.

83. **Delphinium batangense** Finet & Gagnep. Bull. Soc. Bot. France **51**: 478. 1905. FIG. 8, D.

Stem terete, erect or flexuous, 1.5–5 dm. tall, strigulose, divaricately corymbose at summit, few flowered; leaves several, puberulent, sessile or the lower with petioles to 6 cm. long, crowded on lower stem or scattered; blades rounded in outline, 3–4-parted almost to base into obcuneate parts, these deeply cut or dentate, with lance-oblong laciniae 2–5 mm. wide and obtuse at apex; branches of inflorescence to 12 cm. long; bracts sessile,

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6.5 mm.; drawn from *Forrest 6694* (US). F. *D. beesianum*; blade of upper petal 13 mm. long, spur 18 mm.; blade of lower petal 10 mm. long, claw 7 mm.; drawn from *Forrest 6364* (ISOTYPE of *D. calcicola*) (US). G. *D. bhutanicum*; blade of upper petal 9 mm. long, spur 15 mm.; blade of lower petal 8 mm. long, claw 5 mm.; drawn from *Ludlow & Sherriff 887* (E). H. *D. caeruleum*; blade of upper petal 12 mm. long, spur 17 mm.; blade of lower petal 10 mm. long, claw 5 mm.; drawn from *Ludlow & Sherriff 2400* (BM). I. *D. candelabrum*; blade of upper petal 13 mm. long, spur 16 mm.; blade of lower petal 7 mm. long, claw 7 mm.; drawn from *Ludlow 332* (E). J. *D. chefoense*; blade of upper petal 10 mm. long, spur 18 mm.; blade of lower petal 8.5 mm. long, claw 5 mm.; drawn from *Zimmerman 192* (US). K. *D. cheilanthum*; blade of upper petal 16 mm. long, spur 17 mm.; blade of lower petal 13 mm. long, claw 9 mm.; drawn from *Ikonnikov-Galitzky 3428* (UC). L. *D. crispulum*; blade of upper petal 10 mm. long, spur 12 mm.; blade of lower petal 4 mm. long, claw 6 mm.; drawn from *Grossheim & Schiskin 305* (UC).

ca. 2 cm. long, 3-parted, the parts 3-lobed, obtuse; pedicels 2–5 cm. long, strigulose; bracteoles 3-lobed, obtuse, ca. 1 cm. long, situated below the middle of the pedicels; flowers 2–4 on a stem, deep blue, ca. half the length of the pedicels; upper sepal round-ovate, 18–20 mm. long, spur arched-recurved, 20–24 mm. long; other sepals ovate, obtuse, short-strigulose, 20–22 mm. long; lamina of upper petals straight, emarginate, glabrous, 13–14 mm. long, the spur 19–20 mm. long; limb of lower petals obovate-oblong, 2-lobed, bearded in the middle, not ciliate, ca. 7 mm. by 5 mm., the claw 8 mm. long, glabrous, appendaged at base; stamens 6–7 mm. long; follicles 3, densely puberulent, 6 mm. long.

TYPE: Tibet, prov. Batang, Zambala & Yargong, in 1903, *Soulié 3042 bis* (P); seen. It is this number at Paris that was dissected and drawn, but *Soulié 3040, 3041, 3042,* and *3043* were filed with the type. From the same location, also deposited at Paris, *Soulié 3898* and *3899.*

ILLUSTRATION. Bull. Soc. Bot. France **51**: *plate 5, B. fig. 7–11.* 1905.

84. **Delphinium beesianum** W. W. Smith, Notes Bot. Gard. Edinb. **8**: 130. 1913. FIG. 8, E, F.

Delphinium beesianum var. *malacotrichum* Hand.-Mazz. Acta Horti Gothob. **13**: 60. 1939. Based on *Harry Smith 2985,* Tsepula, Szechwan. Isotypes (A, BM) seen.

Delphinium beesianum var. *malacotrichum* f. *radiatifolium* Hand.-Mazz. *loc. cit.* Type number *H. Smith 11939* from Taofu, Sikang. Isotypes (A, BM, MO) seen.

Delphinium beesianum var. *radiatifolium* (Hand.-Mazz.) W. T. Wang, Acta Bot. Sinica **10**: 264. 1962.

Delphinium beesianum var. *latisectum* W. T. Wang, *loc. cit.* 265. Based on *C. W. Wang 64923* and *64995* from Yunnan; not seen.

Delphinium calcicola W. W. Smith, Notes Bot. Gard. Edinb. **8**: 130. 1913. Type. *Forrest 6364* from Lichiang Range, Yunnan (E), seen; isotype (US) seen.

Delphinium beesianum f. *calcicola* (W. W. Smith) W. T. Wang, Acta Bot. Sinica **10**: 264. 1962.

Rootstock slender, covered with fibrous bases of old leaves; stem 1.5–5 dm. tall, flexuous, branched from below, white- and retrorse-strigulose or more loosely pubescent, the hairs sometimes yellow; lower leaves with purplish slender petioles 5–15 cm. long, strigulose, thin and vaginate at the base; leaf blades 5-fid, roundish in outline, 2–6 cm. in diameter, the segments divided to the middle or below into 2–3 lobes 1–3 cm. long, mostly 1–5 mm. wide, acute, strigulose above, longer hairy beneath; flowers 1–few at the ends of the branches in corymbose fashion; bracts mostly foliose, the petiole short, somewhat inflated, the blade trifid into lanceolate lobes, 1 cm. or longer, pubescent; pedicels pubescent, 2–8 cm. long, pilose; bracteoles above the middle of the pedicel, trifid to entire, 8–12 mm. long; sepals blue with deeper veining, densely pilose, the upper sepal ovate, 22–26 mm. long, 10–15 mm. wide, obtuse, the spur 20–25 mm. long, straight or somewhat curved to the blunt tip, 4–5 mm. wide at the base; lateral sepals oblong with rounded tip, 23–30 mm. long, 10 mm. wide; lower sepals ovate, about the same size; petals blue, the blade of the upper straight, 12–13 mm. long, entire to emarginate, the spur 18–24 mm. long; blade of lower petals oblong-obovate, 9–10 mm. long, 5 mm. wide, erose to deeply emarginate, claw 6.5–7 mm. long; stamens ca. 8 mm. long, the filaments ciliate; anthers dark, 1 mm. long; follicles 5, white-hairy, ca. 14 mm. by 3.5 mm., the style an additional 3 mm.; seeds brown, winged, 1.5 mm. long.

TYPE: Yunnan, limestone cliffs on east flank of Lichiang Range, 4500 m., Sept. 1910, *G. Forrest 6694* (E), seen; isotypes (K, P, UC, US) seen.

DISTRIBUTION. At about 4000 to 5000 m., in eastern Tibet and western China.

EXAMPLES. **Tibet:** *Rock 14518, 14520, 14523, 14522, 14460, 22267, 13398*; *Ludlow, Sherriff & Taylor 6379.* **Yunnan:** *Kingdon Ward 1025*; *Forrest 22577, 21007, 20204*; *Rock 24738, 10817, 7763, 5421, 11692, 10788, 10776, 17248, 22852*; *Wang 64995, 69525, 70146.* **Kansu:** *Rock 13092, 14640.* **Szechwan:** *Kingdon Ward 4856*; *Forrest 22967, 20572*; *H. Smith 4243, 4326.* **Sikang:** *H. Smith 12619, 12515, 11712, 12421.*

As here conceived this is rather a variable species both as to pubescence and whether the upper petals are entire or not at the apex.

85. **Delphinium bhutanicum** Munz, sp. nov. FIG. 8, G.

Perennial, to ca. 1 m. high, the stem slender, openly branched above, more or less retrorse-strigulose throughout, scattered leafy; lower leaves withered by anthesis, upper blades 4–10 cm. wide, divided almost to their base into cuneate-rhombic segments finely strigulose above, more or less pubescent beneath especially along the veins, trilobed about halfway, then lobulate into linear-lanceolate to lanceolate lobules 5–15 mm. long, 2–5 mm. wide; petioles slightly dilated at the base; uppermost leaves much reduced and serving as bracts; inflorescence open, 2- to few-flowered, subcorymbose, strigulose, the pedicels suberect, 2–5 cm. long; upper bracts lanceolate, ca. 1 cm. long; bracteoles broadly linear, 4–6 mm. long, slightly below the flower; sepals blue, strigulose, the upper broadly obovate, 15–16 mm. by 11–12 mm., subtruncate at apex, spur 15–16 mm. long, ca. 3 mm. wide at base, spreading-decurved; lateral sepals oblong-obovate, 16 mm. by 8 mm., rounded at apex; lower sepals slightly shorter and wider; petals blue, lamina of upper somewhat oblique, 9 mm. by 3 mm., glabrous, entire at the somewhat rounded tip, spur ca. 15 mm. long; lamina of lower petal obovate, 8–9 mm. by 5–7 mm., bifid ca. 3 mm. into 2 rounded-oblong lobes, white-bearded throughout, the claw 5 mm. long; stamens 5–6 mm. long, glabrous; carpels 3, pubescent, 11–12 mm. by 3.5–4 mm., the style an additional 2–2.5 mm.; seeds winged on the angles.

Planta perennis, ad ca. 1 m. alta, tenuis, supra ramosa, strigulosa; laminae foliorum superiorum 4–10 cm. latae, alte divisae, segmentibus cuneato-rhombicis, supra strigulosae, infra pubescentes, laciniis ultimis 5–15 mm. longis, 2–5 mm. latis; inflorescentia laxa, floribus 2–paucis, subcorymbosa; pedicelli suberecti, 2–5 cm. longi; bracteae foliosae, superiores lanceolatae, ca. 1 cm. longae; bracteolae 4–6 mm. longae; sepala azurea, strigulosa; sepalum superiore late obovatum, 15–16 mm. longum; sepala lateralia oblongo-obovata, 16 mm. longa, apice rotundata; sepala inferiora breviora latioraque; petala azurea, laminae superiores glabrae, integrae, 9 mm. longae, calcaria 15 mm. longa; laminae inferiores obovatae, 8–9 mm. longae, bilobatae; ungues 5 mm. longi; folliculi 3, pubescentes, 11–12 mm. longa; semina alata.

TYPE: Northeastern Bhutan, Me La, Aug. 25, 1934, *Ludlow & Sherriff 887*; holotype (BM); isotype (E).

The proposed species has been collected between 3500 and 4000 m., as follows: open grassy meadows, Me La, Bhutan, *Ludlow & Sherriff 1016* (BM); Kurmatrang, Pumthang, *Cooper & Bulley 2239* (E); Cho La, S. E. Tibet to Bhutan, *Ludlow & Sherriff 873* (BM); Pangotang, Tsampa, *Ludlow & Sherriff 19686* (BM). Its inflorescence is corymbose, not spicate as in some species of the region, e.g., *D. denudatum* and *D. roylei.*

86. **Delphinium caeruleum** Jacquem. ex Camb. in Jacquem. Voy. Bot. **4**: 7. *pl. 6.* 1843. FIG. 8, H.

Delphinium grandiflorum L. var. *kunawarensis* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 98. 1896. New name for *D. caeruleum.*

? *Delphinium caeruleum* var. *obtusilobum* Brühl ex Huth, Bot. Jahrb. **20**: 463. 1895 and *D. grandiflora* var. *obtusiloba* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 99. 1896.

? *Delphinium caeruleum* vars. *corymbosum* Brühl ex Huth and *tenuicaule* Brühl ex Huth, *loc. cit.* 464. 1895 and *D. grandiflorum* var. *tenuicaulis* Brühl in Brühl & King, *loc. cit.* 98. Unfortunately I have been unable to borrow authentic material from the Calcutta Herbarium. Mukerjee (Bull. Bot. Surv. India **2**: 293–296. 1960) refers vars. *corymbosum* and *tenuicaule* to *Delphinium candelabrum* Ostenfeld.

? *Delphinium caeruleum* var. *magnificum* Huth, *loc. cit.*

Stem branched from base, 7–40 cm. tall, branches spreading, densely strigulose below, more loosely pubescent above; leaves suborbicular in outline, 1–4 cm. in diameter, 5–7-parted into cuneate-oblong segments, these incised into linear strigulose lobes tending to be revolute on the margin or less divided in the basal leaves; lower petioles to ca. 1 dm. long, not widened at the base, upper cauline leaves remote, shorter petioled; flowers few, in a loose subcorymbose raceme or panicle; bracts divided into linear segments or entire, about 1 cm. long; pedicels 1–5 cm. long; bracteoles fairly remote from flower, pubescent, linear, 5–8 mm. long; sepals pale to intense blue, pubescent to hairy, the upper sepal 12–16 mm. long, ovate, acutish, ca. 9 mm. wide; the spur almost straight, subhorizontal, 18–25 mm. long, 2.5–3 mm. wide at the base, narrowed to an acute apex; lateral sepals oblong, pubescent along the midrib, 13–16 mm. long, 6–8 mm. wide; lower sepals about as long, more pointed and more pubescent; upper petals bluish, slightly oblique, the blade ca. 7 mm. long, entire, narrow to rounded at apex, spur 14–15 mm. long; lower petals blue, the blade oblong-obovate, 7 by 5.5 mm., with a round hairy patch near the base, otherwise sparsely bearded and ciliate, entire or cleft for about 2 mm., the claw 4.5 mm. long; stamens 5–6 mm. long, the anthers dark, 1 mm. long; carpels 3–5, pubescent, 8 mm. or more long, styles an additional 2.5–3 mm.

TYPE: Cambessedes says "Ad jugum montis Houkio (vulgo Houkio-Ghauti) ad fines Tartariae sinensis et provinciae Kanaor (alt. ca. 5000 m.)." At Paris is a specimen "in herboris altissimis inter Hookis Ghat et Doubling, Kunaweer," *Jacquemont* Cat. No. 1896 (P) (720); (K) isotype seen. The Paris specimen has three pieces, two are low, a few cm. high, the third is taller, spindly, 3–4 dm. high; all have lobules 1–2 mm. wide.

DISTRIBUTION. Apparently at 3000 to 5800 m., Nepal, Sikkim, Tibet. I am unable to divide the subacaulescent from the caulescent forms, both growing in the same area. As here recognized, then, a rather variable species in height, pubescence, and outline of lamina of lower petal, which may be entire and rounded to emarginate and rounded.

EXAMPLES. **Nepal:** *Duthie 5299*; *Lall Dhwoj 556.* **Sikkim:** *Cave 6*; *Smith & Cave 2131, 1935*; *Cooper 760.* **Tibet:** *Strachey & Winterbottom 11, 13*; *Ludlow & Sherriff 10051, 9952, 9751, 779, 11067, 2400, 1977, 1968*; *Spencer Chapman 35*; *Kingdon Ward 9997.* **Bhutan:** *Ludlow, Sherriff & Hicks 17476.*

87. **Delphinium candelabrum** Ostenfeld in Hedin, Southern Tibet 6(3): 80. 1922. (A list of flowering plants from inner Asia collected by Dr. Sven Hedin [compiled by Ostenfeld & Paulsen].) FIG. 8, I.

Low perennial from a slender rootstock arising from a thickened branched elongate root; stem dark, slender, branched or simple, subglabrous or with some spreading hairs, 5–15 cm. high; leaves subrosulate at the base, the lower petioles 2–7 cm. long, very slender, strigulose, dilated at the base; the blades 1–2 cm. in diameter, rounded, palmatisect to the base, then again into oblong-linear segments 1–2 mm. wide, mucronate at the subtruncate apices, rather long-pubescent especially beneath; cauline leaves 1 to few, remote, the upper reduced to trifoliate bracts; flowers about 3 to 6, in an open subcorymbose inflorescence; bracts 5–10 cm. long, simply or compound-laciniate; pedicels arcuate-ascending, very slender, somewhat spreading-villous, 5–10 cm. long; bracteoles entire and linear, to ca. 10 mm. long, 1 mm. wide, or sometimes trilobed, near the middle of the pedicel; sepals blue-purple, sometimes drying brownish, white- or yellow-villous, the upper sepal round-ovate, 20 mm. by 18 mm., the spur often slightly decurved, ca. 20 mm. long, 4 mm. wide at the base; lateral sepals asymmetrically oblong-elliptic, 20–25 mm. long, 13 mm. wide; lower sepals ovate-elliptic, 22 mm. by 15 mm., rounded-apiculate at the tip; upper petals dark violet, quite straight, the lamina ca. 14 mm. long, with a few stiff hairs, rounded and erose at apex, the spur 17 mm. long; lower petals with blade at right angles to the claw, rounded-obovate, 6 mm. by 4.5

mm., unequally 2-lobed, short-bearded on lower half, the claw 6.5 mm. long; stamens glabrous, 7 mm. long; anthers dark, 1 mm. long; carpels 3, hairy.

TYPE: Eastern or Inner Tibet, at 5127 m., Aug. 9, 1901, *Hedin* (s?). Not seen.

ILLUSTRATION. OSTENFELD & PAULSEN, List Fl. Pls. Inner Asia, *pl. 2*. 1922.

SPECIMENS SEEN. **Tibet:** *Ludlow 332* (E); Pomo Tso, *Ludlow & Sherriff 523* (E).

88. **Delphinium chefoense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 170. 1893. FIG. 8, J.

Delphinium gilgianum Pilger ex Gilg & Loesener, Bot. Jahrb. 34. Beibl. **75**: 33. 1904. Based on *Zimmermann 192*, May, 1900, from Tsingtau, Kiau-tschou, Schangtung (Shantung), China; isotypes seen (GH, US).

Delphinium grandiflorum L. var. *gilgianum* (Pilger) Finet & Gagnep. Bull. Soc. Bot. France **51**: 483. 1905.

Stem 5–8 dm. tall, erect, angled, few leaved, retrorse-strigulose and short pubescent, with some glandular hairs; basal leaves largely withered by anthesis, the petioles 5–15 cm. long, but slightly dilated at the base, the laminae parted to the base with short, linear, obtuse segments; upper cauline leaves short-petioled, the blades rounded in outline, 3–8 cm. broad, minutely pubescent mostly with appressed hairs, trifid, then the 2 lateral lobes deeply cut making the blade essentially 5-fid, the parts cuneate-obovate, incised 1/2–2/3 their length into lanceolate or linear lobes mostly 2–5 mm. wide; inflorescence laxly racemose, rather few flowered, somtimes with 1 or 2 basal branches, the axis densely spreading-pubescent, some of the hairs glandular; bracts mostly entire, lance-linear, pubescent, 5–7 mm. long; pedicels ascending, slightly divaricate, 2–5 cm. long; bracteoles 2, linear, remote from the flower, 3–4 mm. long; sepals deep blue, with some white, pubescent, the upper sepal broadly ovate, 20–21 mm. by 15–16 mm., subacute, the spur straight, ca. 20 mm. long, 5 mm. wide at the base, obtuse; lateral sepals elliptic, 20 mm. by 12 mm., rounded-obtuse, generally pubescent; lower sepals elliptic-obovate, 20 mm. by 13 mm., obtuse; upper petals pale, somewhat yellowish at apex, the laminae very oblique, ca. 8 mm. by 4 mm., rounded and glabrous at apex or slightly emarginate, the spur ca. 18 mm. long; lower petals bluish, oblique, the lamina rounded-obovate, ca. 9 mm. in diameter, shallowly notched, with yellow beard near the base, otherwise sparsely hairy and ciliate, the claw 5 mm. long; stamens 7–8 mm. long, dilated below, glabrous; anthers dark, oblong, 1.2 mm. long; follicles 3, pubescent; seeds winged on angles.

TYPE: Chefoo, northern China, prov. Shantung, *Fauvel* (P); seen.

ADDITIONAL MATERIAL. Chefoo, *Carmichael 823* (BM); E. Chungtien, *K. M. Feng 2714* (A).

89. **Delphinium cheilanthum** Fisch. ex DC. Syst. 1: 352. 1817; Prodr. 1: 53. 1824. FIG. 8, K.

Delphinium pauciflorum Reichb. ex Schlecht. Linnaea **6**: 582. 1831, nomen; ex Ledeb. Fl. Rossica **1**: 61. 1841. Based on "In terra Tschuktschorum, ad sinum St. Laurentii," *Eschscholtz* (LE). Seen.

Delphinium davuricum Bess. Cat. pl. h. bot. Cremenec. Suppl. **3**: 9. 1814, not Georgi, 1797–1802.

Delphinium dahuricum Stev. ex DC. Prodr. **1**: 53. 1824; *pro synon.*

Delphinium cheilanthum var. *dahuricum* (Steven in DC.) Huth, Bot. Jahrb. **20**: 466. 1895.

Delphinium sylvaticum Turcz. Bull. Soc. Nat. Moscou **15**: 74. 1842. Type from Dahuria, *Turczaninow*, Herb. Fischer (LE); seen.

Delphinium parviflorum Turcz. *loc. cit.* 75. Type, "Ad fl. Barguzin. 1834, Turcz.," (LE); seen.

Delphinium cheilanthum var. *parviflorum* (Turcz.) Huth, Bot. Jahrb. **20**: 467. 1895.

Delphinium middendorffii Trautv. Florula taimyrensis phaenogama, in Middend., Reise Sibiriens 1(2)[Bot.] 63. 1847. Type "Ad. fl. Taimyr, Aug. 1843, *Middendorf,*" (LE); seen.

Delphinium cheilanthum ssp. *middendorffii* (Trautv.) P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 100. 1896.

? *Delphinium cheilanthum* ssp. *schizophyllum* Brühl, *loc. cit.* Based on a collection by Davidson on China Hill near Naini Tal. Not seen.

Delphinium cheilanthum var. *subglabrum* Ledeb. ex Huth, Bot. Jahrb. **20**: 466. 1895.

Delphinium cheilanthum vars. *laxiflorum* and *chinense* Trautv. ex Huth, *loc. cit.* 467. These three varieties of Huth are, to me, uncertain.

Delphinium cheilanthum var. *albiflorum* Trautv. Act. Horti. Petrop. **5**: 503. 1877. Two sheets bearing this name were loaned from Leningrad, both from Herb. Fischer. One certainly belongs here, the other doubtfully so.

Perennial from a woody crown; stems 1 to several, 2–9 dm. tall, simple or branched, subglabrous below to more or less strigulose above, somewhat ridged, 4–8 mm. thick, rather leafy throughout, the lower petioles to about 1.5 dm. long, slightly dilated at the base, the upper much shorter to almost sessile; blades rounded-pentagonal in outline, 3–12 cm. broad, from subglabrous to strigulose on upper surface, especially the latter along the veins, somewhat paler and pilose beneath, 5-parted, or the upper 3-parted, with cuneate-oblanceolate or -lanceolate segments, these entire in upper leaves or trifid or 5-fid in lower into lanceolate acuminate lobes 2–5 mm. wide; inflorescence racemose, few- to several-flowered, the bracts leaflike, entire to multifid; pedicels erect or ascending, 1.5–3 cm. long; bracteoles lanceolate, to ca. 6 mm. long, 2 just beneath the flower, often a third farther down; sepals rich deep blue, sometimes white, pubescent, the upper one 12–16 mm. long, ovate, the spur straight or somewhat decurved, 15–20 mm. long, 3–4 mm. wide at base, narrowed to an acute tip; lateral sepals rhombic-ovate, 12–16 mm. long, 8–9 mm. wide, obtuse, pubescent along the mid-vein; lower sepals oblong-ovate, 16–20 mm. long, 8–10 mm. wide, acutish, more generally pubescent; upper petals mostly blue, the blade slightly oblique, glabrous, entire, 13–16 mm. long, the spur slightly longer; lower petals mostly blue, the oblong-obovate blade mostly not lobed, ca. 13 mm. by 9 mm., with a small patch of yellow hair near the base; claw broad at summit, 6–7 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.2 mm. long; follicles 3, densely pubescent, 13–15 (–20) mm. long, the styles 2–3 mm. long; seeds winged on the angles.

TYPE: "Hab. in Daouria, circa Doroninsk. *Vlassof*." Photograph seen (BH); specimens seen (LE).

RANGE. Eastern Siberia and northern Mongolia.

ILLUSTRATIONS. GMELIN, Fl. Sibirica **4**: 187. *pl. 76.* 1799; Bot. Reg. **6**: *pl. 473.* 1820.

REPRESENTATIVE SPECIMENS. *Augustinowicz* in 1875; *Ikonnikov-Galitzky 365, 3335, 3428*; *Karo 188*; *Turczaninow* in 1831; *Bunge* in 1883; *Maack 673.*

Huth, Bot. Jahrb. **20**: 466–467. 1895, lists var. *formosum* Hort., and var. *chauvieri* Lem. (*D. hendersonii* Henfr., Gard. Mag. Bot. **2**: 57. *pl. 6.* 1850), both of which seem to be entirely horticultural forms.

90. **Delphinium coleopodum** Hand.-Mazz. Symb. Sinicae 7: 275. 1931. FIG. 9, A, B.

Stem simple, 2–4 dm. tall, mostly glabrous, leafy in lower half; petioles 5–15 cm. long, dilated at base for 2–3 cm., blades pentagonal, 2–8 cm. broad, somewhat shorter, strigulose or with longer hairs especially beneath, deeply pentafid into cuneate-obovate divisions that are incised to about the middle into several lanceolate acuminate lobes 5–15 mm. long, 2–5 mm. wide; inflorescence mostly a simple few-flowered secund raceme 5–20 cm. tall; bracts setaceous and simple to leafy and 3-lobed, the lower with conspicuous inflated petiole base, the upper often 1 cm. long, purplish; pedicels erect, spreading-hairy near the apex, 3–8 cm. long; bracteoles setose, purplish, 7–12 mm. long, placed near the middle of the pedicel; sepals dark blue, rather long-pubescent, the upper sepal ovate, 20–25 mm. long, 12–14 mm. wide, pointed, the spur horizontal or slightly decurved, 18–25 mm. long, ca. 3 mm. wide at the base, rather slowly narrowed to an often blunt tip; lateral sepals 25–27 mm. by 12–13 mm., obtuse, pubescent along the midrib; lower sepals about as large, but more generally pubescent; upper petals bluish, the blade 11–12 mm. long, slightly oblique, entire, the spur 20–21 mm. long; lower petals blue, the oblong blade ca. 12 mm. by 8 mm., cleft 2.5 mm., with very long hairs near the base, scattered shorter ones elsewhere, claw 6 mm. long; stamens 5–6 mm. long, the filaments somewhat ciliate; anthers dark, 1 mm. long; follicles 3, erect, with long yellow hairs, the body 15–18 mm. by 4–5 mm., the style an additional 3 mm.; seeds ca. 1 mm. long, with a whitish membrane folded into longitudinal wings at the angles.

TYPE: Northwest Yunnan at Likiang, no. *4105*, presumably collected by *Handel-Mazzetti* and presumably at (W). Not seen, but it is well illustrated in his Symbolae Sinicae 7: *pl. 5. fig. 6.* 1931.

RANGE. At about 4000 to 5000 m., in the Likiang or Lichiang Snow Range of Yunnan.

REPRESENTATIVE SPECIMENS. *Rock 10777, 11676, 7761, 6110, 10633, 11688, 10764, 24945, 11436, 7765, 10669, 6092, 24738*; *Forrest 6690, 22471, 22483, 22362, 3035, 11363, 16942, 15198, 15173*; *C. Schneider 3029*.

This is one of the most easily differentiated species from western China with its remarkably inflated petiole bases.

91. **Delphinium crispulum** Rupr. Fl. Cauc. 34. 1869. FIG. 8, L.

Delphinium speciosum var. *linearilobum* Trautv. Acta Horti Petrop. **4**: 102. 1886. Based on "Transcaucasia rossica districtu Achalzich, ad lacum Chosapin, 6000′, *G. Radde 212*, Aug. 19, 1874" (LE); seen.

Delphinium linearilobum (Trautv.) N. Busch in Fl. Cauc. Crit. III. **3**: 68. 1902.

Delphinium triste var. *linearilobum* Huth, Bot. Jahrb. **20**: 413. 1895.

Delphinium linearilobum var. *crispulum* N. Busch in Fl. Cauc. Crit. III. **3**: 68. 1902.

Delphinium tomentellum Busch, *loc. cit.* 70. Type, Baku, district Kuba, Mt. Bazar, *Alexsenko 2620* (LE); seen, also photo. (A, K).

Delphinium tomentellum vars. *macranthum* and *araraticum* N. Busch, *loc. cit.* 70, 71.

Delphinium araraticum (Busch) Busch in Davis, Fl. Turkey **1**: 111. 1965.

Delphinium tomentellum var. *angustibracteatum* Busch, Fl. Cauc. Crit. III. **3**: 70. 1902.

Perennial from a woody rootstock; stem 4–7 dm. tall, angled, cinereously finely strigulose throughout, leafy to inflorescence, branched above; leaves rather crowded, petioles dilated at base, the lower 1–2 dm. long, the upper shorter; leaf blades strigose above and beneath, 5–10 cm. long, 5-parted almost to base into narrow segments which are in turn deeply incised into lance-linear lobes 5–25 mm. long, prominently veined; upper leaves tripartite; inflorescence an open panicle, the central raceme densely many flowered, the lateral more lax and few flowered; bracts strigose, linear to lanceolate, 1–2 cm. long; pedicels 1–4 cm. long, ascending; bracteoles strigose, 5–7 mm. long, linear, subtending the flower; sepals light blue, strigose, upper sepal ovate, 13–15 mm. by 5 mm., pointed, the spur almost straight, 14 mm. long, 3 mm. wide at the base, rather narrow at apex; lateral sepals oblong-obovate, 15 mm. by 8 mm., rounded-obtuse; lower sepals 15 mm. by 5 mm., pointed; petals very dark, the upper with a blunt, almost straight, somewhat bidentate, glabrous lamina ca. 10 mm. long, the spur ca. 12 mm. long; lower petals with the blade oblong, bearded, 4 mm. by 2.5 mm., cleft 1/3 its length, the claw 6 mm. long, the blade at right angles to the claw; stamens 6–7 mm. long, with glabrous filaments; anthers dark, oblong, 1 mm. long; follicles 3, pubescent; seeds squamellate.

TYPE: Caucasus orientalis, Gumbet, *Owerin,* July 26, 1861 (LE), seen; photograph (A, K).

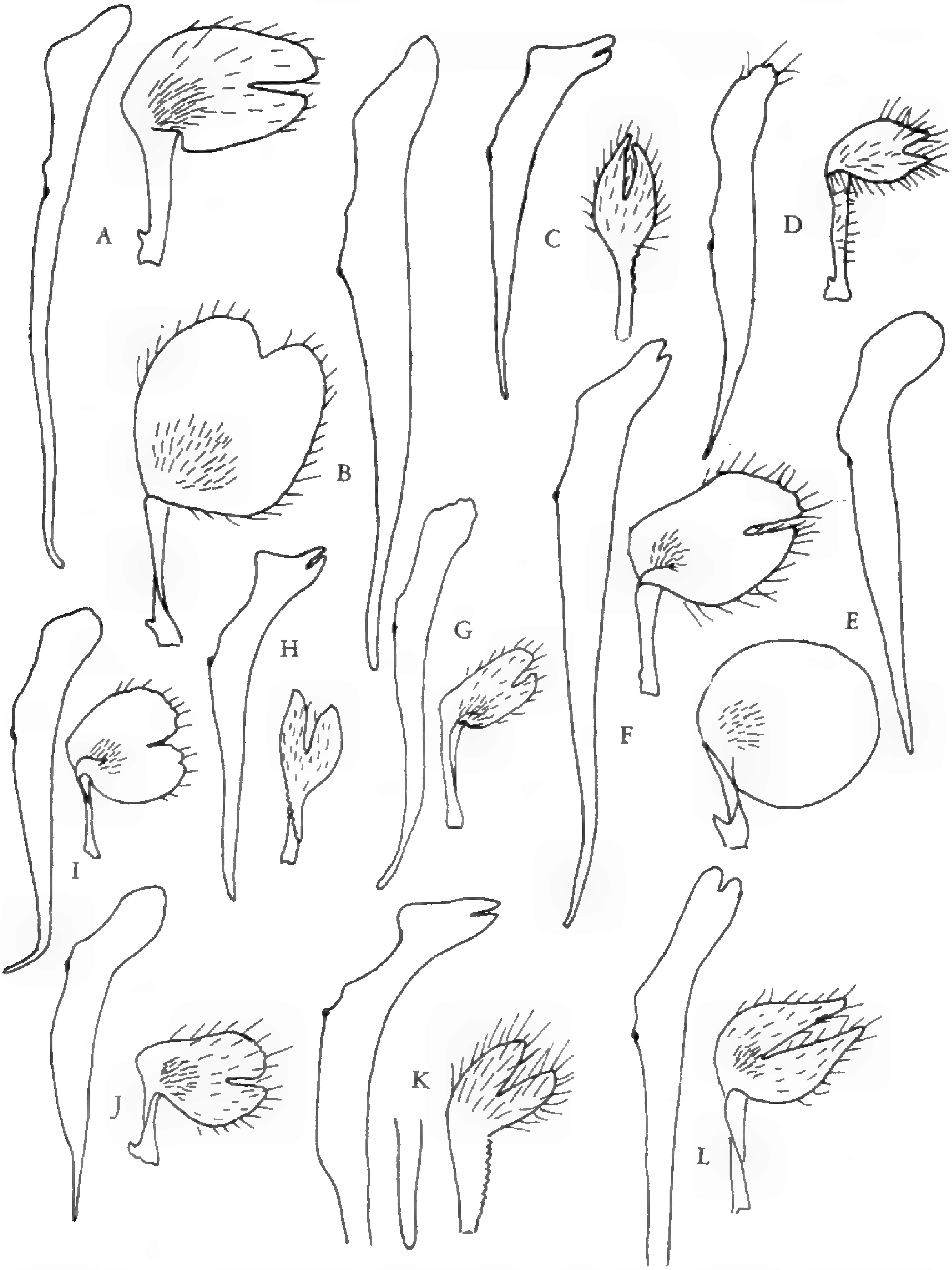

FIGURE 9. **Delphinium,** GROUP VI. Petals, the upper spurred, the lower clawed. A. *D. coleopodum*; blade of upper petal 12 mm. long, spur 21 mm.; blade of lower petal 12 mm. long, claw 6 mm.; drawn from *Rock 11676* (US). B. *D. coleopodum*; blade of upper petal 13 mm. long, spur 23 mm.; blade of lower petal 13 mm. long, claw 8 mm.; drawn from *Rock 10764* (US). C. *D. denudatum*; blade of upper petal 9 mm. long, spur 15 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Fleming 445* (MICH). D. *D. dissectum*; blade of upper petal 11 mm. long, spur 13 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Pavlov 336* (NY). E. *D. grandiflorum*; blade of upper petal 10 mm. long, spur 18 mm.; blade of lower petal 10 mm. long, claw 4 mm.; drawn from *Nikiforow* (MICH). F. *D. henryi*; blade of upper petal

DISTRIBUTION. The plants seem to grow in rocky places between 1000 and 3000 m., from eastern Anatolia to the Caucasus and northwestern Iran.

EXAMPLES. **Transcaucasia:** prov. Tiflis, *Grossheim 305.* **Turkey:** prov. Kars, *Davis 32562* in part; **Turkish Armenia:** *Sintenis 7107* and *7108*; prov. Van, *Davis 23327, 23612*; *McNeill 731*; prov. Erzincan, *Davis 31665*; prov. Coruh, *Davis 32443.* **Iran:** above Zinjanab, *Gilliat-Smith 2514.*

Nevski (Komarov, Fl. U.S.S.R. 7: 143. 1937) cites the synonymy much as I have given it, but Davis (Fl. Turkey 1: 110–111. 1965) maintains *D. linearilobum* and *D. araraticum* as species, as well as *D. tomentellum* and *D. crispulum*, making 4 distinct species. The differences seem very slight; *D. araraticum*, for instance, having bractlets 2–3 mm. wide, while in the others they are 1–2 mm. Without more material than was available to me I cannot be sure of the status of the taxa and follow Nevski.

92. **Delphinium denudatum** Wall. Cat. no. 4719. 1830, *nomen*; ex Hook. f. & Thoms. Fl. Indica 49. 1855. FIG. 9, C.

Delphinium pauciflorum Royle, Illustr. Bot. Himal. 55. 1834, not D. Don, Prodr. Fl. Nepal. 196. 1825.

Stem usually freely and openly branched throughout, 4–8 dm. tall, subglabrous to rather coarsely strigose, especially above, 2–4 mm. thick, terete, sometimes spreading-pubescent above; basal leaves 5–15 cm. broad, roundish in outline, 3–5-parted into rather broad, obovate divisions that are pinnately and divaricately coarsely laciniate into suboblong lobes or teeth 2–3 mm. wide, the petioles to 1.5 dm. long, slender, somewhat dilated at the base; cauline leaves remote, gradually reduced upward and more deeply laciniate into narrower lobes; inflorescence an open panicle of rather few-flowered open racemes; bracts linear, commonly 5–15 mm. long; pedicels ascending, 1–4 cm. long; bracteoles 2, commonly near the middle of the pedicel, 2–4 mm. long; flowers fragrant; sepals blue to violet, the upper sepal ovate, 12–13 mm. by 6–7 mm., acute, pubescent, the spur 14–15 mm. long, 3.5 mm. wide at the base, subacute; lateral sepals oblong-ovate, 13 mm. by 7–8 mm., rounded at apex, pubescent on

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10 mm. long, spur 25 mm.; blade of lower petal 11 mm. long, claw 5 mm.; drawn from *Henry 6952* (GH). G. *D. incisum*; blade of upper petal 9 mm. long, spur 16 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Dhwoj 49* (E). H. *D. koelzii*; blade of upper petal 9 mm. long, spur 13 mm.; blade of lower petal 5 mm. long, claw 5 mm.; drawn from *Koelz 4921* (MICH). I. *D. kamaonense*; blade of upper petal 8 mm. long, spur 14 mm.; blade of lower petal 7 mm. long, claw 5 mm. long; drawn from *Ludlow 781* (E). J. *D. kamaonense*; blade of upper petal 7 mm. long, spur 15 mm.; blade of lower petal 7 mm. long, claw 4.5 mm.; drawn from *Duthie 5299* (MICH). K. *D. lanigerum*; blade of upper petal 11 mm. long, spur 18 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Kotschy 430* (MO). L. *D. malacophyllum*; blade of upper petal 11 mm. long, spur 28 mm.; blade of lower petal 8 mm. long, claw 7 mm.; drawn from *Harry Smith 3385* (BM).

midline; lower sepals oblong-ovate, 14–15 mm. by 7 mm., rounded at apex, pubescent; upper petals white, with blue tinge at apex, the blade 8–9 mm. long, glabrous, bidentate, oblique, the spur 13–15 mm. long; lower petals blue or violet, the claw 5 mm., the broadly elliptical blade bearded, ca. 6 mm. long, cleft almost halfway; stamens somewhat violet, glabrous, 5–6 mm. long; anthers bluish, 0.8 mm. long; follicles 3, sparsely strigose to subglabrous, 10–16 mm. by 3–3.5 mm., the styles an additional 2–3 mm.; seed dark, obpyramidal, 1 mm. long, the scales rather long and not regularly arranged in even rows.

TYPE: Baramula, Kashmir, *Winterbottom 348*, isotype (K); seen.

RANGE. About 1600 m. to 3300 m., Himalaya of northern India, Kashmir and West Pakistan.

ILLUSTRATIONS. COLLETT, Fl. Simlensis 12. 1902; BASU, Indian Medicinal Plants, *pl. 7.* 1918; BLATTER, Beautiful Flowers Kashmir **1**: *pl. 4.* 1927; COVENTRY, Wild Flowers Kashmir **3**: *pl. 7.* 1930.

REPRESENTATIVE COLLECTIONS. **Punjab:** *Koelz 3163, 4963, 1944, 4638, 4841, 8344*; *R. Stewart 6042, 2026 1/2*; *Sherriff 7310*; *Lace 164*; *Duthie* 8–21–1897, 5–25–1897. **Pradish:** *Koelz 21113, 8659*; *Jacquemont 535, 721*; *Fleming 445, 394*; *Sahni 24608*; *Dudgeon & Kenoyer 107*; *Strachey & Winterbottom 3*; *Watt 612*; *Hooker & Thomson*, June 11, 1848. **Kashmir:** *Pinfold 164*; *Ludlow & Sherriff 7671, 8106, 9106*; *Dickason 366*; *Stewart 17468, 9268, 17534, 12147, 19440.*

93. **Delphinium dissectum** Huth, Bot. Jahrb. **20**: 403. 1895. FIG. 9, D.

Stem erect, simple, 2.5–5 dm. tall, strigulose throughout, scattered-leafy to the middle, the lower petioles 5–12 cm. long, dilated at base, strigulose, the upper gradually shorter; leaf blades rounded-pentagonal in outline, the lower 5–10 cm. broad, strigulose on both surfaces, parted almost to the base into narrow-cuneate segments, these much broadened above, deeply pinnately incised and laciniate into linear segments mostly 1.5–2.5 mm. wide; raceme elongate, peduncled, 1–3 dm. long, soft-pubescent, rather laxly flowered; lower bracts laciniate, upper entire, linear-lanceolate, ca. 1 cm. long; pedicels divaricate, mostly 1–3 cm. long; bracteoles lanceolate, 4–6 mm. long, subtending the flower; sepals dilute blue, with slender hairs 1 mm. long, both externally and internally; upper sepal ovate, 16–18 mm. by 10 mm., acutish, the spur stout, decurved, 16–17 mm. long, 4 mm. wide at base, blunt at tip; lateral sepals oblong-elliptic, 18–20 mm. by 8–10 mm.; lower lance-ovate, 20–22 mm. long, 9 mm. wide, subobtuse; petals black, the upper setose at entire tip, the spur 13 mm. long; lower petals oblique, the blade 6 mm. by 3 mm., the 2 lobes gaping, ciliate, 2 mm. long, bearded, the claw 6.5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1 mm. long; follicles 3, more or less pubescent.

TYPE: Mongolia between Tschargachantu and Geltgentei, *Kirilov*, 1841 (LE); seen.

COLLECTIONS SEEN. All from **Mongolia:** *Ikonnikov-Galitzky 785*; *Pavlov 336*; *Krascheninnikov 87.*

94. **Delphinium dolichocentroides** W. T. Wang, Acta Bot. Sinica **10**: 159–160. 1962.

Stems 3–5 dm. high, 2.5 mm. thick at base, white-hirsute below, glabrous above, remotely 1–2-foliate; basal leaves 2–3, long petioled; blades broadly pentagonal, 2.5–5.5 cm. long, 4.5–8 cm. wide, cordate, 3-parted to 1.5–3.5 cm. above the base, the middle part broadly rhombic, cuneate at base, 3-parted to below the middle, the middle lobe broadly or narrowly rhombic, trifid to middle, the lobules linear to lanceolate, 3–5 mm. wide, rarely 1-toothed, the lateral lobes broadly obliquely rhombic, smaller, unequally 2–3-fid; lateral parts broadly obliquely flabellate, unequally 2-parted to base, the upper parts like the middle, the lower broadly rhombic, unequally bifid, densely strigulose beneath, loosely hirsute above; petioles 14–17 cm. long, loosely hirsute, narrowly vaginate at base; upper leaves with few long laciniate entire segments 3–4 cm. long, 5 mm. wide; racemes 5–24 cm. long, glabrous, very open, 3–6-flowered; pedicels 2–8 cm. long, bibracteolate near or above the middle; bracteoles linear, 6–14 mm. long, 0.4–1 mm. wide, loosely puberulous; sepals blue-purple, elliptic-obovate, 14–16 mm. long, appressed puberulent, short-corniculate, these tips 1–1.5 mm. long; spur subulate, 27–28 mm. long, 4.2 mm. wide at base, slightly falcate decurved; upper petals flavescent, glabrous, emarginate; lower petals blue, the limb broad-elliptic, bilobulate, long-ciliate, yellow bearded below the middle, about as long as its exappendiculate claw; stamens glabrous; carpels 3, densely pilose.

TYPE: Szechwan, Muli, Aug. 19, 1937, *T. T. Yü 14008* (PE), not seen; photograph (E), seen.

I have had no material for study. *Delphinium dolichocentroides* was said by the author to differ from *D. dolichocentrum* in its simple hirsute stems, few-flowered racemes, emarginate upper petals; to have the habit of *D. yuanum*, but with the spurs longer than the sepals and decurved; to be near *D. taliense*, but with leaves 3-parted to the base and the parts more deeply divided.

95. **Delphinium grandiflorum** L. Sp. Pl. **1**: 531. 1753. FIG. 9, E.

Delphinium grandiflorum var. *linnaei* Brühl & King, Ann. Bot. Gard. Calc. **5**: 98. 1896.

Delphinium chinense Fisch. Cat. Hort. Gorenk. 1808; Lodd. Bot. Cab. **1**: *pl. 71.* 1817.

Delphinium grandiflorum var. *chinense* Fisch. ex DC. Prodr. **1**: 53. 1824.

Delphinium grandiflorum vars. *bhotanica, paradoxa, setchwanensis* and *tsangensis* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 98, 99. 1896. I have been unable to borrow authentic material.

Delphinium sinense Fisch. ex Link, Enum. Hort. Berol. **2**: 80. 1822.

Delphinium pubiflorum Turcz. Fl. Baic.-Dahur. 73. 1842, *nomen.*

Delphinium grandiflorum var. *pubiflorum* Turcz. *loc. cit.* I have had on loan the following material from Leningrad: "In arenosis ad Baicalem prope Turxam, 1829, Turcz." as "pubiflorum mihi" 2 sheets; and "In arenosis ad ripam Baicalis, prope Turxam, 1823, Turcz. mihi." I take these to be authentic material.

Delphinium grandiflorum var. *acaule* Turcz. ex Huth, Bot. Jahrb. **20:** 461. 1895. A sheet "Ad acidulas Pogromezenses 1829, Turcz." as var. *acaule* (LE) seen. The stems were 1–5 dm. tall, very fine-leaved.

Delphinium grandiflorum var. *gmelinii* Rchb. Ill. Aconit. atque Delph. *pl. 12.* 1823–27. A sheet from (LE) seen, from N. T. Siberia.

Delphinium grandiflorum L. var. *pallidum* Huth, Bot. Jahrb. **20:** 461. 1895, described as having white flowers; may belong here.

Delphinium grandiflorum var. *pumilum* Huth, *loc. cit.* as being about 2 dm. high; may belong here.

Delphinium grandiflorum var. *tigridium* Kitagawa, Rep. 1st Sci. Exp. Manch., Sect. 4, **IV:** 17, 83. *pl. 2.* 1936. Reduced to synonymy by W. T. Wang, Acta Bot. Sinica **10:** 271. 1962.

Delphinium grandiflorum var. *majus* W. T. Wang, *loc. cit.* 273. Said to have unusually large leaves. Based on *Feng 9286* from Yunnan, which I have not seen.

Delphinium grandiflorum var. *leiocarpum* W. T. Wang, *loc. cit.* 274. Based on *K. C. Fu 7900* (which I have not seen), with glabrous carpels.

Delphinium grandiflorum var. *glandulosum* W. T. Wang, *loc. cit.* 272. 1962. The type by *S. T. Wang*, May 2, 1928, from Shensi is not available.

Delphinium virgatum Jacq. ex Sprengel, Syst. **2:** 617. 1825; not *D. virgatum* Poir. Encycl. Suppl. **2:** 458. 1811.

Delphinium fangshanense W. T. Wang, Acta Bot. Sinica **10:** 269, 270. 1962. Based on *T. N. Liou 8258* which has not been available to me.

Stem or stems mostly slender, 2–8 dm. tall (although some forms are semiprostrate), simple or branched above, mostly closely strigulose, more densely so in the inflorescence, leafy, the cauline leaves not crowded, gradually reduced upward; petioles scarcely dilated at the base, slender, the lower to 1.5 dm. long, the uppermost nearly or quite lacking; leaf blades palmately multipartite, 3–10 cm. wide, the segments divided into parts that are in turn laciniate into linear lobes mostly 1–2 mm. wide and up to 2 cm. or more long; inflorescence simple or few branched, the flowers from 1–2 on a branch to several in rather a dense raceme; lower bracts laciniate, 1–3 cm. long, the upper entire, linear, to 1 cm. long; pedicels erect or ascending, strigulose, 2–4 cm. long; bracteoles linear, opposite; sepals mostly deep blue, sometimes albino, strigulose to spreading-hairy, the upper ovate, 12–17 mm. by 6–8 mm., obtuse, the spur straight, horizontal, ca. 18 mm. long, 3 mm. wide at the base, gradually tapered; upper petals pale with slight bluish tinge, the limb almost straight, 8–10 mm. long, subentire or emarginate at the rounded apex, glabrous, the spur 16–18 mm. long; lower petals violet blue, the blade yellow bearded at the center, ciliate or not on margins, almost round in shape, 8–10 mm. in diameter, entire, erose or emarginate, the claw 4–4.5 mm. long; stamens 5–6 mm. long, glabrous or nearly so; anthers dark, 1 mm. long; follicles 3, straight or recurved, hairy or puberulent for most part, 10–16 mm. long, 3.5–4 mm. wide; styles an additional 2.5 mm.; seeds 1 mm. long, with a loose membranous envelope folded into wings.

TYPE: "Habitat in Sibiria"; photograph seen of specimen (LINN).

RANGE. Central to western Siberia, Inner and Outer Mongolia, northern China (mostly Hopei, Shansi, Kansu).

ILLUSTRATIONS. GMELIN, Fl. Sibirica **4:** *pl. 78.* 1769; Bot. Mag. *pl. 1686.* 1815.

EXAMPLES SEEN. **Siberia:** *Sokolow 97*; *Maximowicz* in 1859; *Stukow 1358*; *Tugarinowa*, July 13, 1908; *Ehnberg*, July 19, 1900; *Digby*, 1914; *Nikiforow*, July 10, 1917; *Herb. Ledebour 809*; *Herb. Pallas*, Aug. 1877. **Mongolia:** *Karo 207*; *Prescott* in 1830; *Ohwi 10662*; *Hsia 3159*; *Kozlov 240*; *Ikonnikov-Galitzky 210*; *314a*; *Litvinov 490, 989*; *Dorsett & Dorsett 3367*. **Tibet:** *Ludlow & Sherriff 9814, 9073, 11114*; *Rock 13361*. **Shansi:** *Licent 1305*; *K. Ling 9143*; *Han Ngan 92*; *H. Smith 6526, 8150, 7139*. **Hopei:** *Dorsett & Morse 7051*; *Liou 1405*; *Read 746*; *Liu 1433, 1968*; *Breitschneider 1817*; *H. Smith 173, 468, 1163*; *T. F. King 12689*; *C. F. Li 10707*; *F. N. Meyer 1057*.

There is great variation in flower size and color, and pubescence, as well as in foliage, the ultimate laciniae of the leaves tending to be wider in Chinese plants than in Siberian and Mongolian. However, a careful study of the matter did not make recognition of the var. *chinense* seem worth while. The species has been widely cultivated and I have seen in herbaria specimens that I would consider *D. grandiflorum* bearing the labels *tatsienense*, *sinense album*, *chinense*, *chinense azureum*, *grandiflorum*, *sibiricum*, *grandiflorum* 'Blue Mirror,' 'Blue Butterfly' and 'Farquahar's Victory.'

96. **Delphinium henryi** Franchet, Bull. Soc. Philom. Paris VIII. **5:** 177. 1893. FIG. 9, F.

Delphinium henryi f. *concolor* W. T. Wang. Acta Sinica Bot. **10:** 79. 1962.

Perennial from a very slender rhizome; stem 1–3.5 dm. high, retrorse-strigulose and with long hairs near the nodes, leafy throughout, the leaves only gradually reduced up the stem; petioles somewhat dilated at their base, more or less pubescent, the lower to 10 cm. long, the upper almost lacking; laminae broader than long, somewhat pentagonal in outline, more or less pubescent with rather long appressed hairs, 2–5 cm. broad, 3- to 5-parted almost to base, the segments cuneate at base, deeply cut into few lance-linear lobes 2–3 mm. wide and acute; flowers solitary to few in a subumbellate cluster; bracts largely foliaceous, divided; pedicels retrorse-pubescent, 2–3 cm. long; bracteoles narrow-elliptic, 5–10 mm. long, close to the flower; sepals blue, pubescent; upper sepal 16–20 mm. long, 10–12 mm. wide, ovate, pointed, the spur 25 or more mm. long; lateral sepals oblong-ovate, obtuse, 15–20 mm. long, 8–9 mm. wide, pubescent along the middle; lower sepals 20–22 mm. long, 8–10 mm. wide, acutish-corniculate; petals brownish, with dark dots, the upper petals with a lamina 10 mm. long, very slightly oblique, bidentate, the spur ca. 25 mm. long; lower petals with claw 5 mm. long, lamina oblong-obovate, 11 mm. by 6.5 mm., cleft 4 mm., bearded somewhat at base and ciliate; stamens ca. 7 mm.

long. ciliate; anthers dark, oblong, 1.2 mm. long; follicles 3, silky, suberect, divergent at tips.

TYPE: Central China, Hupeh, *Dr. Henry 6952* (P); seen. Isotypes (BM, E, GH, K, NY), seen. The collection number was published as *6932*, but the sheets cited above are all *6952*.

OTHER COLLECTIONS. **Szechwan:** *Henry 6952A*; *K. H. Yang 65383*. **Chensi:** *Licent 2760*; *Giraldi* in 1897. Two sheets from Szechwan labeled *sutchuense* fide Wang, do not fit the description. These are nearer to *D. henryi* but with a more open habit: *Chu 3807* (E) and *3127* (E).

97. **Delphinium incisum** Wall. Cat. 4717. 1828, *nomen*. FIG. 9, G.

Delphinium ranunculifolium Wall. var. *incisum* Hook. f. & Thoms. Fl. Indica **1:** 51. 1855.

Delphinium elatum L. var. *incisum* Hook. f. & Thoms. Fl. Brit. India **1:** 26. 1872.

Delphinium englerianum Huth var. *incisum* Huth, Bot. Jahrb. **20:** 418. 1895.

To about 1 m. tall, the stem loosely retrorse-pilose, slender, more or less angled, remotely leafy, becoming more retrorse-strigose above, not glandular; cauline leaves pentagonal, the lamina 5–10 cm. wide, somewhat strigose on both surfaces and paler beneath, 5-fid to near the base, the segments somewhat rhombic, 3-lobed to below the middle, then incised into rather few lance-oblong lobules to ca. 1 cm. long and 1.5–3 mm. wide, mucronate; petioles not strongly vaginate, to ca. 1 dm. long, the uppermost leaves almost sessile; inflorescence racemose or few branched, each branch rather few flowered, fairly compact; bracts leafy and dissected or the upper entire, linear-oblong, to ca. 8 mm. long; pedicels erect-ascending, strigose, mostly 1–2 cm. long; bracteoles linear-oblong, strigose, 4–6 mm. long; sepals bluish, strigose, the upper sepal ovate, 14–15 mm. long, 11–12 mm. wide, rounded at apex, the spur spreading decurved, ca. 17 mm. long, 2.5–3 mm. wide at base, blunt; lateral sepals rounded-obovate, 13 mm. long, 12 mm. wide; lower sepals 13 mm. by 7 mm., subacute; petals black, the upper laminae slightly oblique, 9 mm. by 2 mm., entire, glabrous, the spurs 16 mm. long; lower petals with oblong laminae, 6 mm. by 3 mm., with 2 short unequal oblong ciliate lobes and some bearding from the base out, the claw 6 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1 mm. long, oblong; carpels 3, densely pubescent.

TYPE: Kamaon (Kumaun), *Dr. Wallich*, List No. *4717*, isotypes (BM, E, K, NY, P); seen.

COLLECTIONS SEEN. **Nepal:** *Nilo Bi Rh no. 21* (E); *Lall Dhwoj 49* (E), *267* (E).

Near *D. himalayae*, but inflorescence more branched; flowers smaller; upper petals glabrous and entire.

98. **Delphinium kamaonense** Huth, Bull. Herb. Boiss. **1**: 333. 1893. Spelled *camaonense* in Huth, Bot. Jahrb. **20**: 460. 1895. Fig. 9, I, J.

Delphinium grandiflorum L. var. *kumaonense* E. Huth ex Brühl & King, Ann. Bot. Gard. Calc. **5**: 98. 1896.

Perennial from a thick subvertical root; stem branched, 1–5 dm. tall, subglabrous or with some spreading hairs; petioles dilated at the base, the lower 3–8 cm. long; lower leaves pubescent especially beneath, strigulose above, the blades 2–4 cm. across, 5-parted, then 5-fid, the segments cuneate or narrower, laciniate into oblong lobes 2–3 mm. wide, or shallowly lobed with broader divisions; upper leaves with linear lobes 1–2 cm. long, 1–1.5 mm. wide; inflorescence open, divaricately branched; lower bracts tripartite with linear lobes; upper bracts entire, linear, to 1 cm. long; pedicels much longer than flowers, bibracteolate above the middle; bracteoles linear, 3–5 mm. long; flowers deep blue; sepals slightly pilose, to 20 mm. long, with a dark brown subapical spot; upper sepal round-ovate, obtuse, 17 mm. by 12 mm., the spur straight or slightly curved, 12–15 mm. long, 3.5 mm. wide at the base; lateral sepals elliptic-oblong, rounded at apex, 13–14 mm. long, 8–9 mm. wide, lower sepals 14 mm. by 7 mm., oblong-ovate; upper petals dilute brown, the laminae somewhat oblique, 8 mm. long, 3 mm. wide, entire, glabrous, the spurs 14 mm. long; lower petals blue, bifid, yellow bearded, obovate rounded, 7 mm. long, 8 mm. wide, the claw 5 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, 1 mm. long; follicles densely pilose.

Type: N. W. India, Kamaon (Kumaun), Nipshany Valley in Darma, 4300–4600 m., *Duthie* in 1884 (probably g), not seen; isotypes (e, k), seen; they are numbered *2675*, Aug. 31, 1884.

Range. Growing at perhaps 3000 to 4500 m., Kumaun, Nepal.

Representative collections. **Kumaun:** *Duthie 5299*; *Ludlow 781, 775*. **Nepal:** *F. M. Bailey* in 1936; *Arnold 12*; *Stainton, Sykes & Williams 1871, 7216, 2026, 2233, 2200, 7351, 1930, 8035, 7742, 8142*; *Tyson 95*; *Polunin 1576*; *Lowndes 1324, 1229*.

99. **Delphinium kantzeense** W. T. Wang, Acta Bot. Sinica **10**: 161. 1962.

Stem ca. 1 m. tall, 5 mm. thick near base, loosely spreading-hirtellous, branched, equally foliate; median leaves with broadly pentagonal blade, ca. 5.5 cm. long, 7.5 cm. wide, cordate at base, 3-parted to 3–4 mm. above the base, the primary middle parts broadly rhombic, narrow-cuneate at base, 3-parted to below the middle, secondary middle parts narrow-rhombic, trifid to middle into deltoid or lanceolate lobes 2.5–3.5 mm. wide, the secondary laterals lance-ovate, one-lobulate or entire, the primary lateral parts broadly obliquely obovate, 2-parted to 8–9 mm. above the base, upper secondary parts obliquely rhombic, 3-fid, the lower secondary smaller, unequally bifid, loosely strigulose beneath, loosely hirtellous on veins above; petioles slightly longer than blades, not vaginate; racemes terminal, the central ca. 14-flowered, lateral 3–5-flowered, lax; lower bracts trifid, others linear, 5–12 mm. long; pedicels 2–5 cm. long, retrorse-strigulose and yellow-glandular-puberulent, divergent, bracteolate above; bracteoles to 2–3 mm. from base of flowers, linear, 4–9 mm. long, 0.3 mm. wide; sepals ashy-blue, oblong-ovate or narrow-elliptic, 10–11 mm. long, puberulent; spur 16–18 mm. long, subulate, 2–2.5 mm. wide at base, decurved to a right angle; upper petals ashy-blue, glabrous, entire; lower petals ashy-blue, the laminae ovate or elliptic-ovate, rounded at apex, entire to emarginate, ciliate, yellow bearded at base, claw slightly longer, appendiculate; stamens glabrous; carpels 3, glabrous.

TYPE: Kantze, July 8, 1951, *Y. W. Tsui 4303* (presumably PE); not seen.

I have seen no material definitely referable here. The species was described as near *D. yunnanense*, but the pedicels spreading puberulent; spur strongly decurved; carpels glabrous.

100. **Delphinium koelzii** Munz, sp. nov. FIG. 9, H.

Stem slender, 1.5–3 mm. thick, 8–10 dm. tall, strigulose, simple or with a few short branches above; lower leaves mostly withered by anthesis, the blades commonly 2–8 cm. long, less broad, multisect into divisions that are pinnately and divaricately laciniate into lobes 1–2 mm. wide, subglabrous above, somewhat strigulose beneath, but not strongly bicolored, the petioles to 5 cm. long, with dilated base; middle cauline leaves several, short-petioled to subsessile; racemes lax, the terminal to 8-flowered, the lateral with fewer flowers; axis, pedicels, etc., densely and finely strigulose; bracts linear, subsetaceous, to 5 mm. long; pedicels divergent with more or less recurved tip, mostly 1–2 cm. long; bracteoles 2–3 mm. long, below the middle of the pedicel; sepals wine-colored to blue, somewhat strigulose, the upper sepal ovate, 10 mm. by 5 mm., obtuse, the spur 13 mm. by 3 mm., straight, rather blunt; lateral sepals 10 mm. by 6 mm., rounded-oblong; lower sepals rounded, 10–11 mm. by 6 mm.; upper petals pale, oblique, the laminae 8–9 mm. long, shallowly toothed at apex, the spur ca. 13 mm. long; lower petals with laminae 5 mm. long, bearded, subovate, divided for ca. 3 mm., the claw 5 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, 0.8 mm. long; follicles 3, densely strigulose.

Caulis tenuis, 8–10 dm. altus, strigulosus; folia infima marcescentia, laminis 2–8 cm. longis, multifidis, cum laciniis ultimis 1–2 mm. latis; inflorescentia subcorymbosa, racemis laxis; bracteae lineares, 3–5 mm. longae; pedicelli divergentes, 1–2 cm. longi; bracteolae 3–5 mm. longae; sepala vinacea aut azurea, strigulosa, 10–13 mm. longa, calcare 13 mm. longo; laminae petalorum superiorum obliquae, 9 mm. longae, bidentatae; laminae petalorum inferiorum 5 mm. longae, lobatae; stamina glabra; carpella 3, dense strigulosa.

TYPE: Punjab, at Kulu, Kangra, at 1600 m., June, 1933, *W. Koelz 4922* (GH); isotypes (F, MICH, NY, US) seen.

OTHER **Punjab** COLLECTIONS are Kulu, Kangra, *Koelz 4921* (MICH, US) and *4757* (MICH).

The species seems near *D. roylei*, but has a more corymbose inflorescence and smaller flowers.

101. **Delphinium lanigerum** Boiss. & Hohen. in Boiss. Diagn. **8**: 10. 1849. FIG. 9, K.

Perennial from a thickened root, the stem 1–2 m. tall, terete, glabrous, sparsely branched above; lower leaves to 2 dm. across, palmately parted almost to base, the parts divided into broadly lanceolate, acute, elongate lobes 8–10 mm. wide, the petioles to ca. 2 dm. long, dilate-vaginate; upper cauline leaves remote, divided into much narrower lobes; racemes short, lax, few flowered, glabrous; bracts linear, 5–10 mm. long; pedicels slender, spreading, 2–3.5 cm. long; bracteoles near the middle of the pedicels, setaceous, 4–5 mm. long; flowers intense blue; sepals glabrous except for the ciliate apex; upper sepal 12–15 mm. long, 5 mm. wide, ovate, acute, the spur 15–18 mm. long, 4 mm. wide at base, horizontal, almost straight, gradually narrowed to the tip; lateral sepals 12 mm. by 4 mm., oblong, somewhat rounded at apex; lower sepals 13 mm. by 5 mm., elliptic-ovate, acute; upper petals obliquely truncate, the blade ca. 11 mm. long, divided at apex for ca. 1.5 mm., glabrous, the spur 22 mm. long; lower petals 12 mm. long, the claw 6 mm., the blade 6–7 mm. long, divided ca. 4 mm., heavily bearded; stamens 6–7 mm. long, glabrous; anthers dark, almost 1 mm. long; follicles 3, pubescent.

TYPE: Mt. Elbrus, northern Iran, *Kotschy 430*, July 1, 1843; isotypes (BM, MO, P), seen.

Said to be frequent in Dudera valley, Mt. Elbrus. A collection from a wet meadow, Dorud, Luristan, Iran, June 9, 1941, *Koelz 18164* belongs here.

102. **Delphinium malacophyllum** Hand.-Mazz. Acta Horti Gothob. **13**: 52. *fig. 2b.* 1939. FIG. 9, L.

Stem 1–4 dm. tall, simple or corymbosely branched, the entire plant covered with soft hyaline spreading hairs or strigulose, with longer hairs at the nodes, equally and scattered leafy, 1–7-flowered; leaves pentagonal, 3–6 cm. in diameter, trifid to the base, the outer segments often unequally 2–3-parted, all segments trilobed to the middle or less, the ultimate divisions lanceolate, entire, 1–3 mm. wide, acutish, the middle elongate, strigose above, scattered white-hairy beneath; petioles slender, the lower to 10 cm. long, the main cauline evaginate, ca. as long as the blades, the uppermost almost lacking; lower bracts foliose, trifid, ca. 1 cm. long, the upper linear, entire; pedicels 2.5–7 cm. long, ascending; bracteoles small, filiform, in the upper third or fifth of the pedicel; flowers nodding, dark violet; sepals puberulent to hairy; the upper sepal round-ovate, 13–20 mm. long, 10–12 mm. wide, apiculate, the spur slender, straight, 25–35 mm. long, 3 mm. wide at the base; lateral sepals elliptic, 16–20 mm. long, 10–12 mm. wide, rounded at apex, strigulose on midrib and margin; lower sepals ca. the same, more apiculate; upper petals with a broadly linear lamina 9–10 mm. long, glabrous, emarginate; lower petals dark, the narrow claw 6 mm. long, the deflexed lamina 7 mm. long, bifid to the middle or more, the disc yellow bearded; stamens 5–6 mm. long, glabrous or ciliate; follicles densely white-silky.

TYPE: Szechwan, *Harry Smith 3385* from Hsioeh-shan, 4300 m., Aug. 11, 1922 (W), not seen; isotypes (BM, E), seen.

Differs from *D. pylzowii* in softer pubescence and darker petals.

103. **Delphinium maximowiczii** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 164. 1893. FIG. 10, A.

Delphinium grandiflorum L. var. *latisecta* Maxim. Plant. Chin. Potanin. in Acta Horti Petrop. **11**: 30. 1890.

Stem subglabrous below to minutely strigulose, more densely so above, slender, much branched, 3–8 dm. tall, scattered leafy; leaves tripartite to near the base, the segments again parted, so that the leaf outline is pentagonal, commonly 2–8 cm. in diameter, the 5 parts deeply incised into lance-oblong sharply pointed teeth or lobes 2–3.5 mm. wide, green and somewhat strigulose above, paler and strigulose beneath especially along the veins; petioles slender, somewhat strigose, somewhat dilated at the base, the lower to 20 cm. long, the upper 1–3 cm.; flowers few, in a corymbose cluster at end of each branch, sky-blue; bracts mostly 3-parted; pedicels slender, divaricate, 2–4 cm. long, strigulose, the bracteoles lance-linear, 3–6 mm. long, near the middle of the pedicel; sepals strigulose, somewhat lighter in color along the middle line; upper sepal ovate, 12–15 mm. long, obtuse, the spur 16–25 mm. long, 2.5–3 mm. wide at base, narrowed gradually to a pointed apex; lateral sepals oblong, 17–19 mm., by 6–7 mm., rounded at apex, the pubescence along the midvein; lower sepals more rhombic, 15–18 mm. long, 7–8 mm. wide, obtuse; upper petals yellowish with blue tinge, slightly oblique, the lamina 9 mm. long, glabrous, somewhat rounded at the apex; lower petals with an oblong-obovate blade 7 mm. by 5 mm., yellow bearded in a patch near the base, entire to lobed, the claw 6 mm. long; stamens 5–6 mm. long, glabrous; anthers 1 mm. long; follicles 3, puberulent, recurved-divergent; seeds squamate.

TYPE: E. Kansu, Fyn-Shan-Ling Mts., *Potanin* in 1885 (some labels, such as on the sheet at Paris have 1881), (P), seen; isotype (K), seen.

RANGE. Apparently at about 2500 to 3500 m., western China and adjacent Tibet.

SEEN. **Tibet:** Tsarung, *Rock 23243*. **Szechwan:** *Rock 18327*. **Yunnan:** *Rock 24272*; *Yü 10504*.

There is considerable variation in the lamina of the lower petal in the above cited specimens, although it has the same general shape throughout. *Yü 10504* has the lamina entire, with some hair outside the basal patch.

Rock 18327 and *24272* have entire lamina without outside hair. *Rock 23243* and *Potanin* have the lamina partly cleft and with short ciliation as well as the basal patch.

104. **Delphinium mollipilum** W. T. Wang, Acta Bot. Sinica **10**: 268. 1962.

Stem about 3.5 dm. high, 1–2 mm. thick below, loosely spreading-pubescent, simple, equally foliose; middle cauline leaves with pentagonal lamina, 3.3 cm. long, 6 cm. wide, cordate, trisect, the middle segment broadly rhombic, trifid to below the middle, the middle lobes linear, entire, 3.5 mm. wide, the lateral at an obtuse angle, linear, 1–2-lobulate, the lobules obliquely ovate, subglabrous below, loosely pilose above; petioles equaling the laminae, subterete, indistinctly vaginate, spreading-pilose; upper leaves gradually reduced; inflorescence about 2-flowered; lower bracts trifid into linear lobes, the upper entire, linear; pedicels 3–3.6 cm. long, divergent-erect, with spreading white hairs; bracteoles near the middle of the pedicels, 4.5–6 mm. long, loosely puberulent; sepals purplish blue, oblong to oblong-obovate, 16–17 mm. long, white-puberulent; spur ca. 25 mm. long, slender-subulate, ca. 2 mm. thick at base, straight; upper petals glabrous, yellowish, emarginate; lower petals blue, the limb round-ovate, emarginate, yellowish bearded at base, longer than the appendiculate claw; stamens glabrous; carpels 3, loosely puberulent.

TYPE: Kansu, Sept. 24, 1956, Exped. Hunangho *8928* (PE), not seen; photo. (E), seen.

A specimen from Kansu at ca. 3000 m., Aug., 1914, *Farrer & Purdom 225* (E), in part, seems to belong here. The species is supposed to be close to *D. caeruleum*, but with pedicels spreading pubescent and carpels 3. My interpretation of *D. caeruleum* might almost include this, but that species is restricted to an area farther west.

105. **Delphinium monanthum** Hand.-Mazz. Acta Horti Gothob. **13**: 50. 1939. FIG. 10, B.

Delphinium candelabrum (Ostenfeld in Hedin) var. *monanthum* (Hand.-Mazz.) W. T. Wang, Acta Bot. Sinica **10**: 78. 1962.

The stem low, to ca. 1.5 dm. tall, subglabrous, with several leaves, purplish, flexuous; leaves pentagonal, the blades mostly 1–3.5 cm. in diameter, with fine pubescence, deeply cordate, trisect to the base, the 2 lateral segments deeply divided to make 5 more or less cuneate segments, each of these deeply 3- or more-lobed, the final divisions 1–5 mm. long, 2–4 mm. wide, rounded-oblong, mucronate; petioles 1–5 cm. long, purplish, slightly dilated at base; flowers solitary, large, deep purplish blue; pedicels erect to horizontal, 5–15 cm. long, retrorse-pubescent, the hairs longer toward the summit; bracteoles usually 2, like reduced leaves, 5–15 mm. long, often near the middle of the pedicel; sepals with rather long fine hairs, the upper 20–25 mm. long, 12–15 mm. wide, broadly ovate, minutely

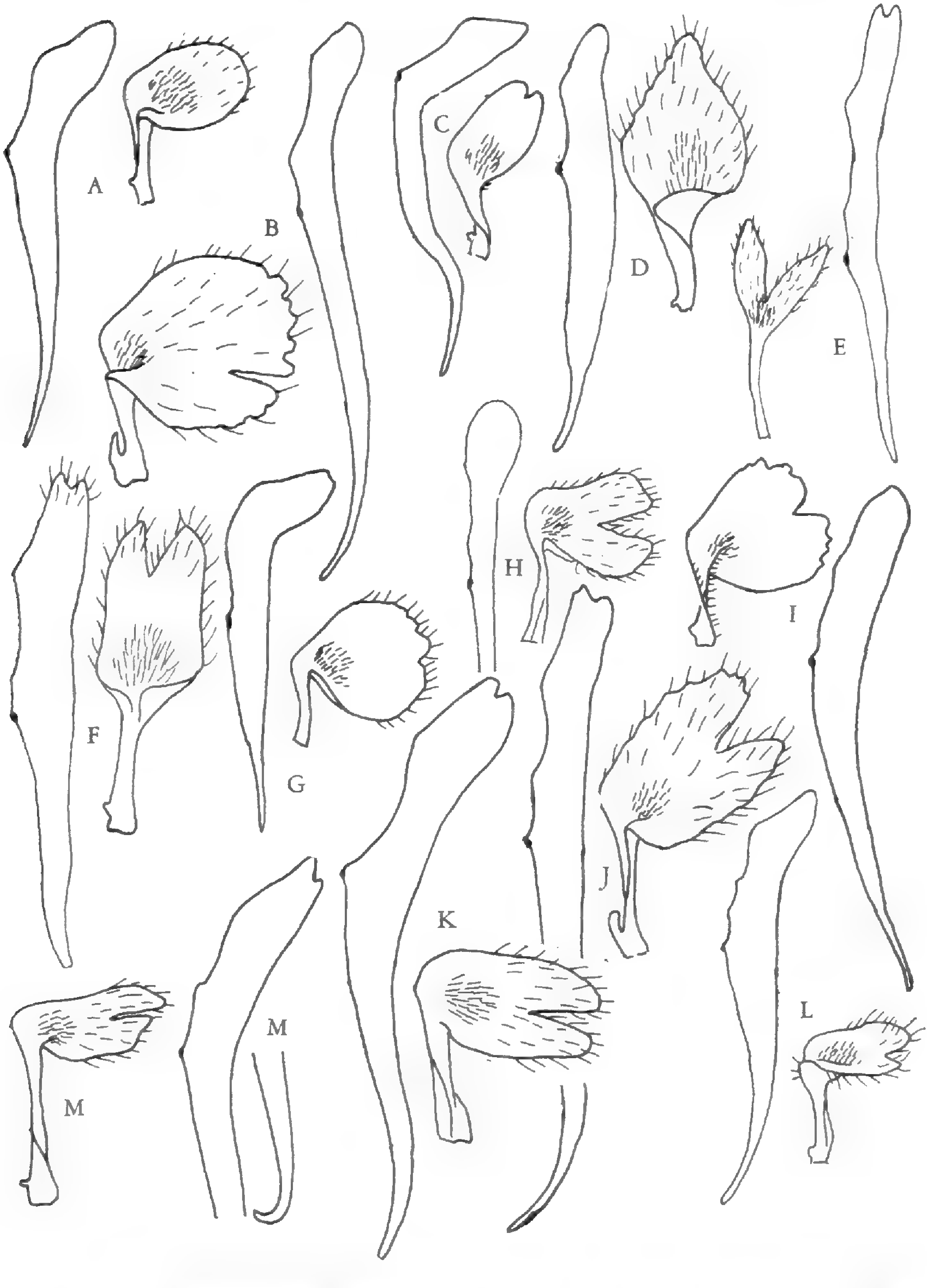

FIGURE 10. **Delphinium,** GROUP VI. Petals, the upper spurred, the lower clawed. A. *D. maximowiczii*; blade of upper petal 9 mm. long, spur 20 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Rock 24272* (UC). B. *D. monanthum*; blade of upper petal 12 mm. long, spur 24 mm.; blade of lower petal 11 mm. long, claw 6 mm.; drawn from *Rock 13185* (GH). C. *D. mosoynense*; blade of upper petal 8 mm. long, spur 18 mm.; blade of lower petal 6 mm. long, claw 4.5 mm.; drawn from *Delavay 8* (NY). D. *D. muscosum*; blade of upper petal 8 mm. long, spur 16 mm.; blade of lower petal 11 mm. long, claw 6 mm.; drawn from the published illustration of the TYPE. E. *D. nortonii*; blade of upper petal 15 mm. long, spur 12 mm.; blade of lower petal 7 mm. long,

apiculate, the spur 25–30 mm. long, ca. 4 mm. thick at base, subcylindric; lateral and lower sepals 25 mm. by 15 mm., somewhat erose on the more or less rounded tips; upper petals blue, slightly oblique, the blade entire, 12 mm. long, the spur 24 mm. long; lower petals blue, the lamina almost round, somewhat bearded and crenulate, 11 mm. by 10 mm., slightly bilobed, claw 6 mm. long; stamens 7–8 mm. long, more or less ciliate; anthers dark, 1.5 mm. long; follicles 3, pubescent to glabrous.

TYPE: Szechwan, Dongrergo, 4800 m., Aug. 9, 1922, *Harry Smith 3131*; isotypes (A, MO), seen.

Other material apparently referable here is from **Szechwan:** *E. H. Wilson 4691* (GH, US). **N. W. Yunnan:** *G. Forrest 20780* (US). **S. W. Kansu:** *Rock 13024* (GH, K, NY, US), *13185* (F, GH, K, NY, US); *Farrer & Purdom 253* (E).

106. **Delphinium mosoynense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 168. 1893. FIG. 10, C.

Delphinium grandiflorum L. var. *mosoynense* (Franchet) Huth, Bot. Jahrb. **20**: 461. 1895.

Delphinium caeruleum var. *majus* Wang, Acta Bot. Sinica **10**: 266. 1962. Wang refers *Rock 13730*, which I had placed in *D. mosoynense*, to this species.

Stem slender, flexuous, branched above, retrorse-strigulose below, usually densely so above, 1–5 dm. tall; lower leaves with long (5–15 cm.) petioles not dilated at base; upper petioles shorter; leaf blades subglabrous to strigulose, divided to base into 5 parts, each of these further incised into divaricate lance-linear lobes mostly 5–20 mm. long, 1–2.5 mm. wide, sharp pointed, more or less inrolled at margins and pale beneath; cauline leaves 1–3, remote; flowers mostly in an open panicle, deep blue, the bracts linear, 5–20 mm. long, or the lowest trifid; pedicels divaricate-ascending, 2–5 cm. long; bracteoles near the middle of the pedicel, linear, 5–8 mm. long; sepals strigulose, the upper 15–18 mm. long, ovate, the spur straight, subulate, ca. 20 mm. long, 3 mm. wide at the base; lateral sepals 12–15 mm. long, 8 mm. wide, obtuse; lower sepals like the lateral; upper petals pale,

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claw 6 mm.; drawn from *Norton 369* (K). F. *D. przewalskii*; blade of upper petal 14 mm. long, spur 15 mm.; blade of lower petal 10 mm. long, claw 8 mm.; drawn from *Przewalski* in 1873 (K). G. *D. pseudograndiflorum*; blade of upper petal 8 mm. long, spur 17 mm.; blade of lower petal 8 mm. long, claw 5.5 mm.; drawn from *Hanbury-Tracy 195* (BM). H. *D. pulcherrimum*; blade of upper petal 13 mm. long, spur 18 mm.; blade of lower petal 8 mm. long, claw 6 mm.; drawn from *Ludlow & Sherriff 1997* (BM). I. *D. pumilum*; blade of upper petal 11 mm. long, spur 26 mm.; blade of lower petal 8 mm. long, claw 5 mm.; drawn from *Rock 18316* (K). J. *D. pylzowii*; blade of upper petal 15 mm., spur 27 mm. long; blade of lower petal 10 mm. long, claw 8 mm.; drawn from *Harry Smith 3135* (A). K. *D. pylzowii*; blade of upper petal 13 mm. long, spur 23 mm.; blade of lower petal 9 mm. long, claw 6 mm.; drawn from *Rock 14482* (NY). L. *D. rockii*; blade of upper petal 11.5 mm. long, spur 15 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Rock 14543* (GH). M. *D. smithianum*; blade of upper petal 13 mm. long, spur 20 mm.; blade of lower petal 8 mm. long, claw 7 mm.; drawn from *Harry Smith 11274* (MO).

somewhat oblique, entire at apex, the limb 8 mm., the spur 18 mm. long; lower petals blue, ca. 6.5 mm. by 5 mm., yellow bearded in center of base of oblong limb, not ciliate; claw 4.5 mm. long; stamens glabrous, 5 mm. long; anthers dark, 1 mm. long; follicles 3, finely pubescent.

TYPE: Yunnan, on Pee-cha-ko, near Moo-so-yn, north of Tali, *Abbé Delavay 717*, Aug. 31, 1884 (P); seen. Photograph (UC).

DISTRIBUTION. Apparently ranging between 2500 and 4500 m., Yunnan, Szechwan, southwestern Kansu.

EXAMPLES. **Yunnan:** *Rock 17338*; *Forrest 6533, 6643, 15233*; *K. M. Feng 2514*; *Maire 7437*; *Delavey 8*; *Ducloux 3875*. **Szechwan:** *Soulié 2389, 2387*; *Handel-Mazzetti 5103*. **Tibet:** *Kingdon Ward 10621.*

107. **Delphinium muscosum** Exell & Hillcoat, Jour. Roy. Hort. Soc. Lond. **78**: 183. 1953. FIG. 10, D.

Perennial from a slender rootstock arising from a thickened elongate root; stems 10–15 cm. tall, many branched from base, hirsute-pilose throughout; basal leaves with petioles to 7 cm. long, flattened at base, pubescent-pilose; blade suborbicular in outline, 2–3 cm. in diameter, trifid to base, the segments divided 3–4 times into ultimate linear pubescent-pilose lobes scarcely 1 mm. wide; cauline leaves short-petioled to subsessile; inflorescence subcorymbose, cymosely branched; flowers solitary at tips of branches, dark blue to dark violet, 3–3.5 cm. long; sepals yellow-hirsute-pilose without, almost glabrous within, the upper elliptic-ovate, 25 mm. by 15–18 mm., the spur 14 mm. by 4.5–6 mm., slightly decurved; lateral sepals elliptic, spatulate, 22 mm. by 11–13 mm.; lower sepals ovate or oblong-ovate, slightly obtusely acuminate, 23 mm. by 14–16 mm., glabrous within; 2 upper petals narrowly elliptic, almost straight, 26 mm. by 4 mm., pubescent within, almost glabrous without, the lamina 8 mm. long, rounded and entire at apex; 2 lower petals with the lamina irregularly ovate, entire, 10–12 mm. by 6–8 mm., yellowish- or whitish-bearded toward claw, the latter 6–7 mm. long; stamens bluish, 7–8 mm. long, glabrous; anthers dark, 1.2 mm. long; follicles 3, tomentellous.

TYPE: Bhutan, Rinchen Chu, at 5000 m., Aug. 7, 1937, *Ludlow & Sherriff 3537* (BM); isotype (E); seen.

RANGE. Growing on open stony wet scree, 4500 to 5500 m., Bhutan.

EXAMPLES SEEN. *Ludlow, Sherriff & Hicks 19725* (BM), *19328* (BM), *19375* (BM), *19399* (BM), *16825* (BM), *17102* (BM); *Cooper 4791* (BM).

A species with leaves as finely dissected as any I have seen.

108. **Delphinium nortonii** Dunn, Kew Bull. **1927**: 247. 1927. FIG. 10, E.

Perennial, 7–10 cm. tall, with dense short spreading pubescence especially above; stems several, 1-flowered; leaves long petioled (2–4 cm.), short-vaginate, the blades orbicular; radical leaves 2–3 cm. in diameter, palmately 3-parted, the segments broadly cuneate, short-petiolulate, imbricate, palmately incised into obtuse lobes 3–5 mm. long, 2–3 mm. wide; cauline leaves few, similar, smaller; flowers large, violet, inflated-globose, long-pubescent; upper sepal 25 mm. long, 18 mm. wide, broadly ovate, obtuse, the spur 10–15 mm. long, 5–7 mm. wide at the base, subcylindric, obtuse; lateral sepals asymmetrically elliptic-ovate, 18 mm. by 15 mm., rounded-truncate; lower sepals slightly longer, more acute; bracts foliaceous, 1 cm. long; pedicels 4–5 cm. long; bracteoles 2, near middle of the pedicel, tripartite to oblong, to ca. 10 mm. long; upper petals almost straight, the lamina 15 mm. long, 3 mm. wide, somewhat emarginate at the blunt apex, spur 10–14 mm. long; lower petals unequally bifid, yellow bearded, the lamina 7–8 mm. long, 5–6 mm. wide, the bearded lobes 5 mm. by 2 mm.; filaments glabrous, 7–8 mm. long; carpels 3, velutinous.

TYPE: Tibet, sandy soil above Kampa Dzong, 12 miles north of Sikkim, 5000 m., June 17, 1922, *E. F. Norton 369* (K); seen.

A specimen from Gyong, E. Himalaya, at 4300 m., by *Rohmoo Lepcha*, Sept. 12, 1912 (E), seems to belong here. The species is in the large-flowered group with *D. muscosum*, and seems to key out independently.

109. **Delphinium przewalskii** Huth, Bot. Jahrb. **20**: 407. 1895.
FIG. 10, F.

Stem sparsely pilose, increasingly so in the inflorescence, erect, branched at the base, 1.5–2.5 dm. tall; leaves glabrous above, somewhat pilose beneath, deeply 3–5-parted, the parts deeply laciniate into 2–3 lobules 2–6 mm. wide; bracts passing into cauline leaves; bracteoles broadly lanceolate and near the flower or spatulate and remote from it, 1–2 cm. long, 5–7 mm. wide; flowers usually terminal, deep blue, 1 to few in a corymbose raceme; sepals 2–2.5 cm. long, 1.2–1.5 cm. wide, loosely pubescent, subcorniculate at tips; upper sepal ovate, 25 mm. by 15 mm., apiculate; lateral sepals elliptic-ovate, 25 mm. by 15 mm.; lower sepals 28 mm. by 18 mm., acute to acuminate; spur ca. 20 mm. long, straight or arcuate, 3.5 mm. wide at base; upper petals more or less ciliate, dark brown, the lamina almost straight, 15 mm. long, 3 mm. wide, glabrous, emarginate, the spur ca. 15 mm. long; lower petals semibifid, white-ciliate, dark brown at base, yellow bearded, less deeply colored in upper part, the lamina to 10 mm. by 4 mm.; claw ca. 8 mm. long, somewhat appendiculate; stamens 7–8 mm. long, glabrous; anthers purple, almost 2 mm. long; carpels 3, densely hairy.

TYPE: W. Mongolia, "Montes Alaschan," *Przewalski* "1874" in Huth. "1871" on herbarium sheet, "1873" (LE), and "1873" (K). The 2 Leningrad specimens (1871 and 1873) are on one sheet, with the label "Syntypus."

110. **Delphinium pseudo-caeruleum** W. T. Wang, Acta Bot. Sinica **10**: 269. 1962.

Stem ca. 9–10 dm. tall, 3 mm. thick at base, indistinctly 5-angled, retrorsely strigulose, many branched, equally foliose; lower cauline leaves long petioled, the upper short or subsessile; blades as in *D. caeruleum* and *D. grandiflorum*, the ultimate lobes linear, 1.5–1.8 mm. wide, more or less revolute, ciliate, ventrally subglabrous, villous along nerves dorsally; petioles subglabrous or retrorse-villous below; inflorescence corymbose, 2–5-flowered; lower bracts trifid into linear lobes, others entire, linear; pedicels densely retrorsely strigulose, 3.2–7.5 cm. long, suberect; bracteoles near middle of pedicel, linear, 4–6 mm. long; sepals deep blue, oblong-obovate or narrow-elliptic, minutely puberulent; spur 20–22 mm. long, subulate, straight or slightly decurved; upper petals dilute blue, glabrous, emarginate; lower petals blue, the limb and claw subequal, the limb yellow bearded at base, subelliptic, bifid to middle into triangular, obtusish, ciliate lobes; stamens glabrous; carpels 3, densely brownish-strigulose.

TYPE: Kansu, Si-Ku, 2500 m., July 29, 1951, *T. P. Wang 14658* (PE), not seen. Isotype and photograph (E), seen.

This species suggests *D. mollipilum*, but has strigose stems and pedicels and bifid lower petals.

111. **Delphinium pseudograndiflorum** W. T. Wang, Acta Bot. Sinica 10: 275. 1962. FIG. 10, G.

Stem about 3–7 dm. tall, almost glabrous and glaucous, with occasional spreading hairs especially about the nodes and on the pedicels just below the flowers; basal leaves few, the blades to ca. 1 dm. in diameter, subglabrous or with a few spreading and some minute appressed hairs, round-pentagonal in outline, divided almost to the base into obovate segments, cuneate and 1 cm. or more wide with little lobing, or more frequently laciniate into linear parts 1–2–3 mm. wide and 1–6 cm. long, acuminate; cauline leaves largely of the latter type, scattered and gradually reduced up the stem; lower petioles to 10 or more cm. long, very slightly vaginate at the base, the upper much shorter; inflorescence open, branched, the racemes lax, few to several flowered; lower bracts trilobed, others entire, linear-subulate, 5–15 mm. long; pedicels arched or erect, 2–10 cm. long; bracteoles linear, 3–7 mm. long, near the flower or lower; sepals deep blue, often tinged purple, strigulose and with longer hairs without, more or less crinkled on margin; upper sepal round-ovate, 13–20 mm. long, rounded-obtuse, the spur 22–26 mm. long, 2.5 mm. wide at base, straight or somewhat decurved; lateral sepals elliptic-oblong, 16–20 mm. by 6–10 mm., rounded at apex; lower sepals elliptic-oblong, similar to but slightly wider than the lateral; upper petals light colored, the blade slightly oblique, 8 mm. by 2.5 mm., glabrous, subentire, the spur ca. 17 mm. long; lower petals blue, the lamina strongly oblique, round-obovate, 8 mm. by 6.5 mm., deeply emarginate, yellow bearded at base, ciliate, the claw 5–6 mm. long; stamens 5–6 mm. long, ciliate; anthers dark, 1 mm. long; carpels 3, hairy, with dark veining, ca. 12 mm. long by 3 mm. wide, the styles an additional 3 mm.; seeds angled, winged, 1.2 mm. long.

Type: Szechwan, Hei-shin, 2400–3300 m., July–Aug., 1957, *H. Li 74016* (PE), not seen; photo. of type and isotype seen (E).

Range. Growing in fields and scrub up to 5000 m., Tibet, western China.

Examples seen. **Tibet:** *Hanbury-Tracy 195*; *Kingdon Ward 10881, 10621, 12077*; *Ludlow & Sherriff 687, 2595, 499*; *Ludlow, Sherriff & Taylor 6093, 5162, 13920*; *Rock 14538.* **Szechwan:** *H. Stevens 458* in part; *Harry Smith 3985.* **Yunnan:** *G. Forrest 16951, 15112, 6538, 23185*; *Schneider 3250*; *Yü 13481*; *H. Wang 41742.* **Sikang:** *H. Smith 13764.* **Kansu:** *R. C. Ching 922, 1070*; *Rock 13178, 14594.*

Near to *D. grandiflorum* and referred here is much of the more western material that formerly was identified as that species. It has longer spurs, a more erose lower petal and sometimes looser stem-pubescence. Wang (p. 275) proposed also var. *glabrescens* with glabrous pedicels and var. *lobatum* (p. 276) with more deeply lobed lower petal-laminae. I have had no material of these, and from descriptions only, must refer them to synonymy.

112. **Delphinium pulcherrimum** W. T. Wang, Acta Phytotax. Sinica 6: 370. 1957. Fig. 10, H.

Stem 1.5–3 dm. tall, equally scattered-leafy, striate, densely retrorse-pubescent or subglabrous, few branched; basal leaves lacking; lower cauline leaves long petioled, upper shorter, 3.5–7.5 cm.; leaf blades pentagonal-orbicular, cordate, 3–4 cm. in diameter, 3-parted almost to the base, middle segments elliptic-rhombic, long acuminate, laciniate, the lobules oblong-linear, 2 mm. wide, acute or rounded at apex, strigose; laterals unequally 2–3-parted, the secondary parts long acuminate, laciniate; petioles 1.5–7 cm. long, vaginate; flowers blue purple; pedicels to 6 cm. long; bracteoles near the flowers, lanceolate to elliptic, 8–11 mm. long, ciliate; sepals round or broadly elliptic, short-acuminate, loosely puberulent without, 17–22 mm. long, 12–17 mm. wide, spur 23–25 mm. long, 3 mm. wide at the base, straight or decurved, obtuse; upper petals 13 mm. long, 2 mm. wide, obtuse, unequally 2-lobulate, glabrous; lower petals 14 mm. long, the limb elliptical, bifid to the middle into 2 ovate, loosely ciliate lobes rounded at apex, yellow bearded below the middle, the claw equaling the limb, appendiculate; stamens 6–7 mm. long, glabrous; carpels 3, densely silky.

Type: Yunnan, A-tun-tze, Pai-ma-shan, Shu-ling, 4240 m., Aug. 3, 1937, *T. T. Yü 9330* (PE), not seen; photo. (E), seen.

Other material referable here. **Southern Tibet:** *Ludlow & Sherriff 1997, 1958*; *Rock 14460.* **Kansu:** *E. Licent 4686*; *R. C. Ching 1123.*

113. **Delphinium pumilum** W. T. Wang, Acta Bot. Sinica **10**: 268. 1962. Fig. 10, I.

Stems 10–16 cm. tall, to 1 mm. thick below, spreading-pilose, 1-foliate above, simple or rarely 1-branched; basal leaves 3–4, long petioled, the blades pentagonal-reniform, 7–14 mm. long, 13–24 mm. wide, cordate, trisect, the middle segment rhombic-obovate, cuneate at base, 3-parted to below the middle, the parts lance- or oblong-linear, 1–2 mm. wide, acutish, entire or with 1 lobule; lateral segments flabellate, unequally bipartite to the base, the upper parts like the middle segment but slightly oblique, the lower subequal to the preceding, unequally twice parted into ultimate linear lobules, slightly revolute, strigose beneath, loosely silky pilose above, the petioles 2–6 cm. long, spreading-pilose, short vaginate; cauline leaf similar; inflorescence corymbiform, mostly 2-flowered; bracts leaflike or small, linear, 6 mm. long; pedicels 2–9 cm. long, subequal, the hairs white, spreading or retrorse and yellow, glandular; bracteoles near or above the middle of the pedicel, linear-subulate, 3–4.5 mm. long, with loose spreading puberulence; sepals blue, elliptic or elliptic-obovate, 12–14 mm. long, loosely puberulent, the spur subulate, 33–38 mm. long, 3–3.5 mm. wide at the base, slightly curved; upper petals glabrous, emarginate; lower petals blue, the limb broad-obovate, yellow bearded at base, ca. 6 mm. long and wide, subtruncate at tip, emarginate, glabrous or loosely puberulent, claw as long as the limb; stamens glabrous; carpels 3, pilose.

TYPE: Szechwan, Muli, Sept. 14, 1959, *S. K. Wu 2662* (PE), not seen; photo. (E), seen.

The author compares *Delphinium pumilum* with *D. caeruleum* and *D. tatsienense*, all three being small plants. I refer here, Szechwan, Muli Kingdom, *Rock 18316*; Mt. Konka, *Rock 16886*. Yunnan, *Yü 14413*.

114. **Delphinium pylzowii** Maxim. ex Regel, Gartenflora **25**: 289–290. *pl. 879*. 1876; Maxim. Bull. Acad. Pétersb. **23**: 307. 1877.

FIG. 10, J, K.

Delphinium pylzowii var. *trigynum* W. T. Wang, Acta Bot. Sinica **10**: 78. 1962, in part, as to *Rock 13194* and *14501* cited by Wang.

Delphinium caeruleum var. *macranthum* Finet, Jour. Bot. Morot **21**: 98. 1908. Based on *Soulié 3903, 3911, 3914* from Yargong, Batang. Seen (P).

Delphinium caucasicum var. *tanguticum* Maxim. *in schedis.*

Delphinium tanguticum (Maxim.) Huth, Bull. Herb. Boiss. **1**: 331. *pl. 15*. 1893. Type. Szechwan, *G. N. Potanin*, 1885 (LE), seen; isotype (K), seen.

Delphinium labrangense Ulbrich ex Rehder & Kobuski, Jour. Arnold Arb. **14**: 11. 1933, *nomen*. Proposed for *Rock 14482, 14483, 14504, 14513*.

Perennial from a more or less woody subterranean base, the stems 1 to several, slender, 1–3 dm. tall, simple and 1-flowered or few branched and few flowered, pilose to retrorsely strigulose, the hairs in the upper part less appressed, very dense, short to rather long and fine; lower leaves 3- or 5-parted, 1.5–2.5 cm. across, the parts more or less cuneate, broad, coarsely 3-toothed at tip, the petioles very slender, 2–5 cm. long, somewhat dilated at base; main cauline leaves few, more deeply laciniate into oblong lobes 2–3.5 mm. wide, 4–10 mm. long; bracts entire to 3-lobed, the lobes entire, to 7 mm. wide or laciniate; pedicels erect, 2–10 cm. long; bracteoles linear,

near the middle of the pedicel, linear to lanceolate, 5–15 mm. long, setaceous, to 5 mm. wide; calyx deep blue; upper sepal ovate, 15–22 mm. long, 10–15 mm. wide, obtuse, with fine rather long hairs, spur somewhat decurved, 24–28 mm. long, ca. 3.5 mm. wide at base, only gradually narrowed into a somewhat obtuse tip; lateral sepals broadly ovate, 20–22 mm. long, 16–18 mm. wide, obtuse; lower sepals 24 mm. by 15 mm., ovate, obtuse; upper petals from yellowish with a blue margin to almost black-purple, the laminae straight, not toothed to erose or emarginate, about 14 mm. long, the curved spur 25 mm. long; lower petals bearded, the elliptic-ovate lamina ca. 8 mm. long, divided to ca. 5 mm., the claw ca. 5 mm. long; stamens 7–8 mm. long, glabrous; anthers dark, narrow, 1.5 mm. long; carpels 5 or 3, pubescent; seeds with low lamellate papillae.

TYPE: Kansu, Terra Tangutorum, *Przewalski, 1872* (LE), seen; isotype (P), seen.

RANGE. About 3500 to 4500 m., Kansu, Szechwan, eastern Tibet.

ILLUSTRATIONS. MAXIMOWICZ, Fl. Tangut. **1:** *pl. 3.* 1889; Gartenflora **25:** *pl. 879.* 1876; Bot. Mag. **145:** *pl. 8813.* 1910.

REPRESENTATIVE MATERIAL. **Kansu:** *Przewalski* in 1880; *Rock 13093, 13041, 14644, 14625, 13086, 13088, 13023, 14641*; *Farrer & Purdom F 710.* **Szechwan:** *Wilson 3094, 4691*; *H. Smith 3135, 2961, 3384, 4283.* **Tibet:** *Ludlow & Sherriff 8854, 9902.*

115. **Delphinium rockii** Munz, sp. nov. FIG. 10, L.

Stem ridged, dark, to ca. 1 m. tall, 4–5 mm. thick, more or less strigulose, branched above, scattered-leafy; petioles scarcely dilated at the base, the cauline to 1 dm. long, somewhat retrorse-pilose; cauline leaf blades generally reduced up the stem, 3–7 cm. in diameter, rounded-pentagonal, strigose above, more loosely so beneath, cleft almost to the base, the divisions rather narrow, 3–8 mm. wide, laciniate or lobed into ultimate parts 1–3 mm. wide, acute; inflorescence open paniculate, the ultimate branches leafy-bracted and bearing umbellate clusters of 3 or more flowers; bracts ca. 1 cm. across, deeply laciniate; pedicels 2–3 cm. long, divergent, strigulose, not glandular; bracteoles subtending the flower, strigulose, 2–3 mm. long, 1 mm. wide; sepals bluish purple, strigulose, the upper sepal oblong-ovate, 18–20 mm. long, 10–11 mm. wide, obtuse, the spur decurved, strigulose, 14–16 mm. long, 3 mm. wide at the base, the other sepals elliptic-ovate, 15 mm. long; petals dark, the upper laminae suberect, glabrous, entire, obtuse, 11–12 mm. long, the spur 15 mm. long; lower laminae oblong, 7 mm. long, unequally shallowly bilobed, the upper surface white-hairy at the base, ciliate; the claw 6 mm. long, appendaged; stamens glabrous; carpels 3, glabrous.

Caulis ad 1 m. altus, 4–5 mm. crassus, strigulosus, supra ramosus; petioli vix dilatati, ad 1 dm. longi, retrorso-pilosi; laminae foliorum caulium 3–7 cm. latae, rotundato-pentagonales, supra strigosae, infra laxe pubescentes, alte lobatae, laciniis ultimis 1–3 mm. latis; inflorescentia paniculata; rami cum bracteis foliosis et umbellis 3–5 florium; pedicelli

2–3 cm. longi, divergentes, strigulosi; bracteolae strigulosae, 2–3 mm. longae; sepala azureo-purpurea, strigulosa; sepalum superiore oblongo-ovatum, 18–20 mm. longum, 10–11 mm. latum; calcar 15 mm. longum; sepala latiora et inferiora elliptico-ovata, 15 mm. longa; petala atropurpurea; laminae superiores glabrae, integrae, obtusae, 11–12 mm. longae; laminae inferiores oblongae, 7 mm. longae; inaequaliter bilobatae, base hirsutae, ciliatae; unguis 6 mm. longus, appendiculatus; stamina glabra; carpella 3, glabra.

TYPE: Eastern Tibet, grasslands between Labrang and Yellow River; valley of Kachiassu, 3000 m., Aug. 5, 1926, *J. F. Rock 14543* (GH).

The proposed new species is near *D. henryi* and *D. trisectum* in the shape of the lamina of the lower petal and in having the bracteoles very near the base of the flower; but differs in its more paniculate inflorescence and its upper petal entire at the apex.

116. **Delphinium smithianum** Hand.-Mazz. Acta Horti Gothob. 13: 49. 1939. FIG. 10, M.

Perennial from an elongate root, with 1 or more stems 3–12 cm. high, simple or few-branched, suberect, more or less purplish, leafy and with short spreading hairs; leaves reniform-pentagonal in outline, the blades 2–5 cm. wide, bifid or trifid to near the base into cuneate obovate divisions, the 2 lateral ones deeply divided to make 5 subequal parts, obovate, 2–3-lobed, these lobes each with 2 or 3 broad teeth rounded at the apex, 1–3 mm. long and ca. 2 mm. wide, the parts somewhat more puberulent beneath than above; petioles slender, 2–6 cm. long, dilated at base, somewhat pubescent; flowers 1–4 on a stem; pedicels 3–8 cm. long, suberect, arising in upper axils; bracteoles 2, leafy, ca. 3-lobed, 6–8 mm. long, placed above the middle of the pedicel; sepals broadly ovate, obscurely violet, fine-hairy; upper sepal 18–20 mm. long, 14 mm. wide; spur 20–22 mm. long, 5 mm. wide at base, subcylindrical, horizontal, blunt; lateral sepals round-ovate, obtuse, pubescent mostly along the purplish midvein; lower sepals 22 mm. by 14 mm., acute, pubescent; upper petals dark, the laminae straightish, 13 mm. long, slightly and unequally bidentate, the spur 20 mm. long; lower petals dark, the oblong blade enlarged somewhat distally, bearded, ca. 8 mm. long, bifid ca. 1/3 its length, the narrow claw 7 mm. long; stamens 7–8 mm. long, glabrous; anthers dark, 1.2 mm. long; carpels silky villous; seeds wingless.

TYPE: Sikang, Kangting (Tachienlu), 4600 m., Aug. 20, 1934; *Harry Smith 11274*, type (W), not seen; isotypes (A, MO), seen.

117. **Delphinium sordidecaerulescens** Ulbrich, Notizbl. Bot. Gart. Berlin 12: 356. 1935. FIG. 13, A.

Erect perennial, sparsely branched, 6–8 dm. tall; stem slender, yellowish green with purplish base, very sparsely hairy; basal leaves gone by anthesis; cauline leaves few, remote, gradually reduced up the stem; lower petioles to 18 cm. long, slightly dilated at the base; blades suborbicular, 4–5 cm. in diameter, about septemfid, the segments 2–3-partite into linear lobes 1–3 mm. wide, acutish, sparsely pilose; upper leaves trifid into entire linear lobes; the inflorescence open paniculate, glabrous to somewhat pubescent on the pedicels with white hairs; bracts linear, 5–20 mm. long; pedicels divergent, 3–9 cm. long, suberect, slightly curved; bracteoles linear, 4–6 mm. long, well below the flower; sepals sordid-bluish, somewhat crisped-pubescent, with a greenish tubercle below the apex; upper sepal ovate, 11–12 mm. long, 8 mm. wide, obtuse, the spur straight, spreading, 22–23 mm. long, 3.5 mm. wide at the base, very slender toward the tip; lateral sepals oblong, 9 mm. long, 7 mm. wide, round-truncate at the apex; lower sepals 14 mm. long, 7 mm. wide, obtuse; petals pale, whitish or yellowish, the upper laminae entire, oblique, ca. 7 mm. long, glabrous, somewhat pointed, the spur about 20 mm. long; lower laminae oblong-obovate, somewhat erose, about 6 mm. long, 4.5 mm. wide, yellow-bearded at the base, short-ciliate on the margin, the claw appendiculate, 5–6 mm. long; stamens 6–7 mm. long, glabrous; anthers dark; carpels 3, pilose, 8–9 mm. long, the filiform styles another 2–3 mm.; seeds glabrous, ca. 3 mm. long.

TYPE: "Szechwan, reg. bor. Huang-chen-kuan, in prato, 3400 m.," *Harry Smith 3983* (UPS; seen through the courtesy of Dr. J. A. Nannfeldt).

This species is very close to *Delphinium pseudograndiflorum* Wang, over which its name has priority. Its flowers are apparently much paler in color and smaller, and without more material for comparison I am maintaining the two species.

118. **Delphinium sutchuense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 178. 1893. FIG. 11, A.

Stem erect, sparsely pubescent to glabrous, scattered-leafy to the top, 4–8 dm. tall; lower petioles slender, not or scarcely dilated; blades 6–9 cm. wide, fine-pubescent, 3–5-sect, the segments oblong, entire at base, narrow-cuneate, ca. 3 cm. wide above, subpetiolulate, distally trifid, then incised into few, long-acuminate, very pointed lobes, 2–4 mm. wide; inflorescence branched, the branches erect, almost appressed to the central stem, bare, with a 2–6-flowered raceme at the summit; upper bracts linear-subulate, the bracteoles subulate, a little below the sepals, 10–12 mm. long, very narrow; pedicels twice as long as flowers, closely strigulose; flowers violet blue, strigulose; upper sepal ovate-oblong, obtuse, 11 mm. by 7 mm., spur 13–18 mm. long, horizontal or slightly ascending, obtuse; other sepals ca. 15 mm. long; petals blue, the upper oblique, the lamina 9 mm. long, emarginate, possibly few-haired at the apex; lower laminae oblong-ovate, 5.5 mm. by 4 mm., bearded at base, ciliate, divided almost halfway into rather broad lobes, claw appendiculate, 5 mm. long; follicles 3, silky.

TYPE: W. China, in north of province of Sutchuen (Szechwan), *Potanin*, 1885 (P); seen.

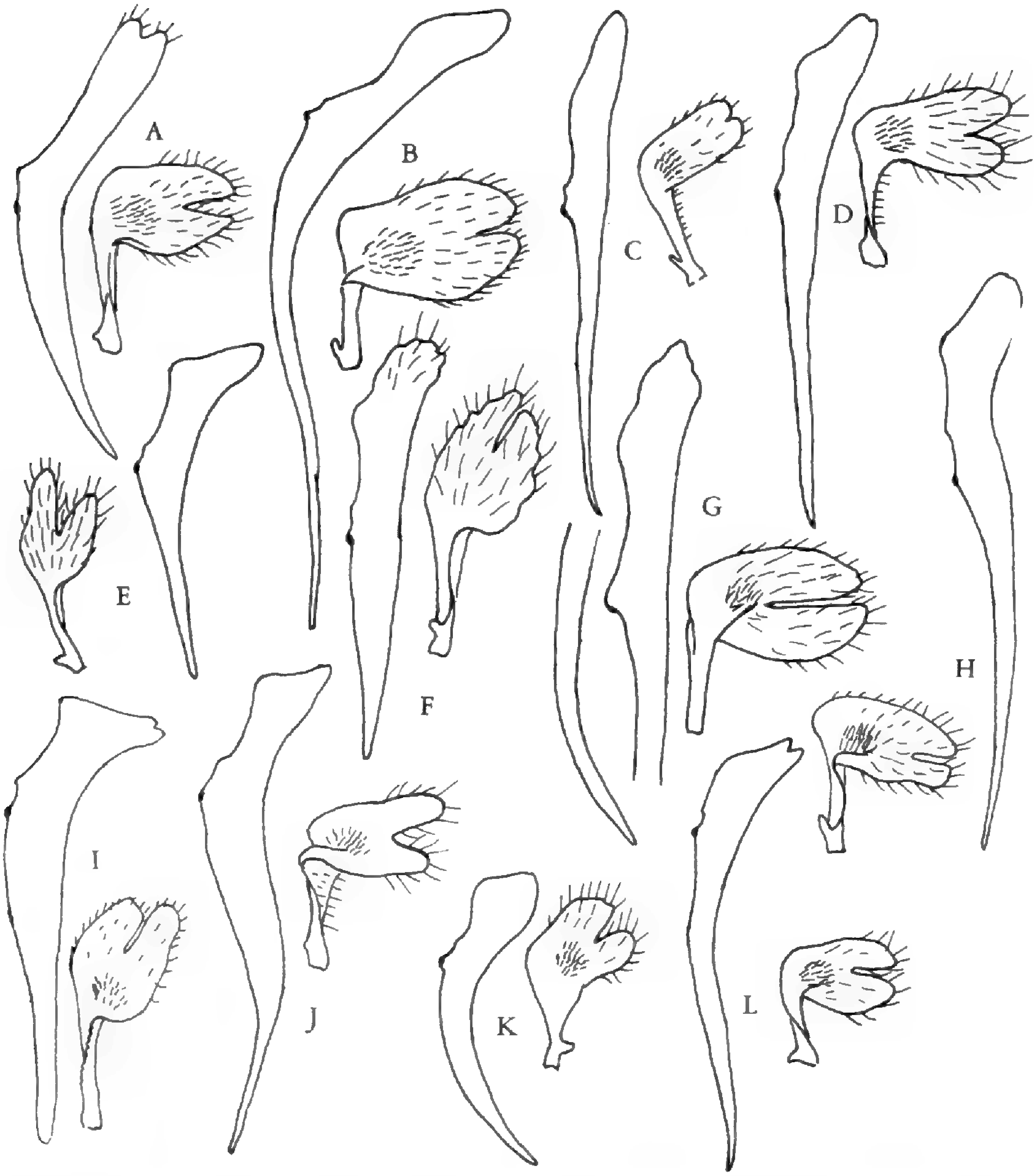


FIGURE 11. **Delphinium,** GROUP VI. Petals, the upper spurred, the lower clawed. A. *D. sutchuense*; blade of upper petal 12 mm. long, spur 15 mm.; blade of lower petal 5.5 mm. long, claw 5 mm.; drawn from *Potanin*, 1885, TYPE (P). B. *D. tatsienense*; blade of upper petal 10 mm. long, spur 30 mm.; blade of lower petal 9 mm. long, claw 5 mm.; drawn from *Stevens 114* (F). C. *D. tenii*; blade of upper petal 10 mm. long, spur 17 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Ten 581* (UC). D. *D. tenii*; blade of upper petal 10 mm. long, spur 18 mm.; blade of lower petal 8 mm. long, claw 6 mm.; drawn from *Schneider 2510* (GH). E. *D. tenuipes*; blade of upper petal 8 mm. long, spur 12 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Stewart & Rahman 25125* (BM). F. *D. triste*; blade of upper petal 12 mm. long, spur 13 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Ikonnikov-Galitsky 82* (UC). G. *D. tsoongii*; blade of upper petal 14 mm. long, spur 25 mm.; blade of lower petal 8 mm. long, claw 5 mm.; drawn from *Rock 13093* (GH). H. *D. tsoongii*; blade of upper petal 10 mm. long, spur 20 mm. long; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Rock 14547* (GH). I. *D. williamsii*; blade of upper petal 10 mm. long, spur 17 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Polunin, Sykes & Williams 1907*

119. **Delphinium tatsienense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 169. 1893. FIG. 11, B.

Delphinium bonatii Lévl. Repert. Sp. Nov. **7**: 99. 1909. Type, Yunnan, *Ducloux 596*, isotypes (E, UC), seen. Lauener & Greene, Notes Bot. Gard. Edinb. **23**: 585. 1961, referred this to *D. grandiflorum*.

Delphinium soonmingense Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) **1**: 175. 1948. Based on *Y. P. Chang 450* from Soonming (PE?); not seen. This referred to synonymy under *D. tatsienense* by W. T. Wang, Acta Bot. Sinica **10**: 267. 1962.

Delphinium pycnocentroides var. *latisectum* W. T. Wang, Acta Bot. Sinica **10**: 164. 1962. Type *C. W. Wang 66226* (PE), not seen; isotype seen (A).

Stem 2–6 dm. tall, slender, simple or with slender branches, subglabrous to strigulose, the hairs tending to be more spreading in upper parts; leaves remote, few, the lower petioles to 1 dm. or longer, slender, strigulose, not vaginate at base; the upper shorter; blades 3–8 cm. or wider, divided to base into 3 or 5 parts that are narrow-cuneiform at their base, deeply incised into obtuse linear lobes commonly 2–4 mm. wide, green and scantily pubescent above, paler and more pubescent beneath; flowers few, in an open corymb or short raceme; lower bracts foliaceous, trifid into linear lobes 1–1.5 cm. long or simple; pedicels arched-ascending to straight, commonly 2–several cm. long, strigulose; bracteoles linear, often more than 2, commonly lance-linear, 4–8 mm. long, near the middle of the pedicel or above; sepals deep blue, pubescent; upper sepal broadly ovate, obtuse, 20 mm. by 12 mm., the spur horizontal, quite straight, 30 mm. long, 3 mm. wide at base, slender, narrowed to rather an acute point; lateral sepals oblong, 17 mm. by 9 mm., rounded-truncate at tip, pubescent along midvein; lower sepals 20 mm. by 10 mm., narrow-obovate, obtuse; upper petals bluish, oblique, 10 mm. long, glabrous, the spur very slender, almost 30 mm. long; lower petals blue, oblong-obovate, the lamina 9 mm. by 6 mm., subentire to cleft at tip for 2 mm., ciliate, densely bearded near base of the blade, the claw 5 mm. long, narrow; stamens 6–7 mm. long, the filaments slightly ciliate; anthers dark, 1.2 mm. long; follicles 3, short-pubescent, 12–15 mm. long, 3–4 mm. wide, the styles an additional 3 mm.; seeds winged on angles.

TYPE: Szechwan, near Tatsienlou, *Henri d'Orléans & Bonvalot*, July 29, 1890 (P); seen. Photographs of type (BH, E, UC); seen.

DISTRIBUTION. Largely at 2500 to 3000 m., western China.

EXAMPLES. **Szechwan:** *Soulié 2027, 2381, 2382, 2489, 2380; H. Stevens 89, 114; H. Smith 4660, 10798, 13764; W. P. Fang 4276; Cunningham 193, 355, 490; Wilson 3096.* **Yunnan:** *Yü 12941, 14527; Forrest 6494, 11449, 22378; Maire 380, 720; Rock 18485, 6292, 7770, 11485, 10686, 11545; Schneider 2739, 2182.* **Tibet:** *Rock 23243; Soulié 3529.*

(BM). J. *D. wilsonii*; blade of upper petal 9 mm. long, spur 19 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *E. H. Wilson 2396* (NY). K. *D. yuanum*; blade of upper petal 6 mm. long, spur 12 mm.; blade of lower petal 5 mm. long, claw 4 mm.; drawn from *Yü 12490* (A). L. *D. yunnanense*; blade of upper petal 7.5 mm. long, spur 22 mm.; blade of lower petal 5.5 mm. long, claw 4 mm.; drawn from *Delavay 967* (NY).

120. **Delphinium tenii** Lévl. Repert. Sp. Nov. 7: 98. 1909.
FIG. 11, C, D.

Delphinium dolichocentrum W. T. Wang, Acta Bot. Sinica **10**: 162. 1962. Based on Yunnan, Atuntze, *T. T. Yü 9885* (PE), not seen; photo. (E), seen.

Stems divaricate, slender, 8–15 (–45) cm. tall, white-villous, simple; leaves basal and a few cauline, the lower petioles very slender, 2–4 cm. long, spreading-villous, somewhat dilated at the base, the cauline not dilated, the upper shorter; leaf blades 2–4 cm. wide, more or less triangular, divided to base to form 3 cuneate-obovate segments, green and finely strigulose above, paler and with longer white hairs beneath, these segments trifid and somewhat additionally lobed into oblong-linear, obtuse parts 2–4 mm. wide; flowers few in an open corymb; bracts ordinary leaves; pedicels strigose or spreading-pubescent, to 6 cm. long; bracteoles leafy, ternate or entire, and elliptical, at about the middle of the pedicel; sepals deep blue, strigose; upper sepals 12–15 mm. long, 8–10 mm. wide, obtuse, the spur decurved toward the apex, 20–22 mm. long, 3 mm. wide near the base, gradually narrowed toward the slender tip; lateral sepals elliptic-oblong, 13–15 mm. long, 6–8 mm. wide, rounded at the apex; lower sepals 12–15 mm. long, 5–8 mm. wide, obtuse; petals bluish, the upper laminae almost straight, entire, glabrous, 10 mm. long, the spur 17 mm. long; lower laminae oblong, emarginate, 6 mm. long, 2.5 mm. wide, bearded near the base and sparsely elsewhere, claw 5 mm. long; stamens 6–7 mm. long, filaments moderately widened; anthers blue, 1 mm. long; follicles 3, hairy, 12–14 mm. long; seeds 2 mm. long, narrowly winged on angles.

TYPE: Yunnan, Lou-Fou near Tong-Tchouan, June, 1906, *Simeón Ten 581* (E), isotype (UC); seen.

EXAMPLES. All from **Yunnan:** *T. T. Yü 9885* (A), *13336* (A); *C. W. Wang 64707, 69117, 64733, 69174, 69397*, all (A); *H. T. Tsai 56240* (A), *51974* (A); *K. M. Feng 2841* (A); *Rock 18205* (A, US); *C. Schneider 2510* (GH).

121. **Delphinium tenuipes** Tamura, Acta Phytotax. Geobot. **16**: 141. 1956.
FIG. 11, E.

Root woody, 5 mm. thick; stem 1 m. tall, 3 mm. thick, simple, terete, erect, glabrous above the white-pilose base; radical and lower stem leaves broadly reniform, 7–9 cm. wide, 3-partite to near the base, the lateral segments bipartite, all cuneate-obovate, pinnatifid into oblong or ovate-oblong lobes, acute or obtuse, glabrous above, sparsely white-hairy beneath; petioles 8–10 cm. long; upper leaves glabrous, 3-parted, the lateral segments 2-parted, all oblong, 1–3-toothed or entire, the blades 4–6 cm. long, 6–7 cm. wide, petioles 3–4 cm. long; racemes laxly branched below, the branches arcuate-divaricate, with about 20–22 flowers; bracts linear, 2.5–5 mm. long; pedicels 15–45 mm. long, slender, arcuate-ascending, bibracteolate above the middle, viscid pilose apically with yellow hairs; bracteoles linear, 2 mm. long; flowers blue; spur cylindric, gibberulate below the apex, 10–11 mm. long, 2 mm. wide; sepals glabrous, 9–11 mm.

long, 3–5 mm. wide; upper petals glabrous, the lamina ca. 8 mm. long, entire, somewhat oblique; lower petals bifid, white bearded; carpels 3, viscid-pilose.

TYPE: Afghanistan, Nuristan, Chatrass, 2100 m., *Kitamura*, Aug. 2, 1955 (KYO, not available).

A specimen from West Pakistan, Swat, Kalam to Utrot, 2500 m., July 20, 1953, *R. R. Stewart & A. Rahman 25125* (BM) seems to me to match the illustration by Kitamura, Fl. Afghan. 125. *fig. 51.* 1960.

122. **Delphinium trisectum** W. T. Wang, Acta Bot. Sinica 10: 80. 1962.

Stems 4.5–5 dm. tall, 3–6 mm. thick at base, densely retrorse-strigulose, simple or with one branch above, subequally foliose; cauline leaves long petioled, the blades broadly reniform (3–)4.5–6.5 cm. long, (5.2–)7.5–12 cm. wide, basally cordate, trisect, the segments broadly obovate or rhombic-obovate, 3-lobed to the middle, the lobes 3-lobulate to the middle, these lobules lance-ovate, entire or 1-toothed, lateral lobes also bifid and much divided; petioles 15–17 cm. long, indistinctly vaginate; racemes 10–14-flowered, lax; lower bracts short petioled and trisect, the segments lanceolate, the upper bracts linear; pedicels 2–7 cm. long, densely retrorse-pubescent; bracteoles near the flowers, lance-linear, 7–9 mm. long, 1 mm. wide, puberulent; sepals purple, elliptic to elliptic-obovate, 14–17 mm. long; spur slightly longer than sepals, cylindric-subulate, straight or slightly decurved; petals dark brown, emarginate, glabrous; lower petals with elliptical laminae, bilobed, long-ciliate, yellow bearded near the base; stamens glabrous; follicles 3, spreading, puberulent.

TYPE: Honan, Shang-Cheng, 400 m., April 19, 1959, *Honan Exped. 149* (PE), not seen; photo. seen (E). Near *Delphinium henryi* and *D. rockii.*

123. **Delphinium triste** Fisch. ex DC. Syst. 1: 362. 1817. FIG. 11, F.

Delphinium obscurum Stev. ex DC. Syst. 1: 362. 1817, *nomen pro synon.*

Stem 3–7 dm. tall, slender, simple or few branched above, leafy, retrorse-strigulose below, the hairs less appressed in the inflorescence; lower petioles slender, somewhat dilated at the base, 5–12 cm. long, the upper shorter; laminae broader than long, subglabrous to strigulose (especially beneath), mostly 4–12 cm. wide, divided quite to the base into 3 or 5 parts, these narrow-cuneate below, obovate, deeply laciniate into linear lobes 1.5–4 mm. wide, acute; racemes lax, 3–15-flowered, the lower bracts trifid, pubescent, to 2 cm. long, others linear-lanceolate, to ca. 1 cm. long; pedicels ascending, pubescent, 2–5 cm. long; bracteoles lance-linear to linear, mostly somewhat below the sepals, 3–6 mm. long; sepals purplish black, cinereous pubescent, the upper sepal ovate, 22 mm. long, 12 mm. wide, rounded-obtuse, the spur almost straight, 12–14 mm. long, 5 mm. wide at the base, obtuse; lateral and lower sepals rhombic-ovate, 14–15 mm. by

10–11 mm., rounded at apex; petals black, the upper laminae slightly oblique, entire but slightly irregular and crisped on the rounded setose tip, ca. 12 mm. long, the spur 13 mm. long; lower laminae bearded on both sides, ovate, 7 mm. long, 5 mm. wide, cleft for about 2 mm. into rather broad lobes, claw 6 mm. long; stamens 7–8 mm. long, the filaments much broadened at base, glabrous; anthers dark, oblong, 1.3 mm. long; follicles 3, somewhat divaricate, densely pubescent, 14–17 mm. long, ca. 4 mm. wide, the styles an additional 3 mm.; seeds brown, 2.5 mm. long, densely clothed with overlapping transverse rows of scales.

TYPE: "Hab. in Daouria circa Doroninsk (Vlassof ex Fisch.)." I have seen a sheet from Dahuria, *Herb. Fischer* (LE, P) which may be type material. Two other specimens loaned from Leningrad both from the Herb. Ledebour are *Turcz.*, 1829 and *Turcz.* no. *929*. The Turczaninow material agrees well with the Herb. Fischer sheets.

ILLUSTRATIONS. KNOWLES & WESTCOTT, Fl. Cabinet **2**: *pl. 54.* 1838; J. W. LOUDON, Ladies' Flower Garden of Ornamental Perennials **1**: *pl. 10.* 1843.

This very distinctive species with dark flowers is represented by the following Mongolian collections: "In alpibus sajanensibus, *Radde*" (K, LE, P); "In pratis ad fl. Dschida" *Turczaninow* (K, P); *Ikonnikov-Galitzky 82* (UC); Lake Kosogol, *Newburg*, in 1924 (A, UC).

124. **Delphinium tsoongii** W. T. Wang, Acta Phytotax. Sinica **6**: 368. 1957. FIG. 11, G, H.

Stem 6–9(–50) cm. long, simple or branched, with short white, usually retrorse hairs, rather equally leafy throughout; lower petioles up to 7 cm. long, slender, with white scattered hairs, somewhat vaginate, progressively shorter up the stem; leaf blades broader than long, cordate, 1–5 cm. in diameter, 5-parted to the base, the petiolulate parts repeatedly divided into ultimate oblong-linear lobes mostly 1–2 (–3) mm. wide; inflorescence glandular-villous with white and yellowish hairs, each branch ending in a 2–7-flowered corymb; lower bracts dissected, foliose, the upper entire, lance-linear; pedicels ascending, 2–5 cm. long; bracteoles linear, slightly above the middle of the pedicel, 2–4 mm. long; sepals dark purplish blue to bright blue or paler, villous; upper sepal elliptic to broadly ovate, 13–16 mm. long, 6–8.5 mm. wide, the spur slender, slightly decurved toward the narrow tip, 20–25 mm. long, 2.5–3 mm. wide at the base; lateral and lower sepals elliptic-oblong, rounded to obtuse at tip, 14–18 mm. long; upper petals dark, with a slightly oblique lamina 10 mm. long, the tip rounded and entire; lower lamina oblong, oblique, 7 mm. by 4 mm., cleft for 2 mm., yellow bearded near the base, subglabrous to white-hairy on remainder, claw 5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.5 mm. long; follicles 3, hairy, divergent at tips, 15–17 mm. long, the styles an additional 2.5 mm. long; seeds black, obpyramidal, 1 mm. long, covered with minute scales.

TYPE: Tibet, between Cha-chia and Chiao-tuao, Aug. 9, 1953, *P. C. Tsoong 6073* (presumably PE, not seen).

If I understand this species at all, I would refer here *Rock 14547* from Tibet (GH, NY); *Rock 13154* (GH, US) and *13193* (GH, NY), both from Kansu; and *R. C. Ching 534* (GH, US) from Kansu.

Delphinium tsoongii is near *D. mosoynense* but has somewhat smaller floral parts and a different range.

125. **Delphinium williamsii** Munz, sp. nov. FIG. 11, I.

Perennial from long branching woody roots; stems rather slender, 4–10 dm. tall, freely and openly branched in upper half, scattered leafy, but the leaves more abundant below, largely glabrous except for the strigulose tips of the inflorescence; lower petioles 5–10 cm. long, very slender, subglabrous, more or less dilated at the base, the upper petioles shorter; leaf blades to 1 dm. broad, 5-fid to near the base, sparingly strigulose to subglabrous, ciliate, variegated, being rather pale near the center, paler on under surface, the segments narrow at the base, obovate-rhombic, lobed then dissected into ultimate parts largely 1–2 mm. wide, acute-mucronate; upper cauline leaves with almost filiform ultimate divisions; inflorescence open, the racemes lax, axes subglabrous, several flowered, to ca. 2 dm. long; bracts linear, 5–12 mm. long, or the lower divided; pedicels divergent, 1.5–5 (–10) mm. long, somewhat strigulose toward the tips; bracteoles near the middle of the pedicels or above, linear to sublanceolate, 2–5 mm. long; sepals dull white with greenish tips, subglabrous except for minute appressed hairs on basal parts; upper sepal oblong-ovate, 14–18 mm. long, 8 mm. wide, apiculate, the spur straight, spreading, subcylindric, 18–21 mm. long, 3 mm. wide at base, rather blunt; lateral sepals elliptic-oblong, 16–18 mm. long, 7–8 mm. wide; lower sepals slightly narrower; petals whitish, the upper lamina strongly oblique, 10 mm. by 4 mm., glabrous, subemarginate, the spur ca. 13 mm. long; lower laminae round-ovate, 6 mm. long, somewhat bearded, short-ciliate, bifid about 1/3 its length into rather broad lobes; claw 6 mm. long; stamens 5–6 mm. long; anthers rather dark, roundish, less than 1 mm. long; carpels 3, strigose.

Caules tenues, 4–10 dm. alti, supra laxe ramosi, disperso-foliosi, praeter strigulosos apices inflorescentiae glabri; petiola basalia, 5–10 cm. longa; laminae ad 1 dm. longae, 5-fidae, subglabrae aut parce strigulosae, ciliatae, segmentis dissectis, laciniis 1–2 mm. latis; inflorescentia laxa, racemi laxi, ad 2 dm. longi; bracteae lineares (aut inferiores divisae), 5–12 mm. longae; pedicelli divergentes, 1.5–5 (–10) cm. longi, plus minusve strigulosi; bracteolae lineares, 2–5 mm. longae; sepala albida, subglabra; sepalum superiore oblongo-ovatum, 14–18 mm. longum, 8 mm. latum, apiculatum, calcar extensum, 18–21 mm. longum; sepala lateralia et inferioria elliptico-oblonga, 16–18 mm. longa; petala albida, lamina superior obliqua, 10 mm. longa, glabra, subemarginata; lamina inferior late ovata, hirsuta, ciliata, bifida, unguis 6 mm. longus; stamina 6 mm. longa; carpella 3, strigosa.

TYPE: Nepal, near Gilam, Tila Valley, 1900 m., April 19, 1952, mainly near cultivated terraces, *O. Polunin, W. R. Sykes & L. H. J. Williams 1907* (BM).

Another collection is from Nepal, Dillihot, 2600 m., banks of cultivated fields, *Polunin, Sykes & Williams 3916* (BM). The proposed species, *Delphinium williamsii*, is near *D. kamaonense*, but with white, not blue, flowers and a longer spur. It is a pleasure to dedicate it to Mr. L. H. J. Williams of the Department of Botany, British Museum (Natural History).

126. **Delphinium wilsonii** Munz, sp. nov. FIG. 11, J.

Root woody; stem terete, slender, 6–8 dm. tall, few leaved in the lower part, glabrous except for a few long hairs near the base; basal petioles 5–12 cm. long, spreading-villous, the cauline shorter, not vaginate; leaf blades rounded pentagonal, 3–7 cm. in diameter, with a few slender hairs along the veins of the under surface, 5-fid to near the base into rhombic segments, each rather deeply lobed into few lance-oblong laciniae 1–2.5 mm. wide; cauline leaves 2–3, reduced; inflorescence rather simple, racemose, few flowered, to ca. 1.5 dm. long, glabrous except for the loosely strigose upper parts of the pedicels; bracts linear, 4–6 mm. long; pedicels suberect, 1–2 cm. long; bracteoles subulate, 2–3 mm. long, near middle of pedicel; flowers blue, the sepals strigulose; upper sepal elliptic-ovate, 13–14 mm. long, obtuse, the spur almost straight, 20 mm. long, 3.5 mm. wide at base; other sepals round-elliptic, 13–14 mm. long; petals bluish, the upper laminae oblique, subacute, 9 mm. long, glabrous, the spur 18–19 mm. long; lower petal laminae oblong-obovate, 7 mm. long, with 2 oblong lobes, hairy near the base, ciliate; the claw 6 mm. long; stamens glabrous; carpels 3, slightly hairy at base of styles.

Caulis teres, tenuis, 6–8 dm. altus, infra paucifolius, subglaber; petiola basalia, 5–12 cm. longa, villosa; laminae foliorum orbiculare-pentagonales, 3–7 cm. longae, infra in venis sparsim villosae, 5-fissae, laciniis 1–2.5 mm. latis; folia caulium 2–3; inflorescentia subsimplex, racemosa, paucis floribus; bracteae lineares, 4–6 mm. longae; pedicelli suberecti, 1–2 cm. longi; bracteolae subulatae, 2–3 mm. longae, in medio pedicelli; sepala azurea, strigulosa; sepalum superiore elliptico-ovatum, 13–14 mm. longum, obtusum, calcar horizontale, 20 mm. longum, base 3.5 mm. latum; sepala lateralia et inferioria orbiculari-elliptica, 13–14 mm. longa; petala subazurea, laminae superiores obliquae, subacutae, 9 mm. longae, glabrae; laminae inferiores oblongo-obovatae 7 mm. longae, bilobatae, base hirsutae, ciliosae, unguis 6 mm. longus; stamina glabra; folliculi 3, apice subhirsuti.

TYPE: W. Hupeh, central China, July, 1901, *E. H. Wilson 2596* (possibly *2396*) (NY). *Delphinium wilsonii* keys to near *D. tenii* and *D.*

dolichocentroides; but it has strigulose rather than glabrous pedicels and comes from Hupeh not Szechwan or Yunnan.

127. **Delphinium yuanum** Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) **1:** 176. 1948. FIG. 11, K.

Stem 10–13 dm. tall, 4–5 mm. thick, glabrous and somewhat glaucous below, subglabrous to somewhat hairy above, remotely leafy, somewhat branched above; lower petiole to 2 or 3 dm. long, somewhat dilated at base, glabrous or with a few spreading hairs; blades pentagonal-orbicular in outline, 5–15 cm. in diameter, 5-fid to base, subglabrous or with scattered hairs and some very short appressed ones, the 2 lower divisions often again deeply parted to make 5 or 7 segments, these cuneate-obovate, the lower leaves with 3 or more blunt oblong lobes 3–5 mm. wide, the upper and middle 3-incised, then again divided into oblong-linear lobes 2–3 mm. wide, subobtuse, mucronulate; inflorescence simple and lax or few-branched, the flowers ca. 15–30; bracts foliaceous or mostly entire, linear, 8–15 mm. long, somewhat hairy; pedicels ascending, more or less arcuate, 1–5 cm. long; bracteoles linear, hairy, 3–6 mm. long, situated somewhat below the flower; sepals blue, white-pubescent with short appressed and somewhat longer, spreading, white and yellow hairs; upper sepal ovate, 12 mm. by 8 mm., obtuse, the spur spreading subcylindric, 14 mm. long, 3 mm. wide at base, obtuse; lateral sepals elliptic, 11 mm. by 6 mm., rounded at apex, the pubescence mostly on the midrib; lower sepals oblong-obovate, 12 mm. by 5 mm., rounded at apex; petals blue, the upper laminae quite oblique, broadened upward, glabrous, 6 mm. long, the spur 12 mm. long; lower laminae oblique, yellow bearded near base, sparsely white-hairy and ciliate beyond, 5 mm. by 4 mm., oblong-obovate, scarcely to shallowly bilobed, dilated below, glabrous, gradually narrowed into a broad claw 4 mm. long; stamens 6 mm. long, glabrous; anthers dark, oblong, 1 mm. long; follicles 3, subglabrous.

TYPE: N. W. Yunnan, Chungtien, 3000 m., *T. T. Yü 12490*, July 27, 1937 (PE), not seen; isotype (A) and photograph of type (E), seen.

I have seen three collections from Yunnan at the Arnold Arboretum, which seem to me to belong here: Atuntze, 3400 m., *T. T. Yü 10547*; Muli, Wachin, 4000 m., *T. T. Yü 14613*; *Chungtien*, 3300 m., *T. Yü 13852*.

128. **Delphinium yunnanense** (Franchet) Franchet, Bull. Soc. Philom. Paris VIII. **5:** 173. 1893. FIG. 11, L.

Delphinium denudatum var. *yunnanense* Franchet, Plant. Delav. 25. 1886.

? *Delphinium yunnanense* vars. *laxum* and *strictum*, Huth. Bot. Jahrb. **20:** 465. 1895. No specimens cited.

Delphinium esquirolii Lévl. & Vaniot, Bull. Herb. Boiss. II. **6:** 505. 1906. I have seen *Esquirol 744* (E) from Lévl. Herb. as *D. esquirolii*; *Esquirol 794* or *793?* (E) as *D. esquirolii* sp. nov.; and *Esquirol 190* (E).

Stem simple or branched, 2.5–7.5 dm. tall, more or less retrorse-strigulose below, subglabrous above, terete; leaves light green, few and remote, finely and thinly pubescent, the petioles slender, mostly 4–8 cm. long, strigulose, dilated at the base, blades more or less round-ovate in outline, 4–12 cm. wide, pentagonal with usually 5 segments to near the base, these cuneate and divaricately and coarsely sharp toothed in the lower leaves or lobed and then toothed with narrow divisions 1–3 mm. wide in the cauline leaves; upper leaves few lobed; flowers few in lax racemes or these in an open panicle, the lowest bracts sometimes foliose, dissected, the upper setaceous, 5–15 mm. long; pedicels mostly glabrous, ascending or erect, 2–5 cm. long; bracteoles opposite, setaceous, 2–5 mm. long, a little above the middle of the pedicel; sepals deep blue, finely strigulose, the upper sepal ovate, 12 mm. long, subacute, the spur horizontal, 20–22 mm. long, ca. 2 mm. wide at the base, slender, narrowed and straight to the fine tip; lateral sepals 10–12 mm. long, strigulose on midrib, rounded at apex, broadly ovate; lower sepals more generally strigulose, about as large; upper petals almost straight, the limb 7.5 mm. long, notched at apex, the slender spur 22 mm. long; lower petals bluish, the blade sparsely bearded except at base, long-ciliate, oblong-obovate, 5.5 mm. long, divided for about 2 mm., the claw 4 mm. long; stamens 5–6 mm. long, the filaments somewhat ciliate; anthers dark, 1 mm. long; follicles 3, subglabrous to strigose; seeds obtusely obpyramidal, transversely wrinkled, with straight wings on the angles.

TYPE: Yunnan, in the plain of Mosoyn, *Delavay 967 bis*, Aug. 31, 1886 (P), seen; isotypes (K, NY), seen; photographs of type (BH, E, UC), seen.

DISTRIBUTION. The species is found at about 1800 to 3800 m., Yunnan.

EXAMPLES. *Forrest 15536, 2977, 7216*; *Henry 13440, 9272*; *Maire 389, 1196*; *Ducloux 7329, 370, 5866*; *Delavay 9, 6515, 6670, 5866*; *Simeón Ten 134*; *T. T. Yü 17375*; *Martin & Bodinier 1789*; *Rock 6551, 6902*; *Ching 21657*; *Feng 89*.

Huth (Bot. Jahrb. **20**: 465. 1890) proposes vars. *laxum* and *strictum* without typification, so one does not know what he had in mind.

NOMEN INCERTUM

129. **Delphinium lepidum** Fisch. & Avé-Lall. Ind. Sem. Horti Petrop. 9: 70. 1843.

Judging from the description which speaks of narrow segments in the leaves and which compares the flowers with those of *D. grandiflorum* L., this plant would fall in my Group VI. It has been compared to *D. triste*, which does not reach nearly so far west as the Caucasus, whence *D. lepidum* was described. I have seen no type specimen and cannot place it at all. Herewith is a translation of the original description.

Leaves 3-sect, the segments divided into entire linear lobes; spur longer than the calyx; lamina of upper petals suboval, subentire, 2-toothed above the middle, long-pilose on both sides and on margin; seeds not lamellate. — Plant showy, 4.5 dm. Stem short-pubescent. Lower pedicels much longer than bract and flower. Calyx deep blue, subglabrous. Lower petals entire at tip, anterior shallowly bifid, with broad cleft. Flowers larger than in *D. grandiflorum* and with suborbicular entire lamina of upper petals, short-ciliate, short-pubescent beneath, bearded to base above. Caucasus at Kobi. Perennial.

Another name about which I am quite uncertain is *Delphinium cheilanthum* subsp. *schizophyllum* Brühl in Brühl & King, Ann. Roy. Gard. Calc. **5**: 99. 1896. It was based on a collection by Col. Davidson on the China hill near Naini Tal, Kumaun. I have seen no material by Davidson and can only guess by the name "schizophyllum" that the plant may belong in Group VI.

[*To be continued*]

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1967

THE YEAR 1967 MARKS the ninety-fifth anniversary of the establishment of the Arnold Arboretum in 1872 by the bequest of James Arnold. Early in the year official greetings were received from several institutions with similar interests around the world. Rather than take particular note of this ninety-fifth anniversary, permission was requested from the Harvard Corporation to prepare special activities for the Centennial year, 1972. Our plans, therefore, are directed toward that year when we may indicate the many accomplishments of the past and make known the goals for the future.

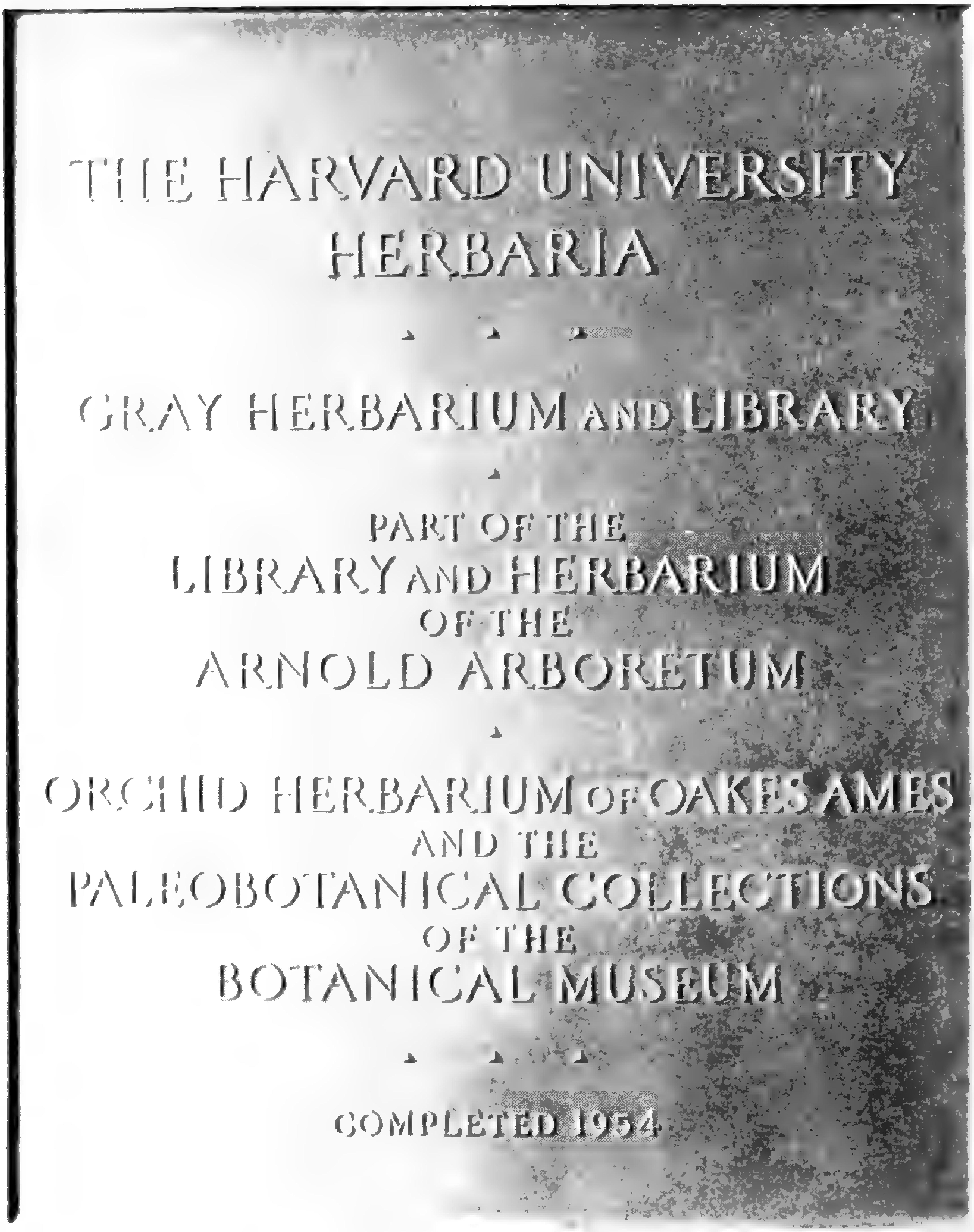
For nearly a decade a legal controversy over the Arnold Arboretum had been conducted in the courts of Massachusetts. This proceeding, which involved the President and Fellows of Harvard College as trustees of the Arnold Arboretum, concerned the legal right and questioned the decision affirming the scientific importance of locating a portion of the herbarium, library, and other research collections and the staff in a building in Cambridge, occupied jointly by members of the Gray Herbarium and the Botanical Museum. A "working herbarium and library" was to be retained in Jamaica Plain in association with the living collections. During the preceding fiscal year the Supreme Judicial Court of Massachusetts dismissed the case subject only to the assurance in a report to be filed, indicating that an adequate library and herbarium do exist in Jamaica Plain; that the location of all books is indicated in the general index files; and that a plaque has been placed in the Cambridge building housing the Arboretum materials. A report indicating that these conditions have been met was accepted by Justice Spaulding for the Court and the case finally has been dismissed.

In association with this action books belonging to the Arnold Arboretum and deposited in the libraries of the Department of Biology and the Harvard Forest since 1933 were recalled and incorporated with the books of the Arnold Arboretum in Cambridge or Jamaica Plain.

The President and Fellows also approved altering the name of the herbarium building in Cambridge to the Harvard University Herbaria, the plural form being the equivalent of "Laboratories," to indicate the multiple occupancy of the building. A bronze plaque was cast and placed in the foyer of the building listing the several independent collections housed in it, and the date of its completion, 1954.

In 1965, the Harvard Corporation approved the establishment of an Institute of Plant Sciences at Harvard to represent the botanical staff of

Photograph of the building newly designated as HARVARD UNIVERSITY HERBARIA.



THE HARVARD UNIVERSITY
HERBARIA

◆ ◆ ◆

GRAY HERBARIUM AND LIBRARY

◆

PART OF THE
LIBRARY AND HERBARIUM
OF THE
ARNOLD ARBORETUM

◆

ORCHID HERBARIUM OF OAKES AMES
AND THE
PALEOBOTANICAL COLLECTIONS
OF THE
BOTANICAL MUSEUM

◆ ◆ ◆

COMPLETED 1954

The plaque recently installed in the building of the HARVARD UNIVERSITY HERBARIA.

the University, the Institute to consist of and represent the staff members of the several botanical organizations at Harvard as well as botanical scientists associated with biological organizations. During the past year the Arnold Arboretum was invited to join in association as part of the Institute of Plant Sciences. This invitation was accepted and membership has been approved by the Corporation. The Corporation also noted that its vote of January 19, 1953, concerning the identity of the Arnold Arboretum is still in effect, and that the procedures for the Director of the

Arboretum to submit recommendations for appointments and for approval of budgets directly to the President are still in order.

Staff:

Although changes in the composition of the staff of an organization are to be expected annually it is always with personal feelings of loss that deaths and retirements of employees of long association are recorded.

Professor Irving Widmer Bailey, Professor of Plant Anatomy, *Emeritus*, died suddenly on May 16th. Although stricken some weeks earlier with a coronary attack, his recovery had seemed probable when death came quickly. Professor Bailey received his A.B. degree from Harvard in 1907, and, except for a few years during World War I, was associated with Harvard continuously. He became associated with the Arnold Arboretum in 1933 when many members of the Bussey Institution staff moved to Cambridge, and he retired officially in 1955. He continued his research in the laboratory of the wood collection he developed for the Arnold Arboretum, and he worked and published on an active schedule to the day before his attack. Tributes to him and for his work have come from all parts of the world. A review of his life will be published in the next volume of this Journal.

Thomas H. Curry, assistant superintendent of buildings and grounds of the Arnold Arboretum, served its living collections in Jamaica Plain for 18 years. He had reached retirement age and would have been retired at the end of the fiscal year. His death occurred, after surgery, on April 30, 1967.

A new appointment during the year was necessary in anticipation of another retirement. Mr. Victor Ferenc Marx was appointed librarian of the Arnold Arboretum and, jointly, librarian of the Gray Herbarium on May 1, 1967. This appointment overlapped briefly that of Mrs. Lazella Schwarten. Mr. Marx came to Harvard from the University of Washington School of Librarianship.

Mrs. Schwarten served the library of the Arnold Arboretum for 23 years and, for the last 13 years, held a joint position as head librarian of the Gray Herbarium and the Arnold Arboretum. She not only served the staff and cared for a major library, but also aided taxonomic botanists, botanical historians, and many others in the field from institutions all over the world. She excelled in all these activities, and her aid has been acknowledged with spontaneous gratitude. Although her efforts in preparing the *Index to American Botanical Literature* published by the Torrey Botanical Club are noted only as items in her bibliography published each year in these reports of the Director, this index is a major tool in taxonomic and general botanical bibliographic research. Her bibliographies of the published writings of many present and former staff members are also most useful. Mrs. Schwarten's greatest effort in the past decade however, has been the organization of the books of the Gray Herbarium and the Arnold Arboretum in Cambridge, and those of the Arnold Arboretum relocated in Jamaica Plain, into working libraries. Only the staff that saw this develop can truly appreciate the tremendous effort involved. Finally, we would note that Lazella Schwarten served the botanical world through the *Journal of the Arnold Arboretum.* Articles by her are not numerous, but the word "Circulation" on the cover is also inadequate to describe her work in making certain that botanists around the world received the Journal.

When the University announced Mrs. Schwarten's retirement, to take place this year, the associated staffs scheduled an appropriate gathering. A gift from the Arnold Arboretum and Gray Herbarium recognized her service to both institutions. In addition a bound volume of letters solicited from her friends who had used the library recorded gratitude from many botanists of numerous countries. The July number of this Journal was also dedicated to Lazella Schwarten. Regretfully, this report of the Director records her retirement from the staff.

Dr. Harrison Leigh Flint whose appointment as Associate Horticulturist was effective on July 1, 1966, for five years, came to our staff from the University of Vermont.

Gordon Parker DeWolf, Jr., was appointed Horticultural Plant Taxonomist, effective March 15, 1967, for a period of five years. Dr. DeWolf received his Ph. D. degree from Cambridge University, having worked under Dr. E. J. H. Corner on the genus *Ficus* in tropical America. He served as an Associate Professor of Botany at Georgia Southern College before joining the Arboretum staff. His research interests in cultivated plants and native floras are supported by his field work and study in such areas as New England, Malaysia, Europe, and Africa.

Two Mercer Fellows completed their studies during the year. Mr. Pablo Legname returned to his position at the University of Tucuman in Argentina and Miss Sandra Shannon accepted a position at the Waltham Field Station of the University of Massachusetts. Dr. Charles C. Tseng completed his studies of the flowers and fruits of the Araliaceae conducted during the summer as a Mercer Research Fellow, and returned to his position at Windham College in Vermont.

Several new assignments were undertaken by the staff. Dr. Richard Howard was appointed to the Commission on Horticultural Nomenclature and Registration for the International Society for Horticultural Science. Dr. Lorin Nevling was appointed a member of the Faculty of Arts and Sciences of Harvard University. He was also appointed Secretary of the American Society of Plant Taxonomists and designated as a representative of the Council of that organization to the American Association for the Advancement of Science, to serve also as Secretary of the Systematic Section of the Botanical Society of America. Dr. Bernice Schubert was appointed Secretary of the Standing Committee on Stabilization of the International Association of Plant Taxonomists. Dr. Carroll Wood was appointed Lecturer on Biology during the year 1966–67, while he was teaching a course in plant taxonomy.

Horticulture:

Recent reports have referred to the drought of the last five years. The rainfall for 1966 was 41.14 inches, 5.55 inches below the normal for Boston. During this period the three conspicuous ponds in the Arboretum were at their lowest since 1937. Watering with metered water was continued through the summer of 1966. The plastic piping which had been run to the top of Bussey Hill made it possible to water and probably to save the large collection of leguminous and ericaceous shrubs there.

The dry spell was broken during the winter, however, and between January 1 and May 31, 1967, approximately 25.6 inches of rain were recorded at the Arboretum. This was an excess of 5.02 inches over the normal. A total of 7.32 inches in May made it the second wettest May in 97 years of official U. S. Weather Bureau records. The wetness was accompanied by unusual cold so that the common lilacs did not come into full bloom until June 3, the latest flowering time in the 36 years we have kept such records.

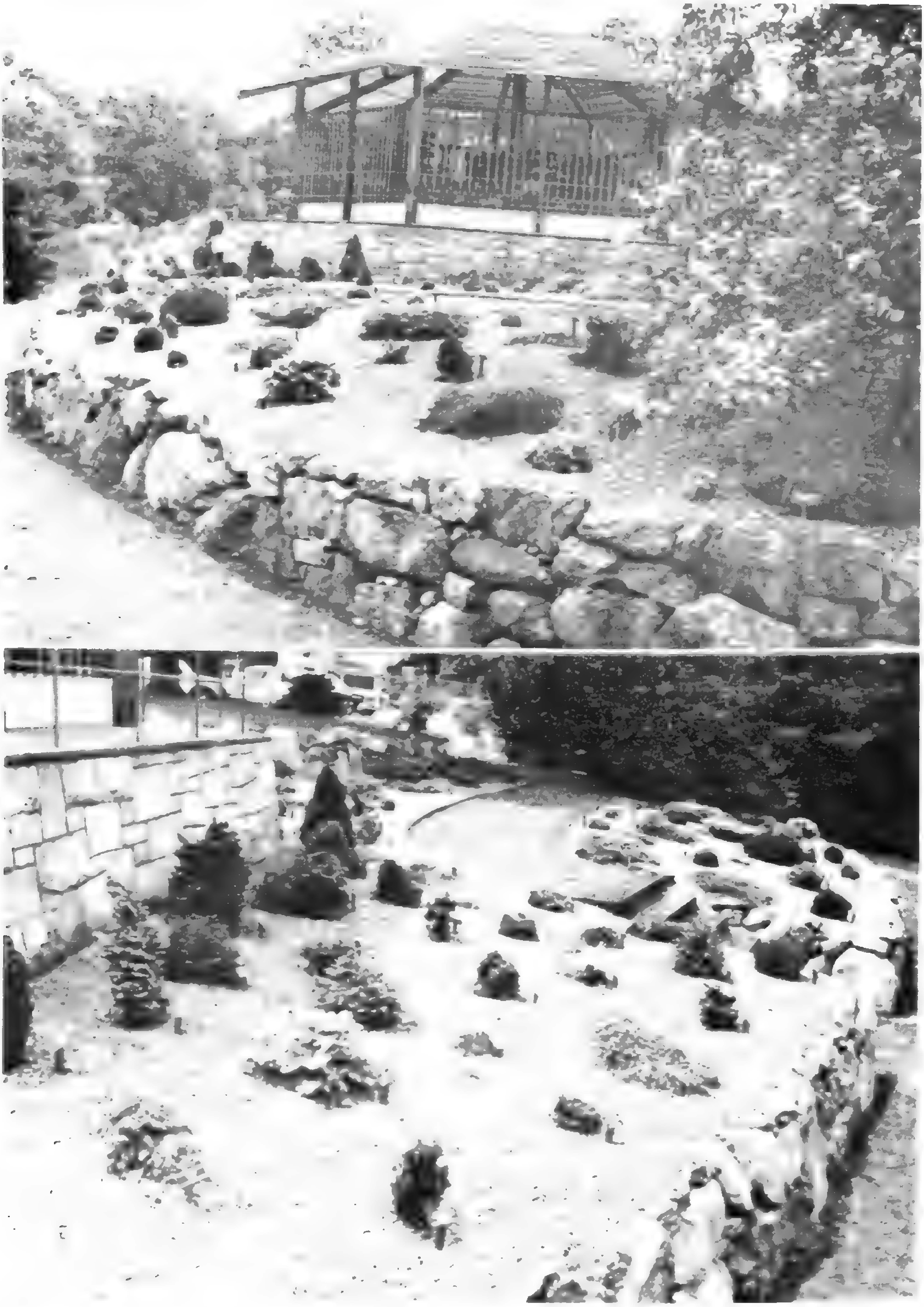
The conditions of fall drought, and excess water and low temperatures in the spring again altered our planting schedule. Plants could not be dug in the nurseries in Weston nor cared for in many areas on the grounds in Jamaica Plain. Eventually, however, 570 plants representing 480 taxa were added to the collections. Most significant was the planting of 50 *Rhododendron fortunei* selections which originated on the Dexter Estate in East Sandwich, Massachusetts. Dr. Wyman has served on a committee to collect and evaluate these widely distributed "Dexter Hybrids" of which the most desirable are now planted on Hemlock Hill. Regular embossed labels identify them as completely as possible and include the location of the original plant.

A severe ice storm again occurred in New England in February causing considerable branch damage. In the *Thuja* and *Chamaecyparis* collection much pruning and repair was needed and duplicate, old, and broken plants were removed to give the healthy specimens additional space.

Work continues on the terracing of the slope below the Larz Anderson bonsai house near the Dana Greenhouses. Field stone walls, graded paths and steps made of railroad ties have enhanced the appearance of the area where more than 125 taxa of dwarf conifers have been planted and mulched with gray stone.

The old Centre Street roadbed in the northwest corner of the Arboretum was excavated to an average depth of two feet. Large quantities of mulch and any available soil were used to fill the road bed. Grading was hardly completed when snow stopped further work; seeding and some planting were delayed until spring. The cost of reclaiming this old road area amounted to $7,000 for contract labor with heavy machinery.

During the winter it was possible to begin a clearing and cleaning operation on the low land adjacent to the Hebrew Rehabilitation Center for the Aged. This hospital was built on land formerly called Joyce Kilmer Park, acquired from the City of Boston. It is adjacent to land owned by Harvard University for the Arnold Arboretum and not under lease from



Two views of the terrace for genetic dwarf conifers below the Larz Anderson bonsai house. The wall is of native field stone. Gray stone is used for mulch.

the City. The unkempt low land served as a barrier during the construction of the hospital but the present operations anticipate development of the area as a formal part of the Arboretum. A major expenditure will be required for fencing, development of roads and paths, and redevelopment of top soil before the land can be fully utilized.

The threat to the Peters' Hill plantings from the bill filed in the Legislature to create a ski tow in the Arboretum required action this year to control access in the winter. The area is normally not ploughed by the City and our own equipment is inadequate for the purpose. A chain link fence was installed for half a mile along Bussey Street giving immediate protection to the half of the area most readily approached by automobile. The police were requested to enforce the regulations of the Park Department regarding skiing. Eventually, additional expenditures for fencing may be required to prevent skiing on the hill and to protect the younger plantings.

During the past year air pollution legislation prohibiting open fires was adopted in Boston. Withholding of permission to burn debris and trash from the grounds has proven to be extremely inconvenient and the added expense of commercial waste-disposal is inevitable.

Previous reports have referred to changes proposed for the buildings in Jamaica Plain if legal directives did not require the return of materials from Cambridge. During the year the first of these changes was completed by the addition of a glass unit consisting of three controlled-environment sections to the Dana Greenhouses. In addition, air conditioning was installed in the laboratory for cytology and morphology, new lighting was installed in the library of the Administration Building and safety flood lights added on to the front and rear of the building for automatic operation during the winter. New lunch room and additional rest room facilities have been completed. Plans have been developed for the construction of a new garage and vehicle repair facility which will stand free yet close to the Administration Building, permitting the removal of motor vehicles and grounds equipment from the basement. Architects' drawings are being prepared prior to a request for bids on construction. Also under construction is a laboratory for plant hardiness studies, including those in cryobiology, in the basement of the Dana Greenhouses. A "Gro-Mor" greenhouse of polyethylene plastic over aluminum frames 11 × 96 feet has been erected in the greenhouse area. A rearrangement of the nursery area has been completed and includes the installation of new ground drainage, watering facilities, and gravel surfaces for the handling of plants grown in plastic containers. Slightly over 1000 square feet are devoted to this purpose.

Through the efforts of Dr. Flint a new coöperative hardiness testing program has been initiated to obtain more reliable information on the characteristics of some of the more important woody ornamental plants in parts of New England colder than the Boston area. This program is to be carried out with the assistance of about 25 coöperators selected as uniformly as possible in hardiness zones 3 and 4. Pot-grown plants of

ABOVE: Rear view of the Dana Greenhouses of the Arnold Arboretum. The unit on the right was newly constructed in 1966.

BELOW: The "Gro-Mor" greenhouse of polyethylene plastic on aluminum frames and the compacted gravel area for the pot grown plants used experimentally for hardiness tests at the Arnold Arboretum.

about 20 taxa will be distributed annually for trial. At the same time observations will be made on plants already under test. To date 19 coöperators have accepted invitations to participate. A limited number of plants was distributed in the Spring of 1967 and the program is expected to reach full scale in 1968. More than 40 taxa have been propagated for distribution in 1967, 1968, and 1969.

Mr. Fordham has continued his long-range program of testing seed germination and propagation procedures for the plants within the Arboretum collections. Ninety-six additional taxa were handled during the year for such information. The search for abnormal plants in natural habitats also continues; eleven seedling populations and 16 asexual propagations from witches'-brooms are presently under study. Seedling plants developed from seeds of abnormal conifers have been followed for several years and the accumulating records now begin to shed light on the nature and cause of the unusual growth forms.

Three members of the horticultural staff, Dr. Wyman, Mr. Fordham, and Mr. Gensel, spent some time in Puerto Rico conducting studies and observations on the growth and reproductive characteristics of plants in the elfin forest project-area. Plant materials were propagated on the site and in nearby areas while comparable materials have been returned to Jamaica Plain for similar tests under more scientifically controlled conditions.

The past winter again produced unusual flowering patterns in many shrubs because of snow protection near the ground and varying levels of cold air above. Mr. Gensel, working with Dr. Flint, has undertaken controlled studies of cold resistance through flower bud development in several taxa grown in the Arboretum. The variations which occurred in taxa of ***Forsythia*** and ***Rhododendron*** under natural conditions during the past winter require much further study before an explanation is possible.

At the Maryland meetings of the American Association of Botanical Gardens and Arboreta the Arnold Arboretum was again appointed National Registration Center for woody plants not otherwise represented by Societies. The International Society for Horticultural Sciences approved the designation of the Arnold Arboretum as International Registration Authority for cultivars in *Weigela* and accepted the list published in *Arnoldia* as the International Registration List. At a special meeting of the IABG Dr. Howard was appointed funding coördinator for a project to test the methods of electronic data processing in relation to the record systems of botanical gardens. The Arboretum will work in coöperation with the University of Tennessee Arboretum where this program will be developed, using the computer systems at Oak Ridge.

Much of the time of the propagation staff is devoted to filling requests for plant parts for propagation or as the basis for special research studies. During the year 66 taxa were propagated for such special requests as part of 184 shipments of material to other gardens and to scientists in 17 countries. The propagation staff received 231 shipments of materials from 32 countries comprising 845 taxa. We supplied healthy materials for other gardens to grow, aberrant material for special developmental studies, diseased material for pathological investigation, foliage for animal food in special research projects, and dried materials for chemical extractions.

Case Estates:

With the increasingly large number of people who visit the Case Estates we have had a growing number of requests for literature, information, or guided tours of the land and the collections. During the past year two regularly scheduled field courses were conducted on the grounds, and two special programs for the Friends of the Arnold Arboretum, consisting of a series of evening lectures in the "Red Schoolhouse" and a series of Sunday afternoon lecture-tours on the grounds, were held.

Special encouragement is given to students and to school classes to visit the grounds and to learn the purpose of the work being done there. Awards for study projects in the elementary school system, initiated this year, should be continued. The students involved have brought their parents to the grounds and appreciation increases for the efforts of the Arboretum within the town of Weston.

During the year a trial bed of 70 taxa of *Allium* was started to contrast with those of *Narcissus*, *Lilium*, and *Hemerocallis*. Most of the *Allium* material was grown from seed and much was a gift of Mr. Nathaniel Whittier. The *Iris* collection previously established for trial was supplemented by a gift of representatives of the Dykes medal winners which show, for teaching purposes, some of the outstanding variation in the bearded irises.

A collection of 79 kinds of native asters of known origin and genetic structure was established on the Case Estates; a section of land was prepared for the studies of a new staff member on the species of *Dahlia*.

A collection of crab apples established several years ago in the big field on Newton Street across from the Junior High School flowered spectacularly this spring. The cultivar of *Malus* 'Henrietta Crosby' developed by Dr. Sax and planted along Wellesley Street was also unusually beautiful.

The isolated location of the Case Estates permits use of the property as a holding area for plants in post-entry quarantine. Almost 500 of the plants introduced by Dr. Wyman from his recent trip to Europe were released during the year and are growing on in the nursery areas. Others remain under continued restriction for future release.

Herbarium:

During the year 24,264 specimens were mounted and added to the herbarium, bringing the total number of specimens to 849,269. Of these, 5,861 were added to the herbarium of cultivated plants which is maintained in Jamaica Plain. That collection now contains 130,531 specimens.

In order to correct some of the unbalance of content in the herbarium of cultivated plants a program of special collecting and special exchanges has been emphasized recently. It is hoped that the result will be an increased representation of cultivated herbaceous plants and a better indication of the range of distribution of many cultivated woody plants. Such development will increase the significance of this particular collection and broaden its function of providing definitive information. The collection in Jamaica Plain is also being checked to insure that all the taxa cited in Rehder's *Manual of cultivated trees and shrubs* and in Bailey's *Manual of cultivated plants* are, in fact, represented in the herbarium of cultivated plants.

A total of 18,863 specimens was received for the herbarium during the year. Of these, 8,791 were in exchange, 3,627 were gifts, 5,388 obtained through subsidy or support of field expeditions, 411 for identification, and 116 by special exchange, with 350 representing staff collections. This material came from herbaria or collectors in the United States, Papuasia, Europe, Western Malaysia, and Mexico and the West Indies in diminishing order, with specimens from seven other geographic areas also. We sent 10,675 specimens in exchange to other institutions; 899 as gifts; and 70 in exchange for identification.

For studies by staff and students a total of 76 loans were requested and received from 26 institutions, 14 in the New World and 12 in the Old World. The total of 7,152 specimens represented an average loan of 94 specimens. We received requests for material from our collections and made 143 loans to 78 institutions which averaged 115 specimens and comprised a total of 16,539 specimens. These were made to 28 foreign institutions and to 45 within the United States.

These series of figures do not indicate the great amount of organization and labor involved in maintaining high standards of quality in the herbarium and in keeping the collections in good order so that the many routine requests for information, photographs, identifications and so forth may be filled competently. Although the growth of the herbarium and the increase in its use is desirable and commendable, such growth continues to present problems of space in light of which plans for future additions to the collections and the buildings must be considered seriously.

The use of the herbarium comprises the basis for diverse studies in the field of botany and may result in monographic work of wide extent, floristic studies, manuals of wild or cultivated plants of extensive or limited geographic areas, and, as a complement to field studies, may produce most valuable data for work on breeding programs, chemical analyses, and various other avenues of research. In short, the projects of the staff often develop into studies of broader aspect than is immediately apparent. Brief statements concerning some of the current work follow.

Mr. Baranov completed his work on the variations in *Sorbus* and continues studies on plants of temperate Asia.

Dr. Brizicky is working on the Generic Flora of the Southeastern United States. His studies, however, often involve broader geographic areas or plant relationships. An example is his valuable contribution on the nomenclature of cotton, *Gossypium*, which forms part of his continuing study of the Malvaceae.

Dr. DeWolf, who has just joined the staff, has had his work interrupted by the change in location. His research interests are in the genera *Ficus* and *Dorstenia* of the Moraceae with special emphasis on the Afro-American relationships involved.

Dr. Hartley completed his study of *Zanthoxylum* in the Malesian area and turned to the genus *Lunasia*, also of the family Rutaceae. He has now named approximately 1,600 of his collections from New Guinea and in the process was able to annotate many tropical Asian specimens in the herbarium.

Dr. Howard spent a portion of the summer continuing his field studies on the elfin thickets or mossy forest on the summit of Pico del Oeste in the Luquillo Mountains of Puerto Rico. This work, which comprises a study of what is in the forest, the conditions under which the plants live. and a day by day account of what the forest is doing, represents one of the comprehensive ecological studies being conducted in the tropics. Other staff members have contributed their special talents to the study area including Miss Powell, Messrs. Fordham and Gensel, Grime and Canoso, and Drs. Wyman, Nevling, and Wood. The duration of the study has been extended to August, 1968, under the same grant from the National Science Foundation. Publication of the program and the special studies contributing to it should begin in the coming winter. In addition. Dr. Howard continues his studies of the vegetation of the Lesser Antilles with the identification of special collections from the area and the compilation of family treatments. Work has also started on a bibliography of the plants under cultivation in the American tropics. Lack of readily available references to the appropriate valid names and synonyms of tropical plants has handicapped progress in areas of science well beyond plant taxonomy. A bibliography will partially solve the problem of correct name and the authority. This is expected to be a long term project which may attract both workers and independent financial support.

Dr. Hu has continued her studies on plants from Asia and has prepared special contributions based on specimens of the Araceae borrowed from European herbaria at Paris and Copenhagen. She has made progress in the study of cultivars of *Hemerocallis* and in the preparation of special chapters in a forthcoming *Hemerocallis* handbook. A collection of plants from Mt. Omei, southwest China, made in 1938–40 by collectors for the Arnold Arboretum, has now been mounted and Dr. Hu is beginning the task of naming and inserting these specimens.

Mrs. Honor Moore of Canberra, Australia, has been appointed a Research Associate during the period her husband is in residence in the area. She is annotating our herbarium material from Australia and indicating the type specimens.

The activities of the herbarium have claimed a large proportion of the time and effort of Dr. Nevling during the year. Nevertheless, his research on *Schoenobiblus* and *Schizophragma*. and on the Thymeleaceae advances. Dr. Nevling is also coöperating with botanists from the Instituto de Biología. in Mexico. on studies of the flora of Veracruz. Approximately 1.400

specimens including duplicates were received during the year representing the initial effort of collectors in the area. Dr. Nevling will spend some time in this region during the summer. The Arnold Arboretum has agreed to subsidize a portion of the collecting in collaboration with the Jardín Botánico of the University of Mexico, and to identify the cultivated plants of the area. Specimens from this project will be available for distribution to other institutions and specialists willing to identify material representing particular families or genera from Veracruz are being sought.

Miss Dulcie Powell is revising for publication a study of the plants transported by the expeditions of Captain William Bligh and is continuing her regular studies of cultivated and native plants of tropical America and the West Indies.

Dr. Schubert has handled an unusually large amount of manuscript in her capacity as editor of the *Journal of the Arnold Arboretum*. Her studies on *Desmodium* are currently focused on the preparation of a treatment for the Flora of Tropical East Africa. Additional studies and identifications are continuing in the genera *Dioscorea* and *Begonia*. As Secretary of the Standing Committee on Stabilization of specific names of plants for the International Association of Plant Taxonomists she has the responsibility of coördinating the opinions of committee members, specialists, and other interested botanists in preparation for the report to be prepared for the next International Botanical Congress.

Dr. Wood continues to coördinate the effort of the small dedicated group of people working on the generic flora of the southeastern United States. With the resignation of Arnold Clapman, who worked as artist on the project, Miss Rachel Wheeler has been appointed staff artist. One of Dr. Wood's tasks is to keep the presentation of visual artistic material and written material as similar as possible to that previously published in the Journal. Dr. Grady Webster, now of the University of California at Davis, spent a portion of the summer of 1966 with Dr. Wood and prepared the treatment of the family Euphorbiaceae in the Southeastern United States. As indicated elsewhere, a new application submitted to the National Science Foundation for renewed support of this work has been approved. During the spring semester Dr. Wood taught an introductory course in the Taxonomy of Flowering Plants and continued his ever generous aid to students.

Library:

The end of the fiscal year marked the retirement of Mrs. Lazella Schwarten as Librarian of the Arnold Arboretum, a post she has held for nearly 23 years. During that time the library has grown from the 59,440 books and pamphlets recorded in the Director's Report of 1945 to a present total of 53,784 bound volumes and 20,879 indexed pamphlets for a total of 74,663. The high quality and good condition of the library, plus the ready availability of the books through the willingness of the librarian and her staff to assist scholars, have made the library of the Arnold

Arboretum outstanding among international botanical libraries. During the past year 488 bound volumes were added to the collections of which 138 were in areas of horticulture and were deposited in Jamaica Plain. Pamphlets numbering 285 were of value and were indexed and added to the collection.

Three additional major changes made during the past fiscal year are not included in the figures cited above. Bound volumes numbering about 600 on temporary deposit in the library of the Biological Laboratories since the 1930's were returned as were over 2,000 books and volumes of periodicals on the subject of forestry from the Harvard Forest. These volumes have always been included in the total count given in annual reports. Their deposit away from the main library of the Arnold Arboretum reflects the crowded conditions existing in Jamaica Plain prior to the construction of the Harvard University Herbaria building and the move to Cambridge. The relocation of these books necessitated changes on all file cards and, in the case of the forestry books, some recataloguing which is in progress. All cards in the general and combined library index of the Arnold Arboretum and the Gray Herbarium now are marked to indicate ownership of the book and its location, by code number and by letters on shelves in Cambridge or in Jamaica Plain.

Index cards, as issued, were added to the Gray Herbarium *Card Index to American Plants*, the Torrey *Index to American Botanical Literature*, and the *Index Nominum Genericorum*. Typed cards exceeding 1,200 were added to the Rehder Index to horticultural literature.

Under the direction of Miss Stephanne Sutton much work was accomplished on the historical correspondence of the staff of the Arnold Arboretum. Letters of former staff members have been arranged chronologically in new files and organized in alphabetical order by correspondents. A master card file indicates the number of letters in each folder and their dates. This work continues. We are pleased to acknowledge here the gifts of Sargent letters as well as photocopies of originals which were loaned to us.

Miss Sutton continues her work toward a biography of Charles Sprague Sargent. The problem of publication of quotations from letters to and from Sargent was solved in part, during the year, when permission was granted by the responsible heirs of Professor Sargent to quote from his correspondence. Mrs. George Slate has also given permission to quote from the letters of her father, the late E. H. Wilson, whose work was so closely connected with the development of the Arnold Arboretum.

Comparative Morphology:

For many years the contributions of the Arnold Arboretum in the area of comparative plant morphology have been primarily those of Professor Bailey and his students and assistants. Our loss is great with his death. Hopefully, we shall seek younger contributors to utilize the great collection of wood samples and microscope slides of plant parts built up during his many years of study. Professor Bailey had completed his investigations of the leaf-bearing cacti, a group which had long occupied him during summer work in Arizona. The final paper of the series will be published posthumously in this Journal. The Marcgraviaceae is a tropical family Professor Bailey knew from British Guiana. Upon completion of his cactus studies he turned to it and his excitement over the initial preparations indicated that another study series would be developed. Regrettably these observations will be denied to us.

Through the interest of Mr. Frank Hankins in the woods of Panama, we have been able to purchase microscope slides prepared from Panama woods previously unsectioned from our own collections and those of the Yale School of Forestry. In addition, approximately 150 slides added to the collection represent material received in exchange for wood samples.

Education:

Two regularly scheduled classes within the College of Arts and Sciences of the University were offered by Arboretum staff members. During the fall semester Dr. Howard taught Biology 209, "The Phylogeny of Flowering Plants," and in the spring semester Dr. Wood taught Biology 103, "The Taxonomy of Vascular Plants." Dr. Hartley taught the course in general botany offered by the Harvard University Commission on Extension Courses. In addition, the staff assisted in the supervision of the research or writing of graduate students and participated, as speakers or as commentators, in the seminars open to undergraduates and graduate students.

Non-credit courses open to the public were offered throughout the year in Weston and in Jamaica Plain as a contribution of the staff. Regular field classes were conducted by Drs. DeWolf, Wood, and Wyman, while, in addition, staff members Flint, Fordham, Howard, Nevling, Williams, and Wood also contributed to a special series of lectures and field trips held in Weston during the spring. Guided tours of the grounds of the Arnold Arboretum and special tours of the Case Estates were available to groups, on written request. These are most frequent in the spring. Because of the unusual weather this year many trips had to be repeated when flowering conditions became more satisfactory. Open Houses, including tours, were held for the Harvard Dames, the staff of the Department of Biology, and several national touring parties of horticulturists.

The staff did not prepare an exhibit for the Spring Flower Show of the Massachusetts Horticultural Society but four staff members, Messrs. Flint, Fordham, and Williams, and Dr. Hu gave lectures and/or demonstrations. A special exhibit of flowering shrubs and trees was prepared for the Worcester County Horticultural Society to supplement its annual *Iris* show.

A coöperative program in training in horticultural and botanical sciences has been conducted with Keuka College and the Jamaica Plain High School. Students from each of these schools have been given short periods of employment under supervision in order that they may learn curatorial, laboratory, or greenhouse techniques from the Arboretum staff. At Weston Junior High School an Interdisciplinary Team Teaching Program this spring selected the Arnold Arboretum and the Case Estates as a study area. Miss Marian Case had encouraged such scholastic interest during the days of the Hillcrest School when she offered prizes for the best studies of Weston School pupils. The Interdisciplinary Team project offered a similar opportunity to reward student interest in the work of the Arboretum. Cash prizes were awarded to Gregory Morrow, Catherine Searle, and Bruce Howard for the three papers judged best by their teachers. Honorary mention awards, reproductions of the drawing "Davidia," by Blanche Ames, were made to Jon Conant, Thomas Griffin, Lois Leonhardt, Richard Powers, and Nancy Raffio.

Staff members were guest lecturers to many groups during the year. Dr. Flint spoke to the Gardeners' and Florists' Club of Boston, the Connecticut Rhododendron Society, and at the University of New Hampshire. Mr. Fordham conducted several special demonstrations and tours of the Arboretum greenhouses for classes from colleges in four New England states and from the Niagara Parks Commission's School of Horticulture. Dr. Howard spoke at Auburn Community College, Auburn, New York, on a visit sponsored by the American Institute of Biological Sciences. He was also a program speaker at the annual Fall Symposium of the Missouri Botanical Garden which considered the subject "Systematics and Natural Areas." The Department of Botany at Miami University, Oxford, Ohio, sponsored his visit to that campus. During the year two programs were prepared for the School of Global Medicine of the U. S. Naval Medical School. These were "Tropical Flora of Medical Importance" and "Edible Plants of the Tropics." Both programs were recorded on closed circuit television in color and prepared for distribution to the Armed Forces as training tapes or 16 mm. film. Dr. Nevling was a guest lecturer to the Department of Botany of the University of Connecticut. Dr. Wyman was the principal speaker at the annual meetings of the American Rhododendron Society in Asheville, North Carolina, the Garden Clubs of Cincinnati, Ohio, and the Northeastern Section of the International Shade Tree Conference in Portland, Maine.

Again this year the staff assumed the responsibility for local arrangements in Cambridge for the midwinter meeting of the Northeast Section of the American Society for Horticultural Sciences.

Travel and Exploration:

The International Horticultural Congress and the annual meeting of the American Institute of Biological Sciences were held simultaneously on the campus of the University of Maryland in College Park. All staff members who could attend did so and many took part in meetings, served on committees, organized symposia or presented papers.

Dr. Wyman organized and conducted a section meeting on amateur horticulture for the International Society of Horticultural Science. He was in charge of the presentation of awards at the banquet of the American Horticultural Society. Dr. Nevling organized a symposium on the Diverse Applications of Plant Taxonomy for the American Society of Plant Taxonomists. Dr. Howard served as a representative at the meeting of the Commission on Nomenclature and Registration and presented an invitational paper in a symposium on the "Nomenclature and Registration of Cultivars."

Dr. Flint attended the annual meetings of the Society for Cryobiology and with Mr. Fordham attended the annual meeting of the International Plant Propagators Society where Flint spoke on testing landscape plants for hardiness in Vermont, and Fordham reported on "Woody plants difficult to root."

Miss Powell represented the Arboretum at the first annual meeting of the Caribbean Conservation Commission, held in Grenada. She explored the area of Morne Quaqua and later, a mountain on St. Kitts, to determine the possibility of using these areas for further studies of elfin thickets. Material from each area was also returned to Boston by air mail to determine the possibilities of such a method of shipment for scientific studies of living specimens.

Dr. Schubert attended the A.E.T.F.A.T. meetings held in Uppsala, Sweden, and before and after these meetings visited and worked in herbaria in Paris, Stockholm, Vienna, and at Kew and the British Museum (Nat. Hist.), in London. Later she again represented the Arboretum at the third Mexican Botanical Congress in Mexico City. She made a short

The 1966 plenary session of the Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale (A.E.T.F.A.T.) held in Uppsala, Sweden. Dr. Bernice Schubert represented the Arnold Arboretum at these meetings.

field trip following the Congress to locate material of *Nanarepenta tolucana* Matuda, purportedly rare, which may well be a species of *Dioscorea* already described.

Dr. Wood attended a special symposium on terrestrial plant ecology held at St. Francis Xavier University in Nova Scotia.

Gifts and Grants:

The Arnold Arboretum is fortunate to receive small monetary contributions from many people who visit the grounds throughout the year. This immediate expression of appreciation is warmly received. We value equally highly the generous response to an annual appeal made to the contributors of longer standing who are the Friends of the Arnold Arboretum. During the past year the gifts for current use have been assigned to support work in horticulture in Jamaica Plain, except for the few specified for other purposes. Additional summer help on the grounds and in the greenhouses was made possible by these gifts. An additional bequest from the estate of Laura Lucretia Case was added to the endowment funds of the Arnold Arboretum.

Gifts and grants were also received in support of specific portions of the living collections and for the research of the staff. Most significant was the grant made for the support of a *Generic Flora of the Southeastern United States* under the direction of Dr. Wood. The project supported by the grant has been approved for a period of five years although the present grant covers only the first two. This continuing study was supported in its initial stages by Mr. George R. Cooley and, more recently, by other grants from the National Science Foundation. Forty-five papers treating 76 families and 249 genera of flowering plants have already been published for this study in the *Journal of the Arnold Arboretum.*

We are pleased to acknowledge the many gifts of plants, books, manuscripts, and similar material items which increase the value of the Arboretum as a research and reference institution. Mr. William J. Flemer of the Princeton Nurseries has supplied valuable plant material for the street tree collection. Mrs. A. F. Bonsal of Upper Montclair, New Jersey, has been instrumental in obtaining for us *Iris* rhizomes of the Dykes medal winners to supplement the display and teaching collection at the Case Estates. Mr. Nathaniel Whittier of Medfield, Massachusetts, has donated many bulbs of interesting taxa of *Allium.*

The University of New Hampshire made a gift of the Latimer Seed Collection which is to be used as a teaching and reference collection at the Dana Greenhouses.

Additional research material on the Caribbean area from the library of the late George H. Hamor was a gift of his widow. Mrs. Van Wyck Brooks presented the Arboretum with the original letters she had received from Professor Sargent.

These gifts and many others are of significance and value to the increasing collections of the Arnold Arboretum.

Publications:

The twelve numbers of *Arnoldia* issued annually, but at irregular intervals, are contributions of the Arboretum staff to the field of horticulture. During the past year several invitational articles of special interest were published. A paper by Dr. John Creech of the United States Department of Agriculture was presented at the annual meeting of the American Horticultural Society in Georgia and published in *Arnoldia* as "Expeditions for New Horticultural Plants." At the International Horticultural Congress Dr. Peter Lapin of the Main Botanical Gardens in Moscow spoke of the efforts of that organization in plant introduction and on the hardiness of ornamental shrubs. He agreed to revise this presentation and describe his research in a special article which we were pleased to publish as "Seasonal Rhythm of Development of Woody Plants and its Importance in Introduction."

The work of Dr. Wyman and Dr. Flint in revising the plant hardiness map which serves as a basis for numerical indication of plant hardiness comprised another issue of *Arnoldia*. The accompanying text compared the several systems of hardiness zonation now in use. Copies of this bright and clear new color reproduction have been distributed to botanists and horticulturists throughout the country.

Dr. Schubert served as editor of the *Journal of the Arnold Arboretum*. Four issues published during the year comprised 387 pages and 22 papers. The first of Dr. Philip Munz's studies of *Delphinium* and *Consolida* of Africa and Asia were published in 1967. This series, treating some important collections of the Arnold Arboretum, will continue through April, 1968.

Dr. Howard was guest editor of the July, 1966, number of the *Newsletter of the American Association of Botanical Gardens and Arboreta* which featured a survey of methods of security and the problems of protection of plants and people in the botanic gardens and arboreta of North America.

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RICHARD A. HOWARD, *Director*

The Board of Overseers of Harvard College
Committee to Visit the Arnold Arboretum

Augustin H. Parker, Jr., *Chairman*, Boston, Massachusetts.
George R. Clark, *Vice-Chairman*, Philadelphia, Pennsylvania.
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Richard P. White, Washington, D.C.
Nathaniel Whittier, Medfield, Massachusetts.

Mercer Research Fellows
during at least part of fiscal year 1966–1967

William Gensel, University of Rhode Island, Providence, Rhode Island.
Pablo Raul Legname, Instituto Lillo, Tucuman, Argentina.
Sandra Shannon, University of Massachusetts, Amherst, Massachusetts.
Charles C. Tseng, Windham College, Putney, Vermont.
Francis H. Wolfe, University of New Hampshire, Dover, New Hampshire.

[†] Died January 6, 1967.

Staff of the Arnold Arboretum

1966–1967

RICHARD ALDEN HOWARD, Ph.D., Arnold Professor of Botany, Professor of Dendrology, and Director.

IRVING WIDMER BAILEY, S.D., Professor of Plant Anatomy, *Emeritus.*†
KARL SAX, S.D., Professor of Botany, *Emeritus.*

PRISCILLA JEAN JAMES-ASHBURNER, Business Secretary.
ANDREY I. BARANOV, Curatorial Assistant.
GEORGE KONSTANTINE BRIZICKY, R.N.Dr., Botanist, Southeastern Flora Project.
MICHAEL ANTHONY CANOSO, M.S., Senior Curatorial Assistant.*
GORDON PARKER DEWOLF, JR., Ph.D., Horticultural Taxonomist.
HENRY DRAPER, Superintendent, Case Estates.
HARRISON LEIGH FLINT, Ph.D., Associate Horticulturist.
ALFRED JAMES FORDHAM, Propagator.
WILLIAM ED GRIME, B.A., Curatorial Assistant.*
THOMAS GORDON HARTLEY, Ph.D., Associate Curator of Pacific Botany.
HEMAN ARTHUR HOWARD, Assistant Horticulturist.
SHIU-YING HU, Ph.D., Botanist.
MARGARET CATHERINE LEFAVOUR, Herbarium Secretary.
VICTOR FERENC MARX, M.Libr., Librarian.*
HONOR CAPEL MOORE, M.Sc., Research Associate.
LORIN IVES NEVLING, JR., Ph.D., Associate Curator and Supervisor of the Herbaria.*
DULCIE ALICIA POWELL, M.A., Research Fellow.
BERNICE GIDUZ SCHUBERT, Ph.D., Associate Curator and Editor.
LAZELLA SCHWARTEN, Librarian.* **
STEPHANNE BARRY SUTTON, A.B., Research Fellow.
ROBERT GEROW WILLIAMS, B.S., Superintendent.
CARROLL EMORY WOOD, JR., Ph.D., Associate Curator.
DONALD WYMAN, Ph.D., Horticulturist.

† Died May 16, 1967.
* Appointed jointly with the Gray Herbarium.
** Retired June 30, 1967.

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