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A MONOGRAPH OF THE GENUS PHILADELPHUS

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With six plates

INTRODUCTION

Philadelphus is geographically one of the most widely distributed genera in nature, ecologically one of the most varied groups in habitat, and horticulturally one of the most popular shrubs in our gardens. Its slightly discontinuous distribution forms a belt girdling the temperate zone of the northern hemisphere, extending to the higher altitudes in the tropics in North America. The early inhabitants of Asia Minor, Eastern Asia and Central America, centers where different culture patterns originated, have independently discovered its merits and have brought under cultivation many species for their showy flowers, their enticing fragrance, or for their medicinal value. In ancient times the Parthians employed the flowers in the preparation of hair perfume, and the advanced people of Mexico, and apparently those of Central America, used the flowers for making garlands, and the leaves for medicine. By the early part of the eleventh century, the Chinese garden forms had developed to such a degree of excellence that they were presented by the people of Szechuan as special tributes to the emperor in Peking. Due to their hardiness, their ability to tolerate a wide range of environmental conditions, their ease of propagation, and their flowering late in the spring season, the species of *Philadelphus* have become garden favorites, especially in the northern hemisphere.

By the latter part of the nineteenth century, forms of both Asiatic and American origin were established in various European gardens. Much was written about them, and very many binomials based on these exotic forms were published. Sometimes several or even up to a dozen different names were assigned to specimens taken from plants of the same origin. Some of the individual authors had only limited material for purposes of comparison, and others lacked specimens from the type localities. Thus it was inevitable that specific names were multiplied and much confusion resulted. In addition, clerical errors in recording names and in labeling living plants and preserved material provided further complication. In

some cases proposed new species were accredited to regions remote from their actual place of origin. Naturally different names came into use for species which not even a specialist could distinguish, and at the same time a single name may have been applied to very different species. Both botanists and horticulturists have complained of this nomenclatural confusion, yet since 1896 there has been no monographic work for the clarification of the entire group. Only scattered papers treating selected species or isolated groups from certain areas have been published. Actually, the lack of uniformity in selecting diagnostic characters by different authors has created further confusion. Thus it is that a practical scheme for the classification of the numerous species in the light of modern taxonomic knowledge and under the regulations of the accepted code of nomenclature is an urgent need.

Unaware of the difficulties in identifying species of this genus, I tried to name some unstudied Chinese material in the Arnold Arboretum herbarium. To my surprise, I was unable to find a workable key which could enable me to distinguish the Asiatic forms. After studying all the original descriptions I found myself even more confused for most of them are so meagre and the characters indicated are so generalized that one description often applies to any one of a number of obviously different species. I turned to more experienced taxonomists and horticulturists for advice and was warned that the species of *Philadelphus* have long been a botanical problem, and it would be wise for me to leave them alone. Though inexperienced in the group and perplexed by the confusion, I had the conviction that the man-made disturbances in the classification of the group could be solved when a real knowledge of the plants themselves had been acquired. I thus commenced an intensive study of the genus involving both living and herbarium material. My hope was that by careful examination of a large number of herbarium specimens collected from various centers of the natural range of the species supplemented with firsthand observations on the living plants cultivated in the Arnold Arboretum, the general pattern of the evolution of the genus might be discovered, and a natural order of relationship of the diversified taxa within the genus might be outlined. Besides the material deposited in the herbarium of the Arnold Arboretum (A) and the Gray Herbarium (G) of Harvard University, large loans were obtained from the Bailey Hortorium of Cornell University (BH), the Chicago Natural History Museum (F), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the University of Tennessee (TENN), and the United States National Herbarium (US). In September 1952, after the annual meeting of the American Society of Plant Taxonomists which took place at Cornell University, I examined the *Philadelphus* collection of the Wiegand Herbarium of that University (CU) and incorporated the notes in my manuscript. With these specimens, vegetative as well as floral characters were carefully analyzed. One by one the characters of geographically remote yet morphologically close taxa were intensively studied. Variations in each character were plotted with due allowance

for changes that may be caused by the age and vitality of the plant as observed in cultivated forms. The more constant characters were distinguished from the variable ones, and thus what I believe to be the fundamental morphological characters essential to proper specific diagnoses were ascertained. At the same time due attention was also given to those characters which might be used to advantage in defining categories above or below the specific level. By using these categories as standards of differentiation, various components of the geographically distinct groups were again investigated. Taxa of the same level were placed in what I assume to be their proper status, and thus a simple scheme of classification expressing the phylogenetic relationship of different groups was constructed on the basis of morphological characters and geographic distributions. It is hoped that this scheme will not only illustrate certain principles in the evolution and distribution of the genus, but also be of some service to horticulturists and to botanists who are concerned with the identification of their *Philadelphus* material, and to cytogeneticists who are interested in the chromosome numbers and behaviors of the various forms of this genus.

In this study the determinations of the taxa are made by comparing the specimens with the types as far as they are available. Since over 40% of the binomials pertaining to this genus were based on cultivated forms with no type ever designated, and sometimes with no actual specimens preserved, material annotated by their authors or specimens prepared from plants cultivated in the gardens indicated in the original publication are used to substitute for the types. In cases like *P. inodorus* Linn. where the taxon was based entirely on a previously published plate and a pre-Linnaean description, specimens from the type locality which best matched the illustration and agreed with the description were selected for identification purposes.

My thanks are due not only to the curators of the herbaria mentioned in the foregoing paragraph for the use of the facilities in their herbaria and libraries or for generous loans of material, but also to Dr. E. D. Merrill for patiently going over a large part of the manuscript with many valuable suggestions, to Dr. C. E. Kobuski for helpful criticisms and suggestions, to Dr. I. M. Johnston for assistance in locating literature regarding North American species, to Dr. K. Sax for consultations on cytogenetic and hybridization problems, to Dr. D. Wyman for the unselfish sharing of his profound knowledge of the living plants as well as the records of the cultivated forms on the grounds of the Arnold Arboretum, to Miss E. E. Upham for her patience in answering my numerous questions concerning both English and Latin, and to Mr. H. Howard for the photographs. I am also indebted to Dr. G. Taylor, Keeper of Botany at the British Museum and Dr. Charles Baehni, Director of the Conservatoire et Jardin Botaniques, Genève. With the help of Mr. Exell, the former gave me a detailed description of the nature of the pubescence on the hypanthium, disk and style of the type of *Philadelphus coronarius* Linn. in the Linnaean Herbarium. Through Professor E. D. Merrill, the

latter sent me the photographs of Schrader's manuscript and drawings together with the photocopies of the types of Schrader's species as published in De Candolle's *Prodromus*.

HISTORY

The first written account of a plant belonging to *Philadelphus* is found in a Chinese poem of the eleventh century describing the fragrance, color and contrast of the white flower with the green foliage, thus: "Herbs for color, trees for shape; None in fragrance to this [*Philadelphus*] compare. Like white foam in a sea of green, Unique among the shrubs it has been." Although this passage, like those of Gerarde, Clusius, Bauhin and other pre-Linnaean authors pertaining to the plant, is nomenclaturally of no importance to modern taxonomists, it nevertheless indicates the antiquity of man's knowledge of the *Philadelphus*.

By the time of Linnaeus, *Philadelphus* had already become a widely cultivated plant in European gardens. In pre-Linnaean literature it appeared as *Syringa* Tournefort, *Frutex coronarius* Clusius, or *Philadelphus Athenaci et Rivinii*. Linnaeus established the genus in 1737 and validated it in 1753. He recognized two species, *P. coronarius* and *P. inodorus*, and distinguished them by their leaf margins. Accordingly, the former species is characterized by its subdentate leaves and the latter by its entire leaves. The fresh material in the gardens of Clifford and Uppsala provided Linnaeus firsthand information about *P. coronarius*. Judging from the material preserved in the Linnaean Herbarium, he correctly identified it as representing Clusius' *Frutex coronarius*. Of the second species, he saw no specimen. His binomial was based wholly on the Catesby description and plate which in turn was based on material observed at the Savannah River region on the border of South Carolina and Georgia.

From the time of Linnaeus to that of A. P. de Candolle, botanists who were interested in *Philadelphus* had their studies limited to the few species of European and American origin, especially the cultivated forms. Miller in 1768 added one dwarf species and a variety with variegated leaves. As he had a larger collection of the living plant belonging to this genus, he perhaps acquired a more intimate knowledge of the group. He had seen sterile specimens of *P. inodorus* Linn. which he raised from cuttings sent him by Dale from Carolina. As these plants were killed by frost when two years old, his records on the height of the plant, the color of the flower and the size of the fruit were probably abstracted from Catesby's accounts. Willdenow in 1809, on the basis of material cultivated in the Botanical Garden of Berlin, described *P. grandiflora*, distinguishing it from *P. inodorus* Linn. by its prominently toothed leaves. About that time, *P. inodorus* Linn. was also in cultivation in a few gardens in England. Sims in 1812 on the basis of a specimen sent him by Wiltey of the Fulham Nursery prepared a colored plate and a description for that species.

During this period, with the exception of Nuttall and Michaux, authors

on American flora had a very dim concept of the published species of American *Philadelphus*. Walter (1788) in the *Flora Caroliniana* presented a very general account of *P. inodorus* Linn. After comparing his statements about this species with that of Linnaeus, one has a feeling that he had never seen a specimen of it for he used even the same wording as Linnaeus. Michaux, being a true field naturalist, had seen the plant and in his *Flora Boreali-Americana* published in 1803 he used hitherto unknown characters about the long acuminate sepals, suboval petals and elongated undivided style for distinguishing *P. inodorus* Linn. Pursh in 1814 recognized four species, one of which, *P. lewisii*, was new. According to the material he cited, he probably had not seen any *P. inodorus* Linn. in America. His description was based on Sims' illustration and the cultivated material in England. Elliott in 1821 admitted that he had seen no specimen of *P. inodorus* Linn. in the various collections of dried plants which he had examined. He further stated that the plant was so rare in nature that no botanists in his day had seen it in the woods.

Nuttall in 1817 described *P. hirsutus* on the basis of his own collection from the bank of the French River near Warm Springs, Tennessee. His description of the species indicates that he was a man of keen and accurate observations and consequently his treatment gives the truest picture of the genus up to his time. He recognized four species. As three of them were American in origin, he was led to conclude that *Philadelphus* is "a North American genus, with the exception of *P. coronarius*." With our present knowledge of the genus, there is a great deal of truth in this statement, for not only the largest numbers of species of the genus occur in North America, but the principal morphological changes of the group are also found here.

Schrader was the first man who attempted to study the entire genus extensively. His dissertation on *Philadelphus* with illustrations which has been cited by De Candolle and Loudon has never been published. The manuscript is preserved in the Conservatoire et Jardin Botaniques, Genève. Part of it was incorporated by De Candolle (1828) in his *Prodromus* III. After Schrader's death, in the "Reliquiae Schraderianae" published in *Linnaea* (1838), an improved form of that dissertation appeared again, but without illustration. In the manuscript as well as the latter paper he included nine species and four varieties of *Philadelphus*. Unfortunately his material was largely limited to the forms then cultivated in European gardens. Having no access to specimens representing species already described by American botanists, he created several synonyms. Moreover, he accepted garden sports or hybrids as representing species and thus created additional confusion. He divided the then known species into two sections on the basis of the habit and the inflorescences, but assigned no sectional names to them. In the section "Caulibus crassioribus strictis, floribus racemosis" he recorded five species and three varieties. The rest were placed in the section "Caulibus tenuioribus virgatis laxis, floribus solitariis ternisve." Schrader's conclusions, whether correct or incorrect,

were followed by European botanists and horticulturists for over half a century.

De Candolle in 1828, using Schrader's manuscript as a standard, published a comprehensive treaty on the genus. He recognized eleven species and three varieties. For the three extra American species not included in Schrader's manuscript, he simply annexed them to Schrader's order and placed them all in the slender-stemmed and solitary-flowered group. This represents a very indiscriminate treatment, for closely related species like *P. coronarius* Linn. and *P. lewisii* Pursh, which are alike in their habit and inflorescences, were placed in separate sections.

Loudon in 1833 in *Arboretum et Fructicetum Britannicum* gave an illustrated comprehensive account of the genus. He recognized ten species and four varieties, placing them in two sections. In the "Stems stiff and straight. Flowers in Racemes" section he included six species and four varieties and in the "Stems more slender, rambling, twiggy and loose. Flowers solitary, or 2 or 3 together" section he had four species. In this classification what we now interpret as inseparable entities, like *P. inodorus* Linn. and *P. grandiflorus* Willd., were placed in different sections.

Philadelphus from Asia and Central America did not appear in botanical literature until the eighteen thirties. Wallich was the first person to discover a species of *Philadelphus* from Asia. In 1831 he named the specimens procured from Gossainthan, Sirmore and Kamaon as *P. tomentosus* and *P. triflorus*. G. Don in 1832 validated the first binomial by giving it a description and Royle in 1839 prepared a colored plate for this Himalayan taxon.

Schlechtendal in 1839 on the basis of Schiede's collection from Jalapa and Ehrenberg's collection from Carmen described *P. mexicanus*, the first species of *Philadelphus* from Central America. About the same time, Bertoloni (1840) published an illustrated account of a Guatemala species under the name *P. myrtoides*, a species which marks the southmost limit of the spontaneous distribution of the genus.

A. Gray in 1849 on the basis of Fendler's collection from Santa Fe Creek, New Mexico, published *P. microphyllus*, the first known xerophytic species. The plant was introduced to Europe in 1883 and hybridists there took advantage of its low habit and very agreeable fragrance and in the autumn of 1887, the Lemoine Nursery of Nancy, France, put into commerce a novelty under the name, *P. lemoinei*, which was announced to be the result of a cross between the American small-leaved species, *P. microphyllus* Gray and the much cultivated European species, *P. coronarius*.

Lindley and Paxton in 1852 published *P. satsumi* Sieb., the first known species of *Philadelphus* from Eastern Asia, on the basis of both living material introduced and the herbarium specimens prepared by Siebold from Japan. Ruprecht in 1856, in a paper of Maximowicz on the important trees and shrubs of the Amur Region, described *P. tenuifolius*, the first known species of *Philadelphus* from the Eastern Asia mainland. A year later in a discussion about *P. tenuifolius* he accidentally published *P. pekinensis* which became the first known Chinese species in the genus.

By the middle of the nineteenth century *Philadelphus* introduced from America and Asia were cultivated under thirty odd names in European gardens. Botanists and growers began to be conscious of the confusion and tried to clarify the nomenclature and to identify the plants. The general tendency shows a lumping effort. Koch in 1859 in an article titled, "Notes on the Genus *Philadelphus*," first published in Germany and then translated by De Borre into French, recognized 16 species. Ten years later, in his *Dendrologie* he reduced the number to 11 species. His species concept was rather vague and he clearly erred in making species of American and Asiatic origin conspecific entities. His work created confusion rather than clarification. Maximowicz in 1867, in a "Revisio Hydrangearum Asiae Orientalis," treated all the species of *Philadelphus* that had racemose inflorescences, including those from Europe, Caucasus, Himalayan Regions, eastern Siberia, northeastern China, Japan and North America, as varieties of *P. coronarius* and thus created a large number of synonyms.

Koehne was the best authority of the group, and he was careful and keen in his observations. Unfortunately the diagnostic characters he chose to delimit subsidiary groups between the species and the genus do not at all well cover the characters of the species involved, and his arrangement proved to be impracticable. In 1893 he selected the exfoliation of the bark as the most important character for distinguishing major groups. He divided the genus into the *Corticatae*, including those species with closed bark and the *Decorticatae* containing those with exfoliate bark. Realizing this character to be unreliable and the scheme not workable, three years later, he selected the size of the stigma as the distinguishing character for dividing major groups. On this basis he proposed two sections, the *Poecilostigma* and the *Stenostigma*. His section *Poecilostigma* represents a conglomeration of phylogenetically unrelated species. This section was subdivided into three subsections, the *Gemmati* with exposed buds, the *Microphylli* containing species with inclosed buds, small leaves and united and more or less separated stigmas; and the *Speciosi* including species with inclosed buds, large leaves and separated broad stigmas. His section *Stenostigma* represents species with inclosed buds and separated narrow stigmas. This was subdivided into four subsections; the *Paniculati* with paniculate inflorescences, the *Gordoniani* with racemose inflorescences, decorticate branchlets and late flowering individuals, the *Satsumani* with racemose inflorescences, decorticate branchlets and early blooming individuals, and the *Coronarii* with racemose inflorescences, corticate branchlets and usually early flowering individuals. In this classification Koehne failed to give a single character which holds true for the *Poecilostigma* as a section, and for the demarcation of the *Stenostigma* he gave two characters, that is, the narrow stigmas and the inclosed buds. At first his statement seems to be acceptable. But as one examines the species that Koehne placed in the *Stenostigma* section, one finds that this section cannot stand as a taxonomic unit, for the first listed species *P. californicus* Benth. has exposed axillary buds, a character which is not

supposed to exist in the section. Moreover, the differences in the size and shape of the stigmas between species of this section is just as great as are those in *Poecilostigma*. As to the characters he chose for distinguishing subsections they are not strong enough even for delimiting species. The manner of the peeling of the bark and the time of blooming are subjected so much to the environmental changes that they are not of much value except for distinguishing closely related garden forms planted in similar conditions. Although Koehne's system of classification has been followed by many authors including Engler in his treatment of the genus in the second edition of *Die Natürliche Pflanzenfamilien*, it is not adopted in this study, for it represents a more artificial and less phylogenetic system.

The beginning of the twentieth century seems to mark a new tendency in the study of *Philadelphus*. Botanists began to show interest in the group on a regional basis. Beadle in 1902 concentrated in a study of *Philadelphus* of the southeastern United States and proposed three new species and one new variety from the homeland of *P. inodorus*. His findings were the basis for the treatment of the genus in Small's *Flora of the Southeastern United States* (1903, 1913) and the *Manual of the Southeastern Flora* (1933) of the same author. He introduced the shape of the base of the capsules for distinguishing species. Thus he characterized *P. inodorus* as a species in which the base of the fruit attenuates into the pedicel and distinguished his new species, *P. gloriosus* from *P. inodorus* by the abruptly contracted fruit base. This character has never been used by any other botanist in the classification of *Philadelphus*. As the shape of the base of the capsule in this genus depends upon the fullness of the fruit which in turn depends partially upon the environmental conditions and partially upon the time when the specimens are collected, it has little value for specific identification.

Rydberg in 1905 prepared a comprehensive treatment of the genus for North America. The principal diagnostic characters he used were the presence or the absence of hairs on the style and disk which he called the upper free part of the ovary, the number of flowers on a flowering branch and the size of the leaf. He recognized 36 species, 10 of which were new. In the key, he grouped those species into six subdivisions, the *Californici*, *Coronarii*, *Grandiflori*, *Hirsuti*, *Microphylli* and *Mexicani*. His work indicates his ability in recognizing differences, and most of his species are good ones. Although some modern botanists may prefer to place the taxa he recognized in subspecific rank, that is only a matter of opinion which does not affect those taxa being distinct entities.

Nakai in 1915 considered the species of Japan and Korea, recognizing seven species, two of which were new. On the basis of bark characters of the second year's growth, whether closed or exfoliate, he raised two of Koehne's subsections into sections. In *Satsumani* he placed a single species, *P. satsumi* and in *Coronarii* he placed all the other species.

Rehder (1920, 1927, 1940, 1949) considered chiefly the cultivated species and varieties. In 1927 he subdivided the genus into six groups:

1. Gordoniani, 2. Sericanthi, 3. Coronarii, 4. Speciosi, 5. Microphylli and 6. Gemmati. Later (1940) he definitely designated these groups as Series. The characters he employed in the key were the number of flowers on a flowering branchlet, the pubescence on the hypanthium, the color of the calyx, etc. He was at times inconsistent when, as an example, he separated a group of species by the pubescence on their hypanthia, yet under certain species of this category he recognized varieties with glabrous hypanthia, as in the case of *P. pubescens* Loisel. var. *intectus* (Beadle) Moore. The diagnostic characters for a series do not always agree with his key characters, as in the case of *P. purpureo-maculatus* Rehd. In the text, he placed this species in series Microphylli which is characteristically a taxon with hidden buds while in the key it is placed under the category of exerted buds. His series concept impresses me as rather vague for in some cases a series consists of species different from each other in many respects. Thus in Series Gordoniani, he placed *P. californicus* Benth. with paniculate inflorescence, glabrous hypanthium and exposed buds as well as *P. pubescens* Loisel. with racemose inflorescence, pubescent hypanthium and inclosed buds; and in Series Sericanthi he placed *P. sericanthus* Koehne with pubescent hypanthium and also *P. delavayi* L. Henry with glabrous hypanthium. Moreover, in some cases morphologically inseparable and geographically closely affiliated taxa like *P. tomentosus* Wall and *P. delavayi* L. Henry are allotted to different series. Rehder's identification formed the basis for Bangham's chromosome count of the genus, and his taxonomic units were adopted by Janaki Ammal in her discussion on the classification and geographical distribution of *Philadelphus*. Rehder's material was restricted to the cultivated species of the temperate regions. This geographical limitation combined with the short-comings of his classification consequently affected the value of the conclusions drawn by the cytologists.

Hitchcock in 1943 studied the American xerophytic species. His work contributes materially to an understanding of the group. He considered four species and thirteen subspecies, all placed in what he called the Microphylli group. According to him, these small-leaved species, "As a unit . . . are readily distinguished from all other North American species of *Philadelphus*, yet it is quite apparent that they have been derived from, and are very closely related to, certain species of the *Mexicani*." I have carefully examined all the taxa that Hitchcock considered as representing a single group, and I can only conclude that this "group" includes heterogeneous elements. The small leaved character impresses me as being misleading. The comparative study of the morphological characters and geographical distribution of all the species of the genus indicates that the elements native of the region considered by Hitchcock are end products of evolution stemming from two or three directions. It is true that three of the four species in Hitchcock's treatment, *P. serpyllifolius* Gray, *P. purpusii* Brandeg. and *P. mearnsii* Evans are related to the Mexican elements. But *P. microphyllus* Gray and its related taxa are surely distant from them in their phylogenetic relationships. In my

judgement his conclusion on *P. microphyllus* Gray being a derivative of *P. purpusii* Brandeg. is too arbitrary. Before me there are several specimens from the Northern Rocky Mountains, chiefly Montana, with characters intermediate between *P. lewisii* Pursh and *P. microphyllus* Gray. The size, form and texture of the leaves and the size of the flowers of these specimens are typical of *P. microphyllus* Gray, but some, or rather, most flowering branchlets possess five flowers which is characteristic of *P. lewisii* Pursh. These spontaneous intermediate forms are good evidence of the origin of *P. microphyllus* Gray and its related species. Nevertheless, Hitchcock's paper takes high rank among all those published on the genus. I believe that it was unfortunate that his studies were limited to the small-leaved forms, for leaf size is indeed an unreliable character, and generalizations can scarcely be made except on the basis of a critical study of all species of the genus.

From the late 1920s up to the present the discoveries of botanists in fields other than taxonomy have broadened our knowledge of *Philadelphus*. Bangham in 1929¹ published the result of his observation on the chromosome number of the genus. Janaki Ammal in 1951² treated the subject in greater detail and discovered triploid and aneuploid individuals in garden forms. These findings will eventually help breeders to obtain better garden forms, for by suitable mating of parents of known chromosome compositions, better hybrids with triploid, or perhaps tetraploid or aneuploid chromosome makeups can be induced. As in many ornamental plants some extra chromosomes often enhance their horticultural merits.

Chaney in 1939 and Condit in 1944³ confirmed the occurrence of fossil *Philadelphus* in the middle upper Miocene. The fossil *P. nevadensis* (Knowlton) Chaney resembles the leaves of *P. lewisii* Pursh which now occurs in northwestern United States. This discovery advances our understanding of the present distribution of the species in this genus.

EVALUATION OF MORPHOLOGICAL CHARACTERS IN THE CLASSIFICATION OF THE GENUS

In the historical review of *Philadelphus* studies I have noted that the habit of the plant, the color and exfoliation of the branchlets, the position of the buds, the size, texture, dentation and indumentum of the leaves, the inflorescences, and the floral parts have all been used either as major or minor diagnostic characters in the classification of the species of the genus. Individual authors have stressed different points and consequently their systems of classification lack uniformity. In the following discussion an attempt is made to evaluate characters stressed by others as well as to add certain fruit and seed data.

¹The Chromosomes of Some Species of the Genus *Philadelphus*. Jour. Arnold Arb. 10: 167-169. 1929.

²Chromosomes and the evolution of Garden *Philadelphus*. Jour. Royal Hort. Soc. 76: 269-275. 1951.

³R. W. CHANEY, Pliocene Floras of California and Oregon, Carnegie Inst. Washington Publication 553. p. 79. pl. 16. fig. 2. 1944.

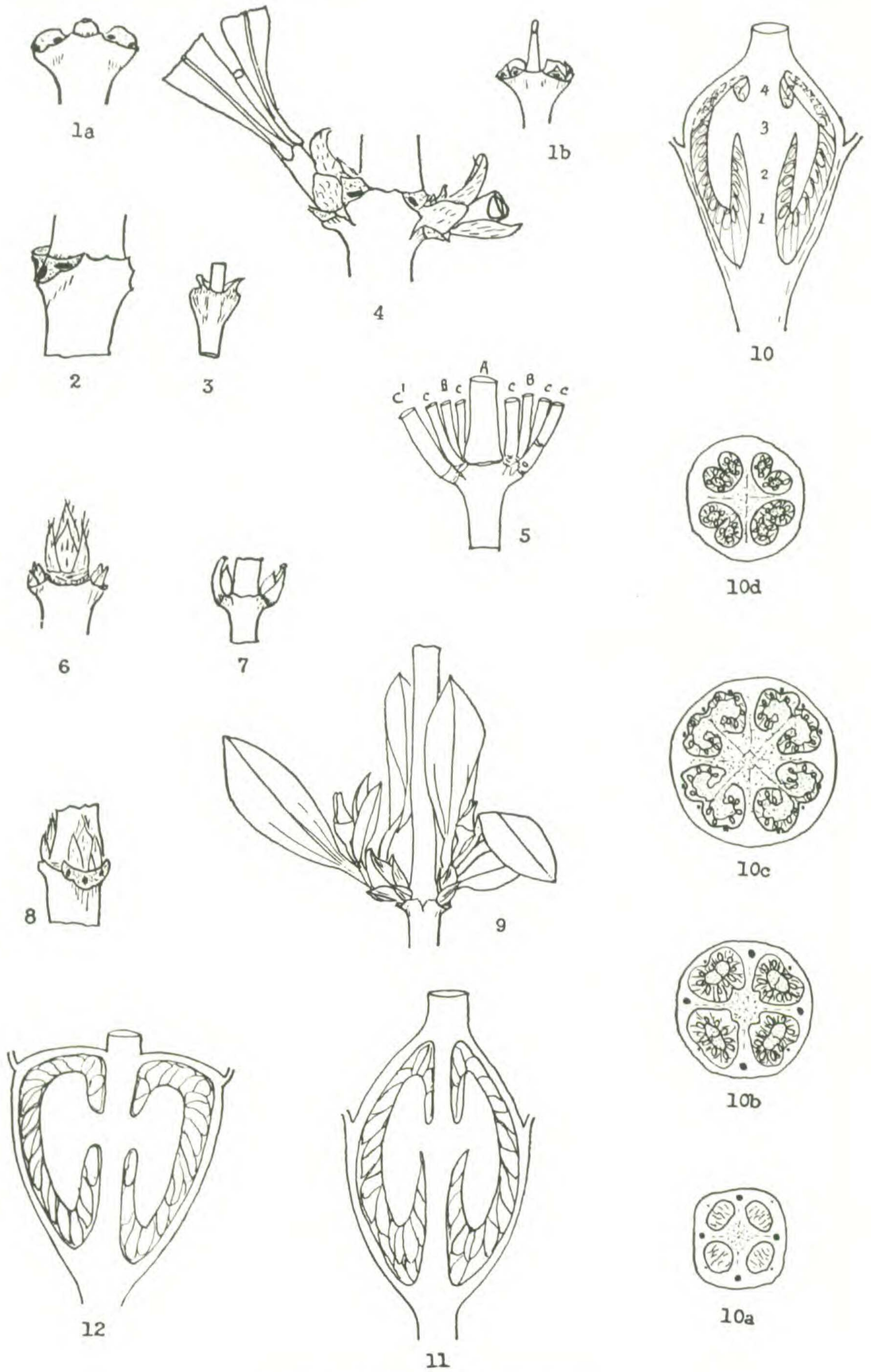
Habit: The habit was used as a principal criterion for separating major groups by early authors like De Candolle and Schrader. As our knowledge of the genus increased, the importance of the habit in the classification of *Philadelphus* gradually decreased. Judging from plants cultivated in the Arnold Arboretum, there seems to be no correlation between the habit of the plant and the other morphological characters such as the position of the buds, or the number of the flowers. Moreover, the habit is often affected by the environmental conditions and the age and vitality of the plant. Possibly the habit, such as upright tall stiff shrub, low widely spreading shrub with twisted branchlets, low compact shrub with upright branches or moundlike tall shrub with arching branchlets, may be used for recognizing special horticultural forms, varieties or even species, but it should not be used for distinguishing taxa above these ranks.

Branchlets: In general practice, a few branchlets constitute the only material a herbarium taxonomist may have for purposes of study and identification. Regarding the branchlets of *Philadelphus*, my discussion will be carried on under the headings of the second year's growth, current year's growth, the axillary buds, and the adventitious growth.

The color and exfoliation of the bark of the second year's growth, whether closed or exfoliate, has been employed by Koehne, Rehder and others for distinguishing species or even taxa of higher rank. It is true that the bark of certain species such as *P. pubescens* Loisel. and its related forms are prevailingly gray. But that of the other species is of various shades of brown, from ash-brown to reddish chestnut. In some species the bark exfoliates in sheets. In others they slowly wear off. It seems to be apparent that the size and the age of the shoot, the rainfall of the growing season, and the amount of snow in the preceding winter are all contributing factors effecting the exfoliation of the bark. Often different shoots on the same plant differ in the degree of exfoliation. As the herbarium specimens represent only very small portions of an individual plant, the actual selection of specimens may govern the evident exfoliation and bark color very materially. When only a few specimens are available, one may interpret the bark color and exfoliation of the second year's growth as forming a definite criterion for species delimitation, but when many specimens from the same general area are examined, the intergradations in color and exfoliation should convince any one that these characters are of little value in recognizing species.

The current year's growth of all species of *Philadelphus* are of two kinds, the sterile shoots bear leaves only, and the flowering shoots each of which bears one to three (or very rarely more) pairs of leaves and a terminal flower or a cluster of flowers. The sterile shoots are more vigorous and their leaves are larger and comparatively more dentate than are those of the flowering branchlets. The bud position on these shoots is very constant.

In one group, the buds are hidden in nodal pouches at the ends of the petioles (Pl. I, fig. 3). When the leaves fall, these buds are covered by



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the abscission layers (Pl. I, fig. 1a, 1b, & 2). As these buds unfold, they burst open the abscission layers (Pl. I, fig. 4) which persist for a long time at the base of the new branchlets. All the plants with such hidden axillary buds bear no terminal buds. Their shoots are determinate. All the Old World species of *Philadelphus* and many of those of the New World are characterized by such hidden buds and determinate branchlets.

In contrast, other species bear prominent conical axillary buds on their sterile and flowering shoots at anthesis (Pl. I, fig. 7, 8). In general, nodes bearing these buds are strongly curved below the insertion of the leaves, while those with hidden buds are but slightly curved. It is doubtful if latitude and temperature have any effect on the production and size of the exposed buds. Thus, *P. hirsutus* Nutt. is a native of the southern Appalachian Mountains, but when cultivated in Boston, which is nearly seven degrees higher in latitude than the original home of the species and Boston has an average annual minimum temperature 10–15 degrees lower than Nashville where the plant grows wild, its axillary buds at anthesis are just as prominent as are those on the Tennessee specimens. Moreover,

PLATE I

1. Shoot apex of the determinate type ($\times 4$, from fresh material collected in the Arnold Arboretum, Jan. 20, 1952). 1a. *P. coronarius* with the lateral buds completely covered by the abscission layer. 1b. *P. microphyllus* with the lateral buds more or less unfolding, the dead terminal portion of the branchlet is more prominent here. 2. Node of *P. delavayi* after the leaves have fallen, showing the lateral buds covered by the abscission layer ($\times 4$, *Rock 16637*). 3. Node of *P. maculatus* with the ends of the petioles attached, showing prominent nodal pouches containing the buds; the curves below the insertion of the leaves are gentle ($\times 4$, *Mueller 2213*). 4. Node of *P. delavayi* with the axillary buds unfolding and each abscission layer has burst open ($\times 3$, *Rock 16173*). 5. Node of a sucker; A, with two branches B, developed from normal axillary buds and six branches developed from adventitious buds. Five of the six are flowering shoots C, and one is a vegetative shoot C'. 6. Shoot apex of the indeterminate type, *P. hirsutus*, with a large terminal bud and two small lateral ones ($\times 4$, from fresh material collected in the Arnold Arboretum on Jan. 20, 1952). 7. Node of *P. texensis* with the petioles on, showing the exposed axillary buds, the curves below the insertion of the leaves are sharp. ($\times 4$, *Reverchon 1523*). 8. Node of *P. hirsutus* after the leaves have fallen, showing two lateral buds exposed ($\times 4$, fresh material collected in the Arnold Arboretum, Jan. 20, 1952). 9. Node of *P. mearnsii* after the buds are unfolded. The unfolding of the buds does not affect the leaf-scars ($\times 5$, *Palmer 11492*). 10. Longitudinal section of a fruit of *P. inodorus*, 1 week after anthesis, showing the attachment of the placentas which are above the insertions of the sepals ($\times 10$). 10a, 10b, 10c, and 10d are transverse sections of the above cut through the points 1, 2, 3, and 4. 10d appears 8-locular. 11. Longitudinal section of a fruit of *P. microphyllus*, 2 months after anthesis, showing the attachment of the placentas which are about the same level as the insertions of the sepals ($\times 10$). 12. Longitudinal section of a mature fruit of *P. hirsutus* showing the attachment of the placentas which are below the insertions of the sepals ($\times 10$).

such plants often bear strong terminal vegetative buds (Pl. I, fig. 6), therefore their shoots are indeterminate. All the species with exposed buds occur in the New World.

The presence or absence of exposed buds is not only constant, but the buds are also very easy to detect. As long as the leaves are mature, no matter whether the branchlets be sterile or fertile, the buds are evident. The morphological constancy and the geographical coincidence indicate that the position of the buds whether hidden or exposed, is a very good character for separating major groups in *Philadelphus*. Accordingly, in this study I take this character as one of the key categories for delimiting the subgenera of the genus.

All species of *Philadelphus* produce adventitious buds at the basal portions of their principal stems or along the upper parts of their branches. In the first case, the buds develop into strong sterile shoots which give rise to flowering branchlets in the following year. In the second case, the buds may develop into a weaker sterile shoot (Pl. I, fig. 5, c'), or usually they form weak flowering branchlets, (Pl. I, fig. 5, c). The leaves of such shoots are generally smaller and the flowers fewer than are those developed from normal buds. The presence of a number of such small flowering branchlets gives the stem somewhat the appearance of a brush. A branch with multiple branchlets at its nodes should always be taken as a sign of old age and reduced vitality in the plant.

Leaves: Authors of the first few species of *Philadelphus* relied chiefly on leaf characters for distinguishing them. Thus Linnaeus distinguished *P. inodorus* from *P. coronarius* by its entire leaves and Willdenow distinguished his *P. grandiflorus* by its dentate leaves. When only a few specimens are compared, there may be seemingly marked differences in the size, shape, texture, venation and margin of the leaves. But when a large number of specimens are available for comparative study, the gradual changes exhibited in these respects prove that what various authors such as Schrader, Koch, Maximowicz, and Rydberg accepted as differential specific characters are not constant. In fact, there is little difference in the size and shape of the leaves of the species of *Philadelphus* of any single area, and also often even between species from distant regions with similar climatic conditions. The differences that existed in the size, shape, texture and margin of related species may also occur as modifications among representative specimens from the same species differing only in age and vigor. Therefore the size and shape in the leaves can only be used as supplementary criteria for distinguishing varieties or garden forms and occasionally even species when it is correlated with characters furnished by flowers and fruits.

The leaves on the sterile shoots and those on the flowering shoots of an individual plant differ in size, shape, apex and margin. In general the leaves on the sterile shoots are larger, more acuminate at the apex, more coarsely dentate at the margin, more pubescent on the surface and even broader at the base than are those on the flowering shoots. Yet, leaves of a flowering shoot developed from an adventitious bud are always much

smaller, more acute, more subentire and more glabrous than are those developed from normal buds. One judges that the age of the plant, the vigor of the shoot, the available water supply may be reflected in the leaves of *Philadelphus*. For this reason, leaf characters based on these aspects should not be employed for the delimitation of taxa above varieties or garden forms.

The nature and the density of the indumentum on the leaf surfaces are rather constant as to leaves on comparable shoots of a species. They usually correlate with certain flower characters, therefore may be used as auxiliary criteria for distinguishing species or categories of even higher rank, such as section and series.

Inflorescences: *Philadelphus* as a genus is characterized by determinate terminal inflorescences, each with 1 or 3 flowers at the last node, and none, one, rarely two single flowers, or very rarely a cyme in the axil of a bract or a leaf on each side of the succeeding nodes. When the succeeding node bears no flower, the branchlet has solitary or ternate flowers. When the succeeding nodes bear flowers the plant has racemose or paniculate inflorescences, depending on the number of flowers in the leaf axils. In many species the bracts are small and caducous. Since De Candolle in 1828 used the term raceme to describe *P. coronarius* Linn. and its related species, it has been used in reference to those species with a terminal cluster of flowers in all major treatments of the genus. But actually when the order of blooming is taken into consideration, none of the *Philadelphus* species really bear true racemes. In this genus, the first opened flower always prohibits the elongation of the flowering shoot and limits the formation of more flower buds. The figures on Plate II actually represent the number of flowers and their relative developments on the branches of *P. californicus* Benth., *P. pubescens* Loisel., *P. lewisii* Pursh, *P. pekinensis* Rupr., *P. inodorus* Linn., *P. microphyllus* Gray, *P. falconii* Sarg., *P. karwinskyanus* Koehne, *P. myrtoides* Bertol., *P. mexicanus* Schlecht., *P. hirsutus* Nutt. and *P. serpyllifolius* Gray. In each case the flowers at each node behave as an independent unit. In cases where many flowers are formed at the end of the flowering branch the terminal one always opens first. Such inflorescence is a determinate raceme or a panicle.

Philadelphus inflorescences may be roughly arranged in six general types, the paniculate, the determinate-racemose, the pauciflorous, the ramiferous, the mexicanus, and hirsutus types. The paniculate type includes inflorescences composed of simple or more or less compound cymes (Pl. II, fig. 1). It is represented by *P. californicus* Benth. and *P. cordifolius* Lange. The determinate-racemose type is the commonest type of inflorescence in the genus. It is best represented by *P. pubescens* Loisel. and *P. lewisii* Pursh in the United States, *P. satsumi* Sieb. of Japan, *P. tenuifolius* Rupr. of the Amur Region, *P. pekinensis* Rupr. and all the other Chinese species, *P. tomentosus* Wall. of the Himalayan Region and *P. caucanus* Koehne and *P. coronarius* Linn. of Caucasia and southwestern Europe. It consists of 3, or very rarely 1, or occasionally in *P. coronarius* Linn. 5, terminal flowers and several pairs of axillary ones at the suc-



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ceeding nodes (Pl. II, fig. 2-5). Sometimes, as in *P. coronarius* Linn., a pair of flowers may appear in a single leaf axil. The upper axillary flowers are often subtended by bracts which fall early in the flowering season. The lower axillary flowers are in general subtended by normal leaves. Great variations exist in the number of flowers in a cluster, the length of the central axis and the size of the bracts in specimens representing a species or sometimes even from a single plant. This is especially true in *P. lewisii* Pursh and *P. pekinensis* Rupr. It seems that the age and vitality of the shoots which give rise to the flowering branches are the controlling factors for such modifications. There are certain garden forms characterized by a predominantly short flowering axis. In such cases the clusters appear rather compact (Pl. II, fig. 4, 5). There are certain species which bear loose determinate-racemes. In such cases the lower two pairs of flowers are borne in the axils of normal leaves (Pl. II, fig. 2, 3); the inflorescences of *P. pubescens* Loisel. and *P. intectus* Beadle are typically of such form.

The pauciflorous type consists of inflorescences with one or three terminal flowers on shoots devoid of exposed axillary buds. This type is best illustrated by *P. inodorus* Linn. and *P. microphyllus* Gray (Pl. II, fig. 6, 7) and their related species. In certain garden forms, the lateral flowers of this type may be replaced by two cymes with elongated peduncles. In such cases, a true dichasium is formed (Pl. II, fig. 8).

The ramiferous types of inflorescences are depauperated panicles. They may appear as racemes or panicles, but each individual flower is on a short pedicel jointed to a woody axis. Thus each flower stalk is morphologically composed of a peduncle and a pedicel. In *P. myrtoides* Bertol. the peduncles of the lower flowers are as long as those of the upper one and the inflorescence appears more or less racemose, but the individual pedicels are jointed (Pl. II, fig. 10). In the more ramified form, as represented by *P. karwinskyanus* Koehne, the inflorescence is composed of elongated lower branches (Pl. II, fig. 9) and shorter upper ones, and it appears like a panicle. Some of the lower branches even bear axillary buds on their basal nodes.

The mexicanus type has one or three terminal flowers on short but jointed stalks, as found in *P. mexicanus* Schlecht. Such an inflorescence

PLATE II

TYPES OF INFLORESCENCE IN PHILADELPHUS (all $\times \frac{1}{2}$). 1. The PANICULATE TYPE, *P. californicus* (Abrams 4649). 2-5. The DETERMINATE-RACEMOSE TYPES. 2. *P. pubescens* (AA 2221). 3. *P. lewisii* with 3 terminal flowers (Thompson 10522). 4. *P. lewisii* with 1 terminal flower (Engberg, June 19, 1905). 5. *P. pekinensis* (Hers 2515). 6 & 7. The PAUCIFLOROUS TYPE. 6. *P. inodorus* (AA 4159-1). 7. *P. microphyllus* (Fendler 266). 8 TRUE DICHASIMUM, *P. falconeri* (Hu, June 14, 1951). 9 & 10. The RAMIFEROUS TYPE. 9. *P. karwinskyanus* (FGW 872). 10. *P. myrtoides* (Carlson 435). 11. The MEXICANUS TYPE, *P. mexicanus* (Standley 65124). 12. The HIRSUTUS TYPE, *P. hirsutus* (Palmer 35517). 13. The SERPYLLIFOLIUS TYPE, *P. serpyllifolius* (Cary 9435).

is probably a reduced or simplified compound inflorescence with the portion above the bracts representing the pedicel and the portion below the joint, the peduncle.

The hirsutus type, as represented by *P. hirsutus* Nutt. and *P. mearnsii* Evans, has inflorescences of solitary or ternate flowers on short flowering branches with exposed axillary buds (Pl. II, fig. 12, 13). Such inflorescence often develops from a terminal bud.

The type of inflorescence in *Philadelphus* is a definite and easily recognizable character. When correlated with the position of the buds, the form of stigma, the shape of fruit, and the appendages of the seed, the type of inflorescence can be employed as a very useful device for distinguishing sections of the genus as well as for assisting in placing the species in its phylogenetic position. In using the inflorescence in the classification of *Philadelphus* several essential points should be observed. (1) All the inflorescences of *Philadelphus*, no matter whether they are composed of a single flower, or three or five up to 20 flowers in simple or ramified branches, are borne at the end of current year's growth. In other words, they are all derivatives of individual buds which are usually axillary. (2) All of them are determinate inflorescences; that is, the terminal flower in each type opens first and they thus limit the elongation of the floral axis. (3) The type of inflorescence of a species is definite, but the number of flowers on each flowering branch is variable. A species with pauciflorous type of inflorescence may have some branches with a single flower, some with three and others with a true dichasium of seven or nine flowers. This variation seems to be a reflection of the environmental condition of the plant as well as the physiological state of the particular flowering branch. In the cultivated *Philadelphus*, good soil, sufficient water supply, proper pruning, vigor of the plant and the bearing year always induce a large number of flowers on a branch. In case of the determinate-racemose type of inflorescence the floral axis is always lengthened.

Rickett in 1944 discussed the inflorescences of *Philadelphus* at length. He used *P. coronarius* Linn., *P. californicus* Benth., *P. lewisii* Pursh, *P. argenteus* Rydb. and *P. hirsutus* Nutt. to illustrate a hypothesis that the terminal dichasium is ancestral in *Philadelphus*. He maintained that this primitive type can be found in *P. hirsutus* Nutt., and suggested that the present forms of the inflorescences of *Philadelphus* are evolved through the reduction of the terminal dichasium to a single flower as found in *P. argenteus* Rydb. Further reduction of the lateral flowering branches leads to the production of axillary flowers of *P. coronarius* Linn. This condensation is accompanied by a lack of dormancy in the new axillary buds, which open the same season as the leaves which subtend them. From flowering branches formed in such a way, derived the floral arrangement as seen in *P. lewisii* Pursh and also the thyrses of *P. californicus* Benth., the latter represents a condensation of the second order, that is, not only are a number of the original flowering branches laterally disposed on a central rachis, but several groups thus constituted are similarly disposed on the main axis of the thyrses. According to this hypothesis the

evolution of the inflorescences of *Philadelphus* has been brought about merely by reduction and condensation of the flowering branches. As I understand the morphology of *Philadelphus*, certain assumptions accepted by Rickett apparently do not conform to what are found in nature. First he selected the inflorescence of *P. hirsutus* Nutt. to represent the ancestral form, but this species is morphologically highly specialized and its low point of placentation and its ecaudate seeds all indicate its advanced position in the evolution of the genus. Secondly, he maintained that the inflorescence of *P. argenteus* Rydb. is a derivative of that of *P. hirsutus* Nutt., but these two species are phylogenetically very remote. They belong to different subgenera. Thirdly, the condensation processes that he assumed to take place between *P. argenteus* Rydb. and *P. coronarius* Linn. and between *P. lewisii* Pursh and *P. californicus* Benth. involve more than a single year's growth. The plant part he took from *P. argenteus* Rydb., or *P. lewisii* Pursh to illustrate his principle represents two year's growth with twigs bearing buds on part of old wood and what he took from *P. coronarius* Linn. or *P. californicus* Benth. represent a single year's growth, originated from a single winter bud. When he assumed that the branch of *P. lewisii* Pursh with a number of flowering branches laterally disposed to be condensed on a central rachis to form an inflorescence corresponding to those of *P. californicus* Benth., he overlooked the age differences of the two elements involved. It is not possible within the organization of the plant to attain such assumed condensation. Moreover a shoot of *P. lewisii* Pursh that bears laterally disposed flowering branches never possesses a terminal bud, so that it is impossible for that shoot to be condensed on the main axis of the thyrses to form a paniculate inflorescence of *P. californicus* Benth. which ends with a terminal flower. Moreover, *P. coronarius* Linn. and *P. lewisii* Pursh have the same determinate-racemose type of inflorescence. When one takes into consideration all factors, it is unnecessary to invoke imagination to explain the evolution of the inflorescences of *Philadelphus*. Rickett was perhaps right in assuming the terminal dichasium as the ancestral type. He was partly correct in recognizing reduction and condensation as a process that brings about the various forms of inflorescences in *Philadelphus* but unfortunately he chose the inflorescence of *P. hirsutus* Nutt. to represent the primitive model. The most primitive type of inflorescence in *Philadelphus* is the pauciflorous type as found in the true terminal dichasium of a healthy vigorously growing flowering branch of *P. inodorus* Linn. Normally such dichasia may be reduced to three or a single terminal flower. The solitary or ternate terminal flower of *P. microphyllus* Gray and all its related species represents a comparatively stable stage of development of such reduced form. The reduction in the height of the plant, the size of the leaves, the number of stamens, the length of style and the size of the stigma all conform with the fact of such reduction in number of flowers. Multiplication as well as reduction, and some times a combination of both processes may have taken place in the evolution of the *Philadelphus* inflorescences. The multiplication in the number of

flowers which are produced in the leaf-axils of the succeeding nodes below the terminal one, gives rise to the determinate-racemose type, and further multiplication which involves the branching of the flowering pedicels gives rise to the paniculate type. The *mexicanus* type is another primitive model which is closely related to the pauciflorous type. The multiplication in the number of flowers and the ramification of the flowering branches of this type give rise to the ramiferous type. The *hirsutus* type is remote from all other types of *Philadelphus* inflorescence. Its slender pedicels with median or super median bracts, its irregular way of branching, and its appearance remind one of the inflorescence of certain *Deutziae*. It is probably derived from some form very remotely related to the *mexicanus* type but the linking form is not known in our present flora.

Pedicels: The length of the pedicels in *Philadelphus* varies considerably. The general tendency is, in the determinate-racemose type, the lower ones are longer than the upper ones, or in the pauciflorous types, the lateral ones longer than the central one. As a criterion for classification, this character has little value. Nevertheless, most species have pubescent pedicels. The nature and density of the trichomes on the pedicels of closely related species are sometimes employed as auxiliary characters for recognizing species or varieties.

Hypanthia: Part of the ovary of *Philadelphus* is fused to the receptacle. In this paper the term hypanthium is used to cover that part called the calyx tube by some authors. For the visible top portion of the ovary the term disk is used.

At anthesis, there is no appreciable difference in the shape and size of the hypanthia of closely related species. But the nature and density of the indumentum which persist in the fruit are very useful for specific identifications, or even for the delimitation of series. Most *Philadelphus* species have yellowish green hypanthia. Certain Chinese species have purplish ones. In such case, color may be used as a handy auxiliary character for identifying species or varieties.

Sepals: The sepals of *Philadelphus* are ovate, rarely deltoid, 4–20 mm. long, acuminate (rarely acute) at the apex. The relatively shortest sepals occur in *P. hirsutus* and the longest ones in *P. inodorus* and *P. mexicanus*. The length, shape and apex of the sepals have been employed by various authors for distinguishing morphologically similar and geographically intermixed species. The study of a large amount of material in this genus reveals that the natural population of any general area belonging to the same section exhibits very little variation in the size and shape of the sepals. Thus, in my opinion, they have no specific significance.

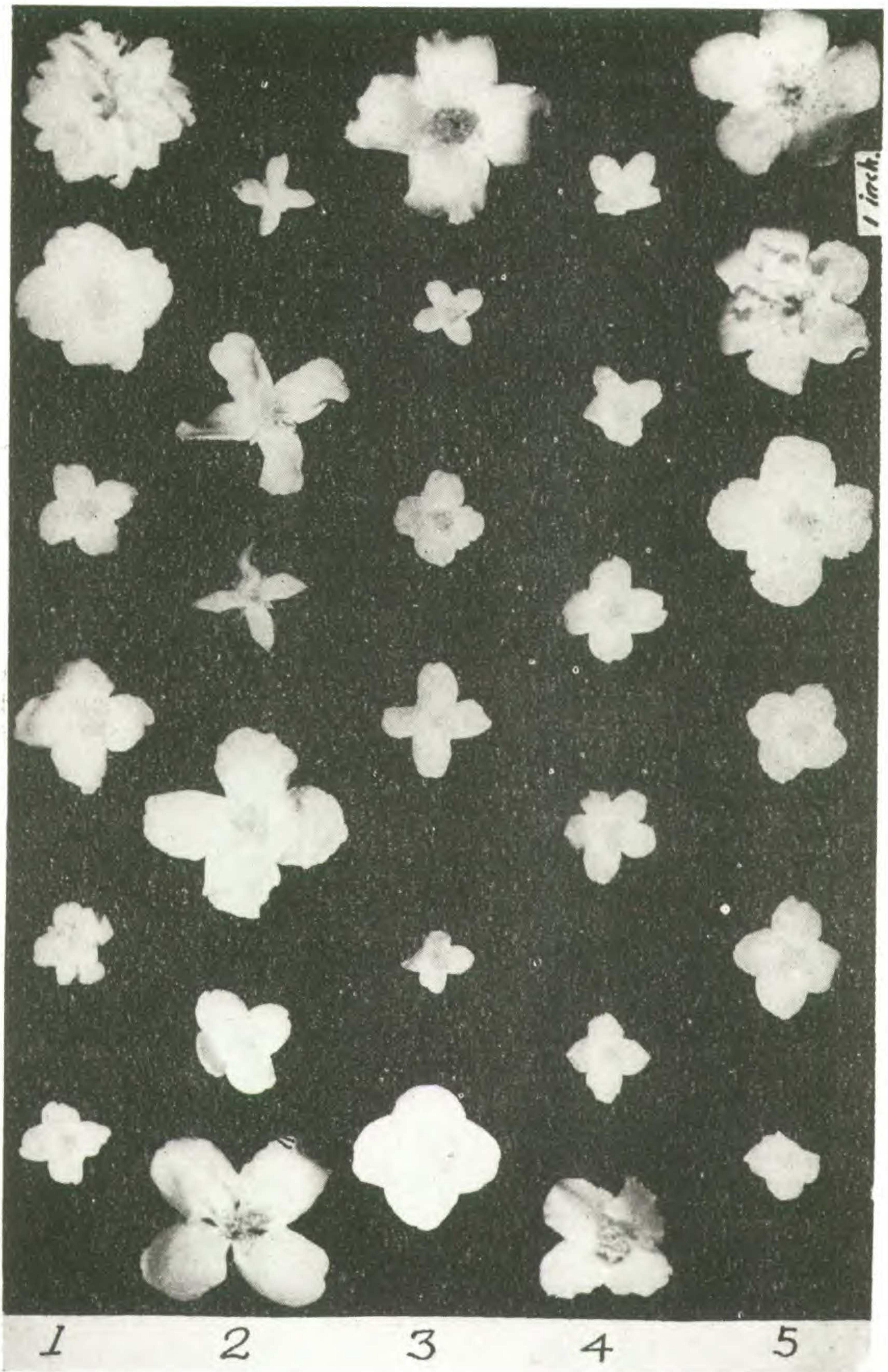
Corolla and petals: Characters of the corolla and the petals have been little used in the classification of the genus. One Central American species has been recognized for its pubescent petals, while another species of northwestern United States has been characterized by its pointed petals.

In shape and size the petals of various species are rather constant. They may be oblong, elliptic, suborbicular or lanceolate. The variations in the shape and size of the petals give the different appearance of the flowers.

Thus *P. inodorus* var. *laxus* (Schrader) S. Y. Hu has oblong petals, and its flowers are distinctly cruciform when fully open (Pl. III, col. 3). The petals of *P. inodorus* Linn. var. *grandiflorus* (Willd.) Gray are suborbicular, and consequently its flowers appear disciform (Pl. III, col. 1). is an important aspect for distinguishing varieties and garden forms, the of *Philadelphus*. It shows a considerable difference in the size, shape and appearance of the corollas in the genus. As the appearance of flowers is an important aspect for distinguishing varieties and garden forms, the size and shape of the petals may eventually have a more important role in demarcating entities subordinate to the species.

Stamens: There is noticeable variation in the number of stamens not only between different species or different plants which clearly represent a single species, but also between different flowers of the same plant. The forms possessing the most stamens are found in *P. inodorus* Linn. and its varieties where as many as 90 stamens have been observed. The smallest number of stamens observed is in *P. mearnsii* Evans where as few as 13 stamens have been counted. But variations in the number of stamens between different flowers on the same plant do exist. With the first cited example as few as 60 stamens and with the second species as many as 20 stamens have been observed. For demarcating morphologically closely related and geographically inseparable species the number of stamens does not seem to have much significance. But there apparently exists a general pattern of stamen number between morphologically different and geographically widely separated groups. Thus the native population of *Philadelphus* of the Southern Appalachian region with pauciflorous inflorescences have the highest stamen count which is between 60 and 90; the xerophytic plants of the southern Rockies with the pauciflorous type of inflorescences have an average count of 30 to 40, rarely as low as 24 or as high as 50 stamens; the native species of Central America with ramiferous inflorescences have 40 to 50 stamens and those with the mexicanus type of inflorescences have 36 to 44 stamens. The Old World species with racemose inflorescences generally have 25 to 35, rarely to 50 stamens. Garden hybrids usually have low stamen counts, and many of them are sterile, with the exception of one form, which has up to 60 stamens, they have 20 to 29, rarely up to 40 stamens. The species with the hirsutus type of inflorescences have the lowest stamen count, ranging 13 to 33. Such a general pattern when correlated with the form of buds, the type of inflorescences and the shape of fruits and the tails of the seeds, may serve as auxiliary criteria for characterizing sections or series of the genus.

Hitchcock was the first person who observed the tendency of the union of the lower portions of the filaments of several adjacent stamens into bundles in *P. argenteus* Rydb. (Pl. IV, fig. 8c), and used this character for distinguishing that xerophytic taxon. Normally the filaments of *Philadelphus* are separated. They are always shorter than the petals. With the exception of the extreme xerophytic dwarf forms like *P. serpyllifolius* Gray or *P. mearnsii* Evans, which has very small flowers and



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short stamens, the length of the filaments in *Philadelphus* is rather constant, with the longest outermost ones being 6–9 mm. long and that of the shortest innermost ones 2–3 mm. long. In the xerophytic forms, the filament of the outer stamens measures up to 4 mm. long and the inner ones 2 mm. long. So far as I know, the longest filament of *Philadelphus* is found in a garden form called *P. "slavini"* hort ex Wymn. with the inner filaments 7 mm. and the outer ones 12 mm. long. The filaments of *Philadelphus* have not and very likely never will furnish outstanding characters for distinguishing taxa of any rank in the classification of the genus.

The anthers of *Philadelphus* are generally oblong, being 1–1.2 mm. long, 0.9 mm. wide. The xerophytic species like *P. serpyllifolius* Gray has subglobose anthers, 0.5 mm. in diameter. There are a few natural populations occurring in Central China and western North America where hair-like processes occur on the thecae of the anthers (Pl. IV, fig. 8c). This is probably an expression of an unusual mutation which eventually may lead to speciation.

Pistil: A normal pistil of *Philadelphus* is composed of four carpels. Occasionally few 5-carpelled or very rarely some 3-carpelled pistils may occur in a garden form. Characters furnished by the parts of the pistil, ovary, style, and stigmas, have been employed for distinguishing taxa of various rank in *Philadelphus*. Schrader recognized *P. speciosus* for its 8-loculed fruit. Pursh distinguished his *P. lewisii* for its relatively long and much divided style. Koehne subdivided the major groups of the genus on the basis of the size of the stigma. Ruprecht, Koehne and many others have proposed species because of the presence of hairs on the style, or disc, or both. Nevertheless, due to our limited knowledge of the pistil in *Philadelphus* unnecessary binomials have been created. A normal *Philadelphus* ovary has four locules and an axile placentation. In each locule there are a pair of more or less fused auricular placentas projecting from the upper portion of the central column (Pl. I, fig. 10–12). The superior lobes of these placentas are much shorter than the inferior ones, the latter are so pressed together that they appear as one organ in cross sections (Pl. I, fig. 10B). In *P. inodorus* Linn., its varieties, and its related species, the inner wall of the roof of each locule, which corresponds

PLATE III

FLOWERS OF PHILADELPHUS CULTIVATED IN THE ARNOLD ARBORETUM SHOWING DIFFERENT FORMS OF THE COROLLA, THE READING IS BY THE COLUMNS 1, 2, 3, AND 4, EACH FROM THE TOP TO THE BOTTOM:

COLUMN 1. *P. "Argentine," P. grandiflorus, P. caucasicus, P. coronarius "speciosissimus," P. coronarius, var. primulaeflorus, P. coronarius;* COLUMN 2. *P. insignis (?), P. incanus, P. falconeri, P. floridus, P. delavayi, P. "Cole Glorious";* COLUMN 3. *P. "Belle Etoile," P. satsumanus, P. lemoinei, P. laxus, P. magdalenae, P. splendens;* COLUMN 4. *P. maximus, P. sericanthus, P. tenuifolius, P. pekinensis, P. nepalensis, P. "bicolor";* COLUMN 5. *P. "Favorite," P. virginalis, P. "Norma," P. zeyheri, P. tomentosus, P. purpurascens.*

to the upper portion of the middle of the carpel, grows down and projects between the superior lobes of the placentas in such a manner that it appears like a false septum separating those lobes. Thus the cross sections made through the upper portion of a normal 4-locular ovary of such species appear 8-chambered (Pl. I, fig. 10D). This was perhaps what Schrader saw in *P. speciosus*. The position of the attachment of the placentas on the central column affects the shape of the fruit and the length of the tail of the seed. In *P. inodorus* Linn. the placentas are attached above the insertion of the sepals. Consequently the fruits are ellipsoid with circumferential sepals. These fruits have long-tailed seeds (Pl. I, fig. 10). On the other hand, the placentas of *P. microphyllus* Gray are attached about the same level as the insertion of the sepals (Pl. I, fig. 11). The fruits are ellipsoid with supermedian persistent sepals, and the seeds are short-tailed. In *P. hirsutus* Nutt. the placentas are attached below the insertion of the sepals (Pl. I, fig. 12). The fruits are obconic with apical persistent sepals and the seeds are ecaudate. This correlation of the attachment of the placentation, the shape of the fruits and the length of the tails of the seeds indicate that the position of the placentas can be used as auxiliary criteria for the delimitation of subgenera or sections of *Philadelphus*.

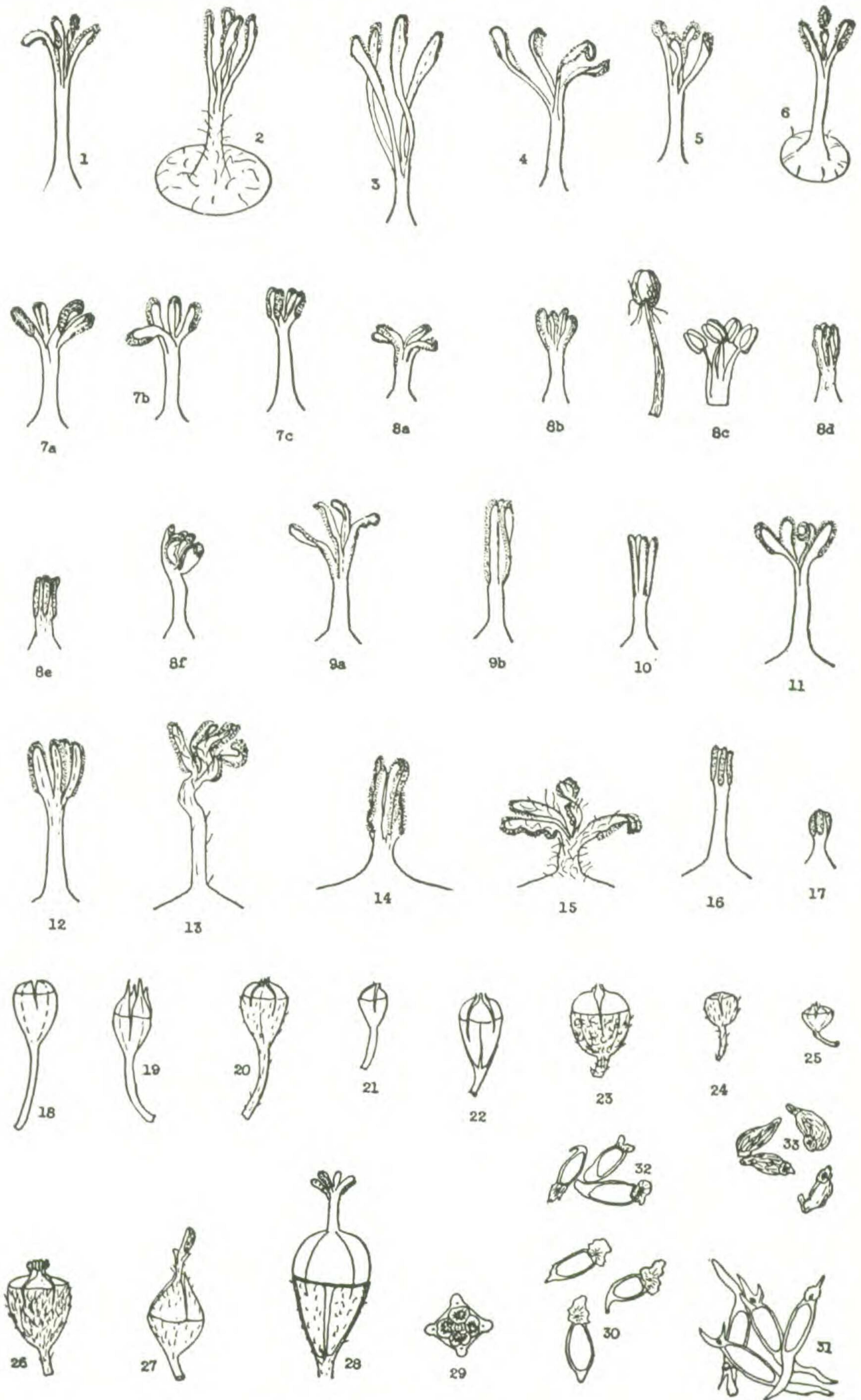
The length and the degree of the union of the style, the number and shape of the stigma and the indumentum of the style and disc have all been used in the classification of *Philadelphus*. Michaux in 1803 in distinguishing *P. inodorus* Linn. from *P. coronarius* Linn. introduced the relative length of the style and the stamens and the degree of union of the style. Since then Pursh has characterized *P. lewisii* as a species with three stigmas and a 3-parted style as long as the stamens, and Nuttall has characterized his *P. hirsutus* as a species with clavate undivided 4-grooved stigma and a style shorter than the stamens. Fortunately the species that Michaux, Pursh and Nuttall dealt with each represents a phylogenetically unrelated group, and incidentally the character holds true for distinguishing them. Later authors including Rydberg and Rehder have used the same character for delimiting closely related species, varieties and garden forms which present varied degrees in the union of the styles. *Philadelphus microphyllus* Gray has been treated as a species with united stigma. But flowers of different collections exhibit varied degree of the union of the styles. Some are completely united, some are partially united and others are completely separated (Pl. IV, fig. 8a, b, e, f). This happens also in *P. argyrocalyx* Wooton (Pl. IV, fig. 9 A-b). So far as I know there is a variation in the degree of the union of the style in every natural population. For this reason such characters fail to be of value for distinguishing species or taxa of lower rank.

There are certain morphological differences existing in the styles and stigmas of geographically separated groups, which, when correlated with characters as the position of buds and the type of inflorescences, may be used as auxiliary criteria for demarcating series or sections. The styles of the southern Mexican species may be long or short, but they all have

elongated cristate stigmas with the fertile papillose surfaces situated largely on the elevated abaxial sides (Pl. IV, fig. 13-15). The styles of the southern Appalachian species with pauciflorous inflorescences are relatively long. They carry oar-shaped stigmas with adaxial as well as abaxial fertile papillose surfaces, the latter though definite in outline, are shorter (Pl. IV, fig. 12). The styles of the Old and the New World species with determinate-racemose inflorescences are comparatively long with clavate or linear stigmas. The fertile surfaces of these stigmas, with the exception of some Yunnan and Japanese species, are longer on the adaxial sides than on the abaxial sides (Pl. IV, fig. 1-6). The styles of the New World xerophytic species with pauciflorous inflorescences are relatively short with linear stigmas, the fertile surfaces of which are largely on the abaxial sides (Pl. IV, fig. 8-9). The styles of the New World species with the hirsutus type of inflorescences are columnar with subcapitate 4-grooved stigmas (Pl. IV, fig. 16-17).

The presence or absence of hairs on the disc and style is a definite and easily recognizable character which may safely be used in the identification of species. Ruprecht in 1857 first used such a character for *P. schrenkii*, Koehne later described *P. lancifolius* from Sikkim, *P. karwinskyanus* from Mexico, *P. subcanus* from Central China and *P. caucasicus* from western Asia on the strength of the same character. Rydberg in 1905 employed this character as the principal criterion in his key. But as abundant material is available for a comparative study of the natural populations of various regions this character is probably not as important as earlier taxonomists considered it to be. In nature among closely related taxa in all regions, there are paired species which differ chiefly in the absence or presence of hairs on the style, disc or both. For example, there are the *P. coronarius* and *P. caucasicus* in southern Europe and western Asia, *P. tenuifolius* and *P. schrenkii* in northeastern Asia, *P. subcanus* and *P. incanus* in Central China, *P. satzumi* and *P. lasiogynus* in Japan, *P. lewisii* and *P. gordonianus* in northwestern United States, *P. stramineus* and *P. pumilus* in southwestern United States, *P. pubescens*, and *P. gattlingii* in southeastern United States, and *P. coulteri* and *P. asperifolius* in Mexico. It is not impossible that such phenomena merely represent an expression of normal Mendelian inheritance of one character. But our knowledge of the genetics of these groups is lacking. For the present, and in the absence of cytogenetic information, the presence or absence of hairs on the disc, style, or both is retained for the purpose of distinguishing certain manifestly closely related taxa.

Capsules: The fruit of *Philadelphus* has not been used to any extent in the classification of its various taxa. The material that I have examined apparently presents subgeneric or at least sectional differences in the shape of the capsules and the position of their persistent sepals. The southeastern Mexican species all possess ellipsoid or obovoid fruits with median sepals while the northeastern Mexican species have globose fruits and subapical sepals (Pl. IV, fig. 26-28). The pauciflorous species have ellipsoid fruits and median persistent sepals while the species of the same



HU, THE GENUS PHILADELPHUS

area possessing the hirsutus type of inflorescences have obconic fruits with apical persistent sepals (Pl. IV, fig. 25). The position of the persistent sepals may be used as a satisfactory auxiliary criterion in distinguishing morphologically close but geographically remote species. *Philadelphus lewisii* Pursh and *P. pekinensis* Rupr. both have pseudoracemose inflorescences and glabrous hypanthia. Besides the geographical separation, the subapical sepals attached to the fruit of the former and the apical ones

PLATE IV

THE STYLE AND STIGMA OF *Philadelphus* (all $\times 2\frac{1}{2}$). 1. *P. coronarius*, the stigmas slightly enlarged, the abaxial surface definite, shorter than the adaxial. 2. *P. caucasicus* with pubescent style and disk. 3. *P. coronarius* var. *duplex* (Kew 1307); the stigmas broadened. 4. *P. tomentosus*, the adaxial surface split into two. 5. *P. pekinensis*, the abaxial surfaces much shorter than the adaxial. 6. *P. kansuensis*, the stigmas often 3, the disk with few hairs, the abaxial surface much longer than that of *P. pekinensis*. 7. *P. delavayi*, a. and c. from Yunnan (Feng 1012), b. from Latong, Tibet (Younghusband). 8. a-b and d-f. *P. microphyllus* with the styles separated in various degrees, the fertile surface of the stigma abaxial (a. Ellis 107, b. Eggleston 18654, d. Heller 3792 and f. Alexander-Kellogg 1785). 9. *P. argyrocalyx* with the stigmas separated or united (a. Eggleston 14541, b. Wootton in 1895). 10. *P. argenteus* with the style slightly separated (Mearns 1617). 11. *P. inodorus* with oar-shaped stigmas, the abaxial surfaces broadened, shorter than the narrow adaxial surfaces (AA15347). 12. *P. "bicolore"* with elongated style and enlarged stigmas (Hu in 1951). 13. *P. affinis*, the style long and hairy, the stigmas elongated with few hairs on the sterile portion (Berlandier 333). 14. *P. calcicolus* with the stigmas more or less united, broadened and cristate, the style short, glabrous (Meyer & Roger 2662). 15. *P. karwinskyanus* with the stigmas cristate and hairy on the sterile portion, the style short and pubescent. 16. *P. hirsutus* with the style comparatively long, the stigmas clavate and undivided, the stigmas on 4 ridges. 17. *P. serpyllifolius* with the style short, the stigmas undivided and subcapitate.

FRUIT OF *Philadelphus* ($\times 1$). 18. *P. tenuifolius* with the apical end rounded (Cen. 263). 19. *P. tomentosus* with the apical end pointed and the persistent calyx almost circumferential (Parker, in 1919). 20. *P. sericanthus* with the apical end rounded, the lower portion pubescent. (Steward, Chiao & Cheo 609). 21. *P. pekinensis* with very small fruit (King 626). 22. *P. inodorus* with ellipsoid fruit. 23. *P. argyrocalyx* with subglobose fruit, the lower portion lanate (Rehder 315). 24. *P. hirsutus* with flat apical end (Biltmore Herb. 4333). 25. *P. hitchcockianus* with very small top-shaped fruit which is broader than long (Moore 3477). 26. *P. sargentianus* with subglobose fruit (Pringle 2094). 27. *P. karwinskyanus* with ellipsoid fruit pointed at both ends (Rose & Hough 4412). 28. *P. mexicanus* with obovoid fruit the lower portion 4-angled. 29. Cross-section of the fruit of *P. mexicanus*, one third from the base.

SEEDS OF *Philadelphus* ($\times 10$). 30. The short-caudate seed of *P. pekinensis* with round-lobed crown. 31. The long-caudate seed of *P. inodorus* with pointed-lobed crown. 32. The short-caudate seed of *P. californicus*. 33. The ecaudate seed of *P. hirsutus*.

SOME UNUSUAL STAMENS OF *Philadelphus*. 8c. Stamens with fused filaments (Eggleston 18654). 8g. Stamen with hirtellous anther (Abram 7200).

to the fruit of the latter are outstanding characters for distinguishing these species.

Seeds: Seeds are minute in all species of *Philadelphus*. Each individual seed consists of a small ellipsoid body about 1–2 mm. long wrapped in a thin testa extending towards both ends. The large portion of this small body is the copious oily endosperm which imbeds the microscopic embryo. The hypocotyl and the radicle constitute two-thirds of the embryo proper. The cotyledons and the epicotyl are very minute. The testa is reticulate, light brown, castaneous, or rarely black. It extends into an irregular collar-like crown at the proximal end and a tail-like wing at the distal end. The crowns of the seeds of different species vary in shape. That of the seed of *P. pekinensis* Rupr. has more or less rounded lobes (Pl. IV, fig. 30), that of the seed of *P. inodorus* Linn. has pointed lobes (Pl. IV, fig. 31), and that of the seed of *P. hirsutus* Nutt. is very minute and inconspicuous (Pl. IV, fig. 33). The length of the seed-tail varies as well as the shape of the crown. *Philadelphus inodorus* Linn. has a long-tailed seed, *P. pekinensis* Rupr. has a short-tailed seed and the seed of *P. hirsutus* Nutt. has no tail. Seed characters have never been used in the classification of *Philadelphus*. The shape of the crown and the length of the tail of the seed correlate with the position of the buds, the type of the inflorescence, and the form of the stigma. In my opinion they are characters of subgeneric or sectional importance. In some cases they can be used to distinguish intricate species. For example, because of the superficial similarities of the leaves and the corollas of *P. lewisii* Pursh and *P. californicus* Benth. and also because of their overlapping geographic distribution, some botanists have placed the latter as a variety of the former. As *P. lewisii* Pursh has long-tailed seeds and *P. californicus* Benth. has short-tailed seeds (Pl. IV, fig. 32), and as this character is associated with the difference in the inflorescences, *P. californicus* Benth. should be considered as a good species.

In summarizing the study of the gross morphology of *Philadelphus*, it seems legitimate to conclude that characters such as the dichasial inflorescence, large number of stamens, elongated stigma with enlarged papillose fertile surface, high insertion point in the placentation, ellipsoid fruit with circumferential calyx lobes, and long-tailed seed can be interpreted as primitive ones, while in contrast, characters like solitary flower, the racemose or paniculate inflorescence, the small number of stamens, the reduced length of the stigma, the low point of insertion in the placentation, the obconic fruit with apical persistent sepals and the short-tailed seed can be interpreted as representing more advance stages in the evolution of the genus.

SUBDIVISIONS OF THE GENUS AND THE PHYLOGENY OF ITS MAJOR GROUPS

Based on the data found in the position of the buds, in the type of inflorescences, in the form of stigmas, in the shape and position of the persistent sepals on the fruits, and the nature of the seeds, I am arranging

the species of *Philadelphus* into four subgenera and nine sections. The characters of these taxa are stated in the following synopsis.

SUBGENUS I. Gemmatus: This subgenus includes all the species with exposed buds; depauperate paniculate inflorescences, one or three terminal flowers with jointed pedicels or many flowers in ramified branchlets; stamens 40–60; semi-inferior ovary, enlarged and often cristate, separated stigmas; obovoid-ellipsoid or subglobose fruits with circumferential sepals; and long-caudate seeds. It contains 14 species in two sections.

SECTION 1. Poecilostigma: Inflorescences compound, 1- up to many-flowered; stamens 40 to 50; stigmas elongated and cristate; fruits obovoid-ellipsoid; southeastern Mexico, Guatemala to Costa Rica.

SECTION 2. Coulterianus: Inflorescences with solitary flowers, rarely 3-flowered; stamens 30–44; stigmas elongate, not cristate; fruit subglobose; northeastern Mexico.

SUBGENUS II. Euphiladelphus: This subgenus includes all the species with enclosed buds, determined branches, determinate-racemose or pauciflorous inflorescences, large or medium number of stamens, clavate or oar-shaped or linear stigmas, and long- or short-tailed seeds. It comprises 41 species in three sections.

SECTION 3. Pauciflorus: Inflorescences true dichasial cymes, often reduced to one or three flowers; stamens 60–90; stigmas oar-shaped; fruit ellipsoid with circumferential sepals; seeds long-tailed with pointed lobes on the crown; two species, native of the Southern Appalachian region of the United States.

SECTION 4. Stenostigma: Inflorescences determinate-racemose; stamens 25–35, rarely over 40; stigmas clavate or linear; fruit ellipsoid with subapical persistent sepals; seeds long- or short-tailed, the crown with pointed or rounded lobes; 30 species in both the Old and the New Worlds.

SECTION 5. Microphyllus: Inflorescences pauciflorous; stamens 25–40, rarely up to 50, stigmas linear; fruit ellipsoid with circumferential or subapical persistent sepals; seeds short-tailed with rounded lobes on the crown; 11 species, Colorado Plateau, Mexican Highland, and northern Mexico.

SUBGENUS III. Marcrothyrsus: This subgenus includes species with exposed buds; determined branches, paniculate inflorescences; medium number of stamens; clavate stigmas, and short-tailed seeds. It has one section including three species, native of California.

SECTION 6. Californicus: Characters as the subgenus.

SUBGENUS IV. **Deutzioides**: This subgenus includes all the species with exposed buds, and indeterminate branches; solitary, rarely ternate flowers; 13–35 stamens; inferior ovary, and columnar or subcapitate 4-grooved stigmas; turbinate or subglobose fruits with apical persistent sepals, and ecaudate seeds. It comprises eight species in three sections.

SECTION 7. **Hirsutus**: Flowers ternate; mesophytic plants; leaves serrate, hirsute, hairs all straight, style 4 mm. long; two species, Tennessee, Alabama.

SECTION 8. **Pseudoserpyllifolius**: Flowers solitary; xerophytic, dwarf plants, leaves entire, strigose or strigose-villose, hairs all straight; style up to 1 mm. long; four species, Texas, New Mexico, and Northern Mexico.

SECTION 9. **Serpyllifolius**: Flowers solitary; xerophytic, dwarf plants, leaves entire, lanate and hirsute beneath, trichomes dimorphous; two species, Texas, New Mexico, Arizona, Northern Mexico.

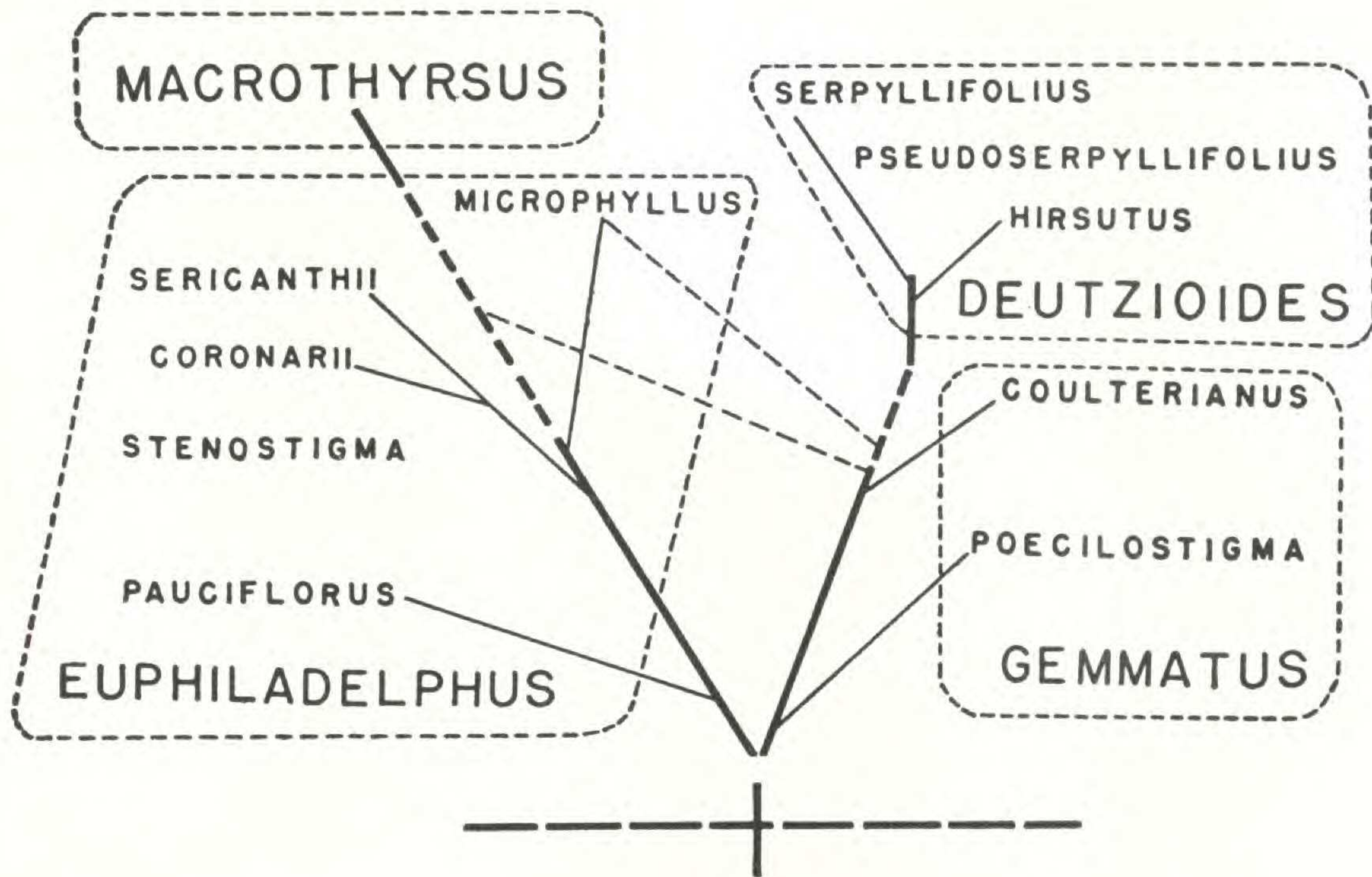
The interrelationship of the subgenera and sections is indicated graphically in the following figure.

In this classification primitive characters such as enlarged stigmas, high point of attachment in the placentation and long-tailed seeds are found both in the section Pauciflorus of the subgenus *Euphiladelphus* and the section Poecilostigma of the subgenus *Gemmatus*. The true dichasial inflorescences and the very large number of stamens of sect. Pauciflorus indicate that species in this section retain more primitive characters than those of sect. Poecilostigma which has apparently reduced compound inflorescences and moderate number of stamens. Yet the exposed buds of sect. Poecilostigma and the elongated cristate stigmas of many of its included species show that this section is more primitive in these respects. Morphological evidences, obviously suggest that our present species of *Philadelphus* seem to express two lines of evolution. They probably have originated from a common stock with exposed buds, dichasial inflorescences, exceedingly large number of stamens, and elongated cristate stigmas. Such a hypothetical "Protophiladelphus" does not exist in our present flora. The species of the section Pauciflorus occur in the mesophyllous forest of the southern Appalachian region, and those of the section Poecilostigma are associated with vegetations constituting the same type of forest in Mexico.¹ Apparently species in these two sections have existed for millions of years with very little changes.² They both represent very ancient stocks in the development of the genus.

¹ A. J. SHARP, Characteristics of the Vegetation in Certain Temperate Regions of Eastern Mexico. *Ecology* 31: 313–333. 1950.

² S. A. CAIN, The Tertiary Character of the Cove Hardwood Forests of the Great Smoky Mountains National Park. *Bull. of the Torrey Bot. Club* 70: 213–235. 1943; and A. J. SHARP. The relation of the Eocene Wilcox Flora to some Modern Floras. *Evolution* 5: 1–5. 1951.

Species of the sect. *Stenostigma* share the character of enclosed buds with the sect. *Pauciflorus*. This section with its determinate-racemose inflorescences, moderate number of stamens and some long-tailed but largely short-tailed seeds seems to have derived from the sect. *Pauciflorus*, the direct link seems to be from the *P. inodorus* type of plant to the *P. lewisii* type of plant. In this process of evolution, the changes involved are: (1) the suppression of the branching of the rachis of the lateral flowers of the true dichasia of the sect. *Pauciflorus*, thus prohibiting the formation of



HYPOTHETICAL PROTOPHILADELPHUS

FIG. 1. Relationships of the subgenera and sections of *Philadelphus* as indicated by morphological similarities. The solid lines indicate relative close relationships while the broken lines indicate lesser affinities.

the lateral cymes, (2) certain genetic modifications which promotes the differentiation of the tissue in the shoot apex, so that flower primordia are formed not only at the terminal nodes, but also in the axils of the leaf primordia, and consequently the determinate-inflorescences of the sect. *Stenostigma* are developed, (3) the reduction of the number of stamens, (4) the narrowing of the stigmatic surfaces, and (5) the lowering of the point of attachment in the placentation. The shortening of the seed-tails represents a more advanced stage of evolution in this section. These changes must have taken place before the Miocene period of geological time for fossil species of *Philadelphus* resembling the present small-leaved forms of *P. lewisii* Pursh existing in the Upper Miocene have been discovered by Chaney in Oregon and Colorado. It is very probable that during the Eocene period when North America, northern Asia and north-

ern Europe supported a temperate and subtropic flora, the species of the section *Stenostigma* were so well established and so widely distributed on the American and Eurasian continents that they had a holarctic distribution and a transcontinental range. The present disjuncted Old World and New World distribution represents its disturbed range and the existing species of this section may hence be considered as "living fossils" corresponding to the situation of *Sequoia* and *Metasequoia*.

The section *Microphyllus* culminates the *Euphiladelphus* line of descent. Its species share the characters of narrow stigmas and short-tailed seeds with the section *Stenostigma*. The majority of them have small leaves and pubescent hypanthia, characters common to xerophytic species. In the course of the evolution of these species the changes involved are chiefly in the development of the dwarf habit of the plant, in the reduction of the size and the increase in the thickness of the leaves, the formation of dense indumentum and in the suppression of the formation of the axillary flowers. These changes must have taken place at or after the end of the Eocene period when America saw the elevation of the Rocky Mountains. The consequent aridity necessitated such adaptation for xerophytic living.

The subgenus *Macrothyrsus*, though small in constitution, has a peculiar position in the classification and evolution of *Philadelphus*. On one hand it shares the moderate number of stamens, the clavate stigmas, the medianly attached placentation and the short-tailed seeds with species in the *Stenostigma* section of the subgenus *Euphiladelphus* but on the other hand its exposed buds link it to the subgenus *Gemmatus*. In addition to this peculiar combination of characters its paniculate inflorescence is very unique. It is probably most closely related to the subgenus *Euphiladelphus*. The general habit, the leaves and the appearance of the individual flowers of its included species, *P. californicus* Benth., resemble those of *P. lewisii* Pursh, a species of the section *Stenostigma* of the *Euphiladelphus*, so much that it has tempted botanists to treat it as a variety of the latter species. Apparently this stock has originated from the subgenus *Euphiladelphus* with a tenuous influence of the section *Gemmatus*.

The species of the section *Coulterianus* share the exposed buds and the long-tailed seeds with the *Poecilostigma*. Apparently this section represents a continuation of the *Gemmatus* line of evolution. In this stock a general tendency in the adaptation for a more xerophytic habitat is very prominent. It is shown both in the reduction of the size of the leaves and in the increased thickness of the indumentum. The stigmas of this section are elongate but not as a rule cristate, and the fruits are more or less globose in outline. In the size of the leaves, the pubescences of the hypanthia and in the form of the fruits, some species of this section, such as *P. sargentianus* S. Y. Hu express a strong resemblance to *P. argyrocalyx* Wooton of the section *Microphyllus* of the subgenus *Euphiladelphus*. These similarities are rather superficial. The gap between these species is wide for they differ in the fundamental criteria as to the position of the buds and the nature of the seeds.

Morphologically the subgenus *Deutzioides* is only remotely related to *Philadelphus*. In the low point of attachment of the placentation, the obconic fruit and the tailless seeds, this subgenus shows a close affinity to the Asiatic genus *Deutzia*. In fact, the appearance of a branch of *P. hirsutus* Nutt., the type species of the section *Hirsutus*, resembles that of a branch of *Deutzia grandiflora* Bge. of West China (Szechuan and Yunnan) more than it does of any American species of *Philadelphus*. Nevertheless, the species of this subgenus should not be separated from *Philadelphus* because of the indefinite number of unappendaged stamens and the simple straight hairs. In *Deutzia* the stamens are usually 10 and are always appendaged, that is, the filaments are winged. The trichomes of *Deutzia* are all stellate. The point of origin of this line of evolution in *Philadelphus* is not clear, but evidently it was not from the stock which gave rise to the *Euphiladelphus* species. The exposed buds of this subgenus indicate its faint affinity with the subgenus *Gemmatus*. Yet its ecaudate seeds, the columnar styles, and the coalescent stigmas imply a wide gap between them. It seems apparent that in the course of the evolution of *Philadelphus*, there has been a tendency towards the production of *Deutzia*-like plants. It appears that in the New World the process stopped in the subgenus *Deutzioides*, while in the Old World the change was more abrupt, the resulting genus, *Deutzia*, once established, diversified more rapidly than *Philadelphus*, and consequently occupies a wider area than *Philadelphus*. This conforms with Professor Sax's finding in the chromosome numbers of the two genera.¹ Accordingly, the basic chromosome number of *Philadelphus* and *Deutzia* are the same, $n = 13$, but in *Deutzia*, many species are polyploids. The xerophytic taxa of the subgenus *Deutzioides* may have the appearance of some species of the section *Microphyllus*. For example, *P. mearnsii* Evans of the section *Pseudoserpyllifolius* resembles *P. pumilus* Rydb., and *P. texensis* S. Y. Hu of the section *Serpyllifolius* has the appearance of *P. microphyllus* Gray. But these resemblances are superficial. *Philadelphus mearnsii* and *P. serpyllifolius* have exposed axillary buds, columnar styles, and ecaudate seeds and *P. pumilus* and *P. microphyllus* have enclosed buds, divided styles and short-tailed seeds. These superficially resembled species are developed from different stocks, the separation of which occurred in remote geological times. The exposed buds and the large serrate leaves of *P. hirsutus* Nutt. resemble those of *P. mexicanus* Schlecht. But the low point of attachment in the placentation, the columnar style and the ecaudate seeds of the former species indicate its advanced position on the genealogical tree of the genus. It is legitimate to assume that the representatives of the section *Hirsutus* were derived from the subgenus *Gemmatus* early in the evolution of the genus, and developed independently into the present forms. The species of the section *Pseudoserpyllifolius* are pygmies of this line of development and come about through the reduction in the size of the leaf to meet changed climatic and topographic require-

¹ K. SAX, Chromosome numbers in the Ligneous Saxifragaceae. Jour. Arnold Arb. 12: 198-204, 1931.

ments characteristic of a xerophytic environment. They are intermediate forms between members of the sections *Hirsutus* and *Serpyllifolius*. In indumentum they resemble the former and in size and general appearance they resemble the latter. The species of the section *Serpyllifolius* represent the climax of this line of evolution.

CYTOLOGY

Investigations of the cytology of *Philadelphus* have been undertaken by W. Bangham in Boston and Janaki Ammal in London. Bangham in 1929¹ examined the pollen mother cells of 37 species, hybrids and varieties of *Philadelphus* grown in the Arnold Arboretum and concluded that there is no marked difference in the chromosome groups among those taxa. He reported that each species had a diploid chromosome count of 26. He observed that the chromosomes of the hybrids were perfectly compatible and there was no evidence of lagging and other aberrant behavior. His observation on the chromosome behavior of a garden form of *P. pubescens* Loisel., which was then assumed by Rehder to be a cross between *P. tomentosus* Wall. of the Himalayan Region and *P. pubescens* Loisel. of southeastern United States, led him to conclude that there must have been very little change in the chromosome makeup of *P. tomentosus* Wall. and *P. pubescens* Loisel. in the millions of years that they, or their ancestors, have been separated.

Janaki Ammal in 1951² studied the chromosome number and behavior of *Philadelphus* grown at the Royal Botanic Gardens, Kew and the gardens of the Royal Horticultural Society at Wisley, England. She confirmed Bangham's findings that the natural species are diploids with the chromosomes $2n = 26$. But her observation of the chromosome behavior of the hybrids differs from that of Bangham. She reported that lagging and other types of aberrant behavior are generally associated with hybridity in *Philadelphus* and consequently give rise to high pollen sterility. In the case of the trispecific hybrids, *P. purpureo-maculatus* Rehd., the chromosome behavior is so irregular that it causes the production of unreduced germ cells. By the fertilization of an unreduced egg cell with a normal pollen, triploid garden forms resulted. She found that *P. "Sybille,"* *P. "Belle Etoile"* and *P. "bicolor"* are all triploids. She also observed a newly produced hybrid, *P. "Beauclerk,"* with tetrasomic diploid chromosome composition, $2n = 28$. She thus concluded, "though differences in chromosome number do not exist in nature, there are differences in morphology of the chromosome which interfere with pairing in their hybrids between widely separated species . . . for the first time since Eocene times polyploidy has been induced in a genus which has remained diploid for millions of years in nature, by the bringing together under cultivation

¹The Chromosomes of Some Species of the Genus *Philadelphus*. Jour. Arnold Arb. 10: 167-169. 1929.

²Chromosomes and the evolution of Garden *Philadelphus*. Jour. Royal Hort. Soc. 76(8): 269-275. 1951.

and the consequent hybridization of races widely separated geographically.”

Bangham worked on plants cultivated in Boston and Janaki Ammal's material was grown in London. These two cities are located out of the natural ranges of the genus *Philadelphus*. The climate of these cities only supports the outdoor growth of a few species and their forms. A close examination of the lists of species studied by Bangham and Janaki Ammal reveals that they covered very limited portions of the geographically widely spread and morphologically much diversified genus. Thus it appears to me that the cytological investigation of the natural species is not inclusive enough for any cytologist to draw a conclusion as to whether differences in the chromosome number of *Philadelphus* do exist in nature or not. A large scale transplanting of natural species from southeastern and western United States and Central America into gardens situated in areas warmer than Boston or London, such as the United States National Arboretum in Washington, D. C. or the Boyce Thompson Southwestern Arboretum for the study of the drought resisting species, will doubtlessly provide better opportunities for more exhaustive cytological studies of the genus and advance our knowledge of the cytotaxonomy in this group.

GEOGRAPHIC DISTRIBUTION

The subgenus *Gemmatus* with its exposed axillary buds, simple, reduced or ramiferous thyrses, high point of attachment in the placenta, broadened usually cristate stigma and long-tailed seeds, represents morphologically, I feel, the more primitive elements of the genus. The species are largely subtropical or tropical in distribution. They are limited to the New World, with eastern Mexico being its center of concentration. The range extends ten degrees toward the north and the south of the Tropic of Cancer. The effect of rainfall, temperature, altitude and latitude on the distribution of the different species of this subgenus in Mexico is very evident. *Philadelphus karwinskyanus* is found only on the Great Cross Range and hence westward along the Pacific Coast at lower altitudes where the climate is warmer. In the warm and humid section of the Sierra Madre Oriental, one finds *P. affinis* with its subglabrous hypanthium. At higher altitudes of the same range grows the small-flowered *P. asperifolius*. Hence northward into the arid northeastern Mexico, occur various endemic species belonging to the Section *Coulterianus*. In the neighborhood of the Tropic of Cancer at high altitude where the rainfall is low, *P. maculatus*, a small-leaved form with reddish purple spot at the base of each petal, grows.

The true *P. mexicanus* with its solitary or ternate flowers and pubescent petals occurs only on the Sierra Madre del Sur, the southern area of the Sierra Madre Oriental, and in Chiapas, hence southwestward to Guatemala. In southern Mexico and Guatemala, a species with pubescent petals and ramiferous inflorescences, *P. myrtoides*, occurs. This species extends southward to the Province of Chiriqui in Panama, the southern limit of the range of distribution in the genus.

The subgenus *Euphiladelphus* includes geographically the more widely distributed elements. Its representatives occur in Europe, Caucasus, the Himalayan region, China Proper, Manchuria, Japan, a large part of the United States, and adjacent southwestern Canada and northeastern Mexico. It is an assemblage of species adapted to the climatic conditions of the North Temperate Zone, between latitudes 25–50° N. in both the Old and the New World.

In the Old World, the subgenus is rather stable. Radical changes did not occur in the course of its evolution. All the Old World species belong to one section, *Stenostigma*. In Europe, it is represented by *P. coronarius* which occurs, according to Hegi, spontaneously in Romania, Austria and southern Germany. In the Caucasus Mountains, it is represented by *P. caucasicus*, a species which differs from *P. coronarius* only in its pubescent discs and styles. The eastward distribution of the section is interrupted in Central Asia. No species is met with until it reaches the Himalayan Mountains. There the species concentrate in Sikkim, Nepal and eastern Punjab where it is represented by *P. tomentosus* and its related forms. In China more marked morphological changes were involved in the course of the evolution of this group. There the section can be subdivided into several series. The Tsingling Range seems to provide a central stage from where the different lines of evolution in the species can be traced. At the western end of this mountain range occurs *P. kansuensis*, a species having the leaf character of *P. pekinensis*, a North China element, the pubescent disc of *P. subcanus*, a Central China element and the pubescent hypanthium of *P. henryi*, a southwestern China element. At the eastern end of this mountain range, occurs *P. sericanthus* and its related forms. South of this range grows *P. purpurascens*, an intermediate form between the Tsingling and the Yunnan species, *P. delavayi*. The latter species morphologically and geographically links the Chinese and the Himalayan elements. North of the Tsingling Range in Shansi, Shensi and Kansu occurs *P. laxiflorus*, a species morphologically and geographically intermediate between *P. pekinensis* and *P. sericanthus*. The northernmost limit of the distribution of this section in the Old World is the wooded valley of the Amur River and its tributaries, the Sungari and Ussuri rivers in Manchuria, where it is represented by *P. tenuifolius* and *P. schrenkii*. These species also occur in Korea. In Japan this subgenus is represented by *P. satsumi* and its related forms.

The distribution of *Philadelphus* in Eastern Asia presents a very interesting phytogeographic phenomenon, that is, the complete absence of the genus from the flora of Taiwan (Formosa). It is a well known fact that Taiwan and Yunnan have very pronounced floristic affinities. Many species as well as genera that occur in one province are also present in the other. But in the case of *Philadelphus*, the genus is abundant in northwestern Yunnan and is completely absent from Taiwan. This fact may be taken as an indicative factor for confirming our belief as to the origin of the genus and for explaining the pattern of its distribution in Eastern Asia. The genera and species that are common to Taiwan and

Yunnan are of Old World origin. *Philadelphus* is obviously of New World origin, and its distribution in Eastern Asia seems to have been southward in direction. Apparently neither the Japanese elements nor the continental Chinese elements of this genus reached Taiwan in their migration.

In the New World, the subgenus *Euphiladelphus* is much more diversified, and consequently three sections are represented. Two of these three sections, *Pauciflorus* and *Microphyllus*, are endemic to the United States. Few species of the section *Microphyllus* also occur at the northern border of Mexico. The third section, *Stenostigma*, America shares with Europe and Asia. In North America the species of the section *Stenostigma* can be subdivided into two series the *Gordoniani* and the *Pubescentes*. Species belonging to the *Gordoniani* series occur along the Snake and Columbia Rivers, hence southward reaching the mountains of the California Coast Range. Among the wild population, there seems to be two elements, *P. lewisii* with a glabrous hypanthium and *P. helleri* with a slightly pubescent hypanthium. Morphologically there seems to be little distinction between them, other than the presence or absence of the hairs on the hypanthium, but ecologically there are certain differences. In the natural population of the general area considered, I have examined 292 individual collections totaling 361 sheets. Of these, 177 have glabrous hypanthia and 115 have slightly pubescent ones. After plotting the localities of these collections on a map and then superposing this figure on Rehder's map of climatic zones,¹ a rather striking fact is revealed. Over 77% of *P. lewisii* occur in zones where the average annual minimum temperature is -10° to -5° F. while over 47% of *P. helleri* occur in zones where the average annual minimum temperature falls to -20° to 10° F. The checking also indicates that the center of distribution of *P. lewisii* is in the lower valley of the Columbia River and in the northern portion of the Pacific Border Province while *P. helleri* occurs largely in the intermontane basin and the deeply dissected mountain uplands of the northern Rocky Mountains. Species belonging to the series *Pubescentes* occur in the Ozark Plateau and the Arkansas Valley of the Interior Highlands and the Interior Low Plateau region of Tennessee, Kentucky, and southern Ohio.

The section *Pauciflorus* with dichasial inflorescences, very large number of stamens, enlarged stigmas, and high point of attachment in the placentation and long-tailed seeds, retains all the primitive characters of the genus. Species of this section concentrate in the mesophyllous forest of the southern Appalachian region with the periphery of their range reaching the Coastal Plain region along the borders of Georgia and Alabama in the south. It seems that species of this section are rather inactive geographically and stable morphologically, for with all the material I have examined, there are very slight variations.

The section *Microphyllus* includes the xerophytic species. Its range covers the southern Rocky Mountains in Central Colorado, the Colorado Plateau in western Colorado, Utah, northern New Mexico and Northern Arizona, the Sonoran Desert region in southern Nevada and southeastern

¹ Man. Cult. Trees, Shrubs pp. xii-xiii, 1940.

California and the Mexican Highland in Eastern Arizona, southwestern New Mexico and western Texas, and the adjoining Mexico. In this large semidesert or desert area the populations are localized and isolated. There are many endemics.

The subgenus *Deutzioides* is strictly a North American taxon. Its three sections occur in two different floristic provinces. The section *Hirsutus*, as represented by *P. hirsutus* Nutt. and its related forms, concentrates in the mesophyllous forests of the Southern Appalachian Mountain areas with the Tennessee River and its tributaries being the center of its range. The other two sections, *Pseudoserpyllifolius* and *Serpyllifolius*, are constituted of xerophytic species which occur in southwestern Texas, New Mexico, southern Arizona, and northern Mexico. It seems that the Mexican Highland is a meeting ground of different elements, the subgenera *Euphiladelphus* from the north, *Deutzioides* from the east and *Gemmatus* from the south.

TAXONOMY

Philadelphus Linn. Sp. Pl. 470. 1753; et Gen. Pl. ed. 5, 211. no. 540. 1754. — Miller, Dict. Gard. ed. 8, 834. 1768. — Willd. Sp. Pl. 2: 947. 1800. — Michx. Fl. Bor. Am. 1: 283. 1803. — Pursh, Fl. Am. Sept. 1: 329. 1814. — DC. Prodr. 3: 205. 1828. — Schrader in Linnaea 12: 388. 1838. — G. Don, Gen. Syst. 2: 807. 1832. — Schlecht. in Linnaea 13: 418. 1839. — Torr. & Gray, Fl. N. Am. 1: 594. 1840. — Endl. Gen. Pl. 1187. 1841. — Walp. Rep. 2: 151. 1843. — Koch in Woch. Gärtn. Pflanzenk. 2: 229. 1859. — Rupr. ex Maxim. in Bull. Phys.-Math. Acad. St. Pétersb. 15: 133. 1856; 15: 365. 1857. — Benth. & Hook. f., Gen. Pl. 1: 642. 1865. — Maxim. in Mém. Acad. Sci. St. Pétersb. VII. 10(16): 35 (Rev. Hydrang. As. Or.). 1867. — Koehne, Deutsche Dendr. 178. 1893; in Gartenfl. 45: 450. 1896; et in Mitt. Deutsche Dendr. Ges. 1904(13): 76. 1904. — Rydb. in N. Am. Fl. 22: 162. 1905. — Schneider, Ill. Handb. Laubh. 1: 1905. — Syreistchikof, Ill. Fl. Mosc. 2: 220. 1907. — Nakai in Bot. Mag. Tokyo 29: 61. 1915. — Moore in Bailey, Stand. Cycl. Hort. 5: 2579. 1916. — Rehd., Man. Cult. Trees Shrubs 270. 1927, ed. 2, 264. 1940; et Bibliogr. Cult. Trees Shrubs 191. 1949. — Engler, Pflanzenf. III, 2a: 69. fig. 36. A-G. 1891; ed. 2. 18a: 190. fig. 110. A-G. 1930. — Hitchcock in Madroño 7: 35. 1944. — Bean, Trees Shrubs ed. 7, 2: 410. 1950; et in Chitt. Dict. Gard. 3: 1545. 1951.

Syringa Adanson, Fam. Pl. 2: 244. 1763. — Moench, Meth. Pl. 678. 1794, non Linn. 1753.

TYPE SPECIES: *P. coronarius* Linn.

Flowers solitary, ternate, in determinate racemes or in depauperate panicles, generally fragrant. Calyx-tubes turbinate or subcampanulate, adnate to the ovary forming the hypanthia, glabrous or pubescent, the

sepals 4, rarely 5, ovate, acute or acuminate; corolla white, rarely with purplish center, the petals 4, rarely 5, in cultivated forms often doubled; stamens 13–90, epigynous, the filaments subulate, free, rarely several united at the base, the anthers oblong, rarely subglobose, glabrous, rarely pilose; ovary inferior or semi-inferior, 4-, rarely in anomalous forms 5-locular, the styles 4, rarely 3 or 5, entirely connate, partially free or rarely in some cultivated forms entirely free, the stigmas free and linear, clavate, oar-shaped, cristate, or coherent and columnar or subcapitate; placentas auriculate, projected from the upper portion of the central axis; ovules numerous, multiseriate, imbricate, pendulous. Capsules ellipsoid, turbinate, hemispherical or subglobose, corticate, the cortex chartaceous, the pericarp cartilaginous, loculicidal. Seeds oblong-subcylindric, the testa brown or nigrescent, membranous, reticulate, generally extending anteriorly into a fimbriate white crown and posteriorly into an obtuse or acuminate tail, the funiculus nigrescent, persistent, the embryo minute, embedded in the carnose and oily endosperm. Shrubs, erect, arching, subscandent or rarely subspinescent; branchlets opposite. Leaves opposite, deciduous, rarely evergreen, serrate or entire, triplinervate or quintuplinervate, glabrous or pubescent, the hairs simple, rarely evergreen, exstipulate; axillary buds exposed or enclosed.

The generic name, *Philadelphus*, is derived from the Greek root *φίλος* meaning love, *δελφός* meaning brother. It was originally used by the ancient Greeks, said to be named for Ptolemy Philadelphus, king of Egypt, 283–247 B. C., for some plant the identity of which is now unknown. Many pre-Linnaean authors called the plants which we now ascribe as *Philadelphus*, "*Syringa alba*." Clusius¹ named his illustration of the plant *Frutex coronarius*. Bauhin was the first man who interpreted the pre-Linnaean "*Syringa alba*" as the *Philadelphus* of the Greeks.² When Linnaeus established the genus, he adopted Bauhin's concept. The vernacular names occurring in various literatures are enumerated in the following list:

English:	<i>Syringa</i> ; common syringa; mock-oranges (for the odor of the flower); pipe tree; pipe privet
French:	<i>Syringa odorant</i>
German:	Pfeifenstrauch; wilder jasmin; falscher jasmin
Dutch:	Witte syring
Chinese:	T'ai-ping-hua = flower of peace; san-mei-hua = mountain mume flower; Mi-tsai = rice fuel.
Spanish:	Geringuilla
Russian:	Tschubuschnik; pustoryl
Central American:	Mosqueta; Acuilotl = water vine; cozticacuilotl; cozticacuilotl xochitl; azahar

¹ *Rariorum Plantarum Historia* 1: 55. 1601.

² *Pinax Theatri Botanici* 399. 1623.

KEY TO THE SUBGENERA AND SECTIONS.

- A. Axillary buds exposed.
- B. Seed long-caudate; stigmas free, broadened, usually cristate; flowers solitary, ternate, or in depauperate panicles; fruit obovoid or subglobose, with circumferential persistent calyx. Subg. I. GEMMATUS.
- C. Leaves acuminate, rarely acute; flowers in a depauperate panicle, 1- up to many-flowered, each on a pointed pedicel; the stigmas broadened, cristate; fruits obovoid-ellipsoid Sect. 1. POECILOSTIGMA.
- CC. Leaves acute or obtuse; flowers solitary or ternate; the stigma elongate but in general not cristate; fruit subglobose Sect. 2. COULTERIANUS.
- BB. Seeds short-caudate; stigmas free, clavate; flowers in panicles of thyrus; fruit ellipsoid with subapical persistent calyx. Subg. III. MACROTHYRSUS (Sect. 6 CALIFORNICUS)
- BBB. Seeds ecaudate; stigmas connate, columnar or subcapitate; flowers solitary or ternate; fruit turbinate or subglobose, with apical persistent calyx Subg. IV. DEUTZIOIDES.
- C. Leaves hirsute or strigose, all hairs straight.
- D. Style 3-4 mm. long; subscandent shrubs; leaves serrate Sect. 7. HIRSUTUS.
- DD. Style 1 mm. long; subspinescent shrubs; leaves entire Sect. 8. PSEUDOSERPYPHYLLIFOLIUS.
- CC. Leaves strigose and lanate beneath; style 1-2 mm. long; subspinescent or small slender shrub Sect. 9. SERPYPHYLLIFOLIUS.
- AA. Axillary buds enclosed Subg. II. EUPHILADELPHUS.
- B. Flowers solitary, ternate or in dichasial cymes.
- C. Large arching shrubs; stamens 60-90; stigmas free, oar-shaped; leaves 4-10 cm. long. Sect. 3. PAUCIFLORUS.
- CC. Erect low shrubs of compact growth or spinescent xerophytic bushes; stamens 35-50; stigmas free or partially connate, linear; leaves 0.5-2.5, rarely up to 3 cm. long. Sect. 5. MICROPHYLLUS.
- BB. Flowers in determinate racemes Sect. 4. STENOSTIGMA.

Subgenus I. *Gemmatus* (Koehne), stat. nov.*Philadelphus* subg. I. *Gemmatus* (Koehne), stat. nov.

Philadelphus Reihe 4. *Decorticatae pauciflorae* Koehne, Deutsche Dendr. 180, 184. 1893, pro parte.

Philadelphus sect. 1. *Poecilostigma* subsect. 1. *Gemmati* Koehne in Gartenfl. 45: 450. 1896, pro parte; et in Mitt. Deutsche Dendr. Ges. 1904(13): 77. 1904. — Engler, Pflanzenf. ed. 2, 18a: 191. 1930.

TYPE SPECIES: *P. mexicanus* Schlechtendal.

Flowers solitary, ternate, or in depauperate panicles; hypanthia obconic, or subglobose, generally dense pubescent; stamens about 40, rarely more or less; ovary semi-inferior, the stigma distinct, broadened or cris-

tate; capsules obovoid-ellipsoid or subglobose, the persistent calyx circumferential or subcircumferential; seeds long-caudate, the crowns with pointed lobes, erect or subscandent shrubs or vines; leaves evergreen or deciduous, remotely denticulate or serrate, triplinervate or quintuplinervate; petioles often twisted; axillary buds exposed.

This subgenus is strictly a Central American taxon. In the southern portion of its range there are several widely spreading species, and in the northern portion, the species are largely endemic to limited areas. It contains two sections including fourteen species. Their geographical distributions are as illustrated in Map 1.

Section 1. POECILOSTIGMA Koehne

Philadelphus subg. I. **Gemmatum** sect. 1. **Poecilostigma** Koehne in *Gartenfl.* 45: 450. 1896; et in *Mitt. Deutsche Dendr. Ges.* 1904(13): 77. 1904, pro parte.

Philadelphus sect. *Poecilostigma* Koehne, ll.cc. — Engler, *Pflanzenf.* ed. 2, 18a: 191. 1930.

Philadelphus Mexicani Rydb. in *N. Am. Fl.* 22: 164. 1905, in clavis, s. stat.

Philadelphus ser. *Gemmati* (Koehne) Rehder, *Man. Cult. Trees Shrubs* ed. 2, 275. 1940; et *Bibliogr. Cult. Trees Shrubs* 194. 1949, pro parte.

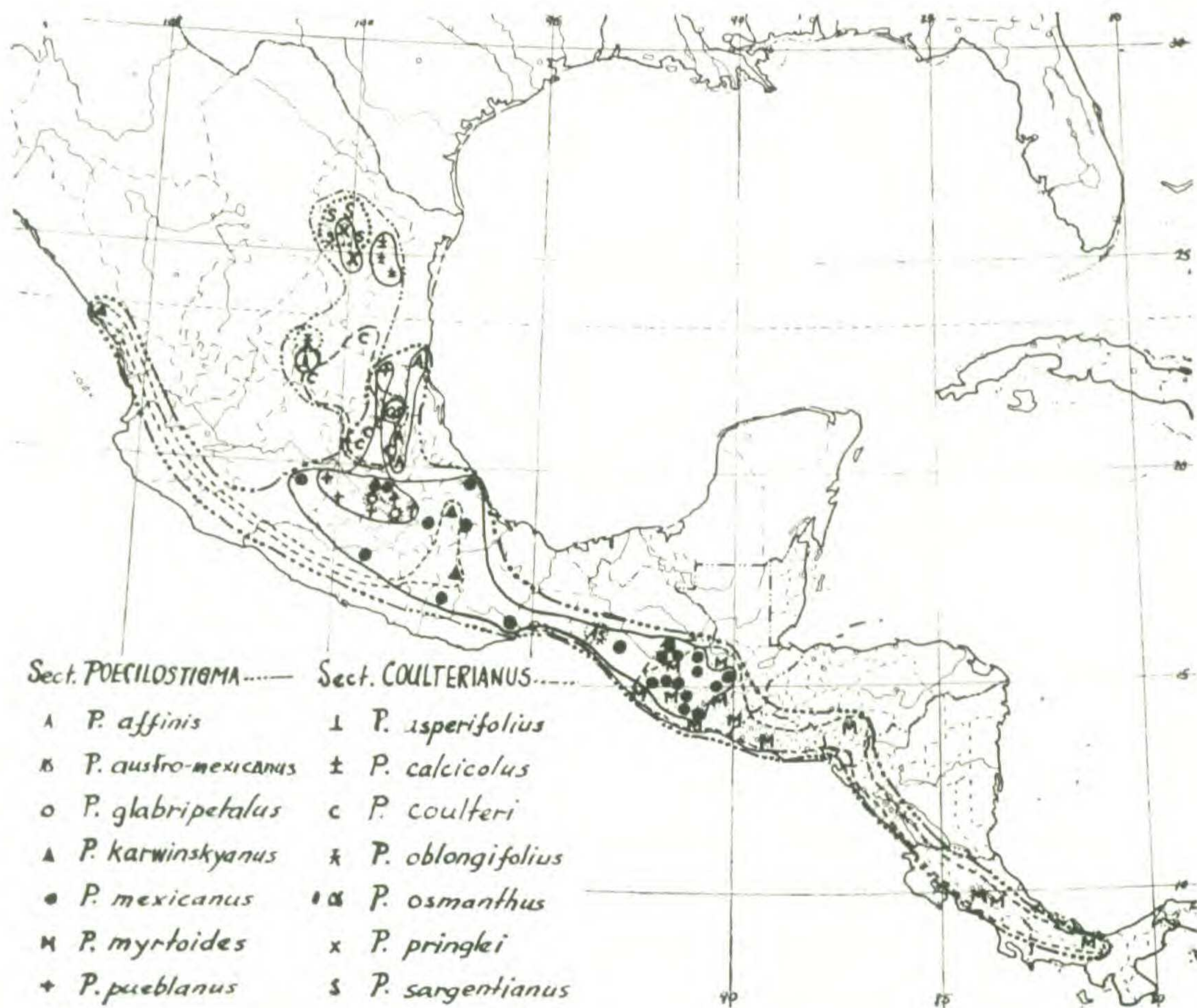
TYPE SPECIES: *P. mexicanus* Schlechtendal.

Arching shrubs or vines, the current year's growth pubescent and usually verrucose, the axillary buds exposed; leaves remotely denticulate or serrate, the base rounded, 3- or 5-nerved, the apex acuminate, rarely acute; inflorescences depauperate panicles, or flowers solitary, the bracts linear or lanceolate, foliaceous; hypanthia subglobose or cyathiform, the sepals foliaceous, (5-) 8-20 mm. long; corolla usually disciform, often pubescent; stamens 40-50; disc conic, style (3-) 4-7 mm. long, the stigma broadened and cristate; fruit obovoid-ellipsoid; seeds long-caudate. Seven species, Mexico to Panama.

KEY TO THE SPECIES

- A. Flowers many on ramified branches; hypanthia subglobose.
 - B. Inflorescences loose, paniculate, the secondary axis of unequal length, 4-30 mm. long, the lower ones longer.
 - C. Hypanthia glabrous or with few weak pilose hairs; base of the hairs on the stem not thickened; axillary buds subglobose 1. *P. affinis*.
 - CC. Hypanthia pubescent; base of the hairs on the stem thickened; axillary buds conic.
 - D. Hypanthia lanate, the underneath tissue obscure; inside of the petals glabrous 2. *P. karwinskyanus*.
 - DD. Hypanthia villose, the underneath tissue visible; petals pubescent on the apical ends 3. *P. pueblanus*.
 - BB. Inflorescences compact, raceme-like, the secondary axis equal in length, 2-4 mm. long, the flowers crowded at the end of elongated leafy branches 4. *P. myrtoides*.

- AA. Flowers solitary or ternate; hypanthia cyathiform or obconic (except *P. glabripetalus*).
- B. Petals pubescent on both surfaces; hypanthia sparsely villose or pilose.
- C. Style and disc pubescent; axillary buds conic; leaves large, 5–11 cm. long, the petioles 8–10 mm. long 5. *P. mexicanus*.
- CC. Style and disc glabrous; axillary buds subglobose; leaves small, 1–3.5 cm. long, the petioles 2–3 mm. long 6. *P. austro-mexicanus*.
- BB. Petals glabrous, at least on the inside; hypanthia lanate 7. *P. glabripetalus*.



MAP 1. Geographical distribution of the species and sections of *Philadelphus* in the subgenus *Gemmatus*.

1. *Philadelphus affinis* Schlecht. in *Linnaea* 13: 419. 1839. — Walp. *Rep.* 2: 151. 1843. — Hemsl. in *Biol. Centr. Am.* 1: 383. 1879. — Koehne in *Gartenfl.* 45: 487. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 78. 1904. — Schneider, *Ill. Handb. Laubh.* 1: 362. 1905. — Rydb. in *N. Am. Fl.* 22: 171. 1905. — Standl. in *Contr. U. S. Nat. Herb.* 23: 511. 1922. — Engler, *Pflanzenf.* ed. 2. 18a: 191. 1930.

Philadelphus zeyheri sensu Hemsl. in *Biol. Centr. Am.* 1: 384. 1880, non Schrader ex DC. 1828.

TYPE: Ehrenberg, Barranca de la Hacienda Del Carmen, S. Mexico.

An arching shrub or vine up to 4 meters high, the flowering branches slender, 10–20 cm. long, bearing 3 to 5 pairs of leaves, sparsely pilose, the base of the hairs not thickened; axillary buds subglobose, pubescent. Leaves ovate rarely ovate-elliptic, 4.5–8 cm. long, 2.5–4.5 cm. wide, rounded, rarely subcordate at the base, 5-nerved, acuminate at the apex, remotely serrate, each side with 2 to 5 teeth, subglobose or very sparsely strigose on both surfaces, more so on the principal nerves beneath, reticulations obscure above, conspicuous beneath, petioles 3–10 mm. long, pilose. Inflorescences depauperated panicles (Pl. V fig. 1) with 5-, rarely 3-, 1-, or 11-flowers, the woody part of the stalk 1–3 cm. long, pubescent as are the branchlets, bracts linear, the pedicels 2–3 mm. long, glabrous, after fruit up to 6 mm. long; hypanthia subglobose, 6 mm. in diameter, glabrous or with few weak pilose hairs, the sepals ovate, acuminate, 10 mm. long, 4–5 mm. wide, glabrous or very sparsely pilose; corolla subdisciform, 3.5–5 cm. across, the petals obovate to suborbicular, 1.3–1.8 cm. in diameter, glabrous, the apex round; stamens about 50, the longest three-fourths the length of the petals; disc subconic, glabrous; style 7 mm. long, undivided or the upper one-fifth separated, hirsute, the stigmas broadened, cristate, the abaxial surfaces broader and longer than the adaxial ones, the sterile portion hirsute (Pl. V fig. 1a). Capsules ellipsoid, the persistent calyx circumferential, the seeds long-tailed.

MEXICO: Hidalgo: Zacualtipán, *P. Maury* 5826 (NY), same locality, *H. E. Moore* 3238 (BH, G); in a barranca below Trinidad Iron Works, *C. G. Pringle* 8833 (F, G, MO, NY, US); Atotonilco, *Schiede*, June 1830 (A, US); Bluff above Cuera Humada, *A. J. Sharp* 4618 (TENN.). Tamaulipas: Tampico, Real del Monte, *M. Berlandier* 333 (F, MO, US). Without precise locality, Herb. Dendrol. *Schneider* (A).

The type not being available, this interpretation is made on the basis of Schlechtendal's original description and Koehne's supplementary remarks. Schlechtendal characterized the inflorescences as 5-flowered racemes, the peduncles and calyces smooth and glabrous. Unfortunately he did not mention the pubescence of the style. For this character I rely upon Koehne who certainly had access to the now destroyed type. According to Koehne the style of this species has loose stiff hairs. I therefore place the Mexican material with 5-flowered depauperate panicles, more or less glabrous hypanthia and calyces, and pubescent styles with *P. affinis* Schlecht. Hemsley in 1880 doubtfully published *Berlandier* 333 from Tampico as *P. zeyheri* Schrad. In this he mistook the material of a spontaneous Mexican species, *P. affinis* Schlecht., for a garden form cultivated in European gardens.

The ovate leaves, the subglobose glabrous hypanthia, the large foliaceous sepals with acuminate apices, the large number of stamens, the broadened stigmas and the ellipsoid capsules with circumferential persistent sepals of this species all suggest relationship to *P. inodorus* Linn. of the southern Appalachian region of the southeastern United States. As

the latter species has enclosed buds and this one has exposed buds their separation must have taken place far back in geological time.

In Mexico this species occurs on the Sierra Madre Oriental at altitudes of 1852–2000 meters, in regions where the annual rainfall attains at least 80 inches per year. Its white fragrant flowers appear from April to June. The specimens collected in July are with fruits.

2. *Philadelphus karwinskyanus* Koehne in *Gartenfl.* 45: 486. 1896; et in *Mitt. Deutsch. Dendr. Ges.* 1904(13): 1904. — Schneider, *Ill. Handb. Laubh.* 1: 362. 1905. — Rydb. in *N. Am. Fl.* 22: 170. 1905. — Standley in *Contr. U.S. Nat. Herb.* 23: 311. 1922.

Philadelphus scandens Moore in Bailey, *Stand. Cycl. Hort.* 5: 2582. 1916.

TYPE: Karwinsky, Tolotapa, Oaxaca, Mexico.

A subscandent shrub up to 4 meters high, branchlets slender, the flowering ones over 50 cm. long, much ramified, terete, striate, villose, the base of the hairs thickened; axillary buds conic, villose. Leaves ovate, 4–7.5 cm. long, 2–3.5 cm. wide, rounded at the base, acuminate at the apex, 5-nerved, reticulations conspicuous beneath, remotely sharp serrate, 5–8 teeth on each side, sparsely strigose on both surfaces; petiole 5–10 mm. long, attached on cushion-like projections of the node. Inflorescences with 5–31 flowers, in a loose depauperate panicle, the woody portion below the pedicel 4–20 mm. long, pubescent, the pedicels 2–5 mm. long, thickly strigose and lanate; hypanthia subglobose, 4 mm. in diameter, strigose-lanate, the sepals ovate, 5–8 mm. long, densely lanate, the hairs entirely obscuring the tissue beneath; corolla 2.5–3 cm. across, the petals obovate-suborbicular 0.8–1.3 cm. in diameter, sparsely pubescent along the median dorsal line, glabrous on the ventral side, the apex rounded; stamens about 45, the longest half as long as the petals; disc subconic, pubescent, stigmas 2.5–3 mm. long, enlarged cristate, the sterile portion pubescent, the abaxial surface with 2 papillose ridges. Capsule and seed not known.

MEXICO: Oaxaca: Tepascalula, *Loesener* 1421(G); Huitzo, *L. C. Smith* 807(G). Vera Cruz: Orizaba, *F. Müller*, Jan. 1853(NY). Sinaloa: Mazatlan, *J. G. Ortega* 6770(F). Without precise locality, *Ortega* 7342(F).

UNITED STATES: Cultivated in California: Altadena, *F. W. Peirson* 79(BH); San Diego, *F. G. Woodcock* 870(F), 871(BH), 872(A, BH); Santa Monica, *L. H. & Ethel Bailey* 7804(BH); Los Angeles, *L. H. & Ethel Bailey* 9117(BH).

A great altitudinal variation is reported for this species. In Oaxaca it has been collected 2000 meters above the sea level and in Sinaloa, it has been reported from humid lowlands almost at sea level. It is an evergreen shrub, flowering all year around. In California where it is an introduced and cultivated species, flowering records cover August, October, December, January, February, March, April and May.

3. *Philadelphus pueblanus*, sp. nov.

Frutex subscandens, usque 4 m. altus, ramulis floriferis, 20–40 cm. longis, teretibus, striatis, 2–4 mm. diametro, dense pilosis et sparse strigosis, pilis basi incrassatis, gemmis axillaribus breviter, villosis; foliis ovatis, 4–7 cm. longis, 2–3.5 cm. latis, basi rotundatis, raro obtusis, quintuplinerviis, apice acuminatis, serratis vel subintegris, dentibus utrinque 1, 2 usque ad 5, utrinque strigosis, petiolo 5–10 mm. longo; inflorescentiis ramosis, 5- usque 31-floribus, pedunculis 4–20 mm. longis, pedicellis 3–6 mm. longis, villosis, verruculosus, hypanthiis subglobosis, 4 mm. diametro, villosis; sepalis ovatis, caudatis, 10 mm. longis, 4–5 mm. latis, sparse villosis; corolla disciformii, 4 cm. diametro, petalis oblongo-suborbiculatis, 2 cm. longis, 1.5 cm. latis, partibus medianis extus hirsutis, apice rotundatis et retusis; staminibus ca. 40; disco subconico, medio hirsuto; stylis 6–7 mm. longis, columnaribus indivisis; pubescentibus; stigmatibus cristatis, 2–3 mm. longis, partibus sterilibus hirsutis; capsulis et seminibus ignotis.

MEXICO: Puebla: vicinity of Puebla, *Bro. G. Arsène (Bro. Nicolas) 171* (A, TYPE; G, MO, NY, US ISOTYPES); Arzobispado, *Bro. G. Arsène 10136*(US); Ixtaccihuatl, *C. A. Purpus 169*(MO, US); Com. Geogr.-Expl. Rep. Mexicana 1022(NY). Tlaxcala: Tlaxcala, *E. K. Balls 4906*(A). San Luis Potosí: Santa Barbara, *Bro. G. Arsène 10093* (US). Mexico: Par Nicolas, *M. Bourgeau 995*(US); Temascaltepec, Rincón, *G. B. Hinton 2362*(A), *5032*(BH, NY, US). Michoacan: Zitacuaro, *G. B. Hinton 13342*(G, NY, US). Morelos: near Cuernavaca, *J. N. Rose & W. Hough 4412*(US).

This species is intermediate between *P. affinis* Schlecht. which has glabrous or subglabrous hypanthium and *P. karwinskyanus* Koehne in which the hypanthium is thickly lanate with the indumentum entirely covering the epidermal tissue. In Puebla it occurs at altitudes between 1700 and 2194 meters as semiscandent shrubs in thickets and among trees in ravines. Its pale yellow sweet-scented flowers appear from March to October.

4. *Philadelphus myrtoides* Bertol. Fl. Guatim. 21. pl. 7. 1840. — Walp. Rep. 2: 151. 1843. — Hemsl. Biol. Centr. Am. 1: 383. 1879. — Koehne in Gartenfl. 45: 487. 1896. — Rydb. in N. Am. Fl. 22: 170. 1905. — Engler, Pflanzenf. ed. 2, 18a: 192. 1930. — Standley in Field Mus. Nat. Hist. Bot. Ser. 18: 474 (Fl. Costa Rica). 1937.

Philadelphus trichopetalus Körnicke in Gartenfl. 16: 73. 1867. — Koehne in Gartenfl. 45: 487. 1869; et in Mitt. Deutsch. Dendr. Ges. 1904(13): 78. 1904. — Smith in Pittier, Prim. Fl. Cost. II. 1: 90. 1898. — Schneider, Ill. Handb. Laubh. 1: 364. 1905. — Engler, Pflanzenfam. ed. 2, 18a: 192. 1930.

Philadelphus mexicanus sensu Moore in Bailey, Stand. Cycl. Hort. 5: 2582. 1916, pro parte. — Standley & Calderón, Pl. Salv. 88. 1925, non Schlechtendal.

Philadelphus sempervirens Hort. ex. Moore in Bailey, Stand. Cycl. Hort. 5: 2582. 1916.

Philadelphus matudai Lundell in Contr. Univ. Mich. Herb. 4: 6. 1940.

TYPE: Botanical Garden of Bologna, Italy.

An arching shrub, 2–4 m. high, flowering branches slender, 21–50 cm. long, with 14 or more pairs of leaves, longitudinally striate, rather densely villose, the trichomes slightly curled, their base more or less thickened; buds small, rounded, densely brown villose. Leaves ovate, 3–4 cm., rarely up to 5.5 cm. long, 1–2.8 cm. wide, sparsely strigose above, more so beneath, the hairs glandular at the base, rounded or rarely obtuse at the base, acuminate at the apex, subentire, or remotely denticulate, with 2 to 6 sharp teeth projecting outward on each side, triplinervate or quintuplinervate, reticulations obscure on both surfaces; petioles 6–9 mm. long, strigose. Flowers 5, rarely 1, 3, or 7, crowned at the end of long slender branchlets, the woody portions below the pedicels uniformly short, 2–4 mm. long, the bracts linear, 5–13 mm. long, the pedicels 3–4 mm. long, white lanate; hypanthia subglobose, 5 mm. in diameter, densely lanate; sepals ovate, acuminate, 8 mm. long, 4 mm. wide, lanate; corolla disciform, 3–4 cm. in diameter, the petals suborbicular-ovate, 1.2–1.8 cm. long, 1.1–1.7 cm. wide, slightly hirsute along the median longitudinal line on both surfaces, the apex rounded; stamens ca. 44, the longest half as long as the petals; disc subconic, pubescent, the style 3–4 mm. long, pubescent, the stigmas 3 mm. long, enlarged, cristate, the abaxial surface as long as the adaxial, the sterile portions hirsute; capsules and seeds not known.

MEXICO: Chiapas: Volcano Tacana, *E. Matuda* 2791 (ISOTYPE of *P. matudai* Lundell, A, F, G, NY, US).

GUATEMALA: Alta Vera Paz: Vicinity of Cobán, *P. C. Standley* 92452(F). Guatemala: near Finca La Aurora, *Ignacio Aguilar* 82(F). Huehuetenango: near Chiantla, *P. C. Standley* 82517(F). Sacatepéquez: near Antigua, *P. C. Standley* 60316(F); *S. Hayes* (G). Quezaltenango: *P. C. Standley* 86561(F, US). Suchitepéquez: vicinity of Finca Alvidas, *J. A. Steyermark* 35458(F).

EL SALVADOR: San Salvador: *S. Calderón* 687 (F, G, US, MO, NY); *M. C. Carlson* 435(F). Ahuachapán: near Ataco, *P. C. Standley & V. E. Padilla* 2726(F).

HONDURAS: Morazan: Tegucigalpa, *J. V. Rodríguez* 3173(F).

COSTA RICA: Cartago, Cervantes, *A. Tonduz* 10444(US); San José, *Tonduz* 1492(US); Las Cónovas, *P. C. Standley* 36006(US); Tapisca de Zaruro, *Austin Smith* 185(US).

PANAMA: Chiriqui: vicinity of Bajo Mona and Quebrada Chiquero, *R. E. Woodson & R. W. Schery* 588(MO).

CULTIVATED: California: Santa Barbara, *E. P. Bradbury*, Oct. 10, 1915(BH).

The identification of this species is based on Bertoloni's description and illustration. In his illustration he characterized *P. myrtoides* as a plant

with rather small ovate-elliptic leaves on the flowering branches which terminate with crowded cluster of several flowers each in the axil of a reduced leaf. Among the available collections of Guatemalan *Philadelphus*, Bertoloni's description and illustration conforms in all respects to *Standley 60316, 82417* and *Steyermark 35458*. It is also well represented by *Calderón 687* from El Salvador. *Matuda 2791* represents the northern limit of the range of the species. Bradbury's collection from Santa Barbara, in Bailey Hortorium, was identified as *P. sempervirens* Hort. This specimen was probably Moore's material basis for the publication of his *P. sempervirens*.

Although 110 years have elapsed since *P. myrtoides* was published, it has not been well understood. Körnicke was probably not aware of Bertoloni's species when he published *P. trichopetalus* from Costa Rica. According to his description the Costa Rica plant has flowers clustered at the end of a branchlet, and the petals of the flowers are softly pilose. I have not seen Körnicke's type. But judging from the Costa Rica and Panama collections I have examined and by our present knowledge of the distribution of the various species of *Philadelphus* in Central America, *P. trichopetalus* Körnicke and *P. myrtoides* Bertol. are conspecific.

Philadelphus myrtoides is the most southern species of the genus. It has been collected on the high mountains from Chiapas in Mexico through Guatemala, El Salvador, Honduras south to Costa Rica and Panama. In Guatemala it occurs in cypress groves at altitudes ranging from 1200 to 1930 meters. Standley suggested the possibility of it being introduced and cultivated in Costa Rica. Some of the El Salvador collections were from gardens. Apparently this species has been widely cultivated in Central America where it flowers from January to August. The creamy white fragrant flowers are sold in the markets for decorative purposes under the name "Mosqueta."

Philadelphus myrtoides is closely related to *P. karwinskyanus* Koehne but the latter species can be distinguished for its elongated peduncles and its petals being glabrous on the inner surface.

5. *Philadelphus mexicanus* Schlecht. in *Linnaea* 13: 418. 1839. — Walp. *Rep.* 2: 151. 1843. — Hemsley in *Biol. Centr. Am.* 1: 384. 1879, excl. spec. Seemann, Coulter, Ghiesbreght. — W. G. Smith in *Gard. Chron.* n.s. 19: 753, fig. 123. 1883. — Burbidge in *Gard. Chron.* III. 34: 218, fig. 89. 1903. — Hook. f. in *Bot. Mag.* 124: pl. 7600. 1898. — Koehne in *Gartenfl.* 45: 487. 1896; et in *Mitt. Deutsch. Ges.* 1904(13): 78. 1904. — Wittmack in *Berl. Gartenz.* 1883: 528, fig. 91. 1883. — Dippel, *Handb. Laubh.* 3: 335. 1893. — Schneider, *Ill. Handb. Laubh.* 1: 362, fig. 234 b-b.² 1905. — Rydb. in *N. Am. Fl.* 22: 170. 1905. — Standley in *Contr. U. S. Nat. Herb.* 23: 311. 1922. — Rehder, *Man. Cult. Trees Shrubs* 280. 1927, ed. 2, 275. 1940; et *Bibliogr. Cult. Trees Shrubs* 195. 1929. — Hansell, *Mexico Pl.* 162. 1935. — Bean, *Trees Shrubs* ed. 7, 2: 419. 1950; et in *Chitt. Dict. Gard.* 3: 1546. 1951.

A scandent evergreen shrub to 5 meters high with long drooping branches, the second year's growth 3–4 mm. in diameter, castaneous, rugose, the bark closed, longitudinally rimulose, the current year's growth 1.5–2 mm. in diameter, hirsute, the trichomes with more or less thickened bases; axillary buds conic, the first few below the flowers often developing into virgin shoots. Leaves ovate, 5–11.5 cm. long, 2–5 cm. wide, very sparsely strigose on both surfaces, rounded or obtuse or subcordate at the base, 5- or rarely 3-nerved, acuminate at the apex, subentire or with 1 to 6 tooth-like projections on each side, reticulations obscure above, conspicuous beneath, the petioles 8–10 mm. long, strigose. Flowers solitary, yellowish white, very fragrant; pedicels hirsute, 1–3 mm. long, bracts lanceolate, 1–2 cm. long; hypanthia cyathiform, sparsely villose, the trichomes slightly curly; sepals foliaceous, ovate, long acuminate or cordate, 10–20 mm. long, 7 mm. wide, sparsely villose, the hairs tending to curl slightly; corolla 3–4 cm. across, the petals suborbicular, hirtellous on both surfaces; stamens ca. 40, the anthers oblong; disc subconic, hirsute at the center, the styles 3 mm. long, pubescent, the upper half divided, the stigmas 3 mm. long, cristate, the abaxial surface much longer than the adaxial one, the sterile portion often hairy. Capsules obovoid-ellipsoid, the lower portion near the base quadrangular, about 12 mm. long, 10 mm. in diameter, the persistent calyx subcircumferential. Seeds long-caudate.

MEXICO: Mexico: Amecameca, *G. L. Fisher* on July 29, 1924(F, MO, US); Federal District, *A. J. Sharp* 445 (A, TENN); Mts. of Toluca, Halstead (NY). Guerrero: Omiltemé, *A. J. Sharp* 441551 (A, TENN). Michoacán: Morelia, Cerro Azul, *Bro. G. Arsène* 5141 (F, G, MO, US). Oaxaca: Cerro de San Felipe, *C. Conzatti & V. Gonzalez* 471(G); *H. Galeotti* 2850(US); *E. W. Nelson* 1398(G, US). Chiapas: Siltepec, *E. Matuda* 1701(A, MO, US). Vera Cruz: Jalapa, *S. Schiede*(G, NY, ISOTYPES); Orizaba, *Botteri* 1105(G, US). Puebla: Cero Guadalupe, *Nicolas*, June 10, 1909(F).

GUATEMALA: Huehuetenango: San Juan Ixcoy, *A. J. Sharp* 4616(F); definite locality not given, *J. D. Smith*, April 9, 1896(G); Cerro Cananá, Sierra de los Cuchuatanes, *J. A. Steyermark* 49059(F); Aguacatán, *P. C. Standley* 91218(F). Quezaltenango: Volcán de Santa María, *P. C. Standley* 83535(F); *J. A. Steyermark* 33985(F); Palestina, *P. C. Standley* 84230(F); Santa María de Jesús, *P. C. Standley* 84860(F); above Mujuliá, *P. C. Standley* 85608(F, US); Zunil, *P. C. Standley* 85647(F); Volcán Santo Tomas, *J. A. Steyermark* 34952(F). Quiché: *O. F. Cook* 31(US); San Miquel Uspantán, *Heyde & Lux* (distributed by *J. D. Smith*) 3046(G, NY, US); Chajul, *A. J. Sharp* 4681(F). Sacatepequez: Volcán de Auga, *P. C. Standley* 65124(F). Chimaltenango: Santa Elena, *D. S. Johnson*, Aug. 10, 1932(F); *A. F. Skutch* 335 (A, US). Sololá: Volcán San Pedro, *J. A. Steyermark* 47253(F, US); Volcán Atitlán, *J. A. Steyermark* 47527(F). San Marcos: Volcán Tajumulco, *J. A. Steyermark* 35661(F). Without precise locality, *F. C. Lehmann*, June 1882(US).

CULTIVATED: California: Berkeley, in the garden of A. Blake, *N. F. Bracelin*, 1354(BH).

As the natives of Mexico had cultivated species of *Philadelphus* from early times it is inevitable that certain garden forms had been produced by them. It happened that the first published Mexican species was based on a double flowered form. Schlechtendal cited three specimens, Schiede from Jalapa, Mühlenpfordt from Oaxaca and a specimen from Mexico in Herb. Lehmann. Of these I have seen only the duplicates of Schiede's collection, which agree with Schlechtendal's description. Thus the double flowered form typifies the species. Apparently this form is found only or chiefly in the states of Vera Cruz and Puebla where the mean annual temperature is between 62–67° F. and the mean annual rainfall is 40–80 inches. The Bracelin collection is the only specimen from a cultivated plant outside of Mexico that I have seen. It has been reported that the cultivated plants climb to 12 meters and their flowers are yellowish or deep cream white.

Specimens collected from the wild population all have simple flowers. Compared with the isotypes of typical *P. mexicanus* Schlecht., I can detect no other characters from the above cited specimens to distinguish them as a form besides their possession of the simple flowers. Like the double-flowered form, their petals are pubescent on both surfaces, the disc and style are pubescent, and the hypanthium is sparsely villose with the trichomes slightly curled. In general, their leaves are larger and more prominently quintuplinervate than the double flowered form. But this 5-nerved condition is also true with the large leaves of the cultivated specimens. It seems that with both the wild and the cultivated material, at the base of each leaf, there is a pair of small nerves originated from the petiole and running along the basal portion of the margin. When the leaves are small, these nerves are so closely pressed against the margin that they appear inconspicuous.

In Mexico this species occurs at altitudes of 2280–3000 meters in Oaxaca. In Huehuetenango, it has been recorded at altitudes of 1950–3160 meters on steep limestone slopes of damp oak forests. In Quezaltenango it occurs at altitudes of 1500–3000 meters in sunny thickets, damp sandy hillside forests or in wet brushy ravines as subscandent shrubs. In Sololá it occurs in damp cloud forests.

The vernacular names reported are "Mosqueta" and "Azahar," the former more widely applied. Hernandez (1651) in "Nova Plantarum Mexicanorum Historia" discussed and illustrated a plant with opposite leaves and a cluster of two simple flowers under the name, *Acuilotl* or *Volubili Aquatica*. He mentioned it as growing in wet places, creeping on the ground or scrambling up trees. This record has been regarded by Schlechtendal, Lindley, Hooker and many modern authors as representing *P. mexicanus* Schlecht. To the Mexican Indians this species is economically rather important. They employ the flowers both in preparing perfume and for making garlands. The leaves are taken in wine for the relief of colic, or crushed and applied as a plaster to ease strained members and dissolve tumors.

The pubescent petals and simple flowers of this species resemble those

of the flowers of *P. myrtoides* Bertol. But the latter species can be readily distinguished by its clustered flowers and densely lanate hypanthium.

6. *Philadelphus austro-mexicanus*, sp. nov.

Philadelphus mexicanus sensu Decaisne in Rev. Hort. III. 1: 381, fig. 20. 1852. non Schlechtendal, 1839.

Frutex ramosissimus, ramulis floriferis brevibus, ca. 3 cm. longis. 1 mm. diametro, castaneis, rugoso-strigosis, pilis basi incrassatis, gemmis axillaribus subglobosis, pilosis; foliis ovatis vel ovato-lanceolatis, 1–3.5 cm. longis, 0.5–1.5 cm. latis, basi subrotundatis, triplinerviis, apice subacuminatis vel acutis, serratis, utrinque 1- usque 5-serratis utrinque sparse strigosis vel praeter nerviis subglabris, petiolo 2–3 mm. longo; floribus solitariis, pedicellis 2 mm. longis, strigosis; hypanthiis obconicis, 3 mm. longis, 4 mm. diametro, sparse pilosis; sepalis ovatis, 9–11 mm. longis, caudatis, sparse pilosis vel subglabris; corolla disciformi, 3.8–4 cm. diametro, petalis obovatis, 1.5–1.7 mm. longis, 1.3 mm. latis, utrinque in partibus mediis hirsutis; staminibus ca. 52, disco glabro, stylis 4 mm. longis, glabris, partibus superioribus liberis, stigmatibus dilatatis, cristatis; capsulis et seminibus ignotis.

MEXICO: Chiapas: *Dr. Ghiesbreght 813* (G. TYPE; F, MO, ISOTYPES; A. fragment of ISOTYPE).

The rugose branchlets, the dentation of the leaves, the large sepals, the pubescent petals, the numerous stamens, the divided style and the dilate-cristate stigmas of this species all suggest a close relationship to *P. mexicanus* Schlecht. But it can be readily distinguished by its small leaves, very sparsely pilose hypanthium and sepals and its glabrous styles.

Decaisne's figure represents a plant with small leaves. His concept of Schlechtendal's species was apparently based on a Ghiesbreght collection, very likely a part of the same collection of which three specimens are available to me. All of them have small leaves and glabrous styles.

7. *Philadelphus glabripetalus*, sp. nov.

Philadelphus mexicanus sensu Lindl. Bot. Reg. 26(Misc.): 37. 1840; et 28: pl. 38. 1842. — sensu Hemsl. in Biol. Centr. Am. 1: 384. 1879, pro parte, non Schlechtendal, 1839.

Frutex ramosissimus, ramulis floriferis 5–15 cm. longis, 1–1.5 mm. diametro, rugoso-hirsutis, pilis basi incrassatis; foliis ovatis vel ovato-lanceolatis, 1.5–6 cm. longis, 1–2.5 cm. latis, basi rotundatis, triplinerviis, apice acuminatis, subintegris vel serratis, dentibus utrinque 1 vel 2, raro 4, supra subglabris vel sparse villosis, subtus sparse villosis; petiolo 3–5 mm. longo, villoso; floribus solitariis vel raro ternatis, pedicellis 3–5 mm. longis, dense villosis, hypanthiis subglobosis, 5 mm. diametro, lanatis; sepalis ovatis, 10–15 mm. longis, 5 mm. latis, acuminatis; corolla 2.5–3 cm. diametro, petalis obovatis, vel suborbicularibus, 1–1.3 cm. longis, 9–10 mm. latis, utrinque glabris, vel extus hirsutis, staminibus ca. 60;

disco medio hirsuto, stylis glabris vel basi hirsutis, 3–4 mm. longis, stigmatibus cristatis, 4 mm. longis, supra liberis; capsulis et seminibus ignotis.

MEXICO: Federal District: Sierra de Ajusco, *C. G. Pringle* 6311(A, TYPE; G, MO, NY, US, ISOTYPES). Puebla: Moria, *Nicolas*, in February 1908(F). Without precise locality, *P. Maury* 3158(NY), 3822(NY).

The shape of the leaves, the solitary flowers and the glabrous petals suggest a relationship to *P. osmanthus* S. Y. Hu, but the latter species has strigose lower leaf-surfaces and hypanthia, and short styles while the present species has villose lower leaf-surfaces, lanate hypanthium, and styles 3–4 mm. long. It differs from *P. mexicanus* Schlecht. in having glabrous petals and smaller leaves. Its solitary or ternate flowers also suggest relationship with *P. coulteri* S. Wats. but the latter species has densely villose hypanthia with the epidermis entirely obscured. In the Federal District, this species occurs at altitudes 2400–2470 meters. It climbs among shrubs up to 5–7 meters high. Specimens collected from June to September all bear flowers. This suggests that like many other Mexican *Philadelphus*, this species has a very long flowering period; of course, local climatic conditions may be involved.

Judging by the figures and the descriptions given by Lindley (1842), his material which was introduced by Hartweg from the Hacienda del Carmen, could not be the true *P. mexicanus* Schlecht. for it has small leaves and a glabrous style while Schlechtendal's species has large leaves and a pubescent style. As Lindley described the hypanthium and calyx of his material as densely pubescent, this eliminates the possibility of it being *P. austro-mexicanus* S. Y. Hu which is another small-leaved Mexican species, for the latter has more or less glabrous hypanthium and calyx, and pubescent style. By the process of elimination, one may logically come to the conclusion that the material Hartweg introduced to the European gardens belongs here.

Section 2. *Coulterianus*, sect. nov.

Philadelphus subg. I. *Gemmatus* sect. *Coulterianus*, sect. nov.

TYPE SPECIES: *P. coulteri* Wats.

Frutex erectus vel subscandens, ramulosis hornotinis pubescentibus, plerumque verrucosis, gemmis axillaribus expositis; foliis integris, raro denticulatis vel inconspicue serratis, basi rotundatis vel obtusis, raro acutis, triplinerviis; apice acutis vel obtusis; floribus solitariis vel raro ternatis; hypanthiis subglobosis, pubescentibus; sepalis ovatis, 3–8 mm. longis, corolla cruciformi vel disciformi; staminibus 30 usque ad 44; disco plano, stylo 1–3 mm. raro 4 mm. longo, stigmatibus noncristatis; capsulis subglobosis; seminibus longo-caudatis.

Seven species, all in northeastern Mexico.

KEY TO THE SPECIES

A. Lower leaf-surface pilose or strigose; stems rugosely hirsute, the base of the trichomes thickened.

- B. Hypanthia pilose, the epidermal tissue visible; the lower leaf-surface pilose 8. *P. osmanthus*.
- BB. Hypanthia densely villose, the epidermal tissue obscure; the lower leaf-surface strigose.
- C. Leaves oblong; pedicels 5–8 mm. long; petals emarginate at the apex 9. *P. oblongifolius*.
- CC. Leaves ovate; pedicels 2–3 mm. long; petals rounded at the apex.
- D. Style and center of disc pubescent; leaves on flowering shoots 2–3 cm. long 10. *P. coulteri*.
- DD. Style and center of disc glabrous; leaves on flowering shoots 1–2 cm. long. 11. *P. asperifolius*.
- AA. Lower leaf-surface densely villose; stem pilose, the base of the trichomes not thickened.
- B. Leaves subcoriaceous, hispid above, densely villose and appearing white beneath.
- C. Style pubescent 12. *P. sargentianus*.
- CC. Style glabrous 13. *P. pringlei*.
- BB. Leaves characeous, weakly pilose above, very sparsely villose beneath; style glabrous 14. *P. calcicolus*.

8. *Philadelphus osmanthus*, sp. nov.

Frutex subscandens, 1.3 m. altus, ramosissimus; ramis robustis, 3–5 mm. diametro, fumeis, longitudinaliter rimulosis, bienniis 2 mm. crassis, castaneis, striatis, rugoso-hirsutis, corticibus clausis, hornotinis 1–1.5 mm. diametro, pilis basi incrassatis, gemmis conicis, strigosis, pilis luteis; foliis ovatis, raro ovato-lanceolatis, 2–6 cm. longis, 0.8 cm. latis, basi obtusis, apice acutis vel obtusis, apiculatis, integris vel utrinque 1 vel 3 serrulatis, utrinque strigosis, pilis eburneis, petiolo 4–9 mm. longo; floribus 1, raro 3, terminalibus, bracteis linearibus, 3–10 mm. longis, pedicellis 5–10 mm. longis, cum hypanthiis et calycibus incano-pilosis, hypanthiis subglobosis, 5–7 mm. diametro; sepalis ovatis, acuminatis, 7–8 mm. longis; corolla subcruciformi, 2.5–3.2 cm. diametro, petalis obovatis, apice emarginatis, 1.2–1.5 cm. longis, 0.7–1.2 cm. latis; staminibus ca. 36; disco medio piloso, stylo brevissimo, 1 mm. longo, vix hirtello, stigmatibus 3 mm. longis, cristatis, supra divisis; capsulis ellipsoideis vel subglobosis, 6–8 mm. diametro, calycibus persistentibus supra medium affixis; seminibus longicaudatis.

MEXICO: Hidalgo: Jacala, V. H. Chase 7310 (NY, TYPE; A, F, G, MO, ISOTYPES).

This species occurs in woods in deep ravines at an altitude of 1525 meters. Unlike other species of the genus, the lateral buds on the branchlets of this one are suppressed from normal development. Thus its flowering shoots are largely developed from the terminal buds, a very unusual character in *Philadelphus*. The thickened base of the epidermal hairs on the branchlets, the elongate stigmas and the pubescent disc of this species suggest relationship to *P. coulteri* Wats. The latter species can be dis-

tinguished by the thickly villose hypanthium. The subentire leaves sparsely strigose and the long-tailed seeds of this species also suggest a remote relationship with the southern Appalachian species *P. inodorus* Linn. which has enclosed axillary buds. The very short style conforms to Körnicke's description of *P. asperifolius*, a species with glabrous style and disc.

9. *Philadelphus oblongifolius*, sp. nov.

Frutex ramosissimus, ramis cinereis, ramulis gracilibus, bienniis 1–1.5 mm. crassis, brunneis, verrucoso-hirsutis, hornotinis 1 mm. diametro, pilis basi incrassatis; foliis oblongis, raro oblongo-ovatis, 1.3–2.5 cm. longis, 4–8 mm. latis, utrinque obtusis, apice apiculatis, margine integerrimis, utrinque strigosis, pilis subtus longioribus et densioribus, petiolo 3 mm. longo; floribus solitariis, pedicellis 6–8 mm. longis, incanis, hypanthiis calycibusque incanis; sepalis ovatis, 6 mm. longis, 2.5–3 mm. latis; corolla cruciformi, 3.5 cm. diametro, petalis obovatis, apice emarginatis, 1.6 cm. longis, 1.1–1.4 cm. latis; staminibus ca. 30; disco praeter medio glabro, stylo 5 mm. longo, supra diviso, basi dense hirsuto, stigmatibus 2 mm. longis. Capsulis ignotis.

MEXICO: San Luis Potosi: Minas de San Rafael. C. A. Purpus 5368b (A, fragment of TYPE; F, TYPE; MO, NY, ISOTYPES).

Through its strigose trichomes on the leaves, and pubescent styles this species is closely related to *P. Coulteri* Wats. It can be distinguished from *P. coulteri* by its slender branchlets, oblong leaves, long pedicellate flowers with emarginate petals and 5 mm. long styles.

10. *Philadelphus coulteri* Wats. in Proc. Am. Acad. 22: 472. 1887.

Philadelphus purpusii Brandegee in Univ. Calif. Publ. Bot. 4: 270. 1912.

TYPE: *Dr. Coulter 77*, Zimapan, Mexico (Gray Herbarium).

A subscandent shrub, the branches ferruginous, the second year's growth 2–3 mm. in diameter, the bark rugose, closed, slightly longitudinally rimulose; the current year's growth rugose and hirsute, the trichomes with thickened bases. Leaves ovate, or ovate-elliptic, subentire, obtuse or acute, apiculate, rounded or rarely obtuse at the base, strigose on both surfaces, more so beneath, those on the flowering branches, 1.5–3 cm. long, 1–1.5 cm. wide, the petioles 3–4 mm. long. Flowers solitary, rarely ternate, the pedicels 2–3 mm. long, thickly villose and white like the hypanthia and calyx, the sepals ovate, 5–6 mm. long; corolla disciform, 2.5–3 cm. across, the petals orbicular-obovate, rounded at the apex; stamens 34–38; disc pubescent at the center, the style 2–3 mm. long, the upper half divided, the stigmas 2–2.5 mm. long, the abaxial surface papillose, 2 mm. long, the adaxial surface half as long. Capsules and seed not known.

MEXICO: Hidalgo: Zimapan, *Dr. Coulter 77* (G, TYPE); woods above Minas Viejas between Zimapan and Jacala, *H. E. Moore, Jr. 2767* (G, BH); Atotonilco, *Schiede*, June 1830 (NY). San Luis Potosi: Minas de San Rafael, *C. A. Purpus 4910* (MO), *5368* (F, G, MO, US ISOTYPES of *P. purpusii* Brandege; A, photo and fragment). Tamaulipas: near Frank Harrison's "Rancho del Ciel" in Sierra de Guatemala above Gomez Tarias, *Sharp, Shank, Wolfe & Hernandez 52201* (A, TENN), *52060* (A, TENN).

Philadelphus coulteri Wats. was essentially based on *Coulter 77* collected from Zimapan. In publishing the species Watson also cited C. S. Sargent's collection from Monterey. As the species was named after Coulter, his number 77 in the Gray Herbarium should be the actual type of the species. Sargent's material is specifically distinct. It differs from the type of *P. coulteri* in having smooth pilose branchlets, leaves hispid above and densely long villose beneath and a very short style. In 1888 Watson published an illustrated account of *P. coulteri*. As Coulter's collection is rather fragmentary, that illustration was unfortunately drawn from Sargent's material. This publication has an out-reaching misleading effect in the identification of the true *P. coulteri* among botanists as well as horticulturists and consequently cytogeneticists.

Philadelphus coulteri Wats. was first collected in Zimapan. Additional material extends its range northward to Gomez in the State of Tamaulipas. At this area, the southeastern end of the Mexican Central Plateau, the plant grows, according to Moore, as a shrub a little over a meter high and its flowers are white, and fragrant. The standard reference books on cultivated shrubs have recorded this species as having purple-centered flowers. This is apparently incorrect.

Watson published this species in 1887 on the basis of a herbarium specimen. He did not know the flower color, nor did he indicate it in the description. The next year an illustrated account was published in *Garden and Forest*. Here no flower color was mentioned either. Three years later, Burbidge wrote Hemsley from Dublin, Ireland, saying, "Can you kindly give me the name of the enclosed? I cannot find it in the books. It exists in one or two old gardens here, where it is called Rose Syringa. Its sweet fragrance and purple-centered flowers are remarkable." What Hemsley reported we do not know, but this was later referred to *P. coulteri*. Meanwhile, Nicholson in the *Supplement to the Garden Dictionary* incorporated Watson's review of *P. coulteri* from the *Garden and Forest*. At the end of his summary Nicholson put down 1888, the year when his source material was published, as the year of the introduction of the plant into cultivation. Burbidge got this reference and in 1903 he published a note saying "There is a variety of *P. mexicanus* called *P. M. Coulteri*, introduced, it is said in Nicholson's *Supplement*, as recently as 1888; but probably this is a mistake as the shrub has existed for many years in old Irish gardens, where it is known as the "Rose Syringa" . . . and it differs from all other species or varieties . . . each of its four white petals has a purplish blotch at its base." This is a misinterpretation of Watson's figure and description and also a misidentifica-

tion of the Irish "Rose Syringa." But since that time in all major works on cultivated shrubs and even in books dealing principally with the flora of Mexico, the error in the flower color of *P. coulteri* Wats. has been perpetuated.

Claims have been made by hybridizers and cytogeneticists that *P. coulteri* Wats. is a grandparent of the triploid garden hybrids, "Belle Etoile," "Sybille" and "bicolor" which are segregates of *P. purpureo-maculatis* Lemoine.¹ There seems to be no record that true *P. coulteri* has ever been introduced into cultivation, thus it is impossible for it to have been a parent of *P. purpureo-maculatus* Lemoine. The above mentioned claims do not seem to have any material support. The Monterey region is better known botanically than Zimapan, the type locality of *P. coulteri*. Consequently the *Philadelphus* that Sargent collected is much better represented in American herbaria than is true *P. coulteri*. It was almost inevitable that these specimens should have been mistaken for *P. coulteri*. When typical *P. coulteri* Wats. was again collected by Purpus in 1911, Brandegee was misled into creating a new binomial, for *P. purpusii* Brandegee is the genuine *P. coulteri* Wats. *Purpus 5368*, the type number of *P. purpusii* Brandegee represents an aggregate of three elements, probably three separate collections combined under one number of which I have examined five sheets. The element with glabrous disc and style belongs to *P. asperifolius* Körnicke. The two other elements both have a pubescent disc and style. One of them has ovate leaves and styles shorter than the stigmas. This one agrees with Brandegee's description of *P. purpusii*, and is identical with the type of *P. coulteri* Wats. The other element has small oblong leaves and elongated style which is longer than the stigmas. It becomes the type of *P. oblongifolia* S. Y. Hu.

11. *Philadelphus asperifolius* Körnicke in Gartenfl. 16: 73. 1867. — Koehne in Gartenfl. 45: 487. 1896; et in Mitt. Deutsche. Dendr. Ges. 1904(13): 78. 1904. — Schneider, Ill. Handb. Laubh. 1: 364. 1905. — Rydb. in N. Am. Fl. 22: 171. 1905. — Standl. in Contr. U.S. Nat. Herb. 23: 310. 1922.

TYPE: *Karwinsky* July 1842, Hacienda Santyaguillo, Mexico (Herb. Hort. Petropol.).

An elegant shrub, 2–3 meters high, branchlets rigidly hirsute, the second year's growth gray, longitudinally rimulose, the bark closed, the current year's growth brown, pubescent, the hairs with thickened bases. Leaves ovate, those on the vegetative shoots up to 3 cm. long, 1.3 cm. wide, those on the flowering shoots 1.3–1.7 cm. long, 0.5 cm. wide, rounded at the base, obtuse and apiculate or subacute at the apex, both surfaces sparsely covered with rigid, straight appressed white hairs, the petioles 1–2 mm. long. Flowers solitary, subsessile, the pedicels 1–3 mm. long, canescent as are the hypanthia and the calyx, the sepals ovate, 3 mm. long; corolla disciform, 1.5–2 cm. across, the petals obovate, rounded at

¹ E. K. JANAKI AMMAL in Jour. Roy. Hort. Soc. 76: 272. 1951.

the apex, twice the length of the sepals; stamens 30–38; disc glabrous, the style short, about 1.5 mm. long, undivided, glabrous, the stigmas separated, 2 mm. long, the abaxial surface twice as broad and as long as the adaxial one. Capsules subglobose, 6–7 mm. long, 7 mm. diameter, the persistent calyx subapical. Seeds long-tailed.

MEXICO: San Luis Potosi: Minas de San Rafael, C. A. Purpus 4910 (A, F, G, US), 5368a (G, MO, NY, US).

Unable to examine the type, the identification of this species is based on the original detailed description published by Körnicke and the diagnostic characters supplemented by Koehne who probably saw the type or an isotype. Körnicke described the species as having ovate or broad-elliptic leaves which are obtuse and apiculate or subacute at the apex, and about 3 cm. long and 1.5 cm. wide on sterile shoots. He did not mention the nature and position of the buds and the presence or absence of hairs on the style. For these characters we have to rely upon Koehne's observations. In his latest synopsis of the genus, under the subsection Gemmati which was characterized as having a smooth almost obsolete and glabrous style he placed *P. asperifolius* and *P. serpyllifolius* Gray. Judging from the style of the latter species, the type of which is before me, Koehne's characters indicate a species in which the styles are short but definitely present, 0.5–1.5 mm. long. By inference, Körnicke's description, which calls for no style and the stigmatic column thick and sessile, may also be interpreted to apply to flowers with short but definite styles. One of the elements of *Purpus* 5368, which I have indicated as 5368a, has small ovate leaves, 0.5–1.7 cm. long, 0.4–0.7 cm. wide on the flowering shoots, and glabrous styles. These characters conform to Körnicke's description of the leaves and Koehne's diagnosis of the style of *P. asperifolius*, thus I interpret that element as representing Körnicke's species. *Purpus* 4910 is a poorly selected fruiting specimen. With the exception of one, all sheets I have examined are sterile, and the only fertile specimen has just one fruit with a broken top. The branching is much looser than is that of *Purpus* 5368a. The leaves seem to fit Körnicke's description of those on the vegetative shoots. The small part of the disc left on the broken fruit appears to be glabrous.

The ovate shape of the strigose leaves, the densely villose hypanthia and the very short pedicel of the flower of this species suggest a very close relationship with *P. coulteri* Wats. Yet it can be readily distinguished from Watson's species by its glabrous disc and style and its rather small leaves on the flowering shoots which are only 1–2 cm. long. *Philadelphus coulteri* Wats. has a pubescent disc and style, with the leaves on the flowering shoot 2–3 cm. long. The fragrant white flowers of this species appear in June.

12. *Philadelphus sargentianus*, sp. nov.

Philadelphus coulteri Wats. in Proc. Am. Acad. 22: 472. 1887, pro parte (quoad col. Sargent, excl. *Coulter* 77); et in Gard. Forest 1: 232, fig. 40.

1888. — Nicholson, Suppl. Dict. Gard. 594. 1900. — Rydberg in N. Am. Fl. 22: 170. 1905. — A. H. Moore in Bailey, Stand, Cycl. Hort. 5: 2582, fig. 2905. 1915. — Standl. in Contr. U.S. Nat. Herb. 23: 311. 1922. — Rehder, Man. Cult. Trees Shrubs 280. 1927; ed. 2. 275. 1940; et Bibliogr. Cult. Trees, Shrubs 159. 1949.

Frutex usque 2.3 m. altus, ramis robustis, bienniis 3 mm. diametro, brunneis, longitudinaliter rimulosis, hornotinis 1.5 mm. diametro, dense hirsutis, pilis basi haud incrassatis, gemmis axillaribus conicis, strigosis, pilis luteis; foliis ovatis vel ovato-ellipticis, 2.5–4.5 (raro 5) cm. longis, 1–2 (raro 2.5) cm. latis, basi rotundatis, apice acutis vel obtusis, apiculatis, supra hispidis, subtus dense argenteo-villosis, 3- vel 5-nerviis, margine inconspicue serrulatis, dentibus utrinque 1 usque ad 5, minutis, petiolo 3–5 mm. longo; floribus solitariis, pedicellis brevissimis, 2–3 mm. raro ad 6 mm. longis, cum hypanthiis calycibusque dense albo-villosis; hypanthiis subglobosis, 5 mm. diametro, pilis longioribus et brevioribus intermixtis; sepalis ovatis, acuminatis, 8 mm. longis, 4–5 mm. latis; corolla usque 4.5 cm. diametro, petalis obovatis, 2 mm. longis, 1.6 cm. latis, apice erosis; staminibus ca. 40, antheris 2 mm. longis; disco medio piloso, stylo brevissimo, 1 mm. longo, stigmatibus 4 mm. longis, liberis; capsulis subglobosis, 1 cm. diametro; seminibus longe caudatis.

MEXICO: N u e v o L e o n : Monterey, Sierra Madre Mts., Diente Canyon, C. H. & M. T. Mueller 544(A, F); C. G. Pringle 2094(A, NY, US); C. S. Sargent in April 1887(A TYPE; G, originally placed under *P. coulteri*); Cerro de la Silla, S. S. White 1470(G).

In the publication of *P. coulteri*, Watson cited two collections, *Coulter* 77 from Zimapan and *Sargent s.n.* from Monterey. Watson's species was published in 1887. Sargent's specimen was collected in April of that year. It is highly possible that Watson had prepared the description of *P. coulteri* before he saw the Sargent specimen. When Sargent sent him his Monterey collection, Watson simply incorporated it in his new species. As the species was named for Coulter, his collection naturally becomes the type of *P. coulteri* Wats. But Sargent's collection is definitely different from the type of *P. coulteri* Wats. which has the rugose branchlets and strigose leaves, characteristic of species like *P. mexicanus* Schlechtendal. Sargent's material has villose branchlets and leaves hispid above and densely white villose beneath, a type of pubescence characteristic to the northern element like *P. madraensis* Hemsl. Yet Sargent's specimen is not Hemsley's species because of its exposed buds, and it is thus described as new here.

Philadelphus sargentianus is endemic to Monterey where it grows at altitudes of 1500–1600 meters, where the mean annual temperature is 62°–67° F. and the mean annual rainfall is limited to 30–40 inches. There its fragrant white flowers appear from early April to July. As far as I know this species has never been introduced into cultivation. Unfortunately misled by the publication of an illustration drawn on the basis of the Sargent collection, several authors of standard references on

the cultivated trees and shrubs had misinterpreted this species as *P. coulteri*.

13. *Philadelphus pringlei*, sp. nov.

Philadelphus coulteri sensu Brandege in Univ. Calif. Publ. Bot. 4: 270. 1912, non Wats.

Frutex, ramis brunneis, bienniis 2 mm. crassis, longitudinaliter rimulosis, hornotinis 1.5 mm. diametro, dense hirsutis, pilis basi incrassatis, gemmis axillaribus conicis, pilosis; foliis ovatis, raro lanceolatis, 2.4–5 cm. longis, 1–1.8 cm. latis, basi rotundatis, obtusis, raro acutis, inconspicue triplinerviis, apice acutis, breviter acuminatis vel raro obtusis, apiculatis, inconspicue serratis, serrulis utrinque 2 usque ad 5, minutis argutisque, supra hispidis, subtus dense argenteo-villosis, petiolo 4–5 mm. longo; floribus solitariis, pedicellis 2–4 mm. longis, cum hypanthiis calycibusque dense albo-villosis; hypanthiis subglobosis, 5 mm. diametro; sepalis ovatis, 8 mm. longis, 5 mm. latis, acuminatis; corolla cruciformi, 4–5 cm. diametro, petalis obovatis, 2 cm. longis, 1.5 cm. latis, apice rotundatis; staminibus 40 usque ad 44, antheris oblongis, 2 mm. longis; disco glabro, stylo 4 mm. longo, glabro, supra diviso, stigmatibus 3–3.5 mm. longis; capsulis subglobosis, immaturis 7 mm. diametro.

MEXICO: N u e v o L e o n : Sierra Madre, above Monterey, *C. G. Pringle 10174* (A, TYPE; F, G, MO, US, ISOTYPES); Diente Canyon, about 12 miles south of Monterey, *C. H. & M. T. Mueller 261*(A, F); Waterway below Alamar, about 15 miles southwest of Galeana, *C. H. & M. T. Mueller 656*(A, F, NY).

Geographically this species has the same range as *P. sargentianus* S. Y. Hu and morphologically they are very similar except *P. sargentianus* has a pubescent disc and style, while this species has glabrous ones. According to the collectors, this taxon is abundant in the open woods and shrub zones of the Sierra Madre Oriental in the state of Nuevo Leon. Its white flowers appear in April and May.

14. *Philadelphus calcicolus*, sp. nov.

Frutex usque ad 5 m. altus, ramulis teretibus, cinereis, bienniis 1.5 mm. crassis, corticibus clausis, hornotinis brunneis, 1 mm. diametro, pilosis, gemmis terminalibus conicis, strigosis, pilis luteis; foliis serratis, lanceolatis vel ovatis, 2.5–5 cm. longis, 1–2 cm. latis, basi acutis vel obtusis, trinerviis apice subacuminatis et apiculatis vel acutis, supra in sicco nigrescentibus, pilosis, subtus olivaceis, sparsissime villosis, petiolo 5–8 mm. longo; floribus solitariis, pedicellis 3–6 mm. longis, incanis, hypanthiis subglobosis, 6 mm. diametro, dense tomentosus, argenteis; sepalis ovatis, acuminatis, 7 mm. longis, basi 4.5 mm. latis, argenteis; corolla 3 cm. diametro, petalis obovatis, apice emarginatis, 1.5 cm. longis, 1.3 cm. latis; staminibus ca. 40, antheris sagittatis, 2 mm. longis; disco glabro, stylo brevissimo, 1.5 mm. longo, stigmatibus 4 mm. longis, cristatis,

coalescentibus; capsulis ellipsoideis, 8 mm. diametro, sepalis persistentibus $\frac{1}{3}$ apicem insertis; seminibus breviter caudatis.

MEXICO: N u e v o L e o n : Dulces Nombres, *F. G. Meyer & D. J. Roger* 2662 (TYPE, MO; fragment A); Canyon above Linare toward Galeana, *A. J. Sharp* 45787 (TENN, A, sterile). T a m a u l i p a s : Road above Ciudad Victoria toward Jaumave, dry canyon slope below 3000 ft., *Sharp, Shanks, Wolfe & Hernandez* 52006, (A, TENN).

This species grows on dry limestone cliffs above a dry stream bed at an altitude of 1300 meters. The white flowers appear in June. It is a very interesting plant for most of the lateral buds on the branchlets are weak, as a rule not visible, and do not develop in the following year. Often only those situated near the apices of the shoots, either the apical alone or the two axillary ones, develop into flowering or vegetative shoots. In this respect as well as by its short styles with long cristate stigmas, emarginate petals, and slender petioles this species resembles *P. osmanthus* S. Y. Hu. The latter species can be distinguished by its pubescent disc, less canescent hypanthium and calyx, and hairs with thickened bases on the stem. Its smooth appressed white indumentum on the hypanthium and calyx and its hairs on the stem not thickened at the base also suggest a relationship with *P. argenteus* Rydb., in the section *Microphyllus* of the subgenus *Euphiladelphus*. Rydberg's species can be distinguished by the enclosed buds and small entire leaves which are densely white pubescent beneath. The coalescent stigmas and the short caudate seeds also suggest some relationship with the southern Appalachian species *P. hirsutus* Nutt., but the latter species can be distinguished by its prominent axillary buds, the style longer than the stigmatic column, and the ecaudate seeds.

(*To be concluded*)