MATERIALS TOWARD A MONOGRAPH OF THE GENUS VERBENA. II

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VERBENA L.

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Herbs, sometimes slightly woody at the very base; stems and branches procumbent, ascending, or erect, glabrous or variously pubescent; leaves mostly decussate-opposite, rarely whorled, dentate (very rarely entire) or variously lobed, incised, or pinnatifid; inflorescence spicate; spikes terminal, usually densely many-flowered, often flat-topped and pseudo-umbellate or fasciculate-capitate, sometimes greatly elongate with densely crowded or scattered flowers, very rarely also axillary, often greatly elongating only after anthesis; flowers small or medium-sized, each solitary in the axil of a usually narrow bractlet; calyx gamosepalous, inferior, usually tubular, 5-angled, 5-ribbed, unequally 5-toothed at the rim, not at all or but slightly changed in fruit; corolla gamopetalous, inferior, salver-form or funnel-form, its tube cylindric, straight or curvate, often slightly ampliate or subinflated at the apex, usually villous at the stamen-insertion within and barbate at the mouth, the limb flat, spreading or oblique, weakly 2-lipped, the lobes 5, usually rather elongate, more or less unequal, varying from obtuse or rounded to emarginate at the apex, the 2 posterior outermost and the anterior one innermost in prefloration; stamens 4, didynamous, inserted in the upper half of the corolla-tube, included; anthers ovate, with 2 parallel or slightly divergent thecae, dehiscing by means of a longitudinal slit, the dorsal connective unappendaged and narrowly muticous or provided with a more or less conspicuous glandular appendage; style single, usually short and equaling the stamens, somewhat dilated, shortly 2-lobed or bifid at the apex, the anterior lobe or branch stigmatiferous and subpulvinate-papillose, the posterior lobe or branch smooth and horny and non-stigmatiferous, not as broad as the anterior one; ovary superior, compound, 2-carpellary, entire at the apex or 4-lobed, situated on a somewhat lobed annular disk, completely 4-celled even at time of anthesis, with one ovule in each cell; ovules attached laterally at or near the base, erect, anatropous; fruiting-calyx herbaceous, mostly ventricose, eventually split, often connivent or contorted at the apex, thin-textured; fruit mostly enclosed by the mature calyx, schizocarpous, with the pericarp hard and dry, readily separating at maturity into 4 one-seeded linear or linear-oblong (rarely elliptic-winged) crustaceous cocci (nutlets); seeds 4, erect, oblong, triangular in cross-section, without or with negligible endosperm, the outer face convex; cotyledons 2, thick, applicate.

Best known to the layman of all the genera of Verbenaceae is the type genus, Verbena, founded by Linnaeus in the first edition of his Systema Naturae in 1737, but with a pre-Linnean history that goes back to the classical days of the ancient Greeks and Romans. In this historic genus over 500 binomials have been published by botanical workers through the years, but a great many of the plants thus referred to do not belong in the true genus Verbena as now recognized. True verbenas are most abundant in the central and south-central portions of the United States, in Mexico, and in southern Brazil, Paraguay, Uruguay, Argentina, and Chile where over 205 species and varieties are concentrated. In the Old World (Europe, Asia, Africa, and Australia) there are only about 5 native species and varieties and 8 or 9 additional ones introduced from America as weeds. Because of the showy flowers of so many of its species, the genus (especially the subgenus Glandularia, which is perhaps worthy of generic rank) has long been an important horticultural subject.

The genus is a complex one of about 355 species, subspecific taxa, and hybrids native to temperate and tropical America; 2 species native to the Mediterranean region and the Near East and introduced elsewhere in the Old World. There are several widely cultivated forms. Several American species have become naturalized in various parts of Europe, Asia, Africa, and Australia. The type species is V. officinalis L.

The generic name "vervain" is a Middle English word and "verveine" an Old French adaptation derived from the Celtic, fer, to take away, and faen, stone, in allusion to the former use of the type species in the treatment of bladder-stones, while "Verbena" appears to be the ancient Latin adaptation of this, used by Virgil and Pliny and later adopted by Linnaeus. I. Acuña (1945) gives the etymology as "lat. herbena — una hierba verde, derivado de herbeo-verdear." Rümpler (1873) gives the common names "Eisenkraut" and "Verbene" in German, and says as to the origin of the generic name "Soll von dem keltischen ferfaen abstammen und aus fer, wegführen, und faen, Stein, zusammengesetzt sein; das Kraut wurde nämlich gegen Blasenstein angewendet. Wahrscheinlich aber ist die Abstammung von dem lateinischen verbum, Wort, weil man bei diesem Kraute schwor und es auch bei Opfern gebrauchte."

At least 100 of the taxa here accepted are known from cultivation. Judging from these, apparently all the verbenas are readily raised from seed in early spring in heat, or from cuttings of shoots which have no flowers. The hardy perennial species may also be raised by division of the rootstocks. All require a rich soil and may be planted in the open border during summer from the middle or end of May in the Northern Hemisphere. Most of the species are somewhat tender, even V. rigida being apt to suffer in hard winters. V. hybrida was at one time commonly propagated by cuttings to keep the various named color forms true, but the plants were found to be difficult to keep through the winter.

Members of this genus apparently hybridize quite readily. Numerous natural hybrids have already been discovered and named; others are suspected. Artificial hybrids have also been produced by experimental workers. A list of the known hybrids follows:

xVerbena adulterina Hausskn. = V. officinalis L. x V. supina L.
xVerbena argentina Moldenke = V. cabrerae Moldenke x V. calliantha Briq.
xVerbena baileyana Moldenke = V. hastata L. x V. officinalis L.
xVerbena bealei Moldenke = V. hispida Ruíz & Pav. x V. litoralis H.B.K.
xVerbena bingenensis Moldenke = V. bracteata Lag. & Rodr. x V. lasiostachys var. septentrionalis Moldenke
xVerbena blanchardi Moldenke = V. hastata L. x V. simplex Lehm.
xVerbena clemensorum Moldenke = V. officinalis L. x V. robusta Greene
xVerbena conata Moldenke = V. officinalis L. x V. halei Small
xVerbena corrupta Moldenke = V. peruviana (L.) Britton x V. phlogiflora Cham.
xVerbena covasii Moldenke = V. santiaguensis (Covas & Schnack) Moldenke x V. tenuisecta Briq.
xVerbena deamii Moldenke = V. bracteata Lag. & Rodr. x V. stricta Vent.
xVerbena dermeni Moldenke = V. bonariensis L. x V. hispida Ruíz & Pav.
xVerbena dissoluta Moldenke = V. phlogiflora Cham. x V. tenuisecta Briq.
xVerbena engelmannii Moldenke = V. hastata L. x V. urticifolia L.
xVerbena fabricata Moldenke = V. hispida Ruíz & Pav. x V. urticifolia L.
xVerbena fecunda Moldenke = V. ambrosifolia f. eglandulosa Perry x V. canadensis (L.) Britton
xVerbena ferax Moldenke = V. canadensis (L.) Britton x V. racemosa Eggert
xVerbena goodmani Moldenke = V. halei Small x V. stricta Vent.
xVerbena hybrida Voss = V. incisa Hook. x V. peruviana (L.) Britton x V. phlogiflora Cham. x V. platensis Spreng.

xVerbena illicita Moldenke = V. stricta Vent. x V. urticifolia L.
xVerbena inhonesta Moldenke = V. lasiostachys Link x V. urticifolia L.
xVerbena intercedens Briq. = V. bonariensis L. x V. ovata Cham.
xVerbena kondai Moldenke = V. racemosa Eggert x V. tenuisecta Briq.
xVerbena lecocqi Moldenke = V. hispida Ruíz & Pav. x V. lasiostachys Link
xVerbena matritensis Moldenke = V. carolina L. x V. hastata L.
xVerbena meretrix Moldenke = V. hispida Ruíz & Pav. x V. officinalis L.
xVerbena moechina Moldenke = V. simplex Lehm. x V. stricta Vent.
xVerbena nequam Moldenke = V. dissecta Willd. x V. tenuisecta Briq.
xVerbena noacki Moldenke = V. hastata L. x V. hispida Ruíz & Pav.
xVerbena notha Moldenke = V. halei Small x V. neomexicana (A. Gray) Small
xVerbena oklahomensis Moldenke = V. bipinnatifida Nutt. x V. canadensis (L.) Britton
xVerbena osteni Moldenke = V. peruviana (L.) Britton x V. platensis Spreng.
xVerbena perriana Moldenke = V. bracteata Lag. & Rodr. x V. urticifolia L.
xVerbena prostibula Moldenke = V. hispida Ruíz & Pav. x V. simplex Lehm.
xVerbena rydbergii Moldenke = V. hastata L. x V. stricta Vent.
xVerbena schnackii Moldenke = V. megapotamica Spreng. x V. peruviana (L.) Britton
xVerbena scorta Moldenke = V. halei Small x V. lasiostachys Link
xVerbena solbrigii Moldenke = V. peruviana (L.) Britton x V. tenuisecta Briq.
xVerbena suksdorfi Moldenke = V. lasiostachys var. septentrionalis Moldenke x V. officinalis L.
xVerbena teasii Moldenke = V. hybrida Voss x V. tenuisecta Briq.
xVerbena torpa Moldenke = V. neomexicana (A. Gray) Small x V. urticifolia L.
xVerbena transitoria Moldenke = V. megapotamica Spreng. x V. tenuisecta Briq.
xVerbena trinitensis Moldenke = V. incisa Hook. x V. tenuisecta Briq.
xVerbena uruguayensis Moldenke = V. peruviana (L.) Britton x V. tenera Spreng.
xVerbena vaga Moldenke = V. megapotamica Spreng. x V. santiaguensis (Covas & Schnack) Moldenke
xVerbena wingei Moldenke = V. canadensis (L.) Britton x V. tenui-

secta Briq.

An intergeneric interfamily hybrid has also been described and illustrated, xVeronicena haartmani Moldenke, said by Haartman, Plantae hybridae 7--8 (1751) and Amoen. Acad. 3: 35, pl. 2 (1756), to be a hybrid between V. officinalis L. and the scrophulariaceous Veronica maritima L. The status of this plant, however, is highly questionable, as has been pointed out by me in Am. Midl. Nat. 59: 363--364 (1958). Its existence seems to have been rather generally ignored by, or unknown to, later workers. I have not as yet seen the type -- if, indeed, any such was ever preserved — but among the 171,938 herbarium specimens of my groups that have passed through my hands in the past 32 years there were two specimens which may possibly have represented this same or a similar taxon. Unfortunately, not being aware myself at that time of Haartman's paper, I returned the specimens to their respective institutional owners with the simple annotation "Not verbenaceous!" and kept no detailed record of them. My recollection of them, however, is that they represented a plant much like the one figured by Haartman. The sheets on which they were mounted -- as I recall them now -- were both quite old and had apparently been bandied about from one genus and family to another, always to be returned to the harbarium owning them with the comment that they did not pertain to that group. I recall "Scroph.?", "Labiat.?", and even "Lobeliac.?" inscribed on at least one of them, with each suggestion later stricken out by pencil. Perhaps the curators of the herbaria in question, on reading this, may recall the specimens and may re-examine them in the light of Haartman's claims. Unfortunately, having studied material of my groups from 260 herbaria, I cannot now recall to which herbaria they were returned.

As far as I am aware, this claim of Haartman is the first for a hybrid between species belonging to entirely different families of either plants or animals. Generally such an inter-family hybrid is regarded as biologically impossible, and this alone tends to cast much doubt on Haartman's claim. It is very possible that his concept of a "hybrid" plant was quite different from our modern concept. A detailed study of the remainder of his paper may throw considerable light on his thinking. In Am. Midl. Nat. 59: 364 (1958) are given the detailed similarities and differences between Verbena and Veronica as genera, and the Verbenaceae and Scrophulariaceae which they represent. The chromosome complements of both supposed parents are also compared.

Cabrera, Covas, Dawson, Gmelin, Mattfeld, Nuttall, Ragonese, Schnack, Rozier, Small, and Solbrig have all suggested the segregation of the genus Glandularia J. F. Gmel. from Verbena. Personally, I think that this is quite justified, but because of the great number of nomenclatorial changes which this would necessitate in widely known species, including cultivated ones, I have not followed this course in the present work. Schnack & Covas, in Bol. Soc. Argent. Bot. 1: 282--284 (1946), summarize the situation as follows: "El estudio de numerosas especies incluídas en el género Verbena (sensu Schauer, en D. C., Prodr., 11: 550, 1847) nos ha permitido confirmar el carácter artificial de esta entidad, y correspondientemente la validez del género Glandularia, recientemente rehabilitado.....y que comprende una serie de antiguas Verbenas. En efecto, hemos podido establecer la concomitancia de una serie de caracteres de la más distinta naturaleza dentro del género Glandularia, por una parte, y del género Verbena (en su sentido actual restringido) por otra. Así, la naturaleza de la banda clorofiliana cortical, la longitud del estilo en relación al ovario, la forma de las anteras, de la corola y de los mericarpios, entre otros caracteres, guardan una correlación tan estrecha entre las especies de Glandularia, y son tan netamente antagónicos con respecto a los caracteres de las especies de Verbena, que no vacilamos en calificar a estos dos géneros como dos entidades perfectamente distintas y naturales, en las que fenóminos de convergencia de formas conducen a una similitud aparente de especies que pertenecen a dos líneas evolutivas distintas."

They summarize the differences as follows: in Verbena (1) the stems are plainly quadrangular, (2) the chlorophyllous cortical parenchyma is discontinuous (interrupted at the angles), (3) the inflorescence is paniculate, many-spicate, (4) the corolla is funnel-form, (5) the thecae of the anthers do not surpass the connective, (6) the style becomes approximately 3 times as long as the ovary, (7) the mericarps are chestnut-reddish in color, with the pericarp not prolonged either laterally or at the base of the embryonal sector, and (8) the chromosomes are x = 7 and small. In Glandularia, on the other hand, (1) the stems are cylindric-quadrangular, (2) the chlorophyllous cortical parenchyma is continuous, (3) the inflorescence is few-spicate, generally 1—3-spicate, (4) the corolla is salver-form, (5) the anther-thecae surpass the connective, (6) the style is variously longer than the ovary, (7) the mericarps are brown-blackish, with the pericarp dilated laterally or rather prolonged beneath the embryonal sector, forming an excavated base, and (8) the chromosomes are x = 5 and comparatively larger. Mattfeld (1951) says: "Die bisher mit Verbena (x = 7) vereinigte Gattung Glandularia Gm. (x = 5).....musz als eigene Gattung abgetrennt werden." Meisner and Walpers used the generic name Shuttleworthia and Bunge proposed Uwarowia for what is essentially this group.

In this connection it is interesting to note that cytologists have reported the following chromosome numbers for species of Verbena (sens. lat., including Glandularia): n = 5, 2n = 10 — V. dissecta, V. erinoides [probably tenuisecta], V. erinoides var. alba [probably tenuisecta var. alba], V. flava, V. grandiflora [probably canadensis], V. hybrida, V. laciniata, V. mendocina, V. microphylla, V. parodii, V. perakii, V. peruviana, V. phlogiflora, V. platensis, V. radicans, V. santiaguensis, V. tenera, V. tenuisecta, and V. teucrioides [=platensis]; n = 10, 2n = 20 — V. crithmifolia, V. hookeriana, V. pumila, V. quadrangulata, V. racemosa, and V. wrightii; n = 15, 2n = 30 — V. ambrosifolia, V.

ambrosifolia f. eglandulosa, V. bipinnatifida, V. cameronensis, V. canadensis var. atroviolacea, V. canadensis var. compacta, V. canadensis, V. ciliata, V. delticola, V. elegans var. asperata, V. gooddingii var. nepetifolia, V. racemosa, and V. teucriifolia; n = 7, 2n = 14 — V. canescens var. roemeriana, V. carolina, V. cloverae, V. halei, V. hastata, V. hispida, V. macdougalii, V. neomexicana, V. neomexicana var. hirtella, V. officinalis, V. perennis, V. plicata, V. prostrata [=lasiostachys], V. simplex, V. stricta, and V. urticifolia; n = 14, 2n = 28 — V. bonariensis, V. brasiliensis, V. ehrenbergiana, and V. litoralis; n = 21, 2n = 42 — V. integrifolia, V. rigida, V. xutha. It is to be noted that workers have obtained different chromosome numbers for V. canadensis and for V. racemosa, perhaps due to misidentification of the material used.

Walpers (1845) classified the genus Verbena as follows:

Sect. 1. Aloysioides Walp.
Sect. 2. Verbenaca Walp.
  § 1. Spinosae Walp.
    A. Seriphioideae Walp.
    B. Erinaceae Walp.
  § 2. Inermes Walp.
    * Folia fasciculata
      A. Selaginoideae Walp.
      B. Thymoideae Walp.
    ** Folia opposita non fasciculata
      A. Junceae Walp.
      B. Foliosae Walp.
        1. Micranthae Walp.
          α. Holophyllae Walp.
          β. Schizophyllae Walp.
        2. Macranthae Walp.
          α. Melindres Walp.
          β. Aubletia (Neck.) Walp.

In this classification his Section 1 is synonymous with the genus Aloysia Ortega; his Spinosae, Seriphioideae, Erinaceae, and Selaginoideae are all congeneric with Junellia Moldenke; his Junceae contains 2 species of Diostea, 2 of Junellia, and 1 Neosparton, as well as 3 true species of Verbena.

Schauer (1847) divided the genus as follows:

Sect. 1. Verbenaca Walp.
  Subsect. 1. Pungentes Schau.
  Subsect. 2. Nobiles Schau.
  Subsect. 3. Pachystachyae Schau.
  Subsect. 4. Verticilliflorae Schau.
  Subsect. 5. Leptostachyae Schau.
Sect. 2. Glandularia (J. F. Gmel.) Schau.

In this classification his Section Pungentes is now a part of the genus Junellia, while his Section Verticilliflorae is divided among Diostea Miers, Junellia Moldenke, and Neosparton Griseb.

In the system adopted by myself in 1959 and later emended, the genera and subgeneric groups of the Tribe Euverbeneae are distinguished as follows:

1. Calyx more or less tubular; fruit dry, included by the fruiting-calyx, usually separating into 4 cocci when ripe.
  2. Fruiting-calyx unchanged, not accrescent; stamens 4.
    3. Woody shrubs or subshrubs of desert and high-alpine regions; leaves usually greatly reduced; inflorescence reduced.
      4. Calyx deeply 5-parted almost to the base, with long filiform lobes, densely long-villous; stigma obliquely capitate, apiculate; leaves densely imbricate; Chile. Genus Urbania R. A. Phil.
      4a. Calyx mostly only 5-toothed, with short, often obscure teeth, rarely long-toothed, usually not long-villous; leaves not usually closely imbricate; Argentina, Chile, Bolivia, and Peru. Genus Junellia Moldenke.
        5. Leaves alternate, simple, fascicled. Group Selaginoideae Walp.
        5a. Leaves opposite.
          6. Flowers in small dense heads; leaves parted or entire, more or less stiff and thorny. Series Acerosae Briq.
            7. Spines distinct from the foliage. Group Seriphioideae Walp.
            7a. Leaves and bracts spinescent. Group Erinaceae Walp.
          6a. Flowers in 1- or 2, rarely few-flowered clusters at the tips of the branches; low, often tufted or sod-like, high-alpine plants with tangled branches. Series Pungentes Schau.
    3a. Herbaceous plants or subshrubs, not limited to desert or high-alpine regions; leaves and inflorescences usually well developed.
      8. Fruit not beaked, composed of 4 cocci, easily separable when ripe. Genus Verbena L.
        9. Anthers unappendaged. Subgenus Verbenaca (Walp.) Lewis.
          10. Plants often subshrubby, usually with greatly reduced or even scale-like leaves. Series Junceae Walp.
          10a. Plants mostly herbaceous; foliage mostly not reduced. Series Foliosae Walp.
            11. Young spikes fastigiate-capitate, Subseries Macranthae Walp.
              12. Leaves crenate, dentate, or subincised. Group Melindres Walp.
              12a. Leaves incised-lobed, pinnatifid, or bipinnatifid. Group Aubletia (Neck.) Walp.
            11a. Young spikes not fastigiate-capitate; corollas mostly small and individually not showy; calyx rare-

ly twice as long as the fruit, not contorted beyond it. Subseries Micranthae Walp.

13. Spikes abbreviated, the flowers crowded. Group Pachystachyae Schau.

13a. Spikes elongated, filiform, the flowers scattered. Group Leptostachyae Schau.

9a. Some anther-connectives usually appendaged; corolla mostly large and showy; calyx usually more than twice as long as the fruit and constricted or contorted beyond it. Subgenus Glandularia (J. F. Gmel.) Lewis.

8a. Fruit beaked, nutlet-like, not readily separating. Genus Stylodon Raf.

2a. Fruiting-calyx accrescent, broadened and inflated at the base; stamens 2. Genus Hierobotana Briq.

1a. Fruiting-calyx broadly campanulate; fruit a 4-celled drupe, with more or less fleshy exocarp and hard endocarp. Genus Ghinia Schreb.

It is worth noting here that Verbena Dill. is a synonym of Priva Adans. and that Verbena Pluk. is synonymous with Stachytarpheta Vahl. The genus Verbena L. was placed in Family 75, Labiatae, Section Verbeneae, by Heinrich Gottlieb Ludwig Reichenbach in Mössler, Handb. Gewächsk., ed. 1, 1: xxxvi (1827) and ed. 3, 1: lxxv (1833), and also by him in his Conspectus Regni Vegetabilis per Gradus Naturalis Evoluti 1: 117 (1828).

Kuhlmann & Kühn, Flor. Dist. Ibiti 182 (1947) say "Verbena spp. — As herbas agrupadas neste genero aparecem geralmente em terrenos baldios, cultivados e nos quintais. A 'camaradinha' ou 'jurujba' é cultivada nos jardins. Produzem flores de colorido variável conforme a espécie ou variedade, também visitadas por Lepidópteros e 'Abelhas'. Os frutos sao secos, nada denunciando de apreciável nas suas relacoes com a Fauna."

Rehder (1949) includes in the synonymy of Verbena the following genera: Burseria Löfl. [actually a synonym of Priva Adans.], Stylodon Raf., Styleurodon Raf. [a synonym of Stylodon], and Junellia Moldenke.

Martin (1946) examined 14 species and reports that the endosperm is "negligible". Junell (1934) discusses the gynoecium morphology. Schauer (1847) says that there are only 2 stamens in one species of the genus (!) and that the ovary is very rarely 6-celled. Schauer, of course, included in the genus what we now separate as Hierobotana, Junellia, and Stylodon. The Gmelin reference cited by me in the bibliography (on previous pages) is often cited by other authors as "Gmelin, Syst. Veg. 920. 1791". The genus Billardiera is sometimes cited to "Moench, Meth. 366. 1794", but "369" is the correct page citation. Verbena is sometimes cited to "L., Syst. Veg., ed. 1. 1737", but I have thus far been unable to trace this reference.

Lewis & Oliver (1961) give a very interesting discussion of the genus under V. ovata Cham.: "This species, found in east-central

South America, might have arisen as an amphidiploid in a cross between an n = 5 and n = 7 species followed by genomic doubling to reach this polyploid level. Dermen's (1936) inability to produce an intersectional hybrid, the rare occurrence of 1 parent in South America, and the unquestioned classification of V. ovata in the section Verbenaca (the taxon is not morphologically intermediate) are all evidences against such an origin. Alternately, V. ovata may be a terminal dodecaploid of an extant x = 6 series which was morphologically more closely related to Verbenaca than to Glandularia. Additional cytological studies might reveal other 'relic' taxa in South America, but the very existence of V. ovata supports the hypothesis of an ancestral x = 6 stock. Since many modern angiosperm genera were differentiated in the Cretaceous, we assume conservatively that the x = 6 prototype was widespread in the tropical environment and lowlands characteristic of this period. With the elevation of the Cordilleras during the Lamaride Revolution, the phylad was reduced considerably in distribution. The opening of the new colder and drier environments adjacent to the tropics in the late Cretaceous and Plaeocene gave the necessary stage for the evolution of new taxa. On the northern boundaries of the phylad's now limited range, the ascending x = 7 aneuploid series originated, perhaps during the (early) Tertiary. This macroevolution gave rise to the now dominant Verbenaca in North America. Similarly, the x = 5 descending aneuploid series in South America was evolved (section Glandularia) and became adapted to the more temperate environment in that continent. By the Miocene these phylads were well-established and diverse in the warm temperate regions of both continents adjacent to the tropical zone. With the restriction of the tropical zone during the Tertiary and particularly from the Miocene to recent times, a great numerical decrease in the ancestral population could be expected. Together with the new competitive factors manifested by these conditions, a general decline in the whole taxon was probably the result. Indefinite multiplication of chromosome numbers could not but have a deleterious effect upon the group (Levan, 1942), and if the high level of polyploidy reached by V. ovata is an example, this factor also may have contributed to the near extinction of the x = 6 phylad. The final result is an amphitropical distribution for Verbena.

"The question of both Verbena sections occurring in North and South America remains to be answered. Migration of diploid or tetraploid Glandularia, from South America via trans-tropical land-bridges, similar to the distribution of V. litoralis, or by long-range dispersal, are plausible explanations. Probably this migration took place during the later Miocene or Pliocene in a period of maximum extension of the upland temperate regions into the tropical forests. Once established and after becoming disjunct, this new population(s) could have given rise to the Glandularia taxa in North America. Very likely a migration southward of one or more North American Verbenaca also occurred during these periods and formed the basis for the high level of polyploidy in South America currently unknown to the north. These species, new to both continents, successfully competed with the taxa already present, and polyploidy as an evolutionary mechanism had a selective advantage over the widespread (diploid) populations."

Vernacular names for the genus as a whole are "aublétia", "aublétie", "camaradinha", "camaradinhas", "cambarás", "cedrón", "chichiantic", "Eisen-hart", "Eisen-hort", "Eisen-klette", "Eisenkraut", "Eisenweich", "herva cidreira", "holy herb", "ijzerhard", "iron-weed", "jujubas", "jujubes", "jurujba", "margarita colorada", "margarita punzó", "moradilla", "salvia montés", "Shah's favourite", "Sha-passan", "tepe-chian", "tlal-ahuehuetl", "verbena", "verbenas", "vervain", "vervains", "verveine", "vervène", "verveyne", "wijkruid", and "yapau". Actually, some of these names obviously apply only to the species which happen to grow in a certain circumscribed area, which, in a few cases, may actually be only a single species; yet authors give these names as generic designations. It is worth noting here that "false verbena" is Cochranea anchusaefolia (Poir.) Gürke in the Heliotropiaceae and "sand-verbena" is the genus Abronia Juss. in the Nyctaginaceae, while the name "verbena" is often applied also to Bouchea prismatica (L.) Kuntze, B. prismatica var. longirostra Grenz., Clerodendrum fragrans var. pleniflorum Schau., Priva lappulacea (L.) Pers., Stachytarpheta cayennensis (L. C. Rich.) Vahl, S. calderonii Moldenke, S. frantzii Polak., S. jamaicensis (L.) Vahl, and S. guatemalensis Moldenke, as well as to Salvia polystachya Ort. in the Lamiaceae; "verbena celeste" is Stachytarpheta frantzii, "verbena de playa" is S. jamaicensis, "verbena manza" is S. jamaicensis and Bouchea prismatica var. longirostra, "verbena cimarrona" is Bouchea prismatica, "verbena de flos grande" is Bouchea rusbyi Moldenke, and "verbena morada" is Stachytarpheta frantzii. "Verveine" is also applied to Phyla nodiflora (L.) Greene and to Stachytarpheta jamaicensis, "verveine queue de rat" is S. jamaicensis, "verveine à fleurs rouges" is S. mutabilis (Jacq.) Vahl, "verveine à trois feuilles" is Aloysia triphylla (L'Hér.) Britton, "verveine bleue" and "verveine queue de rat" are also S. indica (L.) Vahl, "verveine citronelle", "verveine odorante", "verveine du Pérou" are Aloysia triphylla, "verveine du Mexique" is Priva mexicana (L.) Pers., "verveine du pays" and "verveine sauvage" are Phyla nodiflora, "verveine faux-gervaô" is Bouchea fluminensis (Vell.) Moldenke, "verveine caraibe" is Wedelia carnosa Rich. in the Carduaceae, and "verveine puante" is Petiveria alliacea L. in the Petiveriaceae. According to Augusto d'Halmar's "San Miguel y las Verbenas madrileñas", there are some fiesta dances in Spanish-speaking countries known as "verbena". In Chilton County, Alabama, there is a town and post office named "Verbena".

Figure 1. Distribution of Verbena in the United States

Mapping by county done by Andrew R. Moldenke

The maps appearing in this monograph are designed to show at a glance the known distribution of the genus and its constituent species in the United States of America, based on the specimens thus far examined by me. I am deeply grateful to my son, Andrew Ralph Moldenke, for the hundreds of hours of his time which he sacrificed from his entomologic studies in order to prepare these maps for this work. No attempt has been made to indicate the relative abundance of records from a given county -- there may be only one or there may be many -- nor the exact location of the records within the county or parish. A county or parish (or island) is blackened on the map to indicate that we have a record or records of the taxon's occurrence in the wild state there and it may be expected and looked for there by students of the group. Figure 1 indicates the distribution of the genus as a whole in this country. Counties where more intensive collecting is required are plainly shown on this map, since it is hardly likely that the genus does not occur in counties completely surrounded by counties from which we have records of its presence. Students living in or near these counties are urged to search in them for specimens of this genus and communicate them to me so that we may eventually fill in the empty spaces in a future edition of this map and the maps that follow.

In the Linnean Herbarium at London the specimen number "1" under genus 35, Verbena, is Stachytarpheta indica; number "2" is S. jamaicensis -- and they are very different from each other! Number "3" is labeled "prismatica" in the handwriting of Solander and bears the annotation "Br." [=Browne; Patrick Browne's herbarium was purchased for Linnaeus in 1758] and another notation in the handwriting of Smith "Stachytarpheta prismatica Sm. in R. Cycl. No. 11." It is actually Bouchea prismatica (L.) Kuntze, with the beaks of the cocci 1.5--2.5 mm. long. Number "4" is labeled "mexicana" in Linnaeus' handwriting and is Priva mexicana (L.) Pers. Number "5" is labeled "lappulacea" in the handwriting of Solander and bears the notation "Br." It is Priva lappulacea (L.) Pers. Number "6", pinned to number "5", is labeled "lappulacea" in Linnaeus' own handwriting and bears the notation "Br." [=Browne] and "Rolander" [Rolander collected in Surinam after 1754]; it is Salvia occidentalis Sw. Number "7" is labeled "stoechadifolia" in the handwriting of Solander, and is Phyla stoechadifolia (L.) Small. Number "8" is labeled "nodiflora" in the handwriting of Solander, and is Phyla nodiflora (L.) Greene. There are more specimens following of this and other species. On specimen number "1" under genus 755, Phryma, Linnaeus wrote "Leptostachya" on the bottom in his usual handwriting and manner, and "Verbena" on top in a large script [the handwriting verified by Mr. Savage, of the Linnean Society, in each case]. On the reverse side of sheet number "3" there is a description in Linnaeus' own handwriting [verified by Savage] starting out "Verbena. Cal. 1-phyllus cylindricus, etc." The specimen was named "hians" on the front of the sheet by Linnaeus (never published under Phryma until by B. D. Jackson in his Index of the Linnean Herbarium) and is actually Chascanum dehiscens (L. f.) Moldenke. The specimens in his herbarium that are true Verbena species will be discussed hereinafter under the taxa involved.

Following is an alphabetic list of names applying to species and varieties excluded from the genus:

Verbena alatocarpa Troncoso = Junellia alatocarpa (Troncoso) Moldenke

Verbena alpigena Walp. = Aloysia scorodonioides (H.B.K.) Cham.

Verbena alternifolia Herb. = Junellia selaginoides (Kunth) Moldenke

Verbena alternifolia Hort. = Junellia selaginoides (Kunth) Moldenke

Verbena alternifolia Sessé & Moc. = Stachytarpheta incana var. angustibracteata Moldenke

Verbena ameghinoi Speg. = Junellia ameghinoi (Speg.) Moldenke

Verbena americana Mill. = Stachytarpheta jamaicensis (L.) Vahl

Verbena americana flore coccinea spicato Breyn. = Stachytarpheta mutabilis (Jacq.) Vahl

Verbena angustifolia Mill. = Stachytarpheta angustifolia (Mill.) Vahl

Verbena aphylla Gill. = Neosparton aphyllum (Gill. & Hook.) Kuntze

Verbena aphylla Gill. & Hook. = Neosparton aphyllum (Gill. & Hook.) Kuntze

Verbena arborea H.B.K. = Petrea arborea H.B.K.

Verbena arborescens Bojer = Lippia javanica (Burm. f.) Spreng.

Verbena aretioides R. E. Fries = Junellia aretioides (R. E. Fries) Moldenke

Verbena aretioides Hayek = Junellia hayekii Moldenke

Verbena aretoides Hayek = Junellia hayekii Moldenke

Verbena aristata Vahl = Stachytarpheta orubica (L.) Vahl

Verbena asparagoides Gill. = Junellia asparagoides (Gill. & Hook.) Moldenke

Verbena asparagoides Gill. & Hook. = Junellia asparagoides (Gill. & Hook.) Moldenke

Verbena asparagoides var. famatinensis Hieron. = Junellia asparagoides (Gill. & Hook.) Moldenke

Verbena aspera Gill. & Hook. = Junellia aspera (Gill. & Hook.) Moldenke

Verbena aspera Hügel = Priva cordifolia (L. f.) Druce

Verbena azorelloides Speg. = Junellia azorelloides (Speg.) Moldenke

Verbena bifurca Benth. = Bouchea prismatica (L.) Kuntze

Verbena bisulcata Hayek = Junellia bisulcata (Hayek) Moldenke

Verbena bonariensis Rendle = Junellia patagonica (Speg.) Moldenke

Verbena briquetii Macbr. = Junellia seriphioides (Gill. & Hook.)

Moldenke
Verbena bryoides Echeg. = Junellia asparagoides (Gill. & Hook.) Moldenke
Verbena bryoides R. A. Phil. = Junellia bryoides (R. A. Phil.) Moldenke
Verbena caespitosa Gill. & Hook. = Junellia caespitosa (Gill. & Hook.) Moldenke
Verbena cajanensis L. C. Rich. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena cajenensis Rich. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena callicarpiaefolia Kunth = Lippia callicarpaefolia H.B.K.
Verbena cannabifolia Sieb. & Zucc. = Vitex negundo var. cannabifolia (Sieb. & Zucc.) Hand.-Mazz.
Verbena capensis Thunb. = Lippia javanica (Burm. f.) Spreng.
Verbena capensis f. capillaris Ray = Hebenstretia erinoides L. f., Selaginaceae
Verbena capitata Blanco = Phyla nodiflora (L.) Greene
Verbena capitata Forsk. = Phyla nodiflora (L.) Greene
Verbena capitata Hort. = Lippia javanica (Burm. f.) Spreng.
Verbena carnea Medic. = Stylodon carneus (Medic.) Moldenke
Verbena carolinense (Walt.) Gmel. = Stylodon carneus (Medic.) Mold,
Verbena carolinensis Gmel. = Stylodon carneus (Medic.) Moldenke
Verbena carolinensis Small = Stylodon carneus (Medic.) Moldenke
Verbena carolinensis Walt. = Stylodon carneus (Medic.) Moldenke
Verbena carolinensis (Walt.) J. F. Gmel. = Stylodon carneus (Medic.) Moldenke
Verbena carolinensis (Walt.) Small = Stylodon carneus (Medic.) Moldenke
Verbena caroliniana Hort. = Stylodon carneus (Medic.) Moldenke
Verbena caroliniana L. [ex Raf.] = Stylodon carneus (Medic.) Moldenke
Verbena caroliniana Medic. = Stylodon carneus (Medic.) Moldenke
Verbena caroliniana Michx. = Stylodon carneus (Medic.) Moldenke
Verbena caroliniana (Walt.) Michx. = Stylodon carneus (Medic.) Moldenke
Verbena carolinianum L. = Stylodon carneus (Medic.) Moldenke
Verbena caroliniensis (Walt.) J. F. Gmel. = Stylodon carneus (Medic.) Moldenke
Verbena carroo Speg. = Junellia tridens (Lag.) Moldenke
Verbena carróo Speg. = Junellia tridens (Lag.) Moldenke
Verbena castrata Sessé & Moc. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena caudata Salisb. = Stachytarpheta indica (L.) Vahl
Verbena cayannensis Rich. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena cayennensis L. C. Rich. = Stachytarpheta cayennensis (L.

C. Rich.) Vahl
Verbena cedroides Sandw. = Junellia cedroides (Sandw.) Moldenke
Verbena ceratophylla Bonpl. = Hierobotana inflata (H.B.K.) Briq.
Verbena chubutensis Speg. = Junellia wilczekii (Briq.) Moldenke
Verbena cinerascens Schau. = Diostea cinerascens (Schau.) Moldenke
Verbena citriodora Cav. = Aloysia triphylla (L'Hér.) Britton
Verbena citriodora Ort. = Aloysia triphylla (L'Hér.) Britton
Verbena clerodendron Froes = Clerodendrum calamitosum L.
Verbena colchaguensis R. A. Phil. = Junellia lavandulaefolia var. colchaguensis (R. A. Phil.) Moldenke
Verbena comberi Sandw. = Junellia comberi (Sandw.) Moldenke
Verbena connatibracteata Kuntze = Junellia connatibracteata (Kuntze) Moldenke
Verbena connatibracteata f. glomerata Monticelli = Junellia connatibracteata f. glomerata (Monticelli) Moldenke
Verbena connatibracteata f. normalis Monticelli = Junellia connatibracteata (Kuntze) Moldenke
Verbena connatibracteata f. rosulata Monticelli = Junellia connatibracteata f. rosulata (Monticelli) Moldenke
Verbena cordata Hort. = Aloysia chamaedryfolia Cham.
Verbena cordata Mackay = Aloysia chamaedryfolia Cham.
Verbena cordifolia Bourgeau = Priva mexicana (L.) Pers.
Verbena cuneata Willd. = Phyla nodiflora (L.) Greene
Verbena curassavica L. = Ghinia curassavica (L.) Millsp.
Verbena decurrens Moench = Stachytarpheta jamaicensis (L.) Vahl
Verbena dentada Vivian. = Aloysia chamaedryfolia Cham.
Verbena dentata Hort. = Aloysia chamaedryfolia Cham.
Verbena dentata Juss. = Aloysia chamaedryfolia Cham.
Verbena dentata Visian. = Aloysia chamaedryfolia Cham.
Verbena diandra Sessé & Moc. = Bouchea prismatica var. brevirostra Grenz.
Verbena diandria Larrañ. = Bouchea prismatica var. brevirostra Grenz.
Verbena dichotoma Larrañ. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena dichotoma Ruíz & Pav. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena digitata R. A. Phil. = Junellia digitata (R. A. Phil.) Moldenke
Verbena disperma Duchassaing & Sagot = Stachytarpheta jamaicensis (L.) Vahl
Verbena diversifolia Kuntze = Junellia diversifolia (Kuntze) Moldenke
Verbena dolichothyrsa Sandw. = Junellia dolichothyrsa (Sandw.) Moldenke

Verbena echegarayi Hieron. = Junellia echegarayi (Hieron.) Moldenke
Verbena echegayari Hieron. = Junellia echegarayi (Hieron.) Moldenke
Verbena echinata R. A. Phil. = Junellia seriphioides (Gill. & Hook.) Moldenke
Verbena elliptica Willd. = Phyla nodiflora var. canescens (H.B.K.) Moldenke
Verbena ellipticifolia Stokes = Stachytarpheta indica (L.) Vahl
Verbena erinacea Gill. & Hook. = Junellia erinacea (Gill. & Hook.) Moldenke
Verbena etchegarayi Hieron. = Junellia echegarayi (Hieron.) Moldenke
Verbena fluminensis Vell. = Bouchea fluminensis (Vell.) Moldenke
Verbena foliis cordato-ovatis, floribus spicatis, calicibus inflatis, seminatis echinatis P. Browne = Priva lappulacea (L.) Pers.
Verbena foliis verticaliter ovatis, spicis globosis L. = Phyla nodiflora (L.) Greene
Verbena foliis verticaliter ovatis, spicis solitariis ovatis Royen = Phyla nodiflora (L.) Greene
Verbena forskaelaei Vahl = Priva cordifolia (L. f.) Druce
Verbena forskaelei Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskaelii Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskålaei Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskålei Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskalii Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskaolaei Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskaolii Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena forskhalei Vahl = Priva adhaerens (Forsk.) Chiov.
Verbena fragrans Salisb. = Aloysia triphylla (L'Hér.) Britton
Verbena fruticosa Sessé & Moc. = Stachytarpheta incana Moldenke
Verbena gayana Kuntze = Junellia glauca (Gill. & Hook.) Moldenke
Verbena glaberrima Gill. & Hook. = Dipyrena glaberrima (Gill. & Hook.) Hook.
Verbena glauca Gay = Junellia glauca (Gill. & Hook.) Moldenke
Verbena glauca Gill. & Hook. = Junellia glauca (Gill. & Hook.) Moldenke
Verbena glauca var. cisandina Niederlein = Junellia glauca var. cisandina (Niederlein) Moldenke
Verbena glauca β cisandina Niederlein = Junellia glauca var. cisandina (Niederlein) Moldenke
Verbena globifera L'Hér. = Lippia alba (Mill.) N. E. Br.
Verbena globiflora L'Hér. = Lippia alba (Mill.) N. E. Br.
Verbena globiflora Nocca = Phyla nodiflora var. reptans (H.B.K.) Moldenke

Verbena globulifera Auct. = Lippia alba (Mill.) N. E. Br.
Verbena globulifera Spreng. = Lippia alba (Mill.) N. E. Br.
Verbena globuliflora L'Hér. = Lippia alba (Mill.) N. E. Br.
Verbena grandiflora Ort. = Priva grandiflora (Ort.) Moldenke
Verbena gratissima Gill. & Hook. = Aloysia lycioides Cham.
Verbena hastata x stricta Ravenel = Stylodon carneus (Medic.) Moldenke
Verbena heteraphilla Willd. = Hierobotana inflata (H.B.K.) Briq.
Verbena heterophylla Willd. = Hierobotana inflata (H.B.K.) Briq.
Verbena hirta Grah. = Lantana hirta Grah.
Verbena hispida Sessé & Moc. = Priva lappulacea (L.) Pers.
Verbena hyderabadensis Rottl. = Svensonia hyderobadensis (Walp.) Moldenke
Verbena hyderobadensis Rottl. = Svensonia hyderobadensis (Walp.) Moldenke
Verbena hyderobadensis var. maysorensis H. Wight = Svensonia hyderobadensis (Walp.) Moldenke
Verbena hydrabadensis Rottl. = Svensonia hyderobadensis (Walp.) Moldenke
Verbena hystrix Briq. = Junellia seriphioides (Gill. & Hook.) Moldenke
Verbena hystrix R. A. Phil. = Junellia hystrix (R. A. Phil.) Moldenke
Verbena illapelina R. A. Phil. = Junellia illapelina (R. A. Phil.) Moldenke
Verbena imbricata Sessé & Moc. = Stachytarpheta mutabilis (Jacq.) Vahl
Verbena inconcinna Briq. = Junellia ligustrina (Lag.) Moldenke
Verbena indica Jacq. = Stachytarpheta angustifolia (Mill.) Vahl
Verbena indica L. = Stachytarpheta indica (L.) Vahl
Verbena indica lanuginosa fl. rubente Barthol. = Manulea rubra L. f., Scrophulariaceae
Verbena inflata Humb. & Kunth = Hierobotana inflata (H.B.K.) Briq.
Verbena inflata H.B.K. = Hierobotana inflata (H.B.K.) Briq.
Verbena inflata Kunth = Hierobotana inflata (H.B.K.) Briq.
Verbena integerrima Larrañ. = Aloysia lycioides Cham.
Verbena intricata Briq. = Junellia intricata (Briq.) Moldenke
Verbena jamaicensis L. = Stachytarpheta jamaicensis (L.) Vahl
Verbena jamaicensis Vahl = Stachytarpheta jamaicensis (L.) Vahl
Verbena jamaicensis Vell. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena jamaicensis var. campestris Griseb. = Stachytarpheta australis Moldenke
Verbena javanica Burm. f. = Lippia javanica (Burm. f.) Spreng.
Verbena juncea Gill. & Hook. = Diostea juncea (Gill. & Hook.) Miers

Verbena junciformis Phil. = Junellia pseudo-juncea (C. Gay) Moldenke ?
Verbena juniperina Gill. & Hook. = Junellia juniperina (Lag.) Moldenke
Verbena juniperina Lag. = Junellia juniperina (Lag.) Moldenke
Verbena juniperina var. campestris Griseb. = Junellia juniperina (Lag.) Moldenke
Verbena juniperina var. clarenii Kurtz = Junellia juniperina (Lag.) Moldenke
Verbena juniperina var. grisea I. M. Johnst. = Junellia juniperina var. grisea (I. M. Johnst.) Moldenke
Verbena laciniata Sessé & Moc. = Bouchea prismatica var. laciniata Grenz.
Verbena lacunosa Mart. = Stachytarpheta lacunosa Mart.
Verbena laevigata Sessé & Moc. = Bouchea prismatica var. laciniata Grenz.
Verbena lanata Willd. = Phyla nodiflora var. canescens (H.B.K.) Moldenke
Verbena lancifolia Moench = Stachytarpheta indica (L.) Vahl
Verbena lancifolia Steud. = Stachytarpheta indica (L.) Vahl
Verbena lantanoides Willd. = Lippia alba (Mill.) N. E. Br.
Verbena lappacea Jacq. = Priva lappulacea (L.) Pers.
Verbena lappulacea Jacq. = Priva lappulacea (L.) Pers.
Verbena lappulacea L. = Priva lappulacea (L.) Pers.
Verbena lapulacea L. = Priva lappulacea (L.) Pers.
Verbena lapulacea Sessé & Moc. = Priva lappulacea (L.) Pers.
Verbena lapullacea L. = Priva lappulacea (L.) Pers.
Verbena lavandulaefolia R. A. Phil. = Junellia lavandulaefolia (R. A. Phil.) Moldenke
Verbena lavandulaefolia var. colchaguensis Reiche = Junellia lavandulaefolia var. colchaguensis (R. A. Phil.) Moldenke
Verbena lavandulifolia R. A. Phil. = Junellia lavandulaefolia (R. A. Phil.) Moldenke
Verbena lavandulifolia var. colchaguensis Reiche = Junellia lavandulaefolia var. colchaguensis (R. A. Phil.) Moldenke
Verbena leptostachys Mart. = Bouchea fluminensis (Vell.) Moldenke
Verbena ligustrina Lag. = Junellia ligustrina (Lag.) Moldenke
Verbena ligustrina Lay. = Junellia ligustrina (Lag.) Moldenke
Verbena lindleyana Walp. = Buddleia lindleyana Fortune, Loganiaceae
Verbena lobelioides Grah. = Castelia cuneato-ovata Cav.
Verbena lobelioides Hort. = Castelia cuneato-ovata Cav.
Verbena lorentzii Niederlein = Junellia ligustrina (Lag.) Moldenke
Verbena lorentzii Niederlein & Hieron. = Junellia ligustrina (Lag.) Moldenke

Verbena luppulacea L. = Priva lappulacea (L.) Pers.
Verbena lupulina Cham. = Lippia lupulina Cham.
Verbena lychnitis Mart. = Stachytarpheta lychnitis Mart.
Verbena maximiliani Mart. = Stachytarpheta lactea Schau.
Verbena maysorensis Wight = Svensonia hyderobadensis (Walp.) Moldenke
Verbena mexica Sessé & Moc. = Priva mexicana (L.) Pers.
Verbena mexicana L. = Priva mexicana (L.) Pers.
Verbena mexicana trachelii folio fructu aparines Dill. = Priva mexicana (L.) Pers.
Verbena micrantha R. A. Phil. = Junellia micrantha (R. A. Phil.) Moldenke
Verbena microphylla R. A. Phil. = Junellia minutifolia (R. A. Phil.) Moldenke
Verbena minima Meyen = Junellia minima (Meyen) Moldenke
Verbena minutifolia Lag. = Junellia minutifolia (R. A. Phil.) Moldenke
Verbena minutifolia R. A. Phil. = Junellia minutifolia (R. A. Phil.) Moldenke
Verbena morenonis Kuntze = Junellia patagonica (Speg.) Moldenke
Verbena mulinoides Speg. = Junellia mulinoides (Speg.) Moldenke
Verbena muscoides Phil. = Junellia minutifolia (R. A. Phil.) Moldenke
Verbena mutabilis Jacq. = Stachytarpheta mutabilis (Jacq.) Vahl
Verbena mutabilis Willd. = Stachytarpheta mutabilis (Jacq.) Vahl
Verbena mysorensis Wight = Svensonia hyderobadensis (Walp.) Moldenke
Verbena myssorensis Wight = Svensonia hyderobadensis (Walp.) Moldenke
Verbena negundo Royle = Vitex negundo L.
Verbena nervosa Scheele = Buchnera elongata Sw., Scrophulariaceae
Verbena nigrescens Mart. = Stachytarpheta glauca Cham.
Verbena nispida Sessé & Moc. = Priva lappulacea (L.) Pers.
Verbena nodiflora C. Bauh. = Phyla nodiflora (L.) Greene
Verbena nodiflora L. = Phyla nodiflora (L.) Greene
Verbena nodiflora Petagn. = Phyla nodiflora (L.) Greene
Verbena nodiflora arborescens Mart. = Lippia javanica (Burm. f.) Spreng.
Verbena nodiflora var. sublanceolata Née = Phyla nodiflora var. rosea (D. Don) Moldenke
Verbena nodosa Rich. = Phyla nodiflora (L.) Greene
Verbena nubigena Poepp. = Junellia caespitosa (Gill. & Hook.) Moldenke ?
Verbena nubigena Speg. = Junellia spegazzinii Moldenke
Verbena nudiflora L. = Phyla nodiflora (L.) Greene
Verbena ochreata Briq. = Junellia spathulata (Gill. & Hook.) Moldenke

Verbena odorata Desf. = Lippia javanica (Burm. f.) Spreng.
Verbena odorata L'Hér. = Lippia alba (Mill.) N. E. Br.
Verbena officinalis Cuevas = Stachytarpheta jamaicensis (L.) Vahl
Verbena officinalis L. x Veronica maritima L. = xVeronicena haartmani Moldenke
Verbena orchioides Hort. = Castelia cuneato-ovata Cav.
Verbena orchioides Walp. = Castelia cuneato-ovata Cav.
Verbena orubica L. = Stachytarpheta orubica (L.) Vahl
Verbena orubica, teucriifolio, primulae veris flore Herm. = Stachytarpheta mutabilis (Jacq.) Vahl
Verbena ourostachya Briq. = Junellia echegarayi (Hieron.) Moldenke
Verbena oxytetragona Mart. = Stachytarpheta gesnerioides var. cuneata Schau.
Verbena patagonica Moldenke = Junellia patagonica (Speg.) Moldenke
Verbena patagonica Speg. = Junellia patagonica (Speg.) Moldenke
Verbena philippiana Kuntze = Junellia minutifolia (R. A. Phil.) Moldenke
Verbena polycephala Turcz. = Junellia selaginoides (Kunth) Moldenke
Verbena polycnemoides Lag. = Junellia minima (Meyen) Moldenke ?
Verbena prichardi Rendle = Junellia patagonica (Speg.) Moldenke
Verbena prismatica Jacq. = Bouchea prismatica (L.) Kuntze
Verbena prismatica L. = Bouchea prismatica (L.) Kuntze
Verbena prismatica Willd. = Bouchea prismatica (L.) Kuntze
Verbena prismatifolia Pers. = Bouchea prismatica (L.) Kuntze
Verbena pritchardi Rendle = Junellia patagonica (Speg.) Moldenke
Verbena psamophila Mart. = Stachytarpheta canescens H.B.K.
Verbena pseudogervao A. St. Hil. = Bouchea fluminensis (Vell.) Moldenke
Verbena pseudogervaõ St.-Hil. = Bouchea fluminensis (Vell.) Moldenke
Verbena pseudo-gervao A. St.-Hil. = Bouchea fluminensis (Vell.) Moldenke
Verbena pseudo-gervão St. Hil. = Bouchea fluminensis (Vell.) Moldenke
Verbena pseudojuncea Clos = Junellia pseudo-juncea (C. Gay) Moldenke
Verbena pseudo-juncea C. Gay = Junellia pseudo-juncea (C. Gay) Moldenke
Verbena punctulata Hieron. = Junellia punctulata Hieron. & Moldenke
Verbena pygmaea R. Fries = Junellia pygmaea (R. Fries) Moldenke
Verbena repens Bertol. = Phyla nodiflora (L.) Greene
Verbena repens Larrañ. = Phyla nodiflora (L.) Greene

Verbena repens Savi = Phyla nodiflora (L.) Greene
Verbena repens Ten. = Phyla nodiflora var. rosea (D. Don) Moldenke
Verbena reptans Loisel. = Phyla nodiflora var. reptans (H.B.K.) Moldenke
Verbena rhinanthifolia Mart. & Gal. = Priva grandiflora (Ort.) Moldenke
Verbena rubiginosa Gill. = Acantholippia seriphioides (A. Gray) Moldenke
Verbena rubiginosa Hook. = Acantholippia seriphioides (A. Gray) Moldenke
Verbena salviaefolia Hook. & Arn. = Aloysia salviaefolia (Hook. & Arn.) Moldenke
Verbena sanguinea Mart. = Stachytarpheta sanguinea Mart.
Verbena sarmentosa Willd. = Phyla nodiflora (L.) Greene
Verbena scabra Muhl. = Phyla lanceolata (Michx.) Greene
Verbena scirpea R. A. Phil. = Diostea juncea (Gill. & Hook.) Miers
Verbena scoparia Gill. & Hook. = Diostea scoparia (Gill. & Hook.) Miers
Verbena scoparia Hook. = Diostea scoparia (Gill. & Hook.) Miers
Verbena scoparia Hook. & Gill. = Diostea scoparia (Gill. & Hook.) Miers
Verbena scoparium Gill. & Hook. = Diostea scoparia (Gill. & Hook.) Miers
Verbena selaginoides Kunth = Junellia selaginoides (Kunth) Moldenke
Verbena selaginoides var. illapelina Phil. = Junellia illapelina (R. A. Phil.) Moldenke
Verbena selaginoides var. illapelina Reiche = Junellia illapelina (R. A. Phil.) Moldenke
Verbena seriphioides Gill. & Hook. = Junellia seriphioides (Gill. & Hook.) Moldenke
Verbena seriphiodes Gill. & Hook. = Junellia seriphioides Gill. & Hook.) Moldenke
Verbena serpillifolia (Speg.) Speg. = Junellia serpyllifolia (Speg.) Moldenke
Verbena serpyllifolia Speg. = Junellia serpyllifolia (Speg.) Moldenke
Verbena serpyllifolia (Speg.) Speg. = Junellia serpyllifolia (Speg.) Moldenke
Verbena silvestrii Speg. = Junellia silvestrii (Speg.) Moldenke
Verbena spartioides Turcz. = Diostea cinerascens (Schau.) Moldenke
Verbena spartoides Turcz. = Diostea cinerascens (Schau.) Moldenke
Verbena spathulata Gill. = Junellia spathulata (Gill. & Hook.) Moldenke
Verbena spathulata Gill. & Hook. = Junellia spathulata (Gill. & Hook.) Moldenke
Verbena spathulata Hook. = Junellia spathulata (Gill. & Hook.) Mol-

denke

Verbena spathulata var. grandiflora Schau. = Junellia spathulata (Gill. & Hook.) Moldenke

Verbena spathulata var. pseudojuncea Reiche = Junellia pseudojuncea (C. Gay) Moldenke

Verbena spathulata α grandiflora Schau. = Junellia spathulata (Gill. & Hook.) Moldenke

Verbena spathulata β parviflora Schau. = Junellia spathulata (Gill. & Hook.) Moldenke

Verbena spicata jamaicana Pluk. = Bouchea prismatica (L.) Kuntze

Verbena spissa Sandw. = Junellia spissa (Sandw.) Moldenke

Verbena squamosa Jacq. = Elytraria squamosa (Jacq.) Lindau, Acanthaceae

Verbena stenophylla Scheele = Buchnera lavandulacea Cham. & Schlecht., Scrophulariaceae

Verbena stoechadifolia Br. = Phyla stoechadifolia (L.) Small

Verbena stoechadifolia L. = Phyla stoechadifolia (L.) Small

Verbena struthionum Speg. = Junellia struthionum (Speg.) Moldenke

Verbena subfruticosa Aubl. = Phyla stoechadifolia (L.) Small

Verbena succulentifolia Kuntze = Junellia succulentifolia (Kuntze) Moldenke

Verbena suffruticosa Aubl. = Phyla stoechadifolia (L.) Small

Verbena suffruticosa Steud. = Phyla stoechadifolia (L.) Small

Verbena supina Trag. = Bidens tripartita L., Carduaceae

Verbena tetragonocalyx Troncoso = Junellia tetragonocalyx (Troncoso) Moldenke

Verbena thymifolia Lag. = Junellia thymifolia (Lag.) Moldenke

Verbena thymifolia var. minutifolia (Phil.) Speg. = Junellia minutifolia (R. A. Phil.) Moldenke

Verbena thymoides Phil. = Junellia minutifolia (R. A. Phil.) Moldenke

Verbena tiliaefolia Cham. = Lantana tiliaefolia Cham.

Verbena tiliifolia Cham. = Lantana tiliaefolia Cham.

Verbena toninii Kuntze = Junellia ameghinoi (Speg.) Moldenke

Verbena tridactyla Phil. = Junellia tridactyla (R. A. Phil.) Moldenke

Verbena tridactylides Lag. = Junellia tridactylites (Lag.) Moldenke

Verbena tridactylites Lag. = Junellia tridactylites (Lag.) Moldenke

Verbena tridactylitis Lag. = Junellia tridactylites (Lag.) Moldenke

Verbena tridens Lag. = Junellia tridens (Lag.) Moldenke

Verbena tridentata Lag. = Junellia tridens (Lag.) Moldenke

Verbena triflora Peter = Aloysia triphylla (L'Hér.) Britton

Verbena trifoliata P. Beauv. = Veronica spuria L., Scrophulari-

aceae
Verbena trifurcata R. A. Phil. = Junellia trifurcata (R. A. Phil.) Moldenke
Verbena tripartita Phil. = Junellia trifurcata (R. A. Phil.) Moldenke
Verbena triphila Willd. = Aloysia triphylla (L'Hér.) Britton
Verbena triphyla Willd. = Aloysia triphylla (L'Hér.) Britton
Verbena triphylla L'Hér. = Aloysia triphylla (L'Hér.) Britton
Verbena tuberosa R. Graham = Castelia cuneato-ovata Cav.
Verbena tuberosa Sessé & Moc. = Priva grandiflora (Ort.) Moldenke
Verbena ulicina R. A. Phil. = Junellia ulicina (R. A. Phil.) Moldenke
Verbena uncinata Waterfall = Priva mexicana (L.) Pers.
Verbena uniflora R. A. Phil. = Junellia uniflora (R. A. Phil.) Moldenke
Verbena uniflora var. glabriuscula Kuntze = Junellia uniflora var. glabriuscula (Kuntze) Moldenke
Verbena valparaisos Lejeune = Phyla nodiflora var. rosea (D. Don) Moldenke
Verbena variabilis Hort. = Stachytarpheta cayennensis (L. C. Rich.) Vahl
Verbena verbenaefolium Michx. = Stylodon carneus (Medic.) Moldenke
Verbena verticifolia L. = Stylodon carneus (Medic.) Moldenke
Verbena violacea Walker = Stachytarpheta urticaefolia (Salisb.) Sims
Verbena virgata Ruíz & Pav. = Aloysia virgata (Ruíz & Pav.) A. L. Juss.
Verbena wilczekii Briq. = Junellia wilczekii (Briq.) Moldenke
Verbena yamaicensis L. = Stachytarpheta jamaicensis (L.) Vahl

"Vervain sage" is Salvia verbenacea L. in the Lamiaceae, "vervain mallow" is Malva alcea L. in the Malvaceae, and the "vervain hummingbird" is Mellisuga minima of Jamaica. The "lavender verbena" of Andreas Feininger (photographer) in Life 28 (15): 65 & 68--69 [color illustration], April 10, 1950, from the Borrego Desert, San Diego County, California, is Abronia villosa S. Wats. in the Nyctaginaceae.

The Hicken, Sert. And. references in the bibliography of this genus are often dated "1922", but should be 1923. The A. W. Chapm., Fl. South. U. S. (1860, 1865, 1872, 1884, 1887, 1889, and 1892) references in the generic bibliography on pages 100--102 are there erroneously written "Fl. Southeast. U. S." and should be corrected.

The Sharp, Clebsch, & Clebsch 4948, distributed as "Verbena sp.", appears to be a species of composite; the Mrs. Neff Bakker s.n. [Herb. San Diego Soc. Nat. Hist. 12751], also so distributed, is Teucrium occidentale A. Gray in the Lamiaceae, while Goodspeed s.n. [Ft. Lauderdale, Mch. 1930; Herb. Iowa State Coll. 136138] is Pycnothymus rigidus (Bart.) Small in the Lamiaceae, Shreve & Tinkham 9896 is Marilaunidium hispidum (A. Gray) Kuntze in the Hydrophyllaceae, F. C. Gates 21124 is Veronica officinalis L. in the Scrophulariaceae, Hitchcock & Stanford 6952 (Po--266725, Se--58765) is Schobera angiosperma (J. Murray) Britton in the Heliotropiaceae, Rowell 2308 is Elytraria bromoides Ørst. in the Acanthaceae, and Edw. Palmer 13 is something not verbenaceous. In various herbaria sheets of Mimulus moschatus Dougl. (Scrophulariaceae), Hemizonia fasciculata T. & G. (Carduaceae), and Conoclinium coelestinum (L.) DC. (Carduaceae) have been distributed as "Verbena sp." The Rambo 3445, also so distributed, is something in the Lamiaceae.

Isern 2499, in the Madrid and Chicago Natural History Museum herbaria, from Tacora, Peru, is an as yet unidentified species of Verbena. Raimondi (1943) cites his numbers 2063 and 2064 from Cajamarca, Peru, as "Verbena sp.", but these have not as yet been seen by me for further identification. The "Verbena sp." recorded by H. S. Gentry in his "Rio Mayo Plants" (1942) is actually two species -- his no. 557 from Mesa Colorado is V. canescens H.B.K., while nos. 1522 and 1758 from Sierra Chacuro and no. 1923 from Cerro Guicorichi are V. pinetorum Moldenke.

Pulver (1937) says that wire hairpins are useful in pegging down verbena stems, but he is here referring to the prostrate-branching cultivated species such as V. hybrida, V. tenera, V. tenuisecta, etc. Cheesman says that "Verbena spp." are common in gardens on Trinidad. Hoehne (1939) reports that plants of the Verbena and Mint Families are used in Brazil to make perfumes called "cambarás" and "herva cidreira". Von Hagen (1937) affirms that a Verbena species which the Jivaro Indians [Amerinds] call "yapau", when mixed with one of the Amaranthaceae, is efficaceous against fevers in Ecuador.

Noack (1937) discusses the genetics and chromosome numbers in the genus, as do also Schnack & Covas in their various publications. Junell (1934) discusses the gynoecium morphology. Rosengurtt Gurvich (1941) calls the Uruguayan members of the genus "hemicripofitas leñosas". The physico-chemical properties of the sap of a Verbena species in relation to phytogeography are discussed by J. A. Harris in his Physico-chem. Prop. Plant Saps 178 (1934) -- his specimen voucher was taken from low ground back of small sand dunes near the point of Tybee Island, Savannah River, Georgia, no. V.19-755 (1). The genus is mentioned by L. R. Parodi (1943) as growing in the climax steppe formation in the Elionurus viridulus zone, in the department of San Martín, Corrientes, Argentina, along with Cyperus, Fimbristylis, Juncus, Nothoscordum, Spergularia grandis, Oxalis, Melochia, Eryngium, Buchnera, Wahlenbergia, Vernonia, Stevia, and Baccharis.

Although we now recognize 363 taxonomic entities in the genus, Bentham in 1876 and Pearson as late as 1901 regarded the genus as comprising only 80 species.

Westcott (1950) lists as diseases attacking the native species in the United States: Plasmopara halstedii (downy mildew, in New Mexico), Ascochyta verbenae (leaf-spot, in Wisconsin), Cercospora verbenicola (leaf-spot, in Alabama, Louisiana, and Texas) and other species of Cercospora (in Illinois, Kansas, and Mississippi), Phyllosticta texensis (leaf-spot, in Texas), Septoria verbenae (leaf-spot, from Vermont to Mississippi, Texas, and South Dakota), Erysiphe cichoracearum (powdery mildew, general distribution), Puccinia aristidae (rust, in Ohio [January] and Arizona [February & March] on grasses), and Puccinia vilfae (rust, in Ohio [January] and Indiana to Oklahoma to Kansas, Missouri and South Dakota). She states that Cuscuta arvensis Beyr. parasitizes the genus in Oklahoma, while Yuncker (1943) says that members of the genus are parasitized by C. glabrior (Engelm.) Yuncker in Texas. A spider mite, Tetranychus desertorum Bank, winters on a Verbena species in the Paraguayan Chaco. Verbena leaves are said to be eaten by the larvae of Acopa carina Harvey, Catabena lineolata Walker, and Crambodes talidiformis Guenée, according to W. J. Holland, Moth Book 163 (1904) in the United States.

Houard (1933) says that insect galls occur on the leaves of Verbena species. Seymour (1929) reports that on species of this genus may be found the fungi Rhizoctonia solani Kuhn and Sphaerotheca humuli (DC.) Burrill. Felt, in Bull. N. Y. State Mus. 200: 182 (1917), describes a gall on Verbena, reared from the rolled leaves, caused by a probably predaceous itonid gall-fly, Lestodiplosis verbenifolia Felt, originally described by him in Bull. N. Y. State Mus. 104: 408 (1908). In his same 1917 work he describes two galls on unidentified members of the Verbena genus: one is an irregular oval stem-gall 3--5 mm. long, caused by an itonid, Cecidomyia sp. (described by Felt in Journ. Econ. Ent. 4: 474. 1911), the other, reared from marginal leaf rolls, being an itonid known as "Verbena leaf midge", Itonida verbenae Beutm. (described by Beutenmueller in Canad. Ent. 39: 306. 1907).

VERBENA ABRAMSI Moldenke, Am. Midl. Nat. 24: 750--751. 1940.

Synonymy: Verbena lasiostachys var. abramsii (Moldenke) Jepson, Fl. Calif. 3 (2): 381. 1943. Verbena abramsii Moldenke ex Jepson, Fl. Calif. 3 (2): 381, in syn., sphalm. 1943.

Literature: Perry, Ann. Mo. Bot. Gard. 20: 292. 1933; Moldenke, Am. Midl. Nat. 24: 750--751. 1940; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 1], 15 & 101. 1942; Jepson, Fl. Calif. 3 (2): 381. 1943; Moldenke, Phytologia 2: 70 & 114. 1945; Moldenke, Alph. List Cit. 1: 2, 3, 56, 72, 121, & 135. 1946; Moldenke, Phytologia 2: 383. 1947; Hill & Salisb., Ind. Kew. Suppl. 10: 242. 1947; Moldenke, Alph. List Invalid Names Suppl. 1: 22 & 25. 1947; Moldenke, Castanea 13: 113. 1948; H. N. & A. L. Moldenke, Pl. Life 2: 48. 1948; Moldenke, Alph. List Cit. 2: 396, 439, 465, 467, 472, 482, 488, 495, 500, 560, 570, 576, & 587 (1948), 3: 718, 755, 786, 794, 799, 808, 832, & 841 (1949), and 4: 980, 1119, 1177, 1181, 1182, 1215, 1225—1230, & 1252. 1949; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 2], 27 & 197. 1949; Moldenke, Résumé 33, 357, 368, & 470. 1959.

Bushy perennial herb, often somewhat woody at the base, 5—7 dm. tall; stems erect or branching from the base and laxly prostrate-ascending or prostrate, slender, tetragonal, usually thick-margined on the angles, densely short-hirsute with brownish or canescent hairs issuing at right angles to the stem, less so in age; branches similar to the stems, but even more densely and persistently short-hirsute; leaves sessile, oblanceolate or obovate, 1.5--9.5 cm. long, 0.5--3.5 cm. wide, usually small, dark-green on both surfaces, often brunnescent in drying, acute at the apex, cuneate at the base, irregularly incised-dentate except at the cuneate base, sometimes the 2 lowermost divisions lobe-like, densely short-strigose with closely appressed hairs and scabrous or subscabrous above, densely strigose-pubescent or subhirsutulous beneath; inflorescence spicate, terminal; spikes elongate, to 12 or more cm. long, slender, about 5 mm. wide, dense before anthesis, loosely many-flowered after anthesis, the fruiting-calyxes not imbricate; bractlets ovate, about 2 mm. long, acute at the apex, densely hirsutulous-pubescent; flowers very small; calyx very small, 2—3 mm. long in all, densely hirsutulous, its rim very minutely toothed with very short and obscure apiculate teeth; corolla purple or lavender to blue, its tube about 4 mm. long, its limb about 2.5 mm. in diameter.

The type of this distinct species was collected by Edward Palmer (no. 309) at Hot Springs, in the southern part of San Diego County, California, in 1875, and is deposited in the Morong Herbarium of Barnard College at the New York Botanical Garden. The species has in the past been confused and united with *V. lasiostachys* Link, from which its small and minutely toothed calyxes at once distinguish it. It is named in honor of the distinguished California botanist, Dr. LeRoy Abrams, who collected it in the San Gabriel Mountains at an altitude of 3000 feet.

Collectors have found this plant on dry hillsides with grass cover and desert slopes, on gentle slopes near ponds, in damp earth, damp meadows, or damp land in general, meadows or swamps, damp streambanks, river-bottoms, and plains, sometimes in alkaline soil, at altitudes of 500 to 3000 feet, blooming an fruiting from April to October. A popular name is "common vervain". Herbarium material has been misidentified as *V. lasiostachys* Link, *V. menthaefolia* Benth., *V. officinalis* L., *V. polystachya* H.B.K., *V. prostrata* R. Br., *V. scabra* Vahl, and *V. urticifolia* L. Balls found it "spontaneous in Botanical Garden trickle", Los Angeles County. Parish says that it is "The prevalent form here [San Bernardino County], meadows, etc." Twisselmann found it "growing in mud of wet seep in open pasture, scarce in dense growth of *Mimulus* guttatus, Scirpus sp....in grassland of Upper Sonoran" zone in San Luis Obispo County. The label on Blankinship s.n. [Sept. 23, 1928] says "apparently an introduced weed".

Culbertson 4210 is a mixture with V. lasiostachys, and H.210 as well as K. Brandegee s.n. [Jolon, June 19, 1908] are mixtures with V. lasiostachys var. septentrionalis Moldenke, while Abbott s.n. [Monterey, 1889] is a mixture with V. robusta Greene. The K. Brandegee s.n. [Aug. 1905], at first determined as V. officinalis L. by L. W. Reinecke, was later re-determined by him as V. menthaefolia Benth. He says that Miss Perry cites this collection as V. menthaefolia in her monograph of the genus in Ann. Mo. Bot. Gard. 20 (1933), but she does *not*.

Miss Perry (1933) noted the differences between this species and V. lasiostachys, but did not give a name to the plant. She says that "The following specimens differ from the species in having scarcely glandular inflorescences and fruiting calyx only 2.5--3 mm. long shortly conniving beyond the fruit.." and then cites five of the collections which I enumerate herein under V. abramsi, with the following 6 additional specimens which I have not as yet seen: CALIFORNIA: San Bernardino Co.: S. B. Parish 2819 (E); Parish & Parish 969 (F, W). San Diego Co.: Edw. Palmer 309 (E, G). Tulare Co.: Culbertson 4210, in part (E). She also cites Abrams 2481 from Los Angeles County, but I regard this as V. lasiostachys var. scabrida Moldenke.

In all, 62 herbarium specimens, including the types of all the names involved, have been examined by me.

Citations: CALIFORNIA: Fresno Co.: K. Brandegee s.n. [Fresno, July 21, 1905] (Ca--185315). Inyo Co.: Horn s.n. [in Owens Valley and at Fort Tejon, 1863] (N). Lake Co.: Blankinship s.n. [Sept. 23, 1928] (Rs--2766). Los Angeles Co.: Abrams & McGregor 689 (Du--24205, N); E. B. Babcock s.n. [near Pomona, Aug. 24, 1902] (Ca--56930); E. K. Balls 19393 (Au--122335); Braunton 520 (Du--75593, Du--78780), s.n. [Nov. 1902] (Du--75595); J. B. Davy 2859 (Ca--25165); Dressler 69 (Ak--29781, Ak--29784); Illingworth 74 (Po--4009); Munz 6919 (N, Po--18355); Pruett 61 (Po--4126); R. B. Randall 282 (Sd--4255); L. C. Wheeler 13 (La). Mariposa Co.: Congdon C.95 (N). Monterey Co.: E. K. Abbott 1889 (Um--19), s.n. [Monterey, 1889] (Mn--23135, N); K. Brandegee s.n. [Jolon, June 19, 1908] (Ca--112914); H. L. Mason 8149 (Ca--912303); Simontacchi 628 [U. S. Dept. Agr. Forest Serv. 23820] (Ca--124418). Orange Co.: J. T. Howell 448 (Rs--654), 2806 (Gg--176994). Riverside Co.: M. A. King s.n. [Menifee, 1893] (Ca--75796); McClatchie s.n. [near Elsinore, 5/16/1892] (N). Sacramento Co.: Bruce 1977 (Po--71012). San Bernardino Co.: S. B. Parish 2819 (Ob--50826, Po--4002, S, Ur), 6295 (Au), 10548 (Du--91160), s.n. [July 1887] (Ca--25164), s.n. [Sept. 1887] (I), s.n. [Aug. 1889] (Dt), s.n. [July 1894] (Ca), s.n. [6 June 1898] (N), s.n. [May 29, 1901] (Du--143856); Parish & Parish 969 (Al, Br, Ca--192067, Du--91137, Io--92219); Pequegnat s.n. [Coldwater Canyon, 25,VIII.37] (La). San Diego Co.: G. W. Dunn s.n. [San Diego] (Ca--104851); Edw. Palmer 309 (Bc--type, Ca--187503--isotype, Pa--isotype). San Joaquin Co.: Suksdorf 3b (Pl--138410). San Luis Obispo Co.: Eastwood 14984 (Gg--147762); Twisselmann 1485 (Gg--391013). Trinity Co.: E. P. Johnson 1163 (Rs--1109). Tulare Co.: K. Brandegee s.n. [Aug. 1905] (Ca--185373); Culbertson 4210, in part (Po--63887), H.210, in part (Gg--31352). County undetermined: Parry & Lemmon 342 (C, Io).

xVERBENA ADULTERINA Hausskn. in Nyman, Consp. Fl. Eur. Suppl. 2 (1): 245. 1889 [not xV. adulterina Moldenke, 1955].

Synonymy: Verbena officinalis x supina Hausskn., Mittheil. Thüring. Bot. Ver., new ser., 10: 65. 1897. Vitex adulterina Hausskn. ex A. W. Hill, Ind. Kew. Suppl. 6: 210, sphalm. 1926.

Literature: Nyman, Consp. Fl. Eur. Suppl. 2 (1): 245. 1889; Hausskn., Mittheil. Thüring. Bot. Ver., new ser., 10: 65--66. 1897; Durand & Jacks., Ind. Kew. Suppl. 1: 451. 1906; A. W. Hill, Ind. Kew. Suppl. 6: 210. 1926; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 1], 44 & 102 (1942) and [ed. 2], 108 & 200. 1949; Moldenke, Phytologia 5: 132. 1955; Moldenke, Biol. Abstr. 30: 1093. 1956; Moldenke, Am. Midl. Nat. 59: 341--342, 344, & 365. 1958; Moldenke, Résumé 357. 1959; Moldenke, Résumé Suppl. 2: 6, 10, 12, 13, & 15. 1960.

This name was first proposed by Haussknecht in Nyman's 1889 work, cited above, for the natural hybrid between V. officinalis L. and V. supina L. which he found growing wild among the two parents in Greece. It is again discussed by him in the 1897 reference listed above and is correctly listed by Durand in 1906. Curiously, Hill, in 1926, apparently through some clerical error in filing and alphabetizing the card references at Kew, published it as "Vitex adulterina" and it was thus recorded by me in my Known Geogr. Distrib. Verbenac., [ed. 1], 44 & 102 (1942) and [ed. 2], 108 & 200 (1949). Hill credits the name to the 1897 Haussknecht reference, but in this reference Haussknecht is plainly proposing a Verbena hybrid. There is no such thing as a "Vitex adulterina". Not knowing of Haussknecht's Verbena adulterina at the time, in 1955 I proposed another "xVerbena adulterina" for the hybrid between V. officinalis L. and V. halei Small. The latter is now known as xV. conata Moldenke

Recently I have examined material purporting to be the type collection of Haussknecht's plant and am unable to see any differences between it and typical V. officinalis. This specimen will be discussed by me in my treatment of the latter species. Because of this fact. I reduced Haussknecht's name to synonymy under V. officinalis in my Résumé in 1959. Nevertheless, V. officinalis and V. supina grow together in many parts of Europe and the Orient, where they are in most places the only representatives of the genus. A hybrid between them is certainly to be expected. It may well be that future study will reveal that some of the named "varieties" and "forms" of these two species may in actuality represent the hybrid instead. Experience with natural hybrids between other members of this genus (e.g., xV. engelmannii, xV. moechina, xV. rydbergii, etc.) has shown that the hybrid population, when extensive, usually shows every intergradation between the two parent species. It is possible, therefore, that the particular specimen of the type collection which I have seen represents a plant that was on the V. officinalis extreme in its superficial characters.

Haussknecht's original description is as follows: "inter parentes pr. Karditza Th[essalonica]. — Im Allgemeinen besitzen diese hybriden Formen mehr das Aussehen der V. officinalis, unterscheiden sich aber durch kürzere, gedrungenere Stengel, durch kleinere, feiner zertheilte Blätter, durch auffallend kürzer gestielte, später sich jedoch sehr verlängernde Ähren mit dicht gestellten Blüthen, die nur in der unteren Hälfte lockerer sind als bei V. supina; ferner durch breitere, etwas tiefer gespaltene Kelchzipfel und vor allem durch das die ganze Pflanze überziehende graue hispide Indument, welches jedoch schwächer ist als bei V. supina. Die zu Th. anscheinend entwickelten Samen sind im Inneren hohl."

VERBENA ALATA Sweet, Brit. Flow. Gard. 4 [ser. 2, 1]: pl. 41. 1830.

Synonymy: Verbena alata Otto ex Sweet, Hort. Brit., ed. 2, 418. 1830. Verbena alata Cham., Linnaea 7: 258--259. 1832. Verbena alata Link & Otto ex G. Don in Loud., Hort. Brit. Suppl. 1: 602. 1832. Verbena alata Hook. ex Moldenke, Alph. List Invalid Names Suppl. 1: 22, in syn. 1947. Verbena alata Cham. & Schlecht. ex Moldenke, Résumé 357, in syn. 1959.

Literature: Sweet, Brit. Flow. Gard. 4 [ser. 2, 1]: pl. 41. 1830; Sweet, Hort. Brit., ed. 2, 418. 1830; G. Don in Loud., Hort. Brit. Suppl. 1: 602. 1832; Cham., Linnaea 7: 258--259. 1832; Maund, Bot. Gard. 5: pl. 98. 1834—1835; Walp., Repert. 4: 17--18. 1845; Schau. in A. DC., Prodr. 11: 543. 1847; Schau. in Mart., Fl. Bras. 9: 190. 1851; Briq. in Engl. & Prantl, Nat. Pflanzenfam. 4 (3a): 146. 1894; Jacks., Ind. Kew. 2: 1178. 1895; Stapf, Ind. Lond. 6: 428. 1931; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 1], 38 & 101. 1942; Augusto, Fl. Rio Grande do Sul 211, 215, & 233, fig. 100. 1946; Moldenke, Alph. List Invalid Names Suppl. 1: 22. 1947; Moldenke, Phytologia 2: 336. 1947; Moldenke, Castanea 13: 117. 1948; Moldenke, Alph. List Cit. 2: 357 (1948), 3: 687, 751, 845, 922, & 923 (1949), and 4: 1124, 1180, 1233, & 1248—1251. 1949; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 2], 93, 163, & 197. 1949; Moldenke, Phytologia 3: 134 (1949) and 3: 466. 1951; Stellfeld, Trib. Farm. 19 (10): 166. 1951; Moldenke in Chittenden, Roy. Hort. Soc. Dict. Gard. 2208—2210. 1951; Rambo, Sellowia 6:

153 & 165 (1954) and 7: 288. 1956; Moldenke, Résumé 109, 222, 357, & 470. 1959; Moldenke, Résumé Suppl. 2: 5, 8, 10, & 15. 1960; Angely, Fl. Paran. 16: 78 (1960) and 17: 46. 1961.

Illustrations: Sweet, Brit. Flow. Gard. 4 [ser. 2, 1]: pl. 41 (in color). 1830; Maund, Bot. Gard. 5: pl. 98 (in color). 1834--1835; Augusto, Fl. Rio Grande do Sul 215, fig. 100 [as "V. Lindmanii"]. 1946.

Erect, suffrutescent, rather robust perennial bush or subshrub, to 2 m. tall, or suffrutescent only at the base, with a peculiar broom-like appearance; stems subfastigiate, very sharply tetragonal and broadly winged, brachiate; branches sharply tetragonal or the larger ones subalate, appearing as though leafless, the flat sides smooth and canaliculate, slightly striate, the angles sometimes scabrous; nodes contracted; principal internodes 7.5—10 cm. long; leaves very small, sessile, mostly ovate or triangular-oblong, 0.5—2.5 (rarely to 6) cm. long, 2—5 (rarely to 11) mm. wide, acute at the apex, mostly truncate (rarely attenuate) at the base, entire or sharply serrate, 3-nerved, somewhat rugose above, strigillose-scabrous or subglabrescent on both surfaces, the upper ones often much reduced and bract-like or scale-like; inflorescence a terminal cymose panicle, subfastigiate, the spikes short and dense, at first ovoid and about 6 mm. long, later subcylindric and elongating to 2.5 cm.; peduncles slender, sharply 4-angled and canaliculate, strigose-scabrous; bractlets lanceolate, shorter than the calyx, usually about 2 mm. long, acuminate at the apex, strigillose; calyx green with carmine-lilac markings or else entirely carmine-lilac, about 3 mm. long, conspicuously and densely white-strigose with appressed antrorse hairs, its teeth subulate; corolla varying from blue or lilac to violet-blue, violet, or red, its tube usually about 5 mm. long, puberulent on the outside toward the throat, the limb 4--7 mm. wide; style equaling the calyx, its apex drooping; stigma declined; cocci about 2 mm. long, dark on the back, striate, the commissure angulate, white-leathery.

The type of this endemic Brazilian species was collected from cultivated material in England in 1830. Sweet says of it: "this fine specimen was sent to me by the kindness of Robert Barclay Esq. from his superb collection at Bury-hill, the plant had been procured for Mr. Barclay by Mr. Hunnemann, who received it from the Royal Botanical Garden at Berlin in 1828". He adds that "it is a native of Monte Video". Actually, I have seen no material of the species from Uruguay as yet, and the statement may well be an error. The original material without doubt came from seed sent by Friedrich Sellow, who collected it in "Brasilia meridionalis". Chamisso, who proposed the same binomial for the species, apparently independently, in 1832, says that his type material was growing in the Botanical Garden at Berlin, originally collected by Sellow in Brazil. The binomial was apparently used in the Botanical Garden and is sometimes credited to Otto or to Link & Otto. Sweet, however, appears to have been the first to publish it validly. The species has been widely cultivated, being known from gardens in England and Germany as early as 1828, in

Italy in 1849, and also in New Jersey. In its native haunts it is said to inhabit marshes, swamps, and pine woods, the edges of swamps, rather marshy places, woods on varzea land, wet grassy and rather open wet places in general, as well as along small streams and along streams in small woods, at altitudes of 840 to 1600 meters. It has been collected in anthesis from September to January, as well as in March and May, and in fruit in January. The only recorded common names are "winged-stalked vervain" and "winged-stem vervain" in England. According to Maund the plant will grow best in a rich light soil, attaining a height of 6 feet, becoming bold and handsome, although its flowers are not very conspicuous. It is not bushy and needs to be staked up if grown in the open. It may be raised from seeds or occasionally increased by division of the roots. It needs a little protection in winter if grown in areas where there are severe frosts.

The species is mentioned by Irmão Augusto in his "Flora do Rio Grande do Sul", pages 211 and 233 (1946), but his illustration is mis-labelled "Verbena Lindmanii". He says that Emrich collected the species at Arroyo Tiririca, Caracol, Rio Grande do Sul, but this specimen has not as yet been seen by me. Material of this species has been misidentified in herbaria as V. ephedroides Cham., V. litoralis L., V. litoralis Kunth, V. brasiliensis Vell., and even (by Dusén) as Neosparton ephedroides Griseb.

In all, 45 herbarium specimens, including type material of all the names involved, and 3 mounted photographs or illustrations have been examined.

Citations: BRAZIL: Minas Gerais: F. C. Hoehne s.n. [Pouso Alegre, May 2, 1927] (La, N, Sp—19358); Mosén 968 (N, S); Netto 334 (Ja—46550, N); Regnell I.326 [8/2/1865] (S), I.326b (S); Widgren s.n. [1845] (Lu, Ut—11584), s.n. [Brasilia] (N, S). Paraná: Dusén 26 (S), 2788 (S), 3061 (S), 5061 [Herb. Mus. Nac. Rio Jan. 46570] (N), 7541 (S), 10753 (S), 18047 (S); Hatschbach 3366 (Z), 35956 (Rb); Tessmann 3399 [Herb. Mus. Paran. 3399] (N), 3400 [Herb. Mus. Paran. 3400] (N). Rio Grande do Sul: Costa Sacco 411 [Herb. Hort. Bot. 1315] (N); Kleericoper 12 [Herb. Mus. Nac. Rio Jan. 48452] (N); Rambo 436, in part (N), 44083 (N), 49719 (N), 54735 (B). Santa Catarina: F. Müller s.n. [Herb. Mus. Nac. Rio Jan. 31564] (N); Reitz 1965 (N), 6831 (N); Reitz & Klein 5484 (N, Ok); Smith & Klein 8065 (Ok), 9059 (Ok); Ule 1068 (W—1323144). São Paulo: Brade 5737 (S); Leite 3744 (El, N). State undetermined: Sellow s.n. [Brasilia; Macbride photos 17399] (Kr—photo, N—photo, N, Vt). CULTIVATED: France: Herb. Martens s.n. [h. b. Par. 1835] (Br). Italy: Herb. Harvey s.n. [h. P. Septb. 1849] (Du—166469, in part). New Jersey: Guyot s.n. (Pr). MOUNTED ILLUSTRATIONS: Maund, Bot. Gard. 5: pl. 98. 1834--1835 (N).

VERBENA ALATA f. ALBA Moldenke, Phytologia 3: 426. 1951.
Literature: Moldenke, Phytologia 3: 426 & 453. 1951; Moldenke,

Biol. Abstr. 25: 3051. 1951; Moldenke, Résumé 109 & 470. 1959.

This form differs from the typical form of the species in having white or whitish corollas.

The type of the form was collected by Anders Frederik Regnell (no. I.326, in part) at Serra do Caldas, Minas Gerais, Brazil, on October 16, 1861, and is deposited in the Britton Herbarium at the New York Botanical Garden. The same number, collected on February 8, 1865, appears to be typical V. alata Sweet. The white-flowered form is known thus far only from Minas Gerais. In all, 4 herbarium specimens, including the type, have been examined.

Citations: BRAZIL: Minas Gerais: Regnell I.326 [16/10/1861] (N--type, S--isotype, S--isotype), I.326 [20/11/1867] (S).

VERBENA AMBROSIFOLIA Rydb. in Small, Fl. Southeast. U. S., ed. 1, 1011 & 1337. 1903.

Synonymy: Verbena ambrosiaefolia Rydb. apud Wooton & Standl., Contrib. U. S. Nat. Herb. 19: 549. 1915. Verbena ambrosiafolia Rydb. ex Moldenke, Suppl. List Invalid Names 7, in syn. 1941. Verbena ambrosiifolia Rydb. ex Moldenke, Suppl. List Invalid Names 7, in syn. 1941; Rzedowski, Ciencia 15: 147. 1955. Verbena androsaemifolia Ricker, Kodachrome Slides of Wild Fls. [4], hyponym. 1953. Verbena ambrosioides Rydb. ex Moldenke, Résumé 357, in syn. 1959. Verbena ambrosifolia Perry ex Moldenke, Résumé 357, in syn. 1959. Verbena bipinnatifida x wrightii Wooton ex Moldenke, Résumé 358, in syn. 1959. Verbena bipinnatifolia var. latifolia Scholl ex Moldenke, Résumé 358, in syn. 1959. Verbena ambrosaefolia Rydb. ex Moldenke, Résumé Suppl. 2: 10, in syn. 1960. Verbena bipinnatifida var. latifolia Scholl ex Moldenke, Résumé Suppl. 2: 10, in syn. 1960.

Literature: Small, Fl. Southeast. U. S., ed. 1, 1011 & 1337. 1903; Prain, Ind. Kew. Suppl. 3: 187. 1908; Small, Fl. Southeast. U. S., ed. 2, 1011. 1913; Wooton & Standl., Contrib. U. S. Nat. Herb. 19: 549. 1915; Rydb., Fl. Prairies & Plains 678. 1932; Perry, Ann. Mo. Bot. Gard. 20: 248, 312, 325--328, 331, & 354. 1933; Dermen, Cytologia 7: 160--175. 1936; Cory, Texas Agr. Exp. Sta. Bull. 550: 88. 1937; Wyman & Harris, Navajo Ind. Med. Ethnobot. 18, 23, & 44. 1941; Moldenke in Lundell, Fl. Texas 3 (1): 18 & 41--42. 1942; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 1], 8--12, 14, 18, & 101. 1942; Schnack & Covas, Darwiniana 6: 471. 1944; Moldenke, Phytologia 2: 126. 1944; Moldenke, Castanea 10: 39. 1945; Darlington & Janaki Ammal, Chromosome Atlas 270. 1945; Schnack & Covas, Darwiniana 7: 71. 1945; Moldenke, Am. Journ. Bot. 32: 610. 1945; G. L. Fisher, Am. Bot. Exchange List. 1946; Moldenke, Alph. List Cit. 1: 4, 14, 23, 34, 99, 126--129, 144, 154, 158, 175, 182, 242, & 256. 1946; Moldenke, Phytologia 2: 159 (1946) and 2: 327 & 328. 1947; Curtin, Healing Herbs Upper Rio Grande 131 & 272. 1947; Moldenke, Castanea 13: 112. 1948; Moldenke, Wrightia 1: 233. 1948; Moldenke, Alph. List Cit. 2: 370, 392, 393, 396, 398--400, 438, 439, 450, 453--456, 467, 468, 472--477, 482, 491, 493--495, 498, 5003--5006, 511, 517, 523, 525, 527, 539, 549, 572, 594, 618, & 640 (1948), 3: 656, 677, 679, 708, 713, 720, 723, 737, 748, 754, 768, 782—784, 787, 789, 790, 801, 805, 827, 829, 831, 839, 842, 843, 858, 870, 873, 904, 905, 917, 931, 933, 939, 950, 954, 965, 970, & 976 (1949), and 4: 989, 991, 1068, 1072, 1086, 1093, 1094, 1107, 1108, 1110, 1112, 1121, 1122, 1129, 1138, 1141, 1142, 1148, 1150—1152, 1154, 1166, 1167, 1170, 1173, 1174, 1181, 1183, 1203, 1205, 1207, 1212, 1213, 1216, 1220, 1223—1225, 1227, 1229—1231, 1237, 1240, 1243, 1246, 1247, 1252, 1253, 1255, 1289—1291, & 1294. 1949; Moldenke, Am. Wild Fls. 292 & 450. 1949; Moldenke, Phytologia 3: 132. 1949; Moldenke, Known Geogr. Distrib. Verbenac., [ed. 2], 16, 18, 20, 21, 23, 25, 26, 32, & 197. 1949; H. N. & A. L. Moldenke, Anal. Inst. Biol. Mex. 20: 12. 1949; Ricker, Kodacrome Slides of Wild Fls. [4]. 1953; C. M. Rogers, Rhodora 56: 207. 1954; Rzedowski, Ciencia 15: 147. 1955; Moldenke, Résumé 20, 22, 24, 25, 28, 30, 31, 38, 357, 358, & 470. 1959; Moldenke, Résumé Suppl. 2: 3 & 10. 1960.

Annual with short taproot or perennial bushy herb, usually low-growing and spreading in dense circles to 2 m. in diameter; stems more or less diffusely branched from the base, mostly spreading to about 25 cm., occasionally erect and 30 cm. tall or loosely decumbent-ascending, somewhat hirsute; leaves decussate-opposite, short-petiolate, the blades 2—6 cm. long, bipinnatifid with the ultimate segments lanceolate, appressed-hirsute on both surfaces, slightly revolute along the margins; spikes pedunculate or subsessile, fascicle-like during anthesis, somewhat elongate in fruit; bractlets a little shorter than the calyx, lanceolate-subulate, hirsute, ciliate; flowers odorless; corolla varying from purple, reddish-purple, bright reddish-purple, or blue-purple to lavender, magenta, rose, violet, or deep-pink, its tube 1 1/3 to 1 1/2 times as long as the calyx, pubescent outside, its limb 6—8 [—10] mm. wide; fruiting-calyx 8—9 mm. long, glandular-pubescent, hirsute particularly along the nerves, its teeth long-subulate and often coarctate; cocci subcylindric, often with a slightly broadened base, 2.5—3 mm. long, reticulate-scrobiculate above, striate below, the commissural faces muricately scabrous; chromosome number: 2n = 30.

The type of this species was collected by George Everett Osterhout at Rocky Ford, Otery County, Colorado, on June 8, 1900, and is deposited in the Britton Herbarium at the New York Botanical Garden. The type of V. bipinnatifida var. latifolia is Scholl 8 from Culberson County, Texas, deposited in the herbarium of the University of Texas at Austin, while that of V. bipinnatifida x wrightii is Wooton 642 from Dona Ana County, New Mexico, in the Britton Herbarium at the New York Botanical Garden. The homonymous designation, V. ambrosifolia Perry, was used by Demaree on his no. 13335 from Cimarron County, Oklahoma.

Miss Perry says "An examination of the type specimens of V. ambrosifolia and V. wrightii reveals differences probably sufficient to suggest distinct but closely related species. Typically the former is characterized by long calyx-teeth and coarser pubescence; whereas the latter has short calyx-teeth, finer and somewhat viscid pubescence. On the other hand, a study of the aggregate specimens of the two shows a high variability in the combination of these characters; moreover, their geographic ranges practically coincide. For these reasons, V. ambrosifolia is maintained as a species with very doubtful status."

V. ambrosifolia is a fairly widespread species, resembling V. canadensis (L.) Britton in its calyx-lobes and V. wrightii A. Gray in its leaves and glandular pubescence. It is sometimes difficult to distinguish from the latter species, as indicated by the quotation from Miss Perry. Typical specimens of the two species are, however, very distinct. Intermediate material may well be the result of natural hybridization, since hybridization seems to be an established characteristic of the genus and since the ranges of the two species seem to be practically identical.

V. ambrosifolia has been found by collectors on humus soil and gravel, in fields and valleys, deserts and dry grasslands, dry ground or moist loam, gulches and rocky hillside pastures, in sandy or gravelly calcareous soil, washes at the base of buttes, open places and bottom fields, pastures and open fields or mesas, wayside meadows and grassy flats in the foothills, rocky slopes, field margins and deep narrow canyons, pine-oak forests on igneous canyon slopes and dry level land, along sandy roadsides and moist streamsides, on prairies and high or open sandy plains, banks, limestone hillsides, alluvial flats near arroyos, red and blue shale banks, grassy or alkali flats, bluffs and rocky canyon walls, dry ridges and mesas, dry hillsides and foothills, railroad embankments and shady slopes, canyon pine slopes, limestone breaks and plains, in arroyos, on steep shale hillsides, along roadside ditches and dry creek beds, and at the edge of pinyon-cedar forests and wet-weather valley ponds. Ewan describes it as "handsome low-growing plants very abundant on mesas", "occasional along seeps in moist sandstone soils", "scattered over recently flooded floor of alfalfa fields", and "rather common in large clumps on dry hills". Earle says that it is "very common in juniper belt, blooming all summer", while Clute reports that it is "abundant in open places, spreading out in circles flat on the ground." Palmer affirms that it is "common on plains and low dry hills", while Nelson found it in "sandy draws in the hills." Cory says it is "frequent on roadsides and shoulders of highways", Goodman found it in "loose soil near highways", Warnock says it is "scattered along roadsides, infrequent", and Porter reports it "common along roadsides on the plains." Waterfall found it growing with grass and Flourensia on the Verhalen clay, on calcareous soil along ditches, on gravelly calcareous soil along creek beds, at the base of cliffs in yellow pine forests, in gypseous soil on level plains in Prosopis-Gutierrezia association, and on low ridges in fine possibly gypsiferous soil. Hopkins and Van Valkenburgh describe it from black volcanic rock and soil derived from it on dry xeric plateaus, while the Moores say it is "very common in limestone gravel soil on highway embankments", Muller found it "sparse on limestone", while Parks & Turner de-