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MORPHO-GEOGRAPHICAL ANALYSIS OF VERONICA SECTION BECCABUNGA

The University of Oklahoma PH.D. 1983

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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

MORPHO-GEOGRAPHICAL ANALYSIS OF *VERONICA* SECTION *BECCABUNGA*

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

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by

ROGER FRANKLIN SELLERS

Norman, Oklahoma

1983

MORPHO-GEOGRAPHICAL ANALYSIS OF

VERONICA SECTION *BECCABUNGA*

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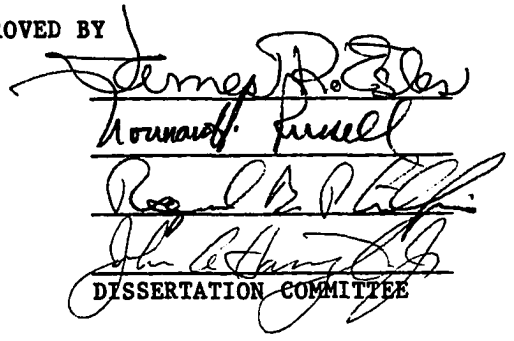

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PREFACE

This dissertation is submitted in the specified form for publication in Systematic Botany. All references to Sellers (1983) refer to maps, exsicata, dendrograms, definitions of geographical areas, and OTU's listed in the appendices of this dissertation.

CONTENTS

MORPHO-GEOGRAPHICAL ANALYSIS OF

VERONICA SECTION *BECCABUNGA*

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ABSTRACT. *Veronica* section *Beccabunga* occurs primarily in the temperate regions of the land masses of the northern and southern hemispheres with the exception of Australia and New Zealand, where it is a rare introduction. Computer assisted techniques involving the General Similarity Coefficient of Gower, UPGMA cluster analysis, Minimum Spanning Tree, and

Duncan and Estabrook's information theoretic optimality criterion model were employed to analyze 760 of 12,039 herbarium specimens based on 28 morphological features. Four species were recognized as a result of these analyses, V. anagallis-aquatica, V. anagalloides, V. beccabunga, and V. scardica. V. beccabunga is composed of two subspecies, ssp. americana and ssp. beccabunga. V. beccabunga ssp. beccabunga is an Old World taxon, whereas V. beccabunga ssp. americana occurs in North America, Kamchatka, and Northern Japan. Based on results when exemplars from other sections are included with this section, Veronica section Beccabunga is a natural taxon.

INTRODUCTION

Veronica section Beccabunga Griseb. (Scrophulariaceae) is composed of semi-aquatic, herbaceous perennials which occur primarily in the temperate regions of all continents of the northern and southern hemispheres, except Antarctica. However, the greatest diversity of Veronica section Beccabunga exists in Europe, and apparently members of the section are only rare introductions in New Zealand and Australia.

Veronica was described by Bauhin (1623) who cited the earlier work of Fuchs. Linnaeus (1753) named V. beccabunga and V. anagallis-aquatica, both of which were later included in the section Beccabunga.

Bentham (1846) and Wettstein (1897) recognized ten sections of Veronica: (1) Paederota (L.) Wettst.; (2) Paederotoides Benth.; (3) Pseudolysimachia Koch; (4) Veronicastrum Benth.; (5) Omphalospora Bess.; (6) Beccabunga Griseb.; (7) Veronica (Chamaedrys sensu Grisebach) ; (8)

Labiatoides Wettst.; (9) Hebe Benth.; and (10) Pygmaea (Hook.) Benth. et Hook. Wettstein (1897) grouped these sections under two larger unnamed taxa, which Pennell (1921), in his revision of new world Veronica, recognized as subgenera: Veronica subgenus Veronicella and Veronica subgenus Veronica (as Euveronica). The subgenus Veronicella of Pennell (1921) includes sections Veronicastrum, Pseudolysimachia, and Alsinebe (Omphalospora of Wettstein 1897; Bentham 1846), whereas subgenus Veronica includes sections Veronica, Labiatoides, and Beccabunga. Pennell (1921) regarded Hebe a distinct genus. The sections Paederota, Paederotoides, and Pygmaea were not included in Pennell's revision. Rompp (1928), however, considered each of these latter three sections to be a separate genus. Section Labiatoides was submerged within the genus Parahebe (Briggs and Ehrendorfer 1968; Van Royen and Ehrendorfer 1970) and section Pseudolysimachion was removed as a genus distinct from Veronica by Hartl (1968). Thus of Wettstein's (1897) original sections only Veronicastrum, Alsinebe, Beccabunga, and Veronica remain, and only the latter two are considered well defined and natural by most authors.

Members of Veronica section Beccabunga are distinguished from other sections by their axillary racemes, semi-aquatic habit, non-incised leaf margin, smaller and round shaped capsules, and smaller seeds. In a flavonoid analysis of the various sections of Veronica, Grayer-Barkmeijer (1973) found an ester pattern unique to section Beccabunga and concluded that the section... "seems to be a natural entity." Although section Beccabunga is clearly demarcated and apparently a natural group, the inclusive taxa appear to be poorly defined.

Bentham assigned 12 species to section Beccabunga, but later monographs and floras have recognized from 10 to 20 species (Rompp 1928; Schlenker 1936; and Stroh 1942). Since 1942, no comprehensive treatment has been conducted to alleviate the confusion that exists within this group. However, several authors (Pennell 1935, 1943; Li 1952; Marchant 1967, 1968; Kulpa 1968; Ozturk and Fischer 1982) have conducted regional studies within the taxon. The limitation of investigations to restricted geographical regions, while the variational patterns are often intercontinental and typically indistinct, has been, at

least partially, responsible for the diversity of taxonomic treatments.

A clearer understanding of the morphological patterns within Veronica section Beccabunga should provide a more meaningful taxonomic system of the group. Fortunately, with the advent of modern methods of numerical analysis, it has become feasible to include a broad array of morphological characters in order to define taxonomic patterns. Phenetic analyses are used to compare Operational Taxonomic Units (OTU's) in multi-dimensional character space in order to provide information about patterns of character state distribution, leading to objective taxonomic decisions.

MATERIALS AND METHODS

Twenty-eight morphological traits have traditionally been used to discriminate among the intrasectional taxa (table 1). All 28 characters were selected for analysis with 22 additional external morphological features, which were based on a preliminary investigation (Sellers unpublished). The primary characters are, for the most part, discrete characters, with the exception of style length, pedicel length, capsule length/width ratio, and leaf length/width ratio. Of the newly added traits, nineteen are continuous characters, including six ratios.

Herbarium specimens were measured using a Wild-Heerburg stereo dissecting scope with ocular micrometer. The specimens were selected from those borrowed from the following herbaria: B, BM, BP, BR, C, DAO, F, G, GH, GOET, H, JE, JEPS, L, MICH, MO, NDG, NY, OKL, OXF, PAD, PH, S, SAM, SGO, UBC, UC, US, W, WIS, WU, and Z (Holmgren, et al. 1981).

The measurements provide the primary data base for establishing and defining the morphological circumscription of the section and delimitation of taxa within the section. All fifty characters were measured for each exemplar specimen, however of these, only 28 (table 1) were ultimately employed in constructing the similarity matrix. Characters were selected based on the following criteria:

(1) Characters which could not be compared for many of the specimens were eliminated. Most of the floral features are of this category. The corolla and epipetalous stamens fall shortly after pollination, thus few herbarium specimens bore flowers. This suite of characters was therefore excluded (character #9, 10, 35, 36 table 1).

(2) Characters which exhibited little or no variation were also not used. The characters of leaf pubescence(#2, table 1), kind of pubescence(#5), bract apex shape(#13), seed color(#14), seed shape(#16), inflorescence position(#6), upper leaf arrangement(#17), leaves incised or not(#21), plants annual/perennial(#24), and number of sepals(#27) were thus eliminated. Although, many of these characters have traditionally been used to define the limits of section

Beccabunga, these characters do not vary significantly for delineation of taxa within the section.

(3) Characters which contributed redundant information were also deleted. Fruit pubescence(#4), upper leaf attachment(#18), sepal length(#28), capsule length(#32), seed width(#38), bract length(#41), and leaf length(#44) were all eliminated. For example, fruit pubescence was perfectly correlated with sepal pubescence and therefore contributed to redundant information. Similarly, upper leaf attachment was highly correlated with lower leaf attachment. Since ratios were employed, either the length or width measure was deleted in order to eliminate weighting of these characters.

Twenty-three geographical areas were established throughout the range of the section frequently corresponding for convenience, with existing political boundaries (Sellers 1983, Appendix C). All available herbarium material from a given geographical region was first examined and then 12-48 specimens were selected for measurement and coding. The number of exemplars selected for any given region was positively correlated with (1) the amount of variation

exhibited by section Beccabunga in that region; (2) the extent of the geographic range of the various taxa within the region; and (3) the size of the geographical zone. Plants were purposely chosen so that the sample would include as much of the perceived variation as possible for the region. Approximately 760 of the 12,039 specimens on hand were measured. A four digit code was assigned to each specimen as they were sequentially selected. To reduce potential bias they were not referred to by taxon.

Both discrete and continuous data were collected. Therefore, the General Similarity Coefficient (GSC) of Gower (1971) was chosen to construct similarity matrices, because it is most appropriate for data sets of mixed character type (GOWER, locally produced). Also, GSC, which ranges the character states, along with the clustering algorithm of unweighted pair group method using arithmetic averages (UPGMA) (Sneath and Sokal 1973), yielded intuitively satisfying results. The cophenetic correlation coefficient (CCC) was employed as a measure of the distortion between the similarity matrix and representative phenogram. A minimum spanning tree (MST) network (Sneath and Sokal 1973)

was constructed for all subsets, in order to determine the nearest neighbors between OTUs for all inclusive character states. UPGMA and MST are part of the NT-SYS (Rohlf, et al. 1971) program in the IBM 3081 computer at the University of Oklahoma. Finally, the data was transformed into multistate data for use by an information theoretic approach (Duncan and Estabrook 1976) to examine character correlation (CHARANAL) in order to identify characters that are highly correlated with the classification and most useful in identification. Distance values for each character of the similarity matrix of figure 4 were calculated and reported (table 1). A low value implied a high correlation between the character and the classification.

Using the exemplar method (Sneath and Sokal 1973), a measure of the taxonomic similarity among taxa from all 23 regions was established. This was done by clustering 3 or 4 representative OTU's from each recognizeable group of a given regional phenogram with those of all other regions. Also, representatives of any taxon which had ever been considered allied to this section were included in the analysis as well as a limited number of specimens of taxa

that are clearly from other sections in order to provide sectional definitions.

Taxonomic decisions were based on information obtained through the various numerical analyses of data, which ultimately was governed by the degree of phenetic similarity among all OTU's selected for study on the basis of the designated morphological characters. Thus, taxa were delimited on the basis of overall external morphological similarity. Type specimens were examined prior to making nomenclatural decisions. The remaining specimens were then examined and compared with the derived taxonomic system and the specimens were annotated.

Although over 100 specific names are available, it soon became obvious that six major groups were most prominently employed and most likely to be ultimately recognized. Taxa will be identified in the following discussions by specific epithet, (e.g., V. americana = AMERICANA). This device is for convenience and does not imply a taxonomic decision. The taxa which will be discussed are V. beccabunga, V. americana, V. scardica, V. anagallis-aquatica, V. catenata, and V. anagalloides.

RESULTS AND DISCUSSION

Exemplars from sections other than Beccabunga cluster with a much lower similarity value (0.6544) in the phenogram derived from GSC, than exemplars within section Beccabunga (fig. 1). This is in spite of the fact that characters employed were chosen more for their discriminating value in defining intrasectional taxa than for delimiting the section itself. Therefore, in addition to being used to discriminate taxa within section Beccabunga, these characters were also useful in demarcating the section. Among the 28 measured characters, stem pubescence, sepal pubescence, and inflorescence position were the most important characters for defining section Beccabunga as determined by CHARANAL (Duncan and Estabrook 1976) with distance values ranging from 0.536 to 0.983 (cf. intrasectional values, table 1). However, there are other external morphological features that distinguish this section--axillary racemes; non-incised leaf margin;

plano-convex, red or yellow seeds; and glandular pubescence. Thus, I conclude that Veronica section Beccabunga is a discrete morphological and natural unit (sensu Sneath and Sokal 1973).

Two taxa, V. ciliata and V. himalanensis, were previously included in section Beccabunga (Bentham 1846; Rompp 1928; Stroh 1942). Exemplars of these taxa cluster at a phenon level of 0.6708 (fig. 1), and hence deviate from this sectional circumscription. Similarly, V. rockii, which is morphologically allied to V. ciliata has also been excluded (see Excluded Names). Based on Rafinesques (1832) description, I believe that V. connata is best considered a synonym of V. scutellata, which is also not of this section.

In the regional phenograms and MSTs (Sellers 1983, Appendix C) of North and South America, Africa, and East Asia, two major clusters are apparent. One group, which includes OTU's representing BECCABUNGA and AMERICANA, tends to form a tight cluster, an indication of little variation within this complex as compared to the other group. Although BECCABUNGA and AMERICANA can be phenetically defined for any given region, this discontinuity breaks down

as the phenogram is expanded to include all regions, resulting in thorough intermixing of the OTU's of both (fig. 2). Therefore, I believe that BECCABUNGA and AMERICANA are best considered conspecific.

OTU's of ANAGALLIS-AQUATICA and CATENATA tend to cluster at lower levels of similarity in most of the phenograms than clusters comprising BECCABUNGA and AMERICANA. A phenogram and MST was constructed employing exemplars of ANAGALLIS-AQUATICA and CATENATA from each regional phenogram (fig. 3). The CCC was 0.587, which is rather low, and indicates a highly distorted phenogram compared to the original similarity matrix. The MST reveals the obvious overlap among the various subclusters. An additional sample of exemplars from the same regional groupings gave similar results. CATENATA, as annotated by Pennell, occurred randomly throughout the cluster, rather than as a distinct unit. Thus, there was no consistent morphological or geographical pattern within this group that could be used to recognize taxa. Consequently, I contend that ANAGALLIS-AQUATICA and CATENATA are conspecific.

Regional phenograms and MSTs in Europe reveal the presence of two additional groups which correspond to ANAGALLOIDES and SCARDICA. Although SCARDICA appears more closely allied to BECCABUNGA in the phenograms (fig 4; Sellers 1983, Appendix C.17), the MST's (fig. 4; Sellers 1983, Appendix C.17) indicate that it is phenetically intermediate between BECCABUNGA and ANAGALLIS-AQUATICA. This intermediate position is largely the result of differences in leaf morphology; newer developing leaves resemble ANAGALLIS-AQUATICA, whereas the mature leaves are more like those of BECCABUNGA.

The MST's and phenograms of regions X and Y (Sellers 1983, Appendix C) as well as the global phenogram and MST (fig. 4) provide evidence of another well-defined group, ANAGALLOIDES, which appears closely allied to ANAGALLIS-AQUATICA. Although ANAGALLOIDES is most similar to ANAGALLIS-AQUATICA, it clusters at a phenon level of 0.7455, making it the most morphologically distinct species in the section.

Although, figure 1 provides information useful in defining sectional limits, the addition of exemplars from other

sections increases the range of the characters, which causes the data to be compressed and the phenogram to be distorted. Consequently, figure 4, without this distortion, more accurately depicts intrasectional groupings than that of figure 1. Four distinct groups can be defined at a phenon level of 0.76.

CHARANAL was used to determine important characters in defining section Beccabunga in figures 1 and 4 (table 1). Three of the most significant characters in descending importance in defining taxa within section Beccabunga, are leaf base shape, lower leaf attachment, and leaf tip shape.

TAXONOMIC TREATMENT

Based on this phenetic analysis, I have concluded that Veronica section Beccabunga is composed of four species with two subspecies. The inclusive taxa are closely allied morphologically and can be easily distinguished from other sections within Veronica. Earlier workers (Bentham 1844; Rompp 1928; Stroh 1942) included V. ciliata and V. himalanesis in section Beccabunga. However, the present analysis, in agreement with Schlenker (1936), shows that these taxa are morphologically inconsistent with section Beccabunga and, therefore, are excluded.

It appears that BECCABUNGA and AMERICANA are perhaps best considered conspecific. Pennell (1921) stated, "Veronica americana appears to be only inconstantly distinguishable from V. beccabunga by its leaf-form and more erect habit." This view is consistent with the present findings. Although the two taxa are strikingly similar, BECCABUNGA and AMERICANA are better treated as subspecies of a single

species, due, in part, to their geographical separation, slightly different leaf morphology, and chromosome number differences (Marchant 1968). AMERICANA occurs primarily in North America, throughout the Aleutian Islands, and in East Asia along the Pacific coast and neighboring islands, while BECCABUNGA ranges mainly throughout much of the Old World. However, isolated pockets of BECCABUNGA do occur in North America, but these are presumably introductions. BECCABUNGA has round or obovate shaped leaves with a round leaf tip; AMERICANA has lanceolate or oblong shaped leaves with an obtuse leaf tip. BECCABUNGA is a diploid (x=9) and AMERICANA a tetraploid (Marchant 1968).

In ANAGALLIS-AQUATICA neither distinct variational nor geographical patterns have emerged. The best summary of all characters indicates that the pattern of variation within this group is best described by treating it as a single taxon. Acknowledging that much intraspecific variation does exist, this study indicates that this taxon may best be considered a polymorphic complex with no obvious regional or morphological patterns.

ANAGALLIS-AQUATICA is by far the most widespread taxon in section Beccabunga. It is a recent introduction in Australia and New Zealand and ranges throughout much of the Old and New World, including many islands of the Mediterranean Sea and Pacific and Atlantic Oceans of the Northern Hemisphere. ANAGALLIS-AQUATICA has become a very successful weed that displays extensive morphological variability.

ANAGALLOIDES is phenetically allied more closely to ANAGALLIS-AQUATICA than to other taxa within the section. However, ANAGALLOIDES possesses a number of character states which delineate it from other intrasectional taxa and make it distinct. This taxon occurs throughout Eurasia west of the Himalayan Mountains and is particularly prevalent in the vicinity of the Mediterranean.

SCARDICA appears morphologically intermediate between ANAGALLIS-AQUATICA and BECCABUNGA. However, SCARDICA is phenetically discrete with a range resticted primarily to the Balkan region of Europe. Label information from many collections indicate that this taxon is frequently associated with both serpentine and volcanic soils.

VERONICA SECTION BECCABUNGA Grisebach. Spicil. Fl. Rumel. 2: 31. 1844.--Type: *Veronica beccabunga* L.

Semi-aquatic perennials; erect or prostrate; often rooting at the nodes. Leaves opposite; margin serrate, crenate, or rarely, appearing entire (although when closely examined minute serrations are always present). Racemes axillary and opposite, rarely alternate. Flowers zygomorphic; Corolla 4-lobed, inferior lobe smaller than the other three; blue or rarely white or pink, dark blue radiating lines; corolla tube wider than long; stamens 2, yellow, epipetalous; pistil hypogynous, style single, stigma capitate. Capsule obcordate, orbicular, or elliptic, somewhat flattened but remaining turgid; bilocular; placentation axillary; dehiscence loculicidal. Seeds many, reddish-brown (yellow), flattened, convex on one side, oval, rarely orbicular.

Keys to taxa of *Veronica*

section *Beccabunga*

Capsule elliptic, 2.5 mm wide or less, typically longer than calyx; leaves linear-lanceolate..... 2. *V. anagalloides*

Capsule orbicular, subcircular, or obcordate, wider than 2.5 mm, typically equal to or shorter than calyx; leaves lanceolate, ovate, round, or obovate.

Leaves petiolate, not clasping..... 3. *V. beccabunga*

Leaves sessile at least on upper one-third of stem, clasping.

Leaves lanceolate, sessile throughout stem; leaf base of upper and lower leaves cordate..... 1. *V. anagallis-aquatica*

Leaves ovate, sessile in upper one-half of stem but petiolate in the lower half; leaf base of upper leaves cuneate, lower leaves petiolate..... 4. *V. scardica*

1. Veronica anagallis-aquatica L. Sp. Pl. 12. 1753.--Type: LINN (photograph of holotype at LINN in Savage's Catalogue of the Linnaean Herbarium; photograph at GH!).

Veronica undulata Wallich in Roxburgh, Flora Indica, ed. 1, 1: 147. 1820.--Type: (no location; no date), N. Wallich, s.n. (holotype: possibly at K; isotype: BM!, C!, L!, PH!, and M!). A small form with highly serrate leaves.

Veronica punctata Hamilton in Don, Prod. Fl. Nep. p. 93. 1825.--Type: "Garam hetty," (Nepal), November 26, 1802, H. (?Hamilton), s.n. (holotype: BM!). A glabrous plant with small capsules and long bracts, sparsely arranged along elongate racemes.

Veronica anagallis Meyer, nomen. illeg., Verz. Pflanz. Kauk. Casp. Meer. p. 12. 1831.--Type: Based on Veronica anagallis-aquatica. A misinterpreted Linnaean name. Linnaeus used a symbol as part of the specific epithet which is transcribed as Veronica anagallis-aquatica (Stafleu, et. al., 1972).

Veronica anagallis β Bertoloni, Fl. Italica 1: 71. 1833. Type: Not seen.

Veronica capensis Fenzl, Linnaea 17: 332-334. 1843.--Type: "Drege," 1841, E. Fenzl, 548 (?holotype: W!).

Veronica oxycarpa Boissier, Diagn. Pl. Or. Nov., Ser. 1, 1(7): 43- 44. 1846.--Type: "Hab. ad fontes alpis Kuh-Daena Persiae australis Kotschy," July 13, 1842, R.F. Hohenacker, 639 (holotype: G!; isotype: C! and GOET!). The acutely tipped capsules make this a rather interesting form.

Veronica lysimachioides Boissier, Diagn. Pl. Or. Nov., Ser. 2, 3(3): 165. 1856.--Type: "Lavadicia ad aquas," (no date), P.E. Boissier, s.n. (hololectotype herein designated G!; isolectotypes G!). A V. anagallis-aquatica with flowers closely packed along the racemes.

Veronica anagallis L. var. umbrosa Koschewnikoff, Bull. Bot. Imp. Naturalistes Moscou 51: 297. 1876.--Type: not seen.

Veronica anagallis L. var. pallidiflora Celakovsky, Prodr. Fl. Bohm. 3: 828. 1881.--Type: not seen.

Veronica comosa Richter ex. Stapf, Akad. Wiss. Wien Math.-Naturwiss. Kl., Denkschr. p. 24. 1885.--Type: "Persia borealis," 1882, J.E. Polak, s.n. (holotype: K; saw photograph in Watsonia 1: 349. 1950). Obviously, a form of V. anagallis-aquatica having long bracts.

Veronica anagallis L. var. latifolia Britton, Bull. Torr. Bot. Club 12: 49. 1885.--Type: "Marble Hill above Phillipsburg, New Jersey," June 24, 1892, Thomas C. Porter, s.n. (isotype: PH!).

Veronica anagallis L. var. anagalloides (Guss.) Buchenau, Fl. Nordw. Tief. p. 445. 1894.--Type: not seen.

Veronica lepida Philippi, Anal. Univ. Chile 91: 110. 1895.--Type: "Cartajeno, Chile," February 1895, E. Albert, s.n. (holotype: SGO!; photograph at PH!). This specimen appears to be a seedling, however, it is unquestionably V. anagallis-aquatica.

Veronica anagallis L. ssp. divaricata Krosche, Allg. Bot. Z. Syst. 18: 83. 1912.--Type: not seen.

Veronica anagallis L. ssp. ambigua Krosche, Allg. Bot. Z. Syst. 18: 84. 1912. Type: not seen.

Veronica anagallis L. ssp. genuina Krosche, Allg. Bot. Z. Syst. 18: 87. 1912.--Type: not seen.

Veronica micromera Wooton and Standley, Contrib. U.S. Nat. Herb. 16: 174. 1913.--Type: "Near Shiprock, Navajo Reservation," (New Mexico), July 25, 1911, Paul C. Standley, 7283 (holotype: US!, photograph at PH! and UC!). A small form of V. anagallis-aquatica.

Veronica anagallis-aquatica L. var. glandulosa Farwell, Rep. Mich. Acad. Sci. 19: 249. 1917.--Type: "Zoo Park, near Royal Oak," July 13, 1916, Oliver Farwell, 4323 (isotype: GH!).

Veronica brittonii Porter ex. Pennell, Torreya 19: 168. 1919.--Type: "Marble Hill, Phillipsburg, New Jersey," June 24, 1892, T.C. Porter, s.n. (holotype: NY; isotype: PH!).

Veronica glandifera Pennell, Torreya 19: 170-171. 1919.--Type: "Suffolk, Nansemond County, Virginia," May 27, 1893, N.L. Britton and J.K. Small, s.n. (holotype: NY; isotype: PH!, US!, and F!). The character state of glandular pubescence as represented here occasionally occurs within each taxon of this section, and, therefore, is not unique.

Veronica catenata Pennell, Rhodora 23: 37. 1921.--Type: "Hot Springs, South Dakota," June 16, 1982, P.A. Rydberg, 926 (holotype: NY, photograph in Watsonia 1: 350. 1950). There is no question that this type is conspecific with Veronica anagallis-aquatica.

Veronica secunda Pennell, Acad. Nat. Sci. Philadelphia Monogr., No. 5, 89-90.--Type: "Hang, Bashahr," (India), July 31, 1934, Negi Parmanand, 771 (holotype: PH!). A form having acute tipped capsules and flowers densely packed along the racemes.

Veronica anagallis-aquatica L. var. terrea Farwell, Pap. Mich. Acad. Sci. 26: 19. 1941.--Type: "Northville, Wayne Co., old woods roads," June 22, 1932, Oliver Farwell, 9105 (isotype: DAO!).

Veronica aegyptiaca Ehrenb., cited in Schlenker, Repert. Spec. Nov. Regni Veg. Beih. 90: 20. 1936.--Type: (no location; no date), Ehrenb., s.n. (isotype: W!).

Succulent, semi-aquatic, perennial. Stem erect or prostrate, rooting at the lower nodes; 24-99 cm tall; internodal length 1.8-12.6 cm; usually glabrous, occasionally glandular. Leaves sessile, clasping; margin with 8-56 serrations along one side; lanceolate; base cordate, rarely round or acute; apex typically acute, rarely obtuse; 14-88 (120) mm long, 3.5-35 mm wide; glabrous. Racemes opposite, rarely alternate; lateral; 4.0-20.0 (32.5) cm long; glabrous or glandular; bracts linear or elliptic; 1.4-5.4 (8.7) mm long, 0.2-1.7 mm wide. Flowers 8-66 per inflorescence alternately arranged along the raceme; pedicels filiform, 2.6-8.8 mm long, usually equal or longer than bracts; calyx linear-elliptic; 2.4-4.8 (5.8) mm long, 0.7-2 mm wide; typically longer than capsule, occasionally shorter; glabrous or glandular; style 0.85-3 mm long. Capsule obcordate, orbicular, or subcircular, somewhat

flattened but remaining turgid; (2.2) 2.6-4 mm long, 2.4-3.9 mm wide; glabrous, although sparsely glandular when present; notch depth 0.17 mm, when present. Seeds 0.33-0.66 mm long, 0.25-0.54 wide.

ANAGALLIS-AQUATICA is the most widely distributed of the inclusive taxa, either introduced or native to every continent except Antarctica. This weedy species, although primarily a temperate plant, may be considered more or less cosmopolitan (fig. 5; Sellers 1983, Appendix D).

2. Veronica anagalloides Gussone, Pl. Rar. p. 5, pl. 3. 1826.--Type: "Sicile," (no date), Gussone, s.n. (holotype: unknown; isotype: Z!).

Veronica salina Schur, Enum. Pl. Transs. Wien 532: 227. 1866.--Type: "Auf schlammigen, etwas salzhaltigen Thonboden, auf der Salzwiese zwischen Hermannstadt, Hammersdorf und dem alten Berg," (no date), P. Schur, s.n., (holotype: unknown; isotype: W! and GH!). Form with wider leaves and a slightly larger capsule.

Veronica anagalloides Guss. β oxytheca Willkomm and Lange, Prodr. Fl. Hisp. 2: 604. 1870.--Type: not seen.

Veronica anagalloides Guss. β dasypoda Uechtritz, Jahresber. Schles. Ges. Vaterl. Cult. 52: 143-144. 1874.--Type: "Nittritz bei Grunberg" (Hellwig), (no date), R. Uechtritz, s.n. (holotype: C!).

Veronica haussknechtii Boissier, Flora Orientalis 4(2): 438. 1879.--Type: "In uliginosis Mesopotamiae ad Surug et fluvium Hassawi," March to June, 1867, C. Haussknecht, 748 (holotype: G!). Capsules noticeably smaller than typical V. anagalloides.

Veronica poljensis Murbeck, Oesterr. Bot. Z. 43: 365. 1893.--Type: "Hercegovina: Gacko polje, in alveo exsiccato rivuli Musica, circ." 950 m.s.m., August 21, 1889, S. Murbeck, s.n. (holotype: S!). The multicellular trichomes on the capsules are unusual for taxa within this section.

Veronica bianoris Sennen, Bol. Soc. Iber. Ci. Nat. 29: 85. 1930.--Type: "Baleares: Torrent et fosses, entre Palma et

Pont d'Inca," August 28, 1917, Fre. Bianor, 3126 (holotype: BM!; isotype: W!).

Veronica anagalloides Guss. var. glabricaulis Lonatschewskij ex Schlenker, Repert. Spec. Nov. Regni Veg. Beih. 90: 22. 1936.--Type: "Rossia. In pratis arenosis inundatis prope 'Tschertoroj' haud procul a 'Kijew'," July 1911, A. Lonatschewskij, 5501 (holotype: B; isotypes: C! and DAO!).

Veronica anagalloides Guss. var. hirsuticaulis Lonatschewskij ex Schlenker, Repert. Spec. Nov. Regni Veg. Beih. 90: 22. 1936.--Type: "Rossia. In pratis arenosis inundatis prope 'Tschertoroj' haud procul a 'Kijew'," July 1911, A. Lonatschewskij, 5500 (holotype: B; isotypes: C!, DAO!, and Z!).

Veronica anagalloides Guss. var. maruensis Fedchenko, Fl. Turkm. 6: 27. 1954.--Type: not seen.

Semi-aquatic, perennial. Stem erect; 10-35.5 cm tall; internodal length 1.2-5.2 cm; glabrous or glandular. Leaves sessile, clasping; margin with 8-56 serrations along one

side; linear-lanceolate; base cordate; apex acute; 2.2-6 cm long, 0.4-1 cm wide; glabrous. Racemes opposite, rarely whorled; lateral; (5) 7-14.5 cm long; glabrous or glandular; bracts linear, 2.2-5.1 mm long, 0.3-1 mm wide. Flowers 25-45 per inflorescence alternately arranged along the raceme; pedicels filiform, 3-6 mm long (except in Africa 1.5-2 mm long), longer than bracts (except in Africa); calyx linear-elliptic, 1.8-3.4 (4.3) mm long, 0.7-1.2 mm wide, usually shorter than capsule, glabrous, rarely hirsute; style (.85) 1-1.36 (1.7) mm long. Capsule elliptic, rarely orbicular, slightly flattened but turgid, 1.9 - 3.6 mm long, 1.4 - 2.4 (2.9) mm wide, glandular, occasionally glabrous, notch lacking. Seeds oval 0.42-0.5 mm long, 0.25-0.33 mm wide.

ANAGALLOIDES is found throughout much of Europe, particularly around the Mediteranean, including the Sinai and West into Persia and the Soviet Union (fig. 5; Sellers 1983, Appendix D).

3. Veronica beccabunga L., Sp. Pl. p. 12. 1753.--Type: Linn (photograph of holotype at Linn in Savage's Catalogue of the Linnaean Herbarium; photograph at GH!).

Succulent, semi-aquatic, perennial. Stem erect or prostrate, rooting at the nodes; 2.6-71 cm tall; internodal length 1.1-9.6 cm; typically glabrous, rarely glandular. Leaves petiolate; margin with 7-30 serrations or crenations along one side; oblong to orbicular (lanceolate); base round or slightly cordate, rarely acute; apex typically round or obtuse, rarely acute; 1.3-8 cm long, (0.7) 1.1-3.4 (4.4) cm wide; glabrous. Racemes opposite, rarely alternate; lateral; 3-19.5 cm long; glabrous or glandular; bracts linear or elliptic, 2-11.4 mm long, 0.2-2.2 mm wide. Flowers 5-37 per inflorescence alternately arranged along the raceme; pedicels filiform, 2.2-12.8 mm long, often longer but sometimes shorter than bracts; calyx linear-elliptic, 2.2-4.9 (5.8) mm long, 0.7-1.9 mm wide, normally equal or longer than capsule, sometimes shorter; glabrous, rarely glandular; style 1.19-3.57 mm long. Capsule obcordate or orbicular, flattened but remaining turgid, 2.2-3.9 (4.3) mm long, 2.4-4.4 mm wide, glabrous, rarely sparsely glandular, notch depth 0-.34 mm. Seeds oval or orbicular 0.33-0.66 mm long, 0.25-0.54 (0.66) mm wide.

V. beccabunga occurs throughout North America, Europe, Asia, and North Africa with an isolated introduction in Pueto Mont, Chile (fig. 5; Sellers 1983, Appendix D).

Keys to the subspecies of Veronica beccabunga

Leaves obovate or round; leaf blade approximately as long as wide.....ssp. beccabunga
Leaves lanceolate or ovate; leaf blade twice as long as wide.....ssp. americana

Veronica beccabunga L. ssp. beccabunga, Sp. Pl. p. 12. 1753.--Type: Linn (photograph of holotype at Linn in Savage's Catalogue of the Linnaean Herbarium; photograph at GH!).

Veronica hjuleri O. Paulsen, Bot. Tidsskr. 27: 212. 1906.--Type: "Pamir, ad locus Jashil Kul. 3800 m," August 28, 1898, Ove Paulsen, 1191 (holotype: C!). A smaller leaved, spreading form.

Stem prostrate, occasionally erect; 2.6-68 cm tall; internodal length 6.5-9.6 cm; glabrous. Leaf margins with 8-23 crenations, occasionally serrations; oval or orbicular; apex typically round; 1.8-6.7 (8) cm long, (0.7) 1.1-3.3 (4.4) cm wide. Racemes 3-17 cm long; bracts 2-8.3 mm long, 0.2-1.2 mm wide. Flowers 7-34 per inflorescence; pedicels 2.2-7 (9.9) mm long; calyx 2.4-4.9 mm long, 0.8-1.7 mm wide, glabrous; style 1.19-3.06 mm long. Capsule 2.2-3.9 mm long, 2.4-4.4 mm wide.

V. beccabunga ssp. beccabunga is found throughout much of Europe and Asia west of the Himilayas, and in northern Africa. There are also several isolated introductions in North America, particularly along major waterways and harbors and at least one introduction in South America in the vicinity of Puerto Mont, Chile. (fig. 5; Sellers 1983, Appendix D).

Veronica beccabunga L. ssp. americana (Raf.) Sellers comb. nov.--Type: "Shenandoah Nat. Park, Rapidan River, near Hoover Camp," June 2, 1934, Elizabeth S. Rawlinson, 21, U.S.

National Herbarium #1736087 (lectotype herein designated: US!).

Veronica beccabunga L. var. americana Rafinesque, Medical Flora 2: 109. 1830.--Type: Believed to be not extant (Pennell 1921).

Veronica americana (Raf.) Schweinitz ex Bentham in DeCandolle, Prodromus 10: 468. 1846.--Type: "Bethl." (interpreted by Pennell, 1921 as Bethlehem, Pennsylvania), (no date), L.v.S. (fide Lewis von Schweinitz), s.n. (isotype: PH!).

Veronica oxylobula Greene, Pittonia 5: 113. 1903.--Type: "Near Golden City, Colorado," 1871, Edw. L. Greene, s.n. (holotype: NDG!, photograph at PH!).

Veronica crenatifolia Greene, Pittonia 5: 114. 1903.--Type: "Mancos River bottom, Southern Colorado," June 22, 1898, C.F. Baker, F.S. Earle, and S.M. Tracy, 33 (holotype: NDG!, photograph at PH!; isotype: US!).

Stem prostrate or erect; 7-71 cm tall; internodal length 1.1-9.4 cm; glabrous, rarely glandular. Leaf margin with 7-30 serrations or crenations; narrowly lanceolate or oblong; apex typically obtuse, rarely acute; 1.3-8 cm long, 1.1-2.8 cm wide. Racemes 3-19.5 cm long; bracts 2.5-11.4 mm long, 0.5-2.2 mm wide. Flowers 5-37 per inflorescence; pedicels 3.4-12.8 mm long; calyx 2.2-4.9 (5.8) mm long, 0.7-1.9 mm wide, glabrous, rarely glandular; style 1.7-3.6 mm long. Capsule 2.4-3.4 (4.3) mm long, 2.5-3.9 (5.3) mm wide.

V. beccabunga ssp. americana occurs through much of North America, across the Aleutian chain to the Kamchatka peninsula and Northern Japan (fig. 5; Sellers 1983, Appendix D).

4. Veronica scardica Grisebach, Spicil. Fl. Rumel. 2: 31. 1844.--Type: "Albania boreali: gregarie in sylvis umbrosis pr. confluentiam utrinsque Drinii locis udis alt. 700'," (no date), Gr. (Grisebach), s.n. (?holotype: GOET!; isotype MO!). The possible type at GOET has label information that is difficult to interpret, making it impossible to make a definite decision concerning this specimen. The specimen at MO is clearly labeled 'Albania boreali' with the initials Gr. (Grisebach) following the species name. Also, the handwriting on both the label at MO and GOET are possibly the same. However, the MO specimen has 'Grisebach mis 1846' on the label, which apparently was added to the label at a later date by someone other than the the collector. Based on this information, I believe the MO plant to be a likely isotype and the specimen at GOET may also be a type, since it was collected by the same author, but at this time the status of the latter can not be satisfactorily resolved.

Veronica anagallis L. β ovalis Visiani, Fl. Dalmatica 2: 45. 1847.--Type: "Sardinia," (no date), R. Visiani, s.n. (holotype: PAD!).

Veronica kovatsii Borbas, Geogr. Atq. Enum. PL. Comit. Castrif. p. 227. 1887.--Type: "Hungaria occidentalis: In fossis Thermarum Hevix comit. Talaviensis sat rara," July 26, 1893, Dr. Vince de Borbas, s.n. (holotype: unknown; isotype: Z!). Similar in all aspects to V. scardica.

Veronica velenovsky Uechtritz, in Engler's Bot. Jahrb. 8: 46. 1887.--Type: not seen.

Veronica velenovsky Uechtr. var. subintegrifolia Borbas, Termeszettud. Kozl. 33: 267-269. 1901.--Type: "Hungaria centr. In humidis calidis ad 'Bekas-Megyer' proper 'Budapest'," September 1894, V. Borbas and L. Richter, 3439 (holotype: M!; isotypes: B! and BP!).

Veronica beccabungoides Bornmuller, Beih. Bot. Centralbl. 22(2): 111. 1907.--Type: "Kerwau, Persia Australis," July 4, 1892, J. Bornmuller, 5001 (holotype: B!).

Veronica maresii Sennen, Bol. Soc. Iber. Ci. Nat. 29: 86. 1930.--Type: "Baleares: Torrent entre Palma et Pont d'Inca," (Spain), July 28, 1917, Fre. Bianor, 3127 (holotype: W!).

Veronica kaiseri Tackholm, Svensk Bot. Tidskr. 36: 250. 1942.--Type: "Ashbel Moja," (Sinai), September 9, 1928, Alfred Kaiser, 538 (holotype: S!). Leaves approximately as wide as long with alternate racemes.

Succulent, semi-aquatic, perennial. Stem erect or prostrate; rooting at the nodes; 13-30 cm tall; internodal length 2.2-6.8 cm; glabrous. Upper leaves sessile, lower leaves petiolate; margin with 6-16 serrations or crenations along one side; ovate or oval; base acute or cuneate, rarely rounded; apex typically acute on upper leaves, obtuse on lower leaves; 1.8-2.7 cm long, 0.9-1.4 cm wide; glabrous. Racemes opposite, rarely alternate; lateral; 5.5-10 cm long; bracts linear, 1.9-3.6 mm long, 0.5-0.7 mm wide. Flowers 14-33 per inflorescence alternately arranged along the raceme; pedicels 4.6-7 mm long, longer than bracts; calyx linear-elliptic, 2.7-3.2 mm long, 1-1.4 mm wide, longer than capsule, glabrous; style 1.19-1.7 mm long. Capsule obcordate or orbicular, flattened but turgid; 2.5-2.7 mm long, 2-2.6 mm wide; glabrous; notch depth 0.17. Seeds oval, rarely orbicular, 0.42-0.58 mm long, 0.25-0.42 mm wide.

V. scardica is primarily restricted to the Balkan States of Europe, but does extend northwest as far as southern Germany (fig. 5; Sellers 1983, Appendix D).

EXCLUDED NAMES

The following taxa do not fall within my circumscription of section Beccabunga. This list includes exemplars from other sections that were employed to help delineate section Beccabunga as well as taxa that were previously included in section Beccabunga.

Veronica anisophylla C.Koch

Veronica cana Wall.

Veronica ciliata Fisch.

Veronica connata Raf.

Veronica eriogyne Winkl.

Veronica grandiflora Gaertn.

Veronica japonensis Makino

Veronica koelzii Pennell

Veronica leucothrix Pennell

Veronica macrocarpa Guss.

Veronica miqueliana Nakai

Veronica montioides Boiss.

Veronica morrisonicola Hayata

Veronica murorum Maxim.

Veronica nana Pennell

Veronica oligosperma Hayata

Veronica riae Winkler

Veronica rockii Li

Veronica umbelliformis Pennell

NAMES OF UNCERTAIN APPLICATION

Names that are believed to be possible synonyms of taxa in section Beccabunga. However, not enough information was available to make a conclusive decision about these names.

Veronica ambigua Luce

Veronica osiliensis Luce

Veronica espadanae Pau

Veronica mucosa Korsh.

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Table 1. List of characters used in phenetic analysis of Veronica section Beccabunga. Distance values are reported for each character employed in constructing the similarity matrix; * = characters employed to generate GSC; + = characters traditionally employed in monographs and floras to discriminate among species of the section.

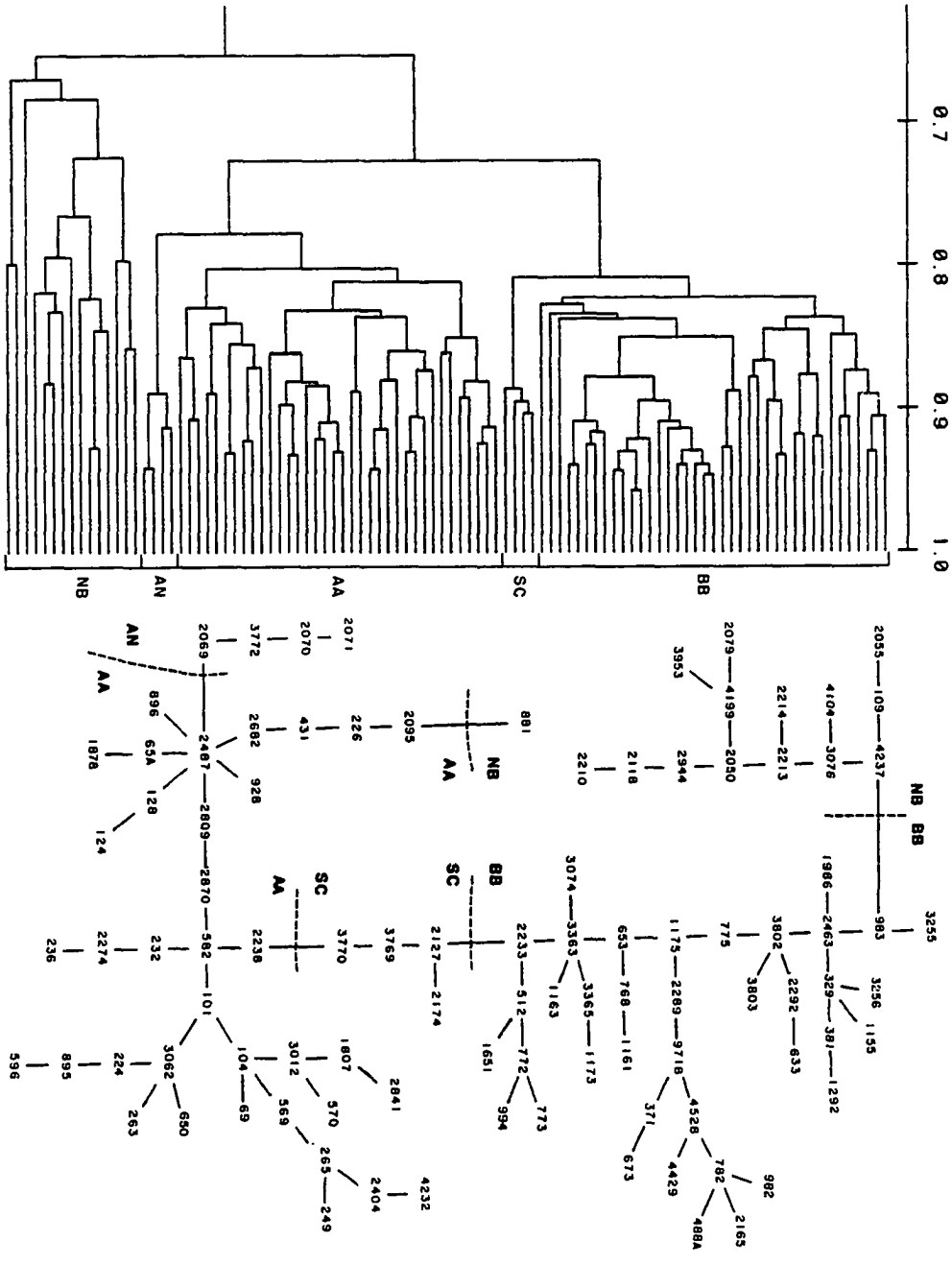
CHARACTERS	CHARANAL VALUE
+*1. Stem pubescence present or absent	.94890
+2. Leaf pubescence present or absent	
+*3. Sepal pubescence present or absent	.85968
+4. Fruit pubescence present or absent	
5. Kind of pubescence	
+6. Inflorescence position	
*7. Inflorescence length	.93519
*8. Number of flowers per inflorescence	.88439
+9. Flower color	

+10.	Corolla shorter/longer than calix	
+*11.	Sepals shorter/longer than capsule	.92629
+*12.	Pedicels shorter/longer than bracts	.97778
+13.	Bract apex shape obtuse/acute	
+14.	Seed color reddish-brown/black	
+*15.	Raceme attachment	.91572
16.	Seeds folded/compressed	
17.	Upper leaf arrangement opposite/alternate	
+18.	Upper leaf attachment	
+*19.	Lower leaf attachment	.46269
*20.	Average serration length	.93037
+21.	Leaves incised or not	
+*22.	Leaf tip shape round/obtuse/acute	.74762
+*23.	Leaf base shape	.34063

	cordate/round/acute	
+24.	Annual/perennial	
+25.	Branched/unbranched	
*26.	Style length of mature fruit	.88202
27.	Number of sepals	
28.	Sepal length	
*29.	Sepal width	.89682
*30.	Sepal l/w ratio	.91050
+*31.	Capsule notch depth	.91075
+32.	Capsule length	
+*33.	Capsule width	.87078
*34.	Capsule l/w ratio	.88151
35.	Number of stamens	
36.	Number of petals	
*37.	Seed length	.94133
38.	Seed width	
*39.	Seed l/w ratio	.92906
+*40.	Pedicel length	.93818
41.	Bract length	
*42.	Bract width	.94997
*43.	Bract l/w ratio	.94885

+44.	Leaf length	
+*45.	Leaf width	.91598
+*46.	Leaf l/w ratio	.87397
*47.	Leaf length/distance from base to widest part ratio	.88233
*48.	Average number of leaf serrations on one side	.94987
*49.	Average internodal length	.95290
+*50.	Plant height	.95048

Fig. 1. Phenogram and MST representing section Beccabunga with exemplars from other sections of Veronica (CCC 0.806). AA = ANAGALLIS-AQUATICA. AN = ANAGALLOIDES. BB = BECCABUNGA. SC = SCARDICA. NB = Veronica not allied to section Beccabunga.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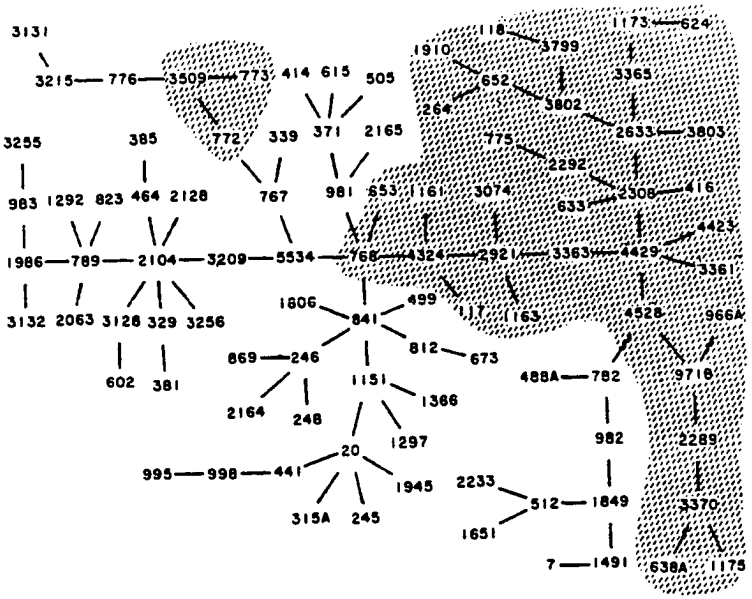
0.8
0.9
1.0
NB
AN
AA
SC
BB

Fig. 2. Phenogram and MST representing the global variation of V. beccabunga (CCC 0.734). Shaded OTUs BECCABUNGA; non-shaded OTUs AMERICANA.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371
2165
3255
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983
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2128
767
981
653
1161
3074
1910
118
3799
1173
624
652
3365
264
3802
2633
3803
775
2292
2308
416
633
4423
1986
789
2104
3209
5534
768
4324
291
3363
4429
3361
3132
2063
3128
329
3256
1806
841
499
117
163
4528
966A
669
246
812
673
488A
782
9718
602
381
1151
2164
248
1366
1297
982
2289
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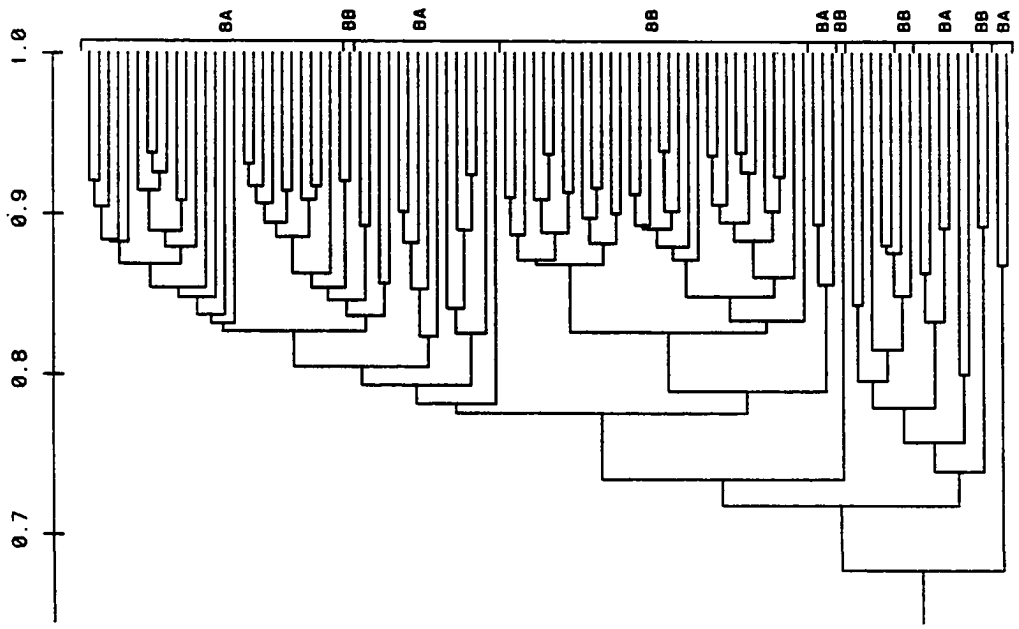
638A
1175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BB
BA
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BA
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BB
BA
BB
BA
1.0
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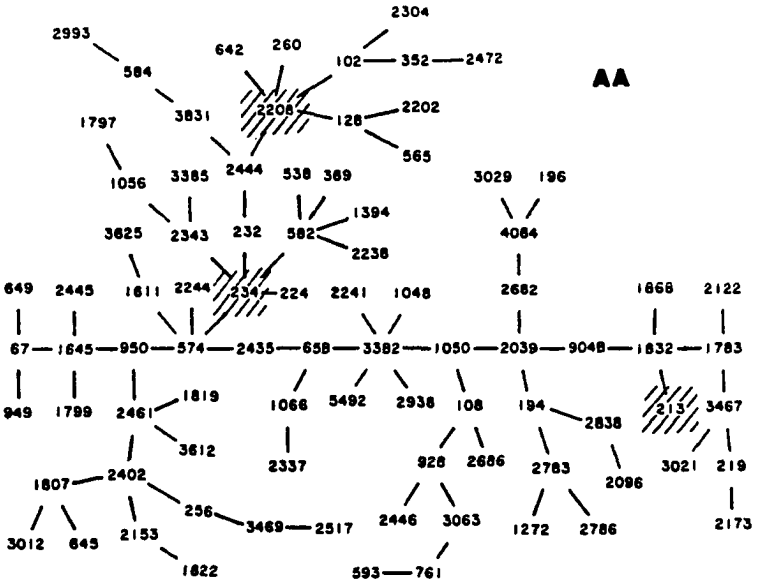
0.8
0.7

Fig. 3. Phenogram and MST representing the global variation of V. anagallis-aquatica (CCC 0.587). Exemplars of CATENATA are defined by (+).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642
260
102
352
2472
584
2208
128
2202
1797
3831
565
1056
3385
2444
538
389
3029
196
1394
3625
2343
232
582
4084
2238
649
2445
1811
2244
234
224
2241
1048
2682
1868
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3469
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2446
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2173
3012
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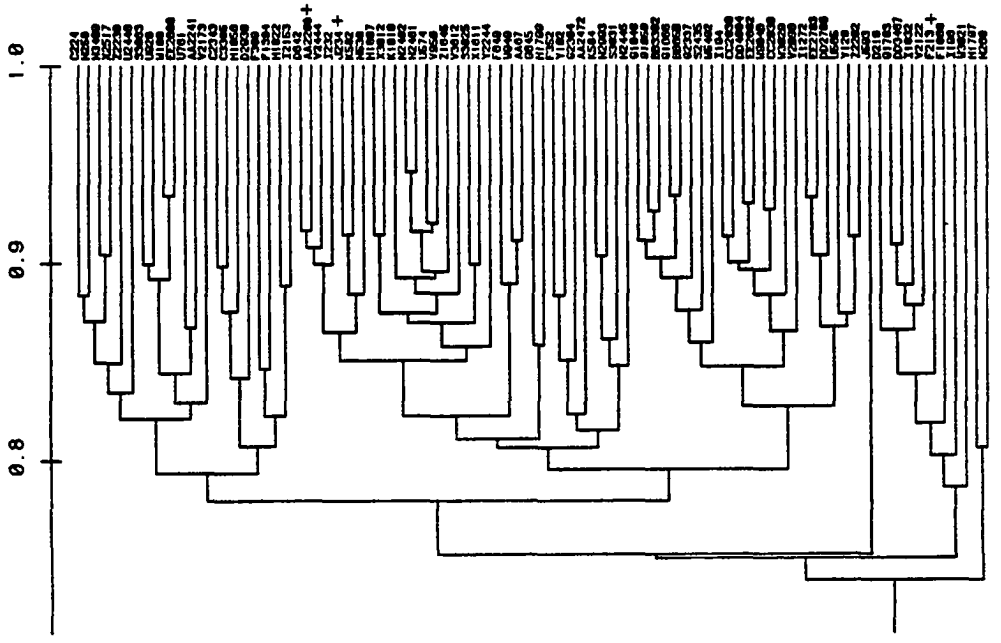
2153
1822
593
761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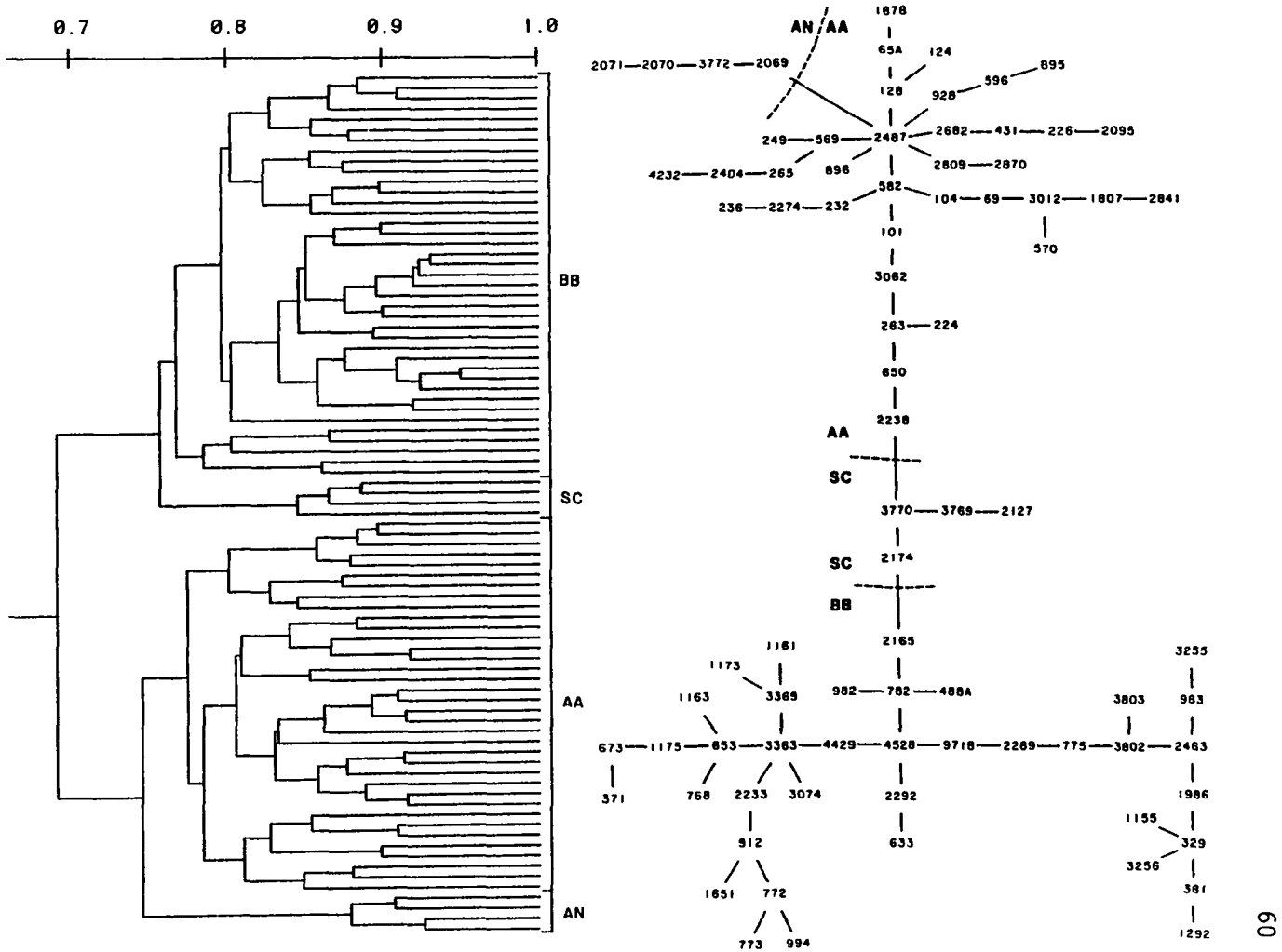
0.9
0.8

Fig. 4. Phenogram and MST representing the global variation of section Beccabunga employing only intrasectional exemplars (CCC 0.697). AA = ANAGALLIS-AQUATICA. AN = ANAGALLOIDES. BB = BECCABUNGA. SC = SCARDICA.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0.8
0.9
1.0
BB
SC
AA
AN
AN/AA
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65A
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2071
2070
3772
2069
128
928
596
895
249
569
2487
2682
431
226
2095
4232
2404
265
896
2809
2870
582
236
2274
232
104
69
3012
1807
2841
101
570
3062
263
224
650
2238
AA
SC
3770
3769
2127
SC
2174
BB
2165
1161
1173
3369
1163
982
782
488A
3803
3255
983
673
1175
653
3363
4429
4528
9718
2289
775
3802
2463
371
768
2233
3074
2292
1986
912
633
1155
329
3256
381
1651
772
773
994
1292

Fig. 5. Distribution map for taxa of *Veronica* section *Beccabunga*.

Top.

V. scardica

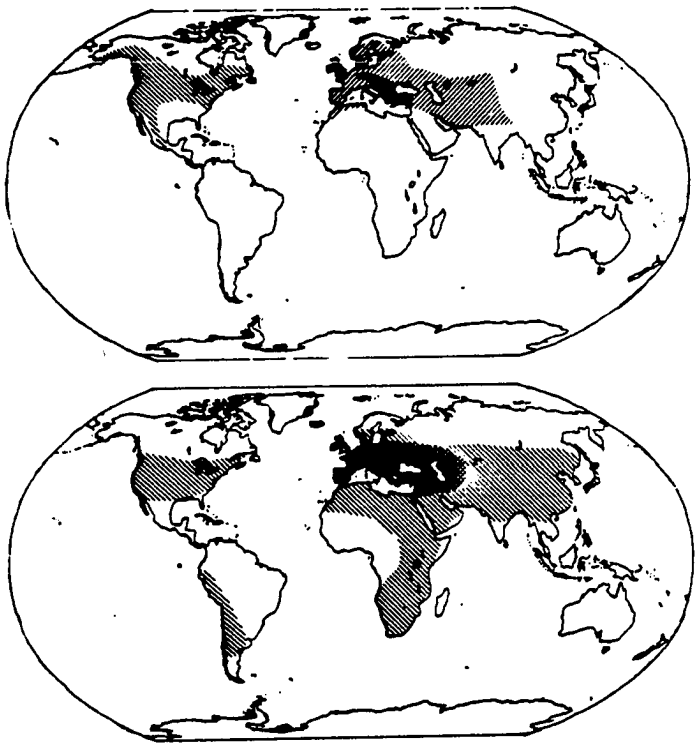
V. beccabunga ssp. *americana*

V. beccabunga ssp. *beccabunga*

Bottom.

V. anagallis-aquatica

V. anagalloides



Appendix A

GEOGRAPHICAL AREAS

SYMBOL	AREA
A....	U.S.A. (Alaska, Aleutian Islands)
C....	Canada (Yukon, Northwest Territories, Alberta, British Columbia, Saskatchewan, Manitoba)
D....	Iceland, Greenland, Canada (Labrador, New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, Quebec)
F....	U.S.A. (Connecticut, Illinois, Indiana, Maine, Maryland, Massachusetts, Michigan, New Jersey, New Hampshire, New York, Ohio, Pennsylvania, Rhode Island, Vermont, W. Virginia, Wisconsin)

G.... U.S.A. (Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, N. Carolina, S. Carolina, Tennessee, Virginia, District of Columbia)

H.... U.S.A. (Colorado, Kansas, Missouri, New Mexico, Oklahoma, Texas)

I.... U.S.A. (Iowa, Minnesota, Nebraska, North Dakota, South Dakota, Wyoming)

J.... U.S.A. (Idaho, Montana, Oregon, Washington)

K.... U.S.A. (Arizona, California, Nevada, Utah)

L.... Mexico, Belize, Coasta Rica, Guatemala, Honduras, Nicaragua, Panama, El Salvador

N.... Argentina, Bolivia, Brazil, Chile, Colombia, Peru

S.... Japan (Hokkaido, Okinawa, Oshima, Ryukyu Islands), Taiwan

U.... China, Korea, Mongolia, Vietnam

V.... Burma, India, Nepal, Pakistan

W.... Cyprus, Afghanistan, Iran, Iraq, Israel, Jordan, Lebanon, Saudi Arabia, Syria, Turkey, Yemen

X.... Soviet Union

Y.... Austria, Bulgaria, Czechoslovakia, Denmark, Germany, Greece, Hungary, Netherlands, Poland, Romania, Yugoslavia

Z.... Finland, Norway, Sweden

AA... Belgium, France, Italy, Portugal, Spain, Switzerland

BB... Ireland, United Kingdom

CC... Algeria, Morocco, Canary Islands, Tunisia

DD... Angola, Botswana, Burundi, Lesotho, Mozambique, Republic of South Africa (Namibia), Rwanda, Swazi, Tanzania, Zambia, Zaire, Zimbabwe

EE... Egypt, Ethiopia, Kenya, Libya, Somalia, Sudan, Uganda

Appendix B

EXEMPLAR SPECIMENS

V. anagallis-aquatica

REGION C: 224--Boivin, 13900 (GH); 2343--Breitung, 4687 (MO); 1429--Macoun, 12421 (F); 3421--McCalla, 8441 (UBC); 3422--McCalla, 8551 (UBC); 3385--McCalla, 9038 (UBC); 2714--Turner, 4343 (MO).

REGION D: 2017--Grassl, 5420 (MICH); 2938--Jonsson, s.n. (US) 2036922; 326--Marie-Victorin and Rolland-Germain, 46222 (GH); 219--Marie-Victorin, Rolland-Germain, and Raymond, 56024 (GH); 642--Montgomery, 919 (GH); 2148--Morton and Venn, NA8493 (MICH); 3011--Sorensen, 38 (US); 103--Sorensen, 38 (GH); 4235--Smith, 2724 (PH).

REGION F: 1072--Allard, 9077 (GH); 1299--Bennett, 2504 (F); 389--Bissell, s.n. (GH) s.n.; 185--Deam, 42185 (GH); 2095--Farwell, 4323 (MICH); 2093--Farwell, 9105 (MICH); 2094--Farwell, 9105 (MICH); 189--Gleason, s.n. (GH) s.n.; 658--Hermann, 7998 (GH); 356--House, 19272 (GH);

213--House, 19565 (GH); 355--House, 21504 (GH); 352--Muenscher and Maguire, 2529 (GH); 1394--Pennell, 10100 (F); 361--Pennell, 10100 (GH); 650--Porter, s.n. (GH) s.n.; 649--Porter, s.n. (GH) s.n.; 1868--Voss, 2267 (MICH); 1870--Voss, 14306 (MICH); 216--Wiegand, 12895 (GH); 1532--Williams, s.n. (F) 161609; 184--Winona and Yunker, 10793 (GH).

REGION G: 2701--Allard, 8894 (MO); 1049--Churchill, s.n. (GH) s.n.; 1066--Fernald and Long, 8847 (GH); 1062--Fernald and Long, 12183 (GH); 1063--Fernald and Long, 12469 (GH); 1050--Fernald and Long, 12805 (GH); 644--Fogg, 14948 (GH); 1070--Grimes, 4587 (GH); 1073--Hunnewell, 5421 (GH); 645--Hunnewell, 18227 (GH); 2147--Leonard, 2398 (MICH); 2304--Leonard, 2398 (MO); 2943--Mohr, s.n. (US) s.n.; 643--Radford and Haesloop, 7285 (GH); 316--Redford, 45012 (GH); 1045--Ruth, 104 (GH); 2337--Ruth, 577 (MO); 1783--Schuette, 4.32.88 (F); 657--Seurgent, 51 (GH); 1048--Shaver, s.n. (GH) s.n.; 1878--Small and Heller, 316 (MICH); 1310--Small and Heller, 316 (F); 1323--Small and Heller, s.n. (F) 400930; 1438--Small and Heller, s.n. (F) 401231.

REGION H: 1790--Bergey, 24 (OKL); 1053--Correll, 37280 (GH); 1358--Eggleston, 15013 (F); 1391--Ellis, 28 (F); 2092--Erlanson, 1277 (MICH); 2091--Erlanson, 1278 (MICH); 1809--Glassman, 1172 (OKL); 1797--Glassman, 1400 (OKL); 1700--Goodman and Hess, 7688 (OKL); 1815--Goodman and Lawson, 8460 (OKL); 1807--Goodman and Lawson, 8517 (OKL); 1802--Govett, 36 (OKL); 1056--Harms, 1702 (GH); 236--Horr, E533 (GH); 1812--Hotchkiss, et. al., 69-6-24-8 (OKL);1795--Massey and Nighswonger, 1560 (OKL); 1810--Pearse, 1265 (OKL); 2138--Rogers, 5736 (MICH); 1256--Steyermark, 23363 (F); 1786--Steyermark, 23468 (F); 1184--Steyermark, 27948 (F); 207--Thomas, 9721 (GH); 585--Waterfall, 3178 (GH); 1822--Weedon and Magrath, 6619 (OKL); 2137--Whitehouse, 15706 (MICH).

REGION I: 1272--Combs, 577 (F); 194--Combs, 577 (GH); 1726--Grime, 218 (F); 1395--Hayward, 1568 (F); 197--Hotchkiss and Fassett, 3326 (GH); 1060--Hulbary, 9434 (GH); 226--Johnson, 470 (GH); 518--Kiener, 15358 (GH); 1044--Kiener, 17483 (GH); 1043--Kiener, 19660 (GH); 2297--Larson, 3328 (MO); 2296--Larson, 3370 (MO); 2295--Larson, 3449 (MO); 1059--Magrath, 6005 (GH); 1188--Maybi, 2293 (F); 1832--Moore, 11542 (OKL);

232--Nelson, 9539 (GH); 195--Ownbey, 2780 (GH); 238--Palmer, 37432 (GH); 1051--Porter and Miller, 5971 (GH); 196--Sandberg, s.n. (GH) s.n.; 2153--Voss, 13086 (MICH).

REGION J:1437--Canby, s.n. (F) 149464; 201--Pennell, 15171 (GH); 593--Sheldon, S.10525 (GH); 234--Suksdorf, 886 (GH); 596--Suksdorf, 7661 (GH); 265--Suksdorf, 7661 (GH).

REGION K: 584--Clokey, 8119 (GH); 2146--Gibson and Horak, 3231 (MICH); 587--Goodding, 767 (GH); 582--Graham, 6246 (GH); 583--Holmgren and Reveal, 1054 (GH); 2299--Nelson, 1684 (MO); 813--Raven and Thompson, 14620 (GH); 1819--Seigler, DS-7164 (OKL).

REGION N: 2404--Alvitez, et. al., 8989 (MO); 1637--Ammann, 99 (F); 2408--Bocher, Herferting, and Rahn, 1172 (MO); 2410--Cabanillas, et. al., 8075 (MO); 1649--Fischer, 165 (F); 258--Goodspeed, 23343 (GH); 242--Gunkel, 5813 (GH); 528--Gunkel, 11043 (GH);2406--Hunziker, 2063 (MO); 524--Hutchison, 129 (GH); 250--Jaffuel and Parion, 3215 (GH); 244--Johnston, 3685 (GH); 253--Johnston, 5849 (GH); 2993--Killip and Pisano, 39754 (US); 2402--Krapovickas, et. al., 22567 (MO); 5540--Kuhlmann, 22643 (PH);

2407--Lopez, et. al., 7494 (MO); 260--Morrison, 16597 (GH); 522--O'Donell, 1133 (GH); 538--O'Donell and Rodriguez, 1274 (GH); 249--Parodi, 11368 (GH); 257--Pennell, 12708 (GH); 256--Pennell, 12631 (GH); 255--Pennell, 12851 (GH); 2461--Solomon, 4321 (MO); 2445--Solomon and Crosby, 4820 (MO); 1646--Stafford, 628 (F); 1647--Stafford, 1150 (F); 2986--Vargas, 15080 (US); 251--Werdermann, 992 (GH); 3469--Werdermann, 992 (JEPS); 254--West, 4735 (GH).

REGION S: 3043--Amano, 6258 (US); 896--Furuse, s.n. (GH) s.n.; 577--Furuse, s.n. (GH) s.n.; 895--Furuse, s.n. (GH) s.n.; 3825--Furuse, 20382 (JEPS); 3048--Ichikawa, 195 (US); 3827--Jamaka, 41 (JEPS); 3831--Makono, 36972 (JEPS); 3828--Makino, 36979 (JEPS); 576--Maximowicz, s.n. (GH) s.n.; 578--Oldham, 640 (GH); 3044--Shimura, s.n. (US) 206039; 766--Suzuki, s.n. (GH) s.n.; 2083--Tanaka and Shimada, 11021 (MICH); 3063--Tanaka and Shimada, 11021 (US); 2435--Tanaka and Shimada, 11021 (MO); 5301--Tanaka and Shimada, 11021 (PH); 579a--Wright, 223 (GH).

REGION U: 3067--Beach, S-25 (US); 2446--Chaney, 318 (MO); 3062--Ching, 483 (US); 564--Ching, 6618 (GH); 565--Chung, 8178 (GH); 568--Feng, 1930 (GH); 571--Henery, 3533 (GH); 3606--Ikonnikov-Galitzky, 149 (JEPS); 561--Ikonnikov-Galitzky, 463 (GH); 570--Ikonnikov-Galitzky, 3844 (GH); 3049--Kozlov, 111 (US); 569--Licent, 11873 (GH); 4191--Maire, 391 (PH); 562--Skvorizov, s.n. (GH) s.n.; 574--Skvorizov, s.n. (GH) s.n.; 572--Steward and Cheo, 272 (GH); 944--Tai, 1239 (GH); 3057--Thompson, s.n. (US) 2500540; 3073--Tsang, 23730 (US); 599--Wang, 61462 (GH); 928--Wang, 62705 (GH); 953--Wang, 66339 (GH); 761--Wang, 71512 (GH); 2277--Wills, s.n. (MO) 1606732.

REGION V: 2204--Cooper, 5372 (MICH); 2122--Dickason, 1697 (MICH); 2123--Dickason, 1698 (MICH); 914--Dickason, 7168 (GH); 3849--Drummond, 26260 (JEPS); 5220--Iajilbash, s.n. (PH) 917708; 2081--Koelz, 4207 (MICH); 2173--Koelz, 4209 (MICH); 2082--Koelz, 4897 (MICH); 2171--Koelz, 5707 (MICH); 947--Koelz, 6222 (GH); 2170--Koelz, 7224 (MICH); 2052--Koelz, 29220 (MICH); 3065--Nicolson, 86 (US); 2096--Parmamand, 771 (MICH); 965--Polunin, Sykes, and Willaima, 5101 (GH); 3612--Rodin, 5603 (JEPS);

2444--Santapau, 11997 (MO); 5490--Schlagintweit, s.n. (PH) s.n.; 2126--Singah, 200 (MICH); 4258--Stewart, 5466 (PH); 4252--Stewart, 9726 (PH); 4207--Stewart, 9987a (PH); 950--Stewart, 13698 (GH); 910b--Stewart, 13821 (GH); 906b--Stewart, 13987 (GH); 3033--Stewart, 17766 (US); 5212--Stewart, 19378 (PH).

REGION W: 3449--Balls, B2741 (JEPS); 436--Becker, s.n. (GH) s.n.; 2433--Bornmuller, 110 (MO); 5493b--Bornmuller, 2826 (PH); 4221--Bornmuller, 4261 (PH); 108--Dinsmore, 188 (GH); 2285--Esfandiari, 4235 (MO); 5491--Field and Lazar, 10 (PH); 5468--Field and Lazar, 982 (PH); 2432--Gibbons, 247 (MO); 5394--Koelz, 11526 (PH); 904b--Koelz, 11938 (GH); 949--Koelz, 12096 (GH); 3069--Kocher, B-445 (US); 95b--Kotschy, 225, (GH); 3053--Kuntz, s.n. (US) s.n.; 3451--Larsen, 825 (JEPS); 2198--Miller, 257 (MICH); 3021--Pitcher and Polack, 1679 (US); 64--Pravitz, 202 (GH); 2292--Rasheuju, 106 (PH); 2199--Rechinger, 638 (MICH); 3029--Rechinger, 5748 (US); 101--Shepard, s.n. (GH) s.n.; 2439--Stapf, 204 (MO).

REGION X: 2517--Andreev, 4148 (MO); 2074--Andreev, 4148 (MICH); 2279--Becker, s.n. (MO) 103695; 2937--Grentved, 2017 (US); 105--Joad, 4 (GH); 99--Joad, 8 (GH); 1611--Joad, 457 (F); 3608--Kornocybanya, 12 (JEPS); 5479--Kossinsky, 1082 (PH); 3012--Litwinow, 1791 (US); 1619--Raeintz, s.n. (F) 29156; 5481--Roshevitz, 818b (PH); 10--Samokish, 1619 (GH); 2431--Savortsov, s.n. (MO) 2351028; 5483--Schipczinsky, 888 (PH).

REGION Y: 129--Braun, 2620 (GH); 5399--Cypers, s.n. (PH) 605853; 102--Franchschi, 268 (GH); 4323--Hansen and Svendsen, 427 (PH); 5398--Heimerl, s.n. (PH) 673981; 5391--Jacobsen and Svendsen, 108 (PH); 2244--Jacobsen and Svendsen, 108 (MO); 68b--Patten, 27 (GH); 128--Poeverlein, 460 (GH); 2487--Raeintz, s.n. (MO) 103748; 104--Smejkal, 1469 (GH); 111--Uechtritz, 4130 (GH); 2236--Wisniewska and Blaszcyk, 456 (MO); 3484--Wisniewska and Blaszazyk, 456 (JEPS).

REGION Z: 125--Fries, s.n. (GH) s.n.; 73--Fries, s.n. (GH) s.n.; 1643--Fries, 1400 (F); 3652--Holmberg, s.n. (JEPS) 206418; 2238--Holmberg, s.n. (MO) 1006415; 124--Holmberg,

s.n. (GH) s.n.; 1645--Johansson, s.n. (F) 824599; 2202--Jordal, 467 (MICH); 2515--Magnusson, 912 (MO).

REGION AA: 69--Bequinot and Pampanini, 149 (GH); 4726--Bernet, s.n. (PH) 33656; 2208--Duvigneaud, 7836 (MICH); 63--Godet, s.n. (GH) s.n.; 1609--Juglar, s.n. (F) 336403; 66--Paoletti, 900 (GH); 67--Raine, s.n. (GH) s.n.; 4249--Reynier, s.n. (PH) 806437.

REGION BB: 2870--Ball, s.n. (US) 683075; 4233--Britton, s.n. (PH) 600187; 3382--Cowan, s.n. (UBC) 43312; 3415--Druce, 3697 (UBC); 3412--Little, 1258 (UBC); 77--Raine, s.n. (GH) s.n.; 65a--Sterling, s.n. (GH) s.n.; 65b--Sterling, s.n. (GH) s.n.; 4232--Twining, s.n. (PH) 600186.

REGION CC: 2685--B.M., 460 (MO); 2683--B.M., 801 (MO); 2841--Chevallier, 601 (US); 107--Cook, 487 (GH); 3447--Faure, s.n. (UC) 317242; 2838--Faure, s.n. (US) 1674050; 2845--Harshberger, 1124 (US); 2041--Lems, 2345 (MICH); 2040--Lems, 5754 (MICH); 2039--Lems, 6074 (MICH); 3600--Ouer, 582 (UC).

REGION DD: 2492--Amshoff, 2394 (MO); 80--Bayliss, 7248 (GH); 431--Finke, 3678 (GH); 2843--Finke, 3678 (US); 2688--Giess, 8252 (MO); 2798--Gill, 87 (MO); 2684--Guillarmod and Mazamane, 304 (MO); 4084--Heady, 1593 (UC); 3467--Liebenberg, 5832 (UC); 433--Linder, 2498 (GH); 2491--Loubser, 3458 (MO); 2786--Richards, 27705 (MO); 2836--Rodin, 3651 (US); 434--Ront, 187 (GH); 2274--Russell, s.n. (MO) 2653567; 432--Seydel, 3678 (GH); 2356--Vollese, 2459 (MO).

REGION EE: 2735--Abdallah and Khattab, 1039 (MO); 2681--Amshoff, 5453 (MO); 2682--Amshoff, 5789 (MO); 2686--Amshoff, 7355 (MO); 2687--Ash, 743 (MO); 2844--Burger, 1881 (US); 3768--Daiser, 83 (UC); 2500--DeWilde, 4503 (MO); 2781--Geesteranus, 4796 (MO); 2050--Gilbert, 242 (MICH); 2785--Hadidi, Kosinova, and Charte, s.n. (MO) 1907357; 2782--Ibrahim, et. al., s.n. (MO) 2252848; 2840--Lynes, 15 (US); 2275--Marsh, s.n. (MO) 103113; 2783--Mwangangi, 1715 (MO).

V. anagalloides

REGION X: 2454--Lonaczevsky, 419a (MO); 2070--Lonaczevsky, 419a (MICH); 2455--Lonaczevsky, 419b (MO); 2069--Lonaczevsky, 4149a (MICH); 2073--Lonatschewskij, 5501 (MICH); 79--Maximov, 4147 (GH); 2514--Maximov, 4147 (MO); 2071--Maximov and Schadek, 4149c (MICH); 2456--Maximov and Schadek, 419c (MO); 95a--Rahntz, s.n. (GH) s.n.

REGION Y: 2453--Baldacci, 88 (MO); 3648--Becking, s.n. (JEPS) 26013; 97--Ginzberger, 2621 (GH); 2459--Ginzberger, 2621 (MO); 3772--Zigmundik, 453 (JEPS); 96--Zigmundik, 453 (GH); 2072--Zigmundik, 453 (MICH); 1627--Zigmundik, 453 (F).

REGION AA: 7700--Contre, 4949 (L); 1624--Deseglise, 1284 (F); 2241--Fernandes and Sousa, 3010 (MO); 2809--Gandoger, s.n. (MO) 103751; 2451--Gandoger, s.n. (MO) 104200; 1164--Jeanpert, s.n. (F) 781286; 2242--Matos and Dinis, 9540 (MO); 2240--Paiva, Matos, and Marques, 7968 (MO); 5477--Reynier, s.n. (PH) 806535.

REGION EE: 2846--Schweinfurth, 195 (US).

V. beccabunga ssp. americana

REGION A: 381--Anderson, 6374 (GH); 382--Calder, 6826 (GH); 371--Hulten, 257 (GH); 2104--Jordal, 2687 (MICH); 2101--Jordal and Miller, 3040 (MICH); 3128--Muller, 1203 (US); 3126--Nelson, 3457 (US); 407--Scamman, 409 (GH); 374--Scamman, 3751 (GH); 2186--Shacklette, 7516 (MICH); 3132--Taylor, 12 (US); 3131--Thomas, 6358 (US); 401b--Walker, 850 (GH); 376--York, 44374 (GH).

REGION C: 502--Argus, 4338 (GH); 3393--Arnold, 94 (UBC); 3243--Ashford, 76 (UBC); 3343--Beamish, et. al., 8471 (UBC); 3310--Beamish and Krause, 630112 (UBC); 3394--Blais and Kuijt, 1948 (UBC); 508--Cody and Gutteridge, 6992 (GH); 3396--Cody and Gutteridge, 7119 (UBC); 3335--Davidson, Bell, and Eastham, 19 (UBC); 3215--Eastham, 5647 (UBC); 3217--Faris, 53 (UBC); 3291--Florian, 65 (UBC); 3268--Harrison, 52.1 (UBC); 3344--Joslin, 43 (UBC); 3264--Krajina, s.n. (UBC) 101916; 3290--Krajina, Pojar, and Parsons, s.n. (UBC) 152741; 3240--King, s.n. (UBC) 29660; 3272--Luitjens, 504.27 (UBC); 3209--Luitjens, 504.70 (UBC); 2266--Macoun, s.n. (MO) 102379; 501--Macoun, s.n. (GH) s.n.; 3338--McCalla,

7784 (UBC); 3337--McCalla, 8215 (UBC); 3395--Moss, 4156 (UBC); 3391--Noel, s.n. (UBC) 29687; 3304--Pinder-Moss, 102 (UBC); 392b--Porsild and Breitung, 10853 (GH); 392a--Porsild and Breitung, 11490 (GH); 393--Raup and Correll, 10926 (GH); 3392--Schofield and Crum, 7578 (UBC); 18--Scogan and Baldwin, 7599 (GH); 3256--Selby, 169914 (UBC); 2658--Shaw, 1128 (MO); 1357--Swink, 3051 (F); 1201--Swink, 3152 (f); 3305--Szczawinski, 5742 (UBC); 3235--Taylor, Calder, and Parmelee, 18475 (UBC); 505--Turner, 57 (GH); 506--Turner, 2000a (GH); 507--Turner, 2276 (GH); 3255--Wright, 168525 (UBC).

REGION D: 146--Blake, 5477 (GH); 322--Breed, et. al., 204 (GH); 617--Chamberlain and Knowlton, s.n. (GH) s.n.; 463--Collins and Fernald, s.n. (GH) s.n.; 476--Fernald, Long, and Fogg, 397 (GH); 461b--Fernald, Long, and Fogg, 1982 (GH); 478b--Fernald and Wiegand, 3948 (GH); 150--Fernald, Bean, and White, 22461 (GH); 480--Garton, 1255 (GH); 614--Gauthier, 11451 (GH); 321b--Krotkov, 7774 (GH); 141--Long, et. al., 8006 (GH); 329--Hosie, Losee, and Bannan, 2169 (GH); 2187--Malte and Watson, 474 (MICH); 602--Marie-Victorian, 8537 (GH); 611--Marie-Victorian, Germain, and Meilleur, 43608 (GH); 615--Marie-Victorian,

et. al., 44024 (GH); 606--Marie-Victorian and Rolland-Germain, 45196 (GH); 610--Marie-Victorian and Rolland-Germain, 49172 (GH); 464--Marie-Victorian and Rolland-Germain, 49442 (GH); 462--Marie-Victorian and Rolland-Germain, 49443 (GH); 149b--Pease and Linder, 22459 (GH); 140--Pease, 26617 (GH); 3174--Rouleau, 3946 (US); 319--Taylor, Losee, and Bannan, 1210 (GH); 323--Taylor, et. al., 2330 (GH); 1748--Umbach, s.n. (F) 94992; 144b--Weathery, 7261 (GH).

REGION F: 1849--Chase, 13733 (OKL); 441--Churchill, s.n. (GH) s.n.; 8--Churchill, s.n. (GH) s.n.; 313--Davis, 4851 (GH); 1896--Ehlers, 3441 (MICH); 1496--Fernald, 89 (F); 11--Hartley, 7692 (GH); 998--Long, 53943 (GH); 7--Pease and Bean, 26506 (GH); 456--Seymour, 700 (GH); 15--Seymour, 14273 (GH); 1491--Small, s.n. (F) 169579; 1297--Steyermark, 11116 (F); 995--Wahl, 701 (GH); 1503--Watson, s.n. (F) 434997; 994--Wilkens, 5878 (GH); 1910--Gleason, s.n. (MICH) s.n.; 264--Matthews, 3860 (GH).

REGION G: 315a--Freer, 1623 (GH); 20--Ruth, 103 (GH); 981--Small, s.n. (GH) s.n.; 982--Steele, 63 (GH); 983--Wood, 5820 (GH).

REGION H: 2063--Baad, 353 (MICH); 2061--Baad, 1302 (MICH); 1945--Erlanson, 1847 (MICH); 851--Goodwin, s.n. (GH) s.n.; 488a--Hermann, 5666 (GH); 798--Hinckley, s.n. (GH) s.n.; 2128--Koelz, s.n. (MICH) s.n.; 1155--Marcelline, 1919 (F); 1210--Pennell and Schaeffer, 22342 (F); 340--Pennell and Schaeffer, 22342 (GH); 1806--Taylor, 2551 (OKL); 339--Waterfall, 3271 (GH); 1838--Weber and Salamun, 12566a (OKL).

REGION I: 1366--Campbell, s.n. (F) 427508; 1151--Dann, et. al, 2243 (F); 1041--Hartley and Thorne, 6240 (GH); 494--Jozwik, 22 (GH); 1922--Kauffman and Erlanson, 38 (MICH); 513--Mogle, 202 (GH); 512--Moore, 16019 (GH); 414--Nelson, 6085 (GH); 482--Nelson, 7370 (GH); 1364--Pratt, s.n. (F) 432964; 1937--Rusby, s.n. (MICH) s.n.; 516--Rydberg, 927 (GH); 520--Rydberg, 1332 (GH); 1831--Smith, 282 (OKL); 1855--Stevens, 286 (OKL); 1298--Stevens, 286 (F); 1547--Stolze, 302 (F); 519--Tolstead, 121 (GH); 2233--Willenbring, 751 (MO).

REGION J: 1856--F.A.A., s.n. (OKL) 11006; 2033--Bartlett and Grayson, 981 (MICH); 1289--Bennett, 7733 (F);

418--Cotton, 396 (GH); 87--Cronquist, 3061 (GH); 1292--Everdam, 982 (F); 661--Henderson, 5509 (GH); 875a--Hitchcock and Muhlick, 13375 (GH); 82--Jones, 66 (GH); 870--Kirkwood, 2364 (GH); 1833--Lawson, 116 (OKL); 387--Lyon, 66 (GH); 496--Macbride and Nelson, 194 (GH); 498--Macbride, 456 (GH); 495--Payson, 1819 (GH); 385--Pennell, 15648 (GH); 869--Pennell, 20566 (GH); 85--Pennell, 20648 (GH); 83--Pennell and Constance, 20994 (GH); 690--Pennell and Meyer, 21185 (GH); 384--Pennell, 26128 (GH); 868--Stickney, 1222 (GH); 865--Suksdorf, 185 (GH); 695--Suksdorf, 1460 (GH); 673--Thompson, 6927 (GH); 864--Shaw, s.n. (GH) s.n.; 499--Thompson, 13837 (GH); 681--Weldert, 156 (GH); 674--Zeller, 831 (GH).

REGION K: 416--Baker, 1078 (GH); 2600--Collom, 244 (MO); 1986--Collom, s.n. (MICH) s.n.; 789--Collom, 244 (GH); 783--Eastwood, 209 (GH); 846--Eggleston, 14118 (GH); 828--Garrett, 1635 (GH); 844--Gentry, 1590 (GH); 2140--Goodding, 64-47 (MICH); 2110--Goodding, 79-47 (MICH); 1859--Goodman, 138 (OKL); 820--Heller, 5839 (GH); 792--Heller, s.n. (GH) s.n.; 803--Heller, 12767a (GH); 1857--Hess, 455 (OKL); 823--Hobson, 91 (GH); 845--Holmgren and Reveal, 1504 (GH); 830--Maguire and Hobson, 16088

(GH); 841--Maguire, 16956 (GH); 824--Maguire, 19611 (GH); 782--Munz and Johnston, 8528 (GH); 839--Pennell and Schaeffer, 22548 (GH); 847--Pennell and Schaeffer, 22865 (GH); 843--Pennell and Schaeffer, 23069 (GH); 812--Raven and Solbrig, 13277 (GH); 781--Ross, 64050 (GH); 807--Smith, 3781 (GH); 840--Vickery and Wiens, 1646 (GH); 2598--Welsh and Holmgren, 13887 (MO); 2597--Welsh and Taylor, 14429 (MO).

REGION L: 1038--Hartman, 531 (GH); 2164--Hernandez and Alexander, 305 (MICH); 1651--Hinton, 4203 (F); 2165--Knobloch, 105 (MICH); 248--Moore, 3422 (GH); 2463--Oliver and Verhoek-Williams, 558 (MO); 245--Pennell, 18388 (GH); 3453--Roivainen, s.n. (JEPS) s.n.; 2160--Rzedowski, 27914 (MICH); 246--Straw and Gregory, 1073 (GH); 2166--Straw and Gregory, 1073 (MICH); 2161--Ventura, 3485 (MICH).

REGION S: 776--Furuse, s.n. (GH) s.n.; 767--Furuse, s.n. (GH) s.n.; 772--Maximowicz, s.n. (GH) s.n.; 773--Tokubuchi, s.n. (GH) s.n.; 3509--Tokubuchi, s.n. (JEPS) s.n.

REGION X: 5532--Augustinowicz, s.n. (PH) 738382; 5534--Steinger, 166 (PH).

V. beccabunga ssp. beccabunga

REGION D: 652--Macoun, 67838 (GH); 653--Williams, s.n. (GH) s.n.

REGION N: 768--Pennell, 12632 (GH).

REGION U: 775--Yu, 5876 (GH).

REGION V: 2289--Stewart, 6260 (MO); 971b--Stewart, 19459 (GH).

REGION W: 2292--Gibbons, 540 (MO); 4423--Haussknecht, 2552 (PH); 4530--Koelz, 11899 (PH); 966a--Koelz, 11931 (GH); 4528--Mundkur, s.n. (PH) 810643.

REGION X: 1163--Dabkowska, s.n. (F) 927149; 3074--Litwinow, 1782 (US); 4324--Litwinow, 1924 (PH); 4422--Luga, 458 (PH).

REGION Y: 118--Getronk, 891 (GH); 3361--Hansen, 10184 (JEPS); 627--Jeppesen and Holm-Nielsen, 625 (GH);

117--Klammerth, 785 (GH); 2555--Schneider, 333 (MO); 1175--Smith, s.n. (F) 840532; 1159--Werdermann, 198 (F).

REGION Z: 631--Blaise, s.n. (GH) s.n.; 5474--Bokman, s.n. (PH) 654621; 2633--Florstrom, 913 (MO); 2661--Fredskild, s.n. (MO) 2386946; 3370--Magnusson, 13031 (JEPS); 1173--Johansson, s.n. (F) 824598; 1161--Kjellmert, s.n. (F) 1553415.

REGION AA: 633--Cavana and Spencer, s.n. (GH) s.n.; 113--R.M.G., s.n. (GH) s.n.; 3799--Pisani, s.n. (UC) 996465; 2921--Gross, s.n. (US) 1666340; 624--Lawalree, 13763 (GH); 1174--Munros, s.n. (F) 67546; 635--Raine, s.n. (GH) s.n.; 3805--Roivainen, s.n. (UC) 113135; 4429--Sennen, 6633 (PH).

REGION BB: 3363--Baggs, s.n. (UBC) 71340; 638a--Ball, s.n. (GH) s.n.; 3365--Cowan, s.n. (UBC) 3101; 625--Milderis, 647 (GH); 5473--Pennell, s.n. (PH) 681639.

REGION CC: 628--Balansa, s.n. (GH) s.n.; 2308--Gandoger, s.n. (MO) 104180; 3803--Quer, 370 (UC); 3802--Quer, 411 (UC).

V. cana

REGION V: 2079--Reid, 5863 (MICH).

V. capitata

REGION U: 4199--Delavay, 2668 (PH).

V. cephaloides

REGION V: 3076--Polunin, Sykes, and Williams, 2624 (US).

V. ciliata

REGION U: 4104--Ikonnikov-Galitzky, 1122 (JEPS).

V. himalanensis

REGION U: 881--Gahm, s.n. (GH) s.n.

V. hirta

REGION V: 2213--Parmanand, 993 (MICH).

V. koelzii

REGION V: 2214--Koelz, 5509 (MICH).

V. grandiflora

REGION A: 2944--McDonald, 395 (US).

REGION X: 2210--Everdam, s.n. (MICH) s.n.

V. montana

REGION AA: 109--Patten, 293 (GH).

V. morrisonicola

REGION S: 2118--Bartlett, 6204 (MICH); 3953--Kanehira and Sasaki, 21778 (JEPS).

V. orientalis

REGION W: 2055--Koelz, 17476 (MICH).

V. rockii

REGION U: 4237--Rock, 14600 (PH).

V. scardica

REGION Y: 2174--Degen, 871 (MICH); 3771--Degen, 871 (JEPS); 2127--Moesz and Javorka, 871 (MICH); 3770--Moesz and Javorka, 871 (JEPS); 3769--Rechinger, 18573 (JEPS).

Appendix C

REGIONAL PHENOGRAMS AND MST'S

LEGEND

Symbol

AA- *V. anagallis-aquatica*

AN- *V. anagalloides*

BA- *V. beccabunga* ssp. *americana*

BB- *V. beccabunga* ssp. *beccabunga*

SC- *V. scardica*

NB- *Veronica* not allied to section *Beccabunga*

In all of the regional phenograms and MST's throughout North America, excluding region L and A (Mexico and Alaska, respectively), two distinct groups, V. anagallis-aquatica and V. beccabunga, are readily apparent. CHARANAL distance values revealed these two groups to be monothetic for leaf base shape. The exemplars of regions L and A comprise only one taxon, V. beccabunga, of section Beccabunga.

Region N consists of exemplars of section Beccabunga throughout South America. V. anagallis-aquatica ranges throughout the Andes Mountains, while V. beccabunga, represented by OTU #768, is present as only an isolated introduction in Puerto Mont, Chile.

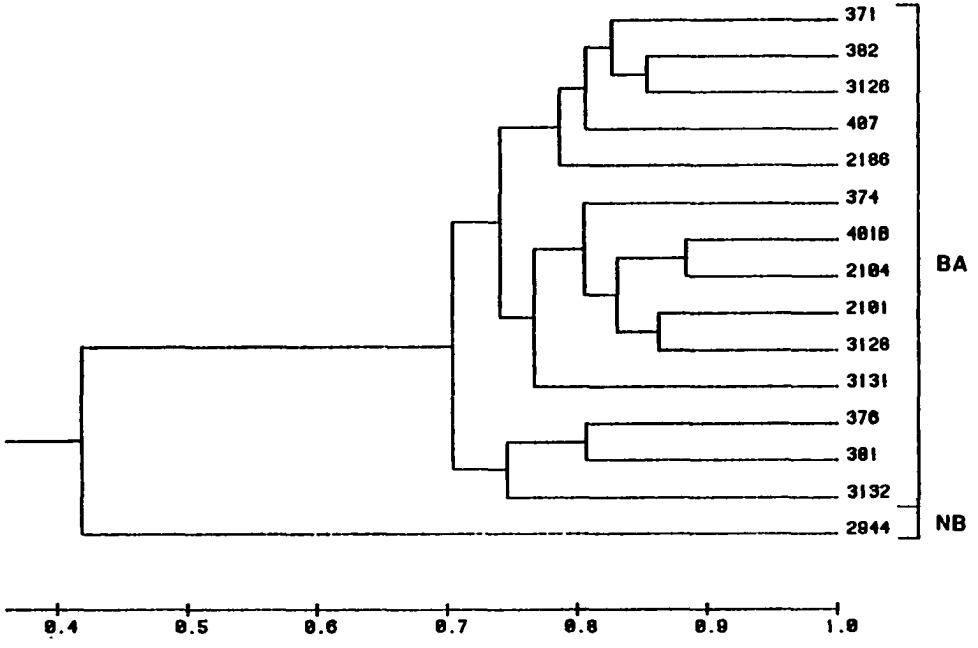
Regions CC, DD, and EE are in Africa. V. anagallis-aquatica is found throughout much of Africa as well as on nearby islands off the northwest coast. Only one taxon, V. anagallis-aquatica, of section Beccabunga is evident in southern Africa (fig. C.22). In regions CC and EE of northern Africa, V. beccabunga is in Morocco and Algeria, while V. anagalloides extends into Egypt.

Regions of eastern Asia, S and U, reveal two taxa within section Beccabunga, V. anagallis-aquatica and V. beccabunga,

consistent with phenograms of North America. In regions S and U, exemplars of other sections, labeled NB, were included in the analysis in order to define sectional parameters. Also, in region U, exemplars of taxa that were formerly included in this section were included. Consequently, V. himilanensis (#881) and V. ciliata (#4104) should be excluded from section Beccabunga.

The following discussion involves the regions of western Asia and Europe, where the greatest diversity within this section occurs. In regions V, W, Z, and BB two distinct groups, V. anagallis-aquatica and V. beccabunga, are indicated. In regions X and AA three taxa are apparent, V. anagallis-aquatica, V. anagalloides, and V. beccabunga. In region Y, the Balkan region of Europe, four taxa are clearly illustrated, V. anagallis-aquatica, V. anagalloides, V. beccabunga, and V. scardica.

Fig. C.1. Phenogram and MST of *Veronica* section *Beccabunga* in region A (CCC .899).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2101
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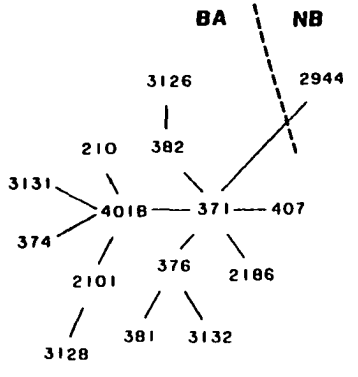
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NB
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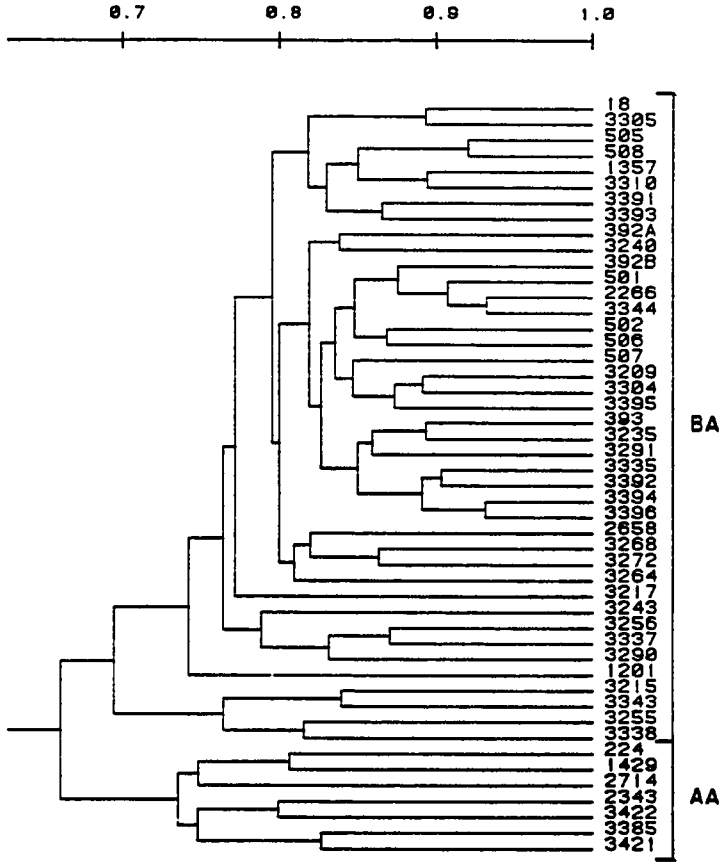
2944
210
382
3131
4018
371
407
374
376
2101
2186
381
3132
3128

Fig. C.2. Phenogram and MST of *Veronica* section *Beccabunga* in region C (CCC .813).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392B
501
2266
3344
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393
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3291
3335
3392
3394
3396
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3256
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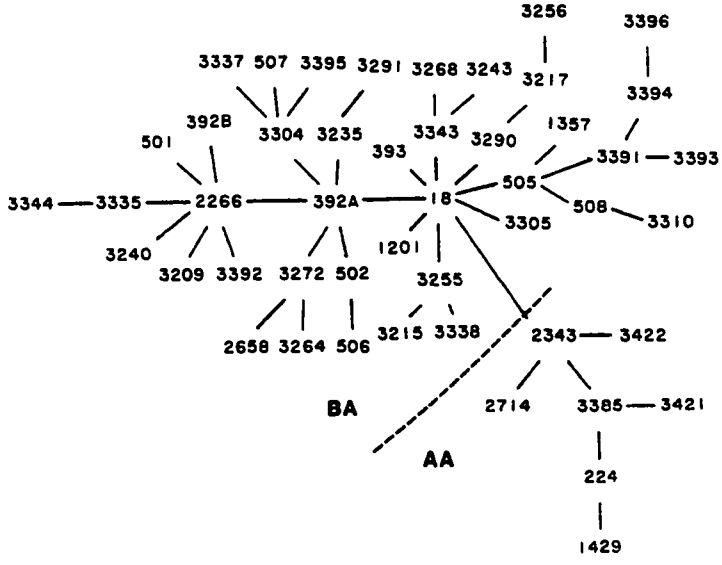
AA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3337 507 3395 3291 3268 3243
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392B
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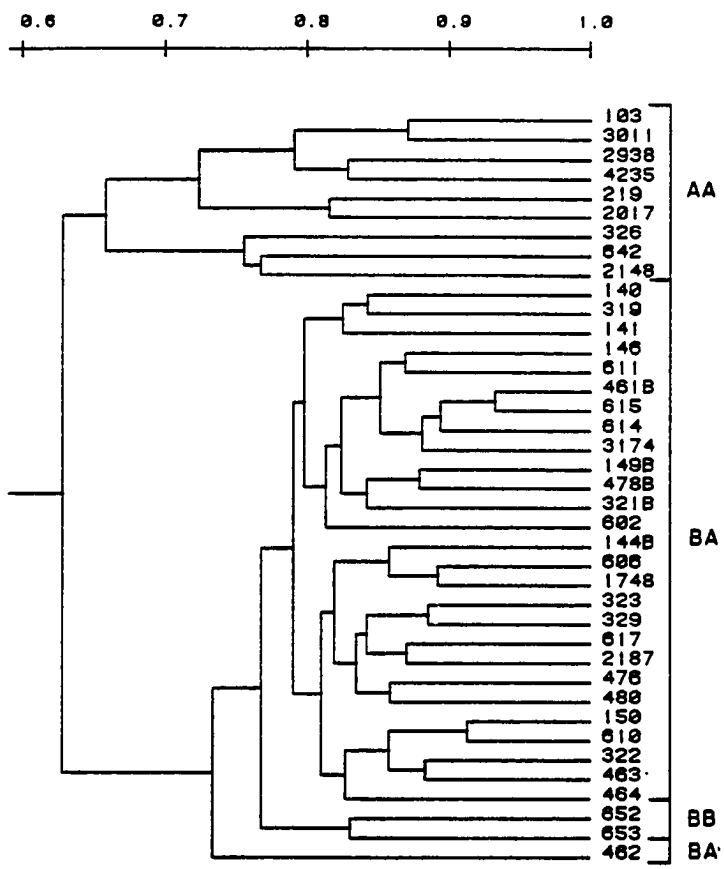
1357
501
393
3391 — 3393
505
3344 — 3335 — 2266 — 392A — 18
508 — 3310
3305
3240
1201
3209 3392 3272 502
3255
2658 3264 506
3215 3338
2343 — 3422
BA
2714
3385 — 3421
AA
224
1429

Fig. C.3. Phenogram and MST of Veronica section Beccabunga in region D (CCC .89).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611
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614
3174
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3218
602
1448
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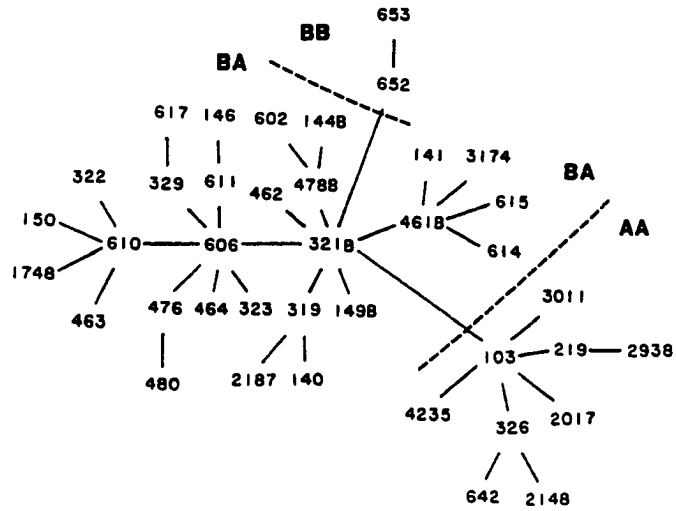
BA
BB
BA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3011
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464
323
319
1498
219
2938
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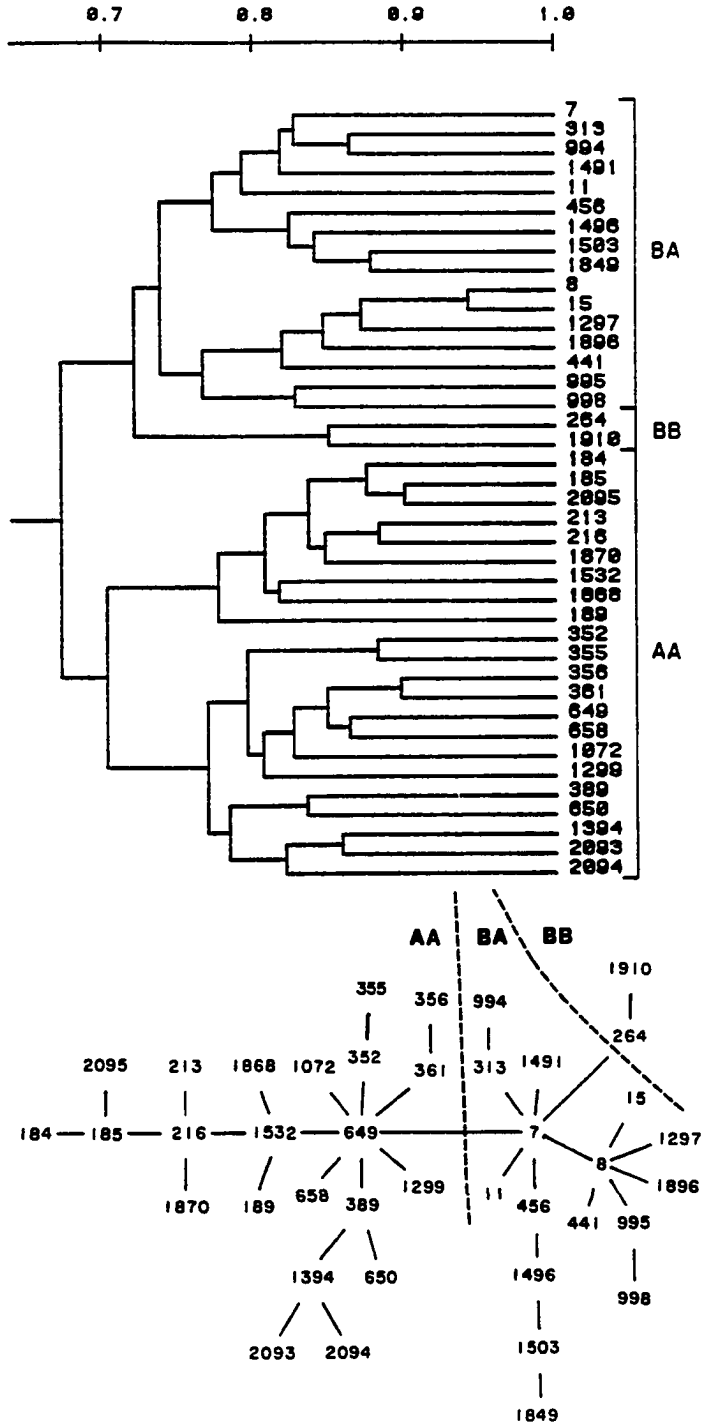
326
2017
642
2148

Fig. C.4. Phenogram and MST of Veronica section Beccabunga in region F (CCC .72).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995
998
264
1910
184
185
2095
213
216
1870
1532
1868
189
352
355
356
361
649
658
1072
1299
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1394
2093
2094
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BB
AA
AA
BA
BB
1910
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994
2095
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8
1896
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11
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441
995
1394
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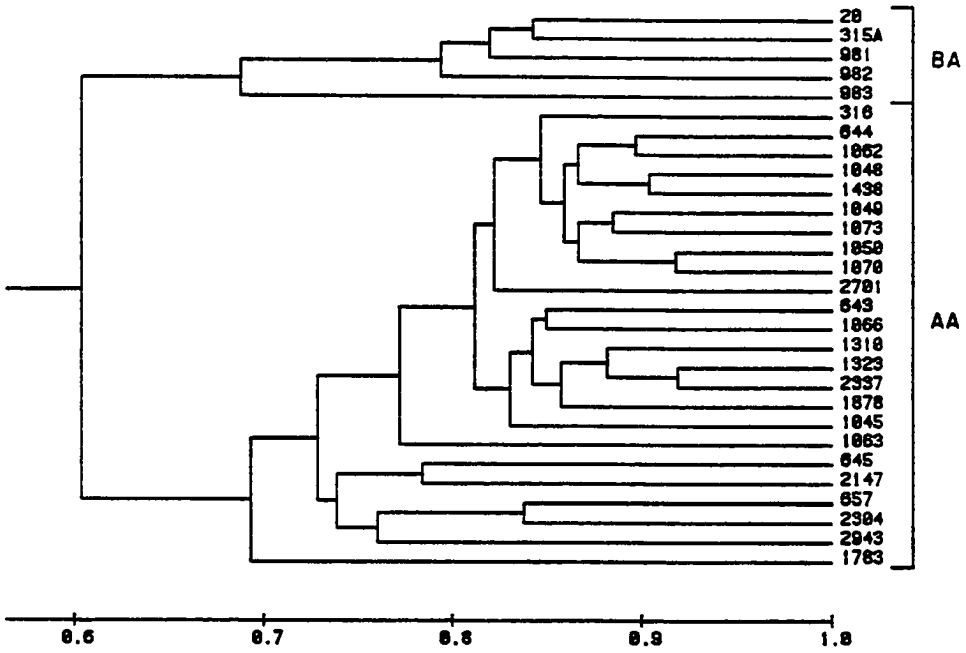
2094
1503
1849

Fig. C.5. Phenogram and MST of *Veronica* section *Beccabunga* in region G (CCC .91).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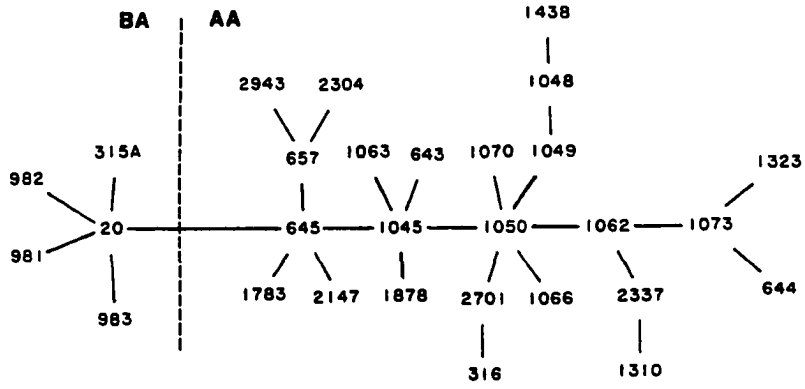
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1073
981
983
1783
2147
1878
2701
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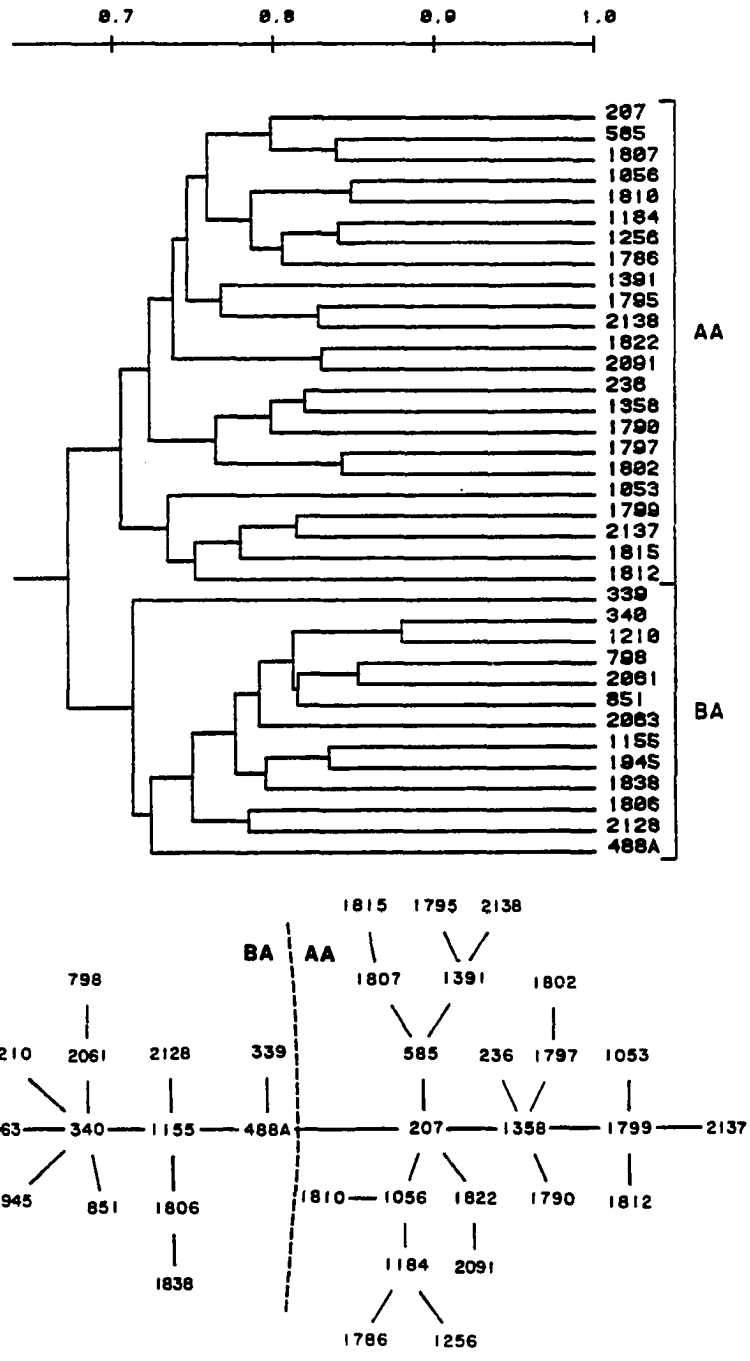
644
316
1310

Fig. C.6. Phenogram and MST of *Veronica* section *Beccabunga* in region H (CCC .65)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1815
1812
339
340
1210
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851
2063
1155
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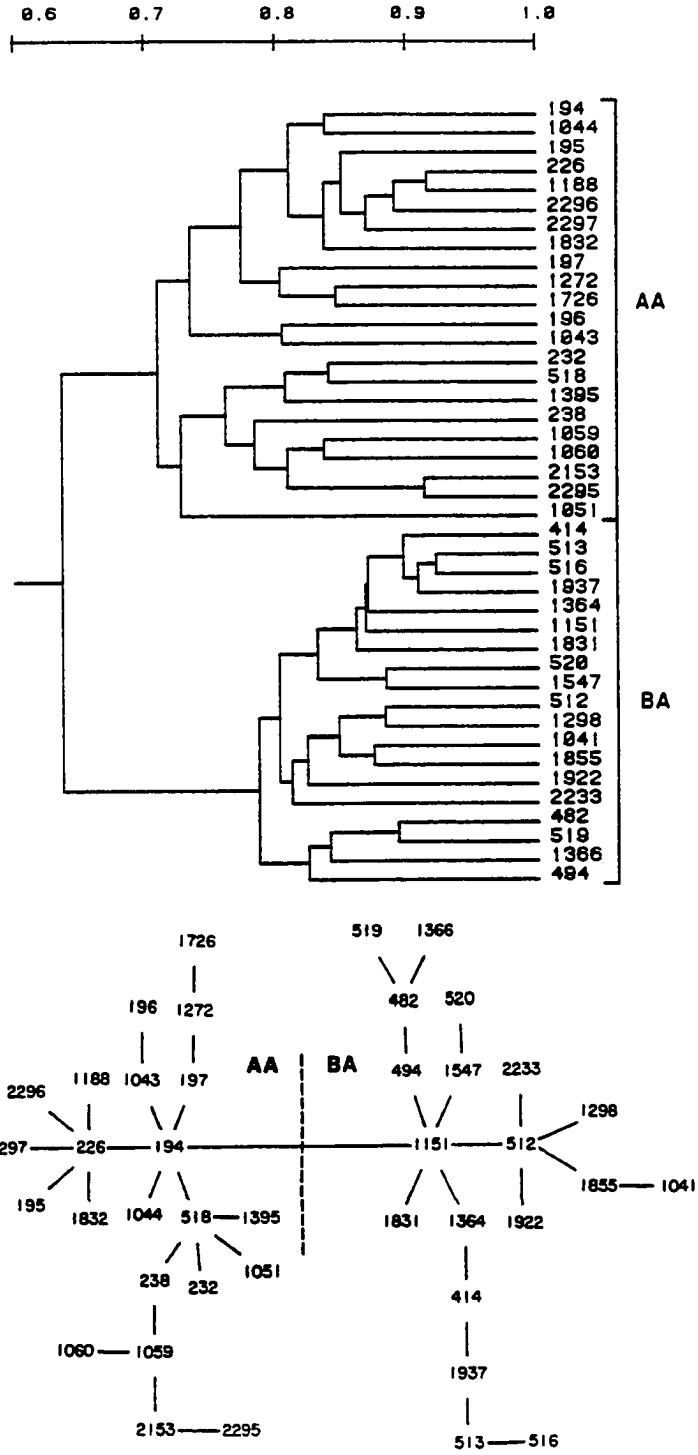
AA
BA

Fig. C.7. Phenogram and MST of *Veronica* section *Beccabunga* in region I (CCC .837).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1832
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1922
238
232
1051
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2295
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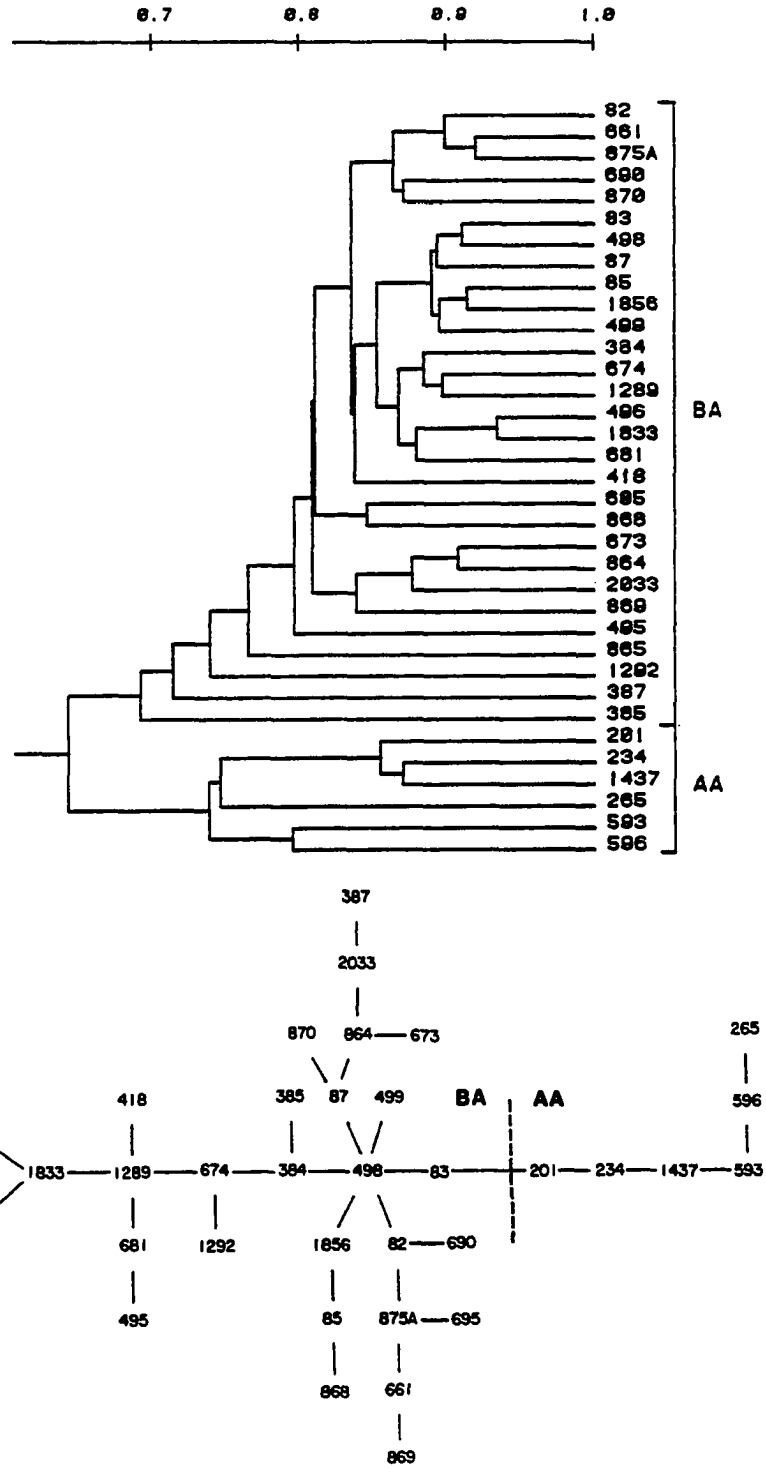
516

Fig. C.8. Phenogram and MST of *Veronica* section *Beccabunga* in region J (CCC .873).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673
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596
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387
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498
83
201
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1437
593
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681
1292
1856
82
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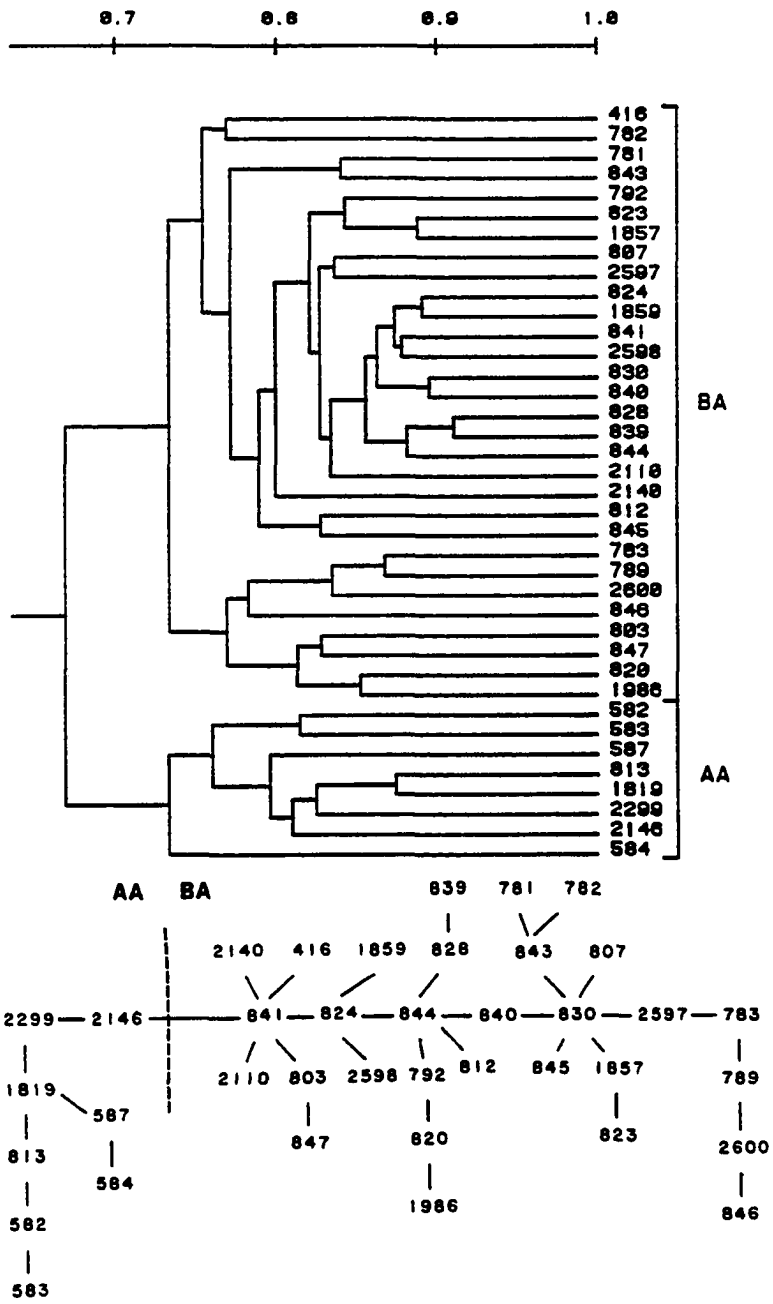
Fig. C.9. Phenogram and MST of *Veronica* section *Beccabunga* in region K (CCC .723).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830
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828
839
844
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803
847
820
1986
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584
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783
2110
803
2598
792
812
845
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789
1819
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820
823
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584
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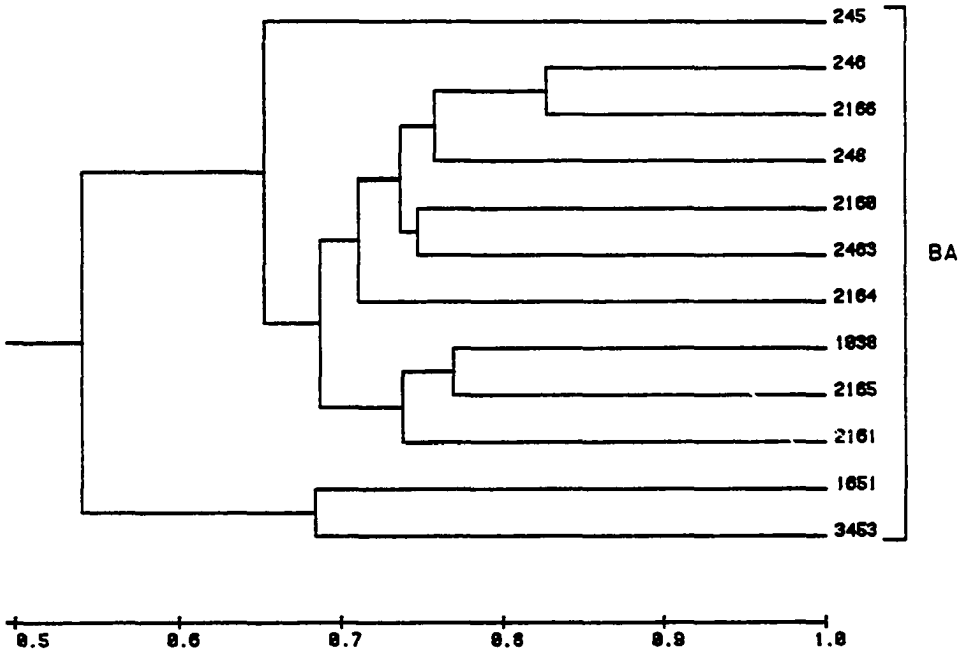
846
583

Fig. C.10. Phenogram and MST of Veronica section Beccabunga in region L (CCC .769).


245
246
2166
248
2168
2463
2164
1038
2165
2161
1651
3453
BA
0.5
0.6
0.7
0.8
0.9
1.0

BA

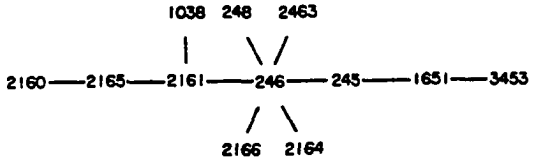
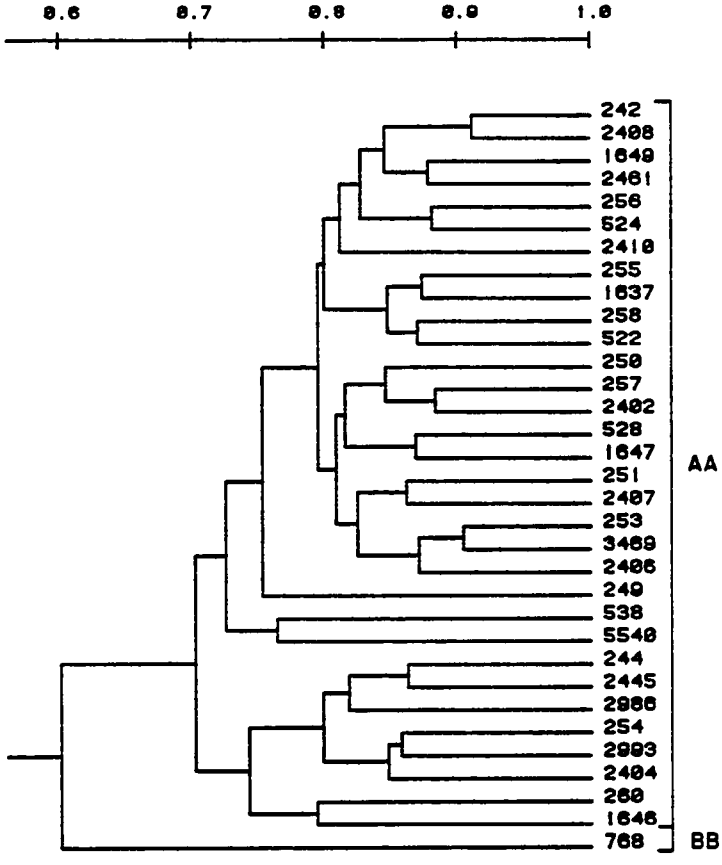

1038
248
2463
2160
2165
2161
246
245
1651
3453
2166
2164

Fig. C.11. Phenogram and MST of *Veronica* section *Beccabunga* in region N (CCC .803).


0.6
0.7
0.8
0.9
1.0
242
2408
1649
2461
256
524
2410
255
1637
258
522
250
257
2402
528
1647
251
2407
253
3469
2406
249
538
5540
244
2445
2986
254
2993
2404
260
1646
768
AA
BB

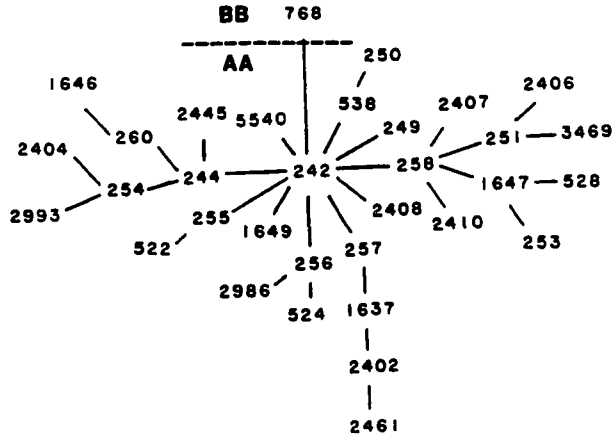
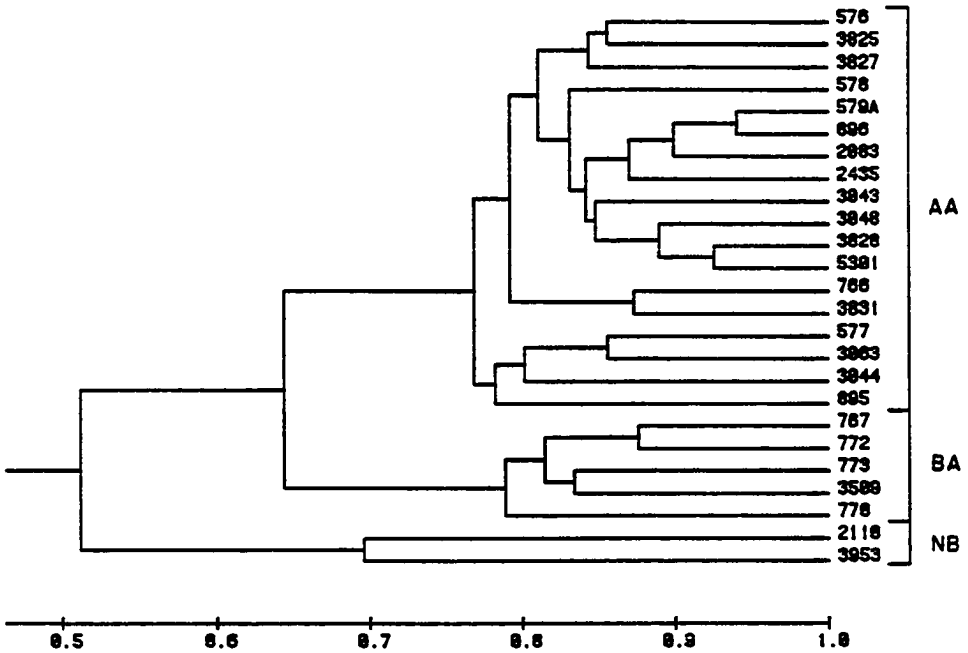

BB
768
AA
250
1646
538
2406
2407
2445
5540
249
251
3469
2404
260
258
244
242
1647
528
254
2408
2410
2993
255
1649
253
522
257
256
2986
524
1637
2402
2461

Fig. C.12. Phenogram and MST of *Veronica* section *Beccabunga* in region S (CCC .93).


576
3825
3827
578
579A
696
2083
2435
3843
3848
3828
5391
766
3831
577
3063
3844
695
767
772
773
3509
776
2118
3953
AA
BA
NB
0.5
0.6
0.7
0.8
0.9
1.0

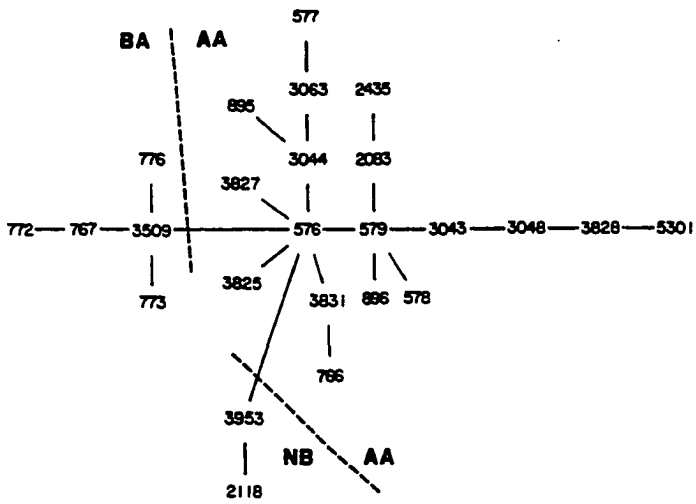
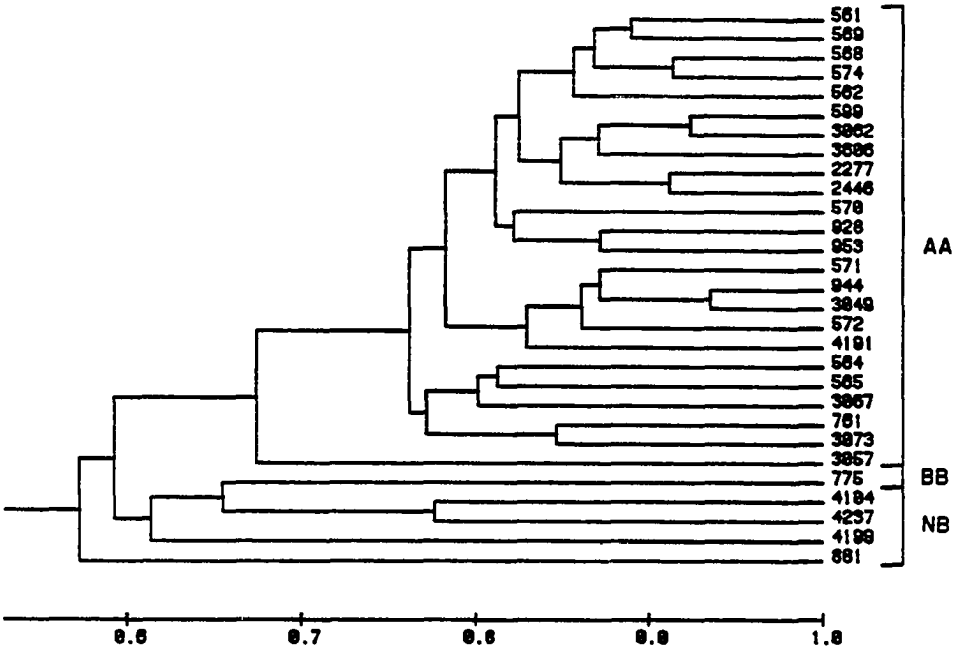

577
BA
AA
3063
2435
695
3044
2083
776
3827
772
767
3509
576
579
3043
3048
3828
5301
3825
773
3831
696
578
766
3953
NB
AA
2118

Fig. C.13. Phenogram and MST of *Veronica* section *Beccabunga* in region U (CCC .907).


561
569
568
574
562
599
3862
3686
2277
2446
578
928
953
571
944
3849
572
4191
564
565
3867
761
3873
3857
775
4184
4237
4199
881
AA
BB
NB
0.6
0.7
0.8
0.9
1.0

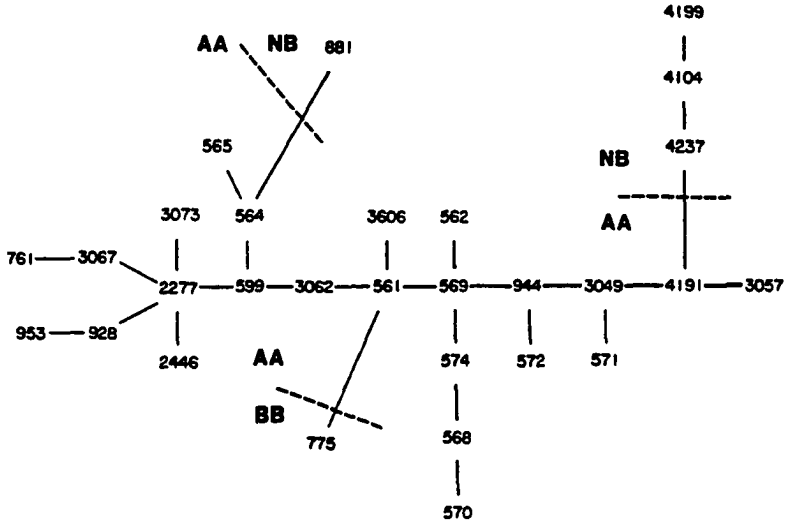
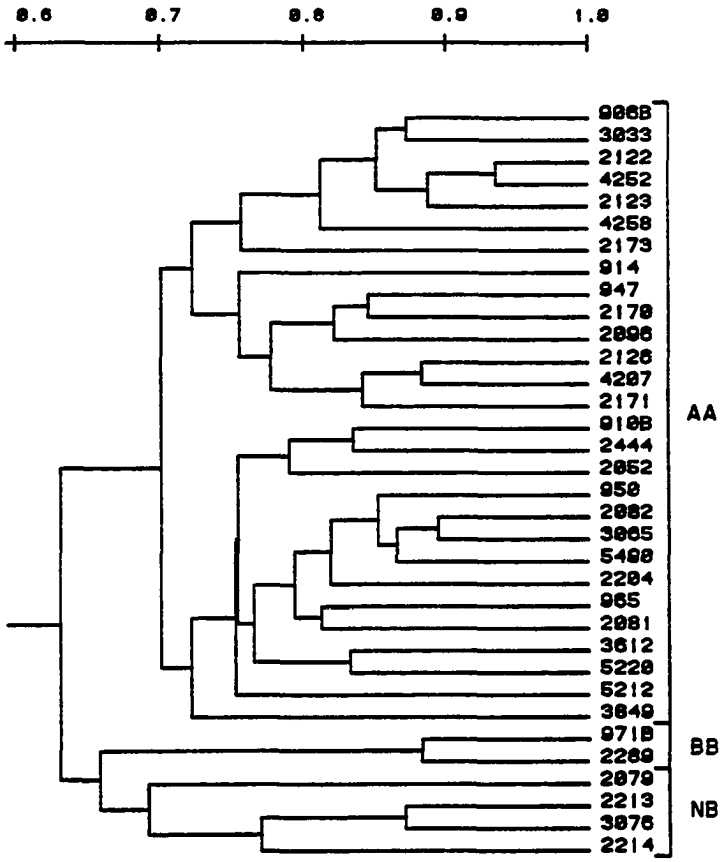

AA
NB
881
565
3073
564
3606
562
4199
4104
4237
NB
AA
761
3067
2277
599
3062
561
569
944
3049
4191
3057
953
928
2446
AA
574
572
571
BB
775
568
570

Fig. C.14. Phenogram and MST of *Veronica* section *Beccabunga* in region V (CCC .772).


0.6
0.7
0.8
0.9
1.0
9068
3033
2122
4252
2123
4258
2173
914
947
2170
2096
2126
4207
2171
AA
9108
2444
2052
950
2082
3065
5490
5212
3612
5220
3849
9718
BB
2289
2079
2213
3076
2214
NB

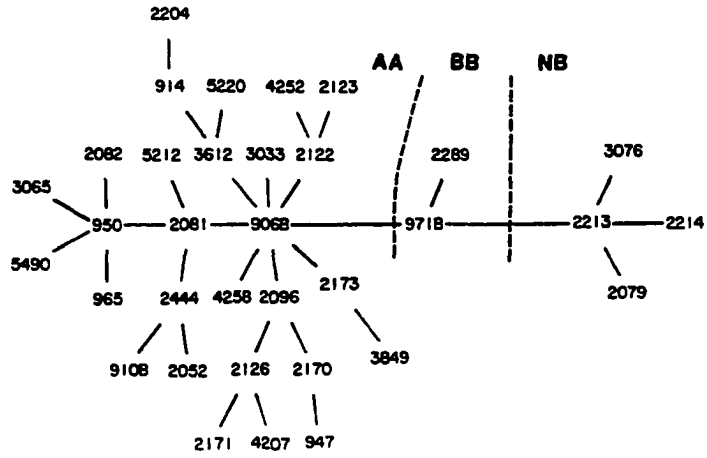
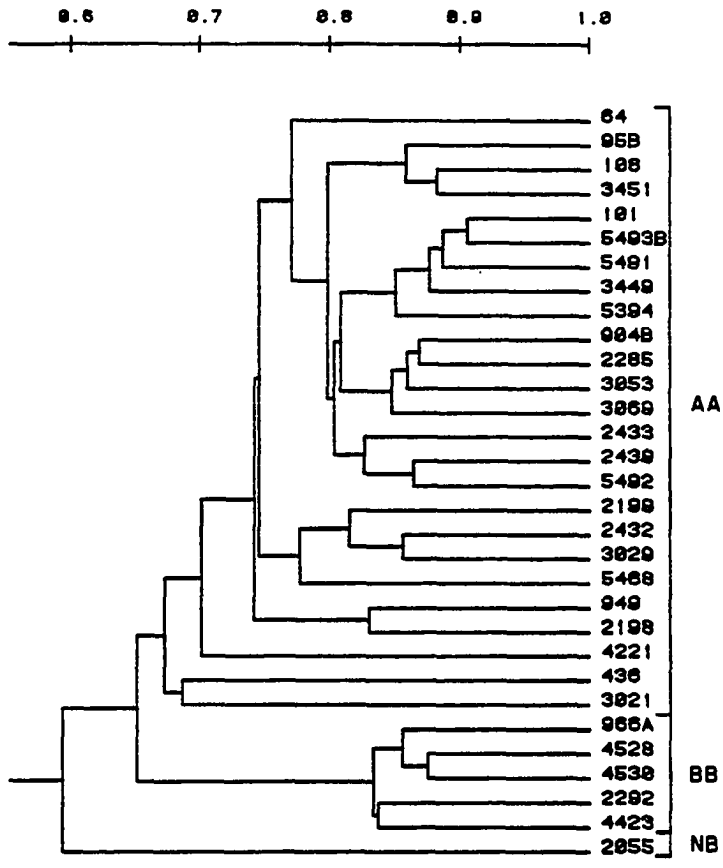

2204
914
5220
4252
2123
AA
BB
NB
2082
5212
3612
3033
2122
2289
3076
3065
950
2081
9068
9718
2213
2214
5490
965
2444
4258
2096
2173
2079
9108
2052
2126
2170
3849
2171
4207
947

Fig. C.15. Phenogram and MST of *Veronica* section *Beccabunga* in region W (CCC .85).


0.6
0.7
0.8
0.9
1.0
64
95B
108
3451
101
5493B
5491
3449
5394
904B
2285
3053
3069
AA
2433
2439
5492
2199
2432
3029
5468
949
2198
4221
436
3021
966A
4528
4530
BB
2292
4423
2055
NB

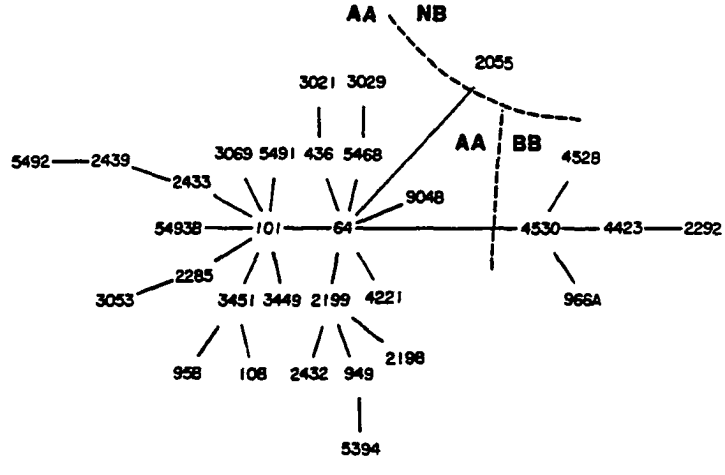

AA
NB
2055
3021 3029
AA
BB
5492
2439
2433
3069 5491 436 5468
4528
9048
5493B
101
64
4530
4423
2292
2285
3053
3451 3449 2199 4221
966A
958
108
2432
949
2198
5394

Fig. C.16. Phenogram and MST of Veronica section Beccabunga in region X (CCC .869).

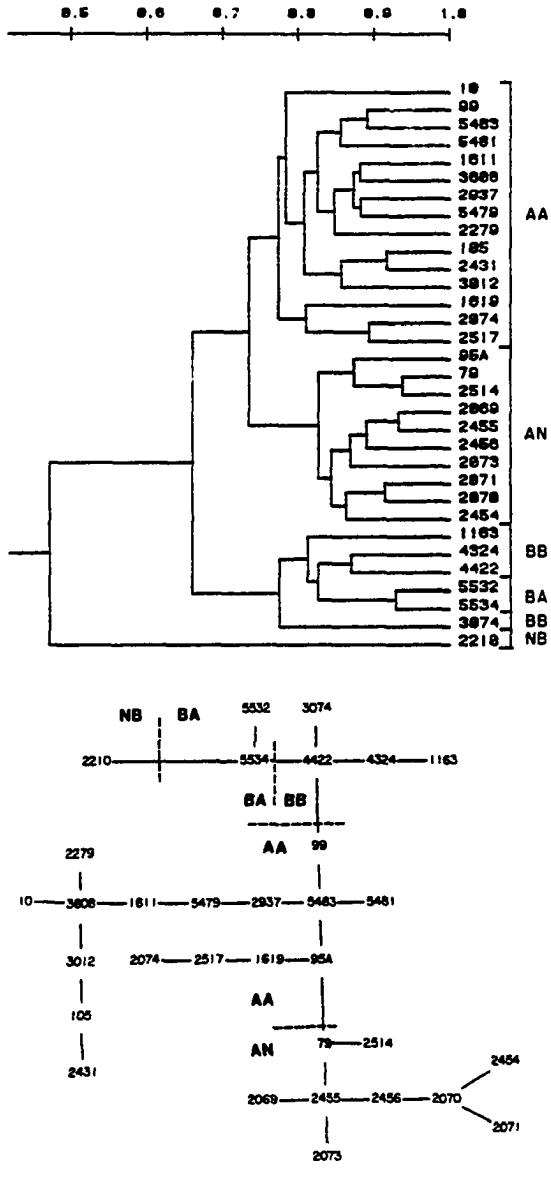

0.5
0.6
0.7
0.8
0.9
1.0
10
99
5483
5481
1611
3808
2937
5479
2279
185
2431
3012
1619
2074
2517
AA
95A
79
2514
2069
2455
2456
2070
2454
2071
AN
1163
4324
4422
BB
5532
5534
BA
3074
BB
2218
NB
NB
BA
5532
3074
2210
5534
4422
4324
1163
BA
BB
AA
99
2279
10
3808
1611
5479
2937
5483
5481
3012
2074
2517
1619
95A
AA
105
AN
79
2514
2454
2431
2069
2455
2456
2070
2071
2073

Fig. C.17. Phenogram and MST of Veronica section Beccabunga in region Y (CCC .769).

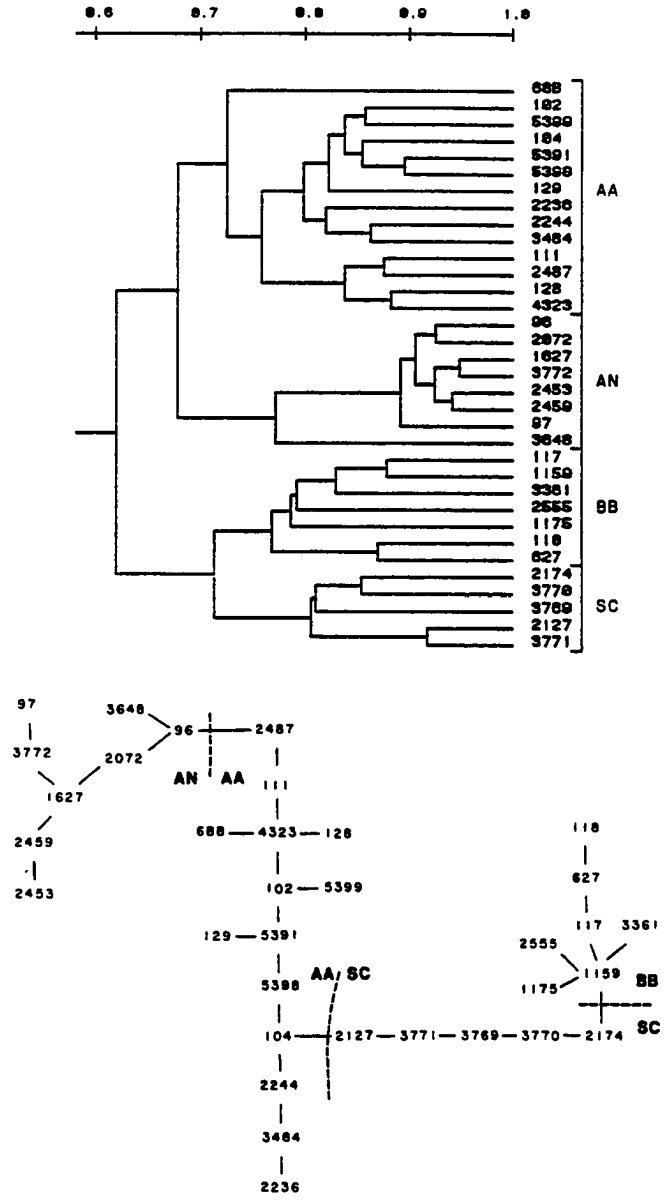
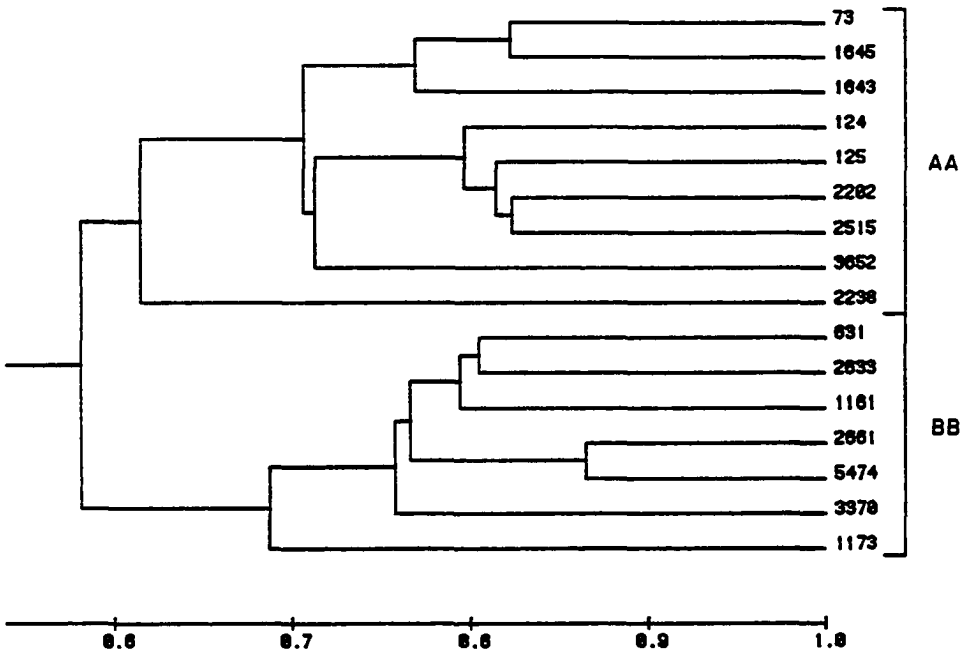

0.6
0.7
0.8
0.9
1.0
688
182
5399
184
5391
5398
129
2236
2244
3484
111
2487
128
4323
96
2072
1627
3772
2453
2459
97
3648
117
1159
3361
2555
1175
118
627
2174
3770
3769
2127
3771
AA
AN
BB
SC

Fig. C.18. Phenogram and MST of *Veronica* section *Beccabunga* in region Z (CCC .814).


73
1645
1643
124
125
2202
2515
3652
2238
AA
631
2633
1161
2661
5474
3978
1173
BB
0.6
0.7
0.8
0.9
1.0

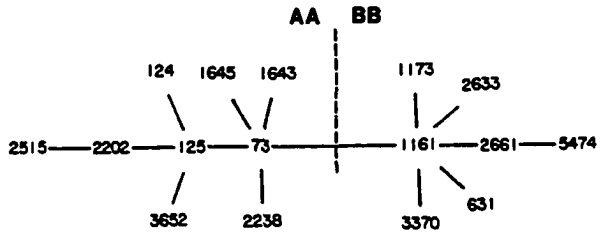
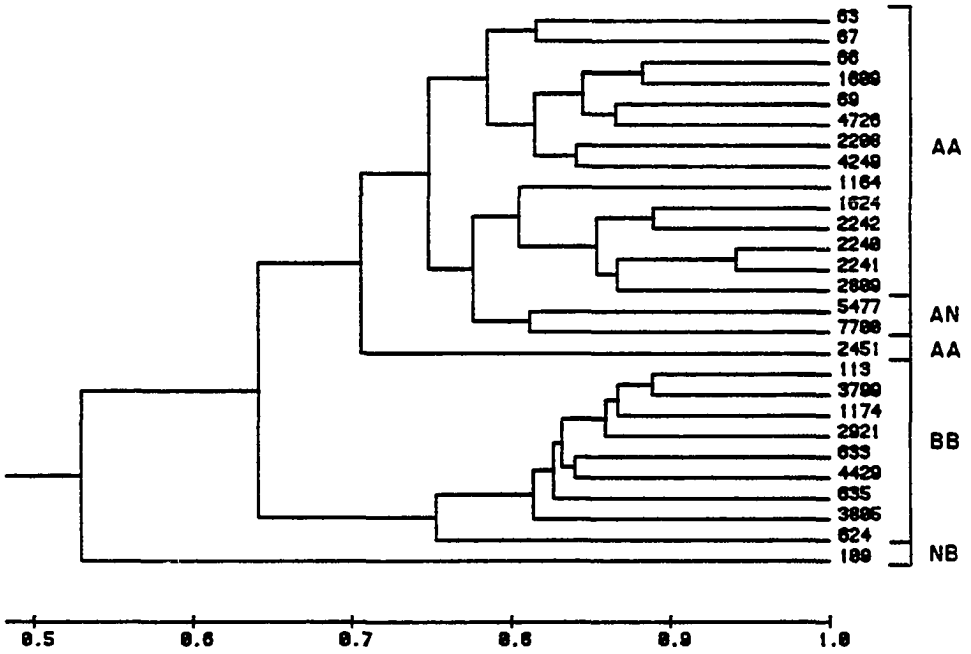

AA
BB
124
1645
1643
1173
2633
2515
2202
125
73
1161
2661
5474
3652
2238
3370
631

Fig. C.19. Phenogram and MST of Veronica section Beccabunga in region AA (CCC .807).


63
67
66
1609
69
4726
2208
4249
1164
1624
2242
2240
2241
2809
5477
7700
AA
AN
AA
2451
113
3799
1174
2921
635
633
4429
635
3805
624
189
NB
BB
0.5
0.6
0.7
0.8
0.9
1.0

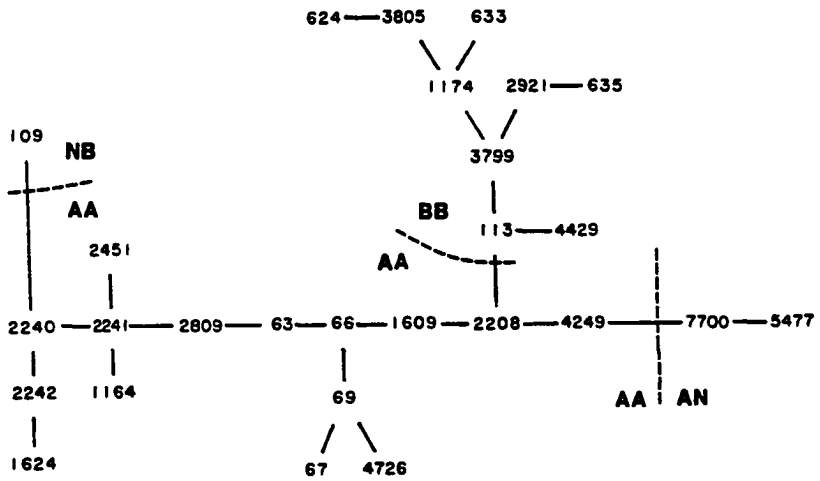
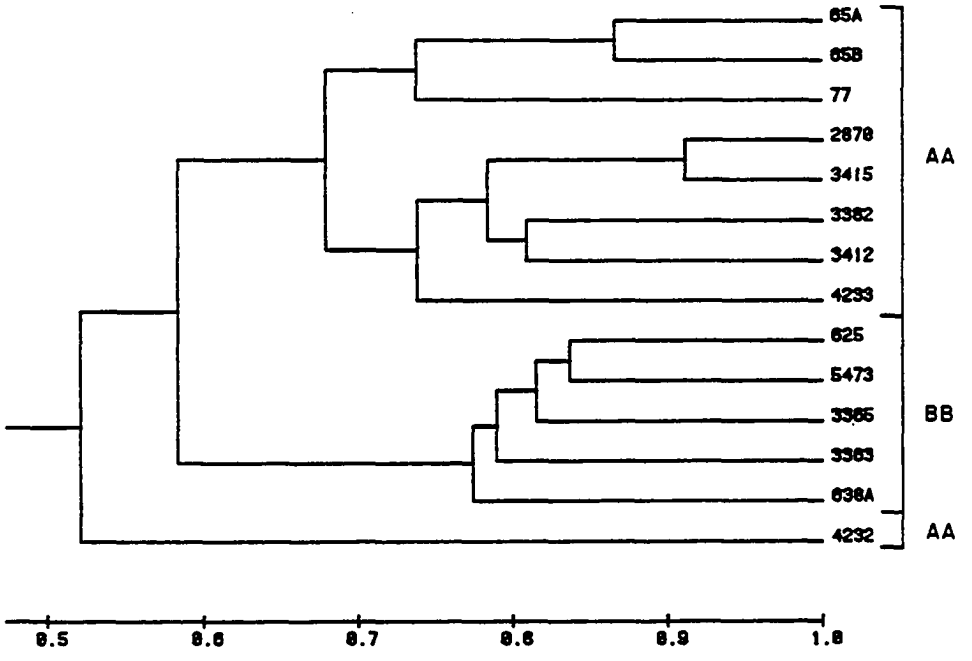

624
3805
633
1174
2921
635
3799
109
NB
AA
BB
113
4429
AA
2451
2240
2241
2809
63
66
1609
2208
4249
7700
5477
2242
1164
69
AA
AN
1624
67
4726

Fig. C.20. Phenogram and MST of *Veronica* section *Beccabunga* in region BB (CCC .871).


65A
65B
77
2870
3415
3382
3412
4233
AA
625
5473
3365
BB
3363
638A
4232
AA
0.5
0.6
0.7
0.8
0.9
1.0

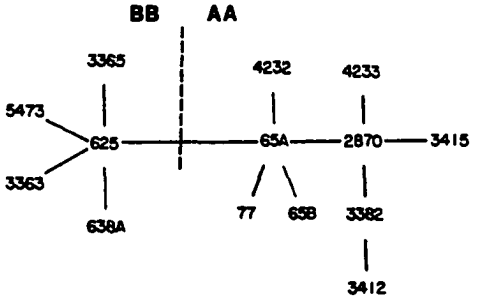
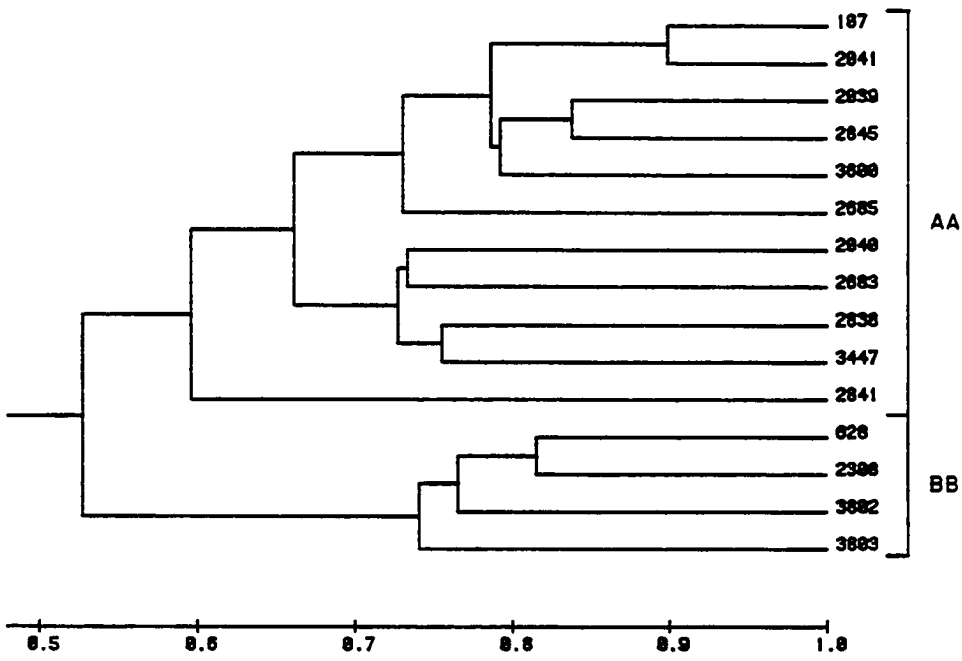

BB
AA
3365
4232
4233
5473
625
65A
2870
3415
3363
77
65B
3382
638A
3412

Fig. C.21. Phenogram and MST of Veronica section Beccabunga in region CC (CCC .894).


187
2841
2839
2845
3600
2685
AA
2840
2683
2838
3447
2841
628
2308
BB
3802
3803
0.5
0.6
0.7
0.8
0.9
1.0

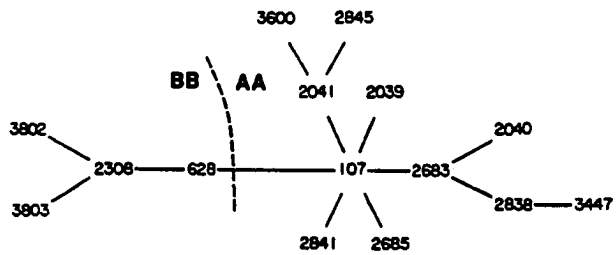
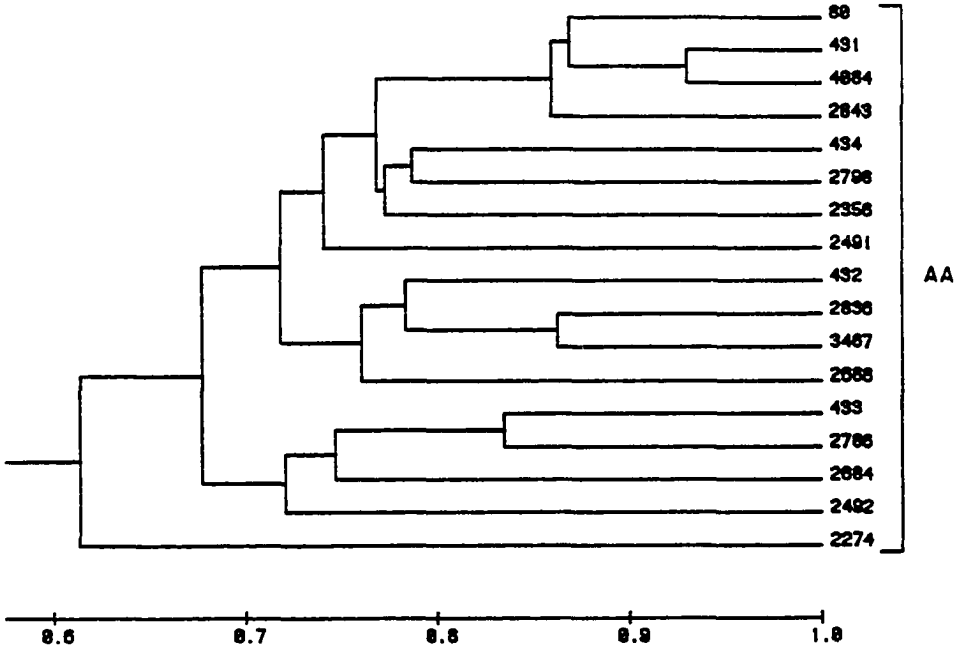

3600
2845
BB
AA
2041
2039
3802
2040
2308
628
107
2683
3803
2838
3447
2841
2685

Fig. C.22. Phenogram and MST of *Veronica* section *Beccabunga* in region DD (CCC .774).


80
431
4084
2843
434
2798
2356
2491
432
2836
3467
2688
2492
2684
433
2786
2274
AA
0.6
0.7
0.8
0.9
1.0

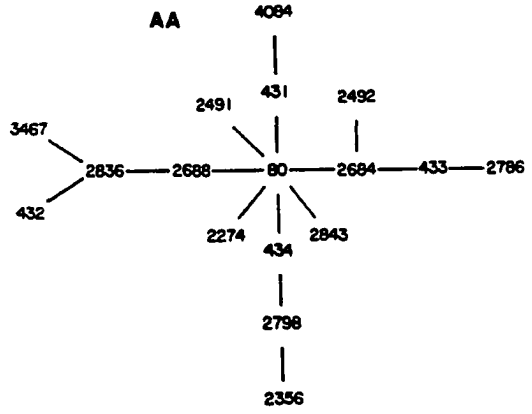
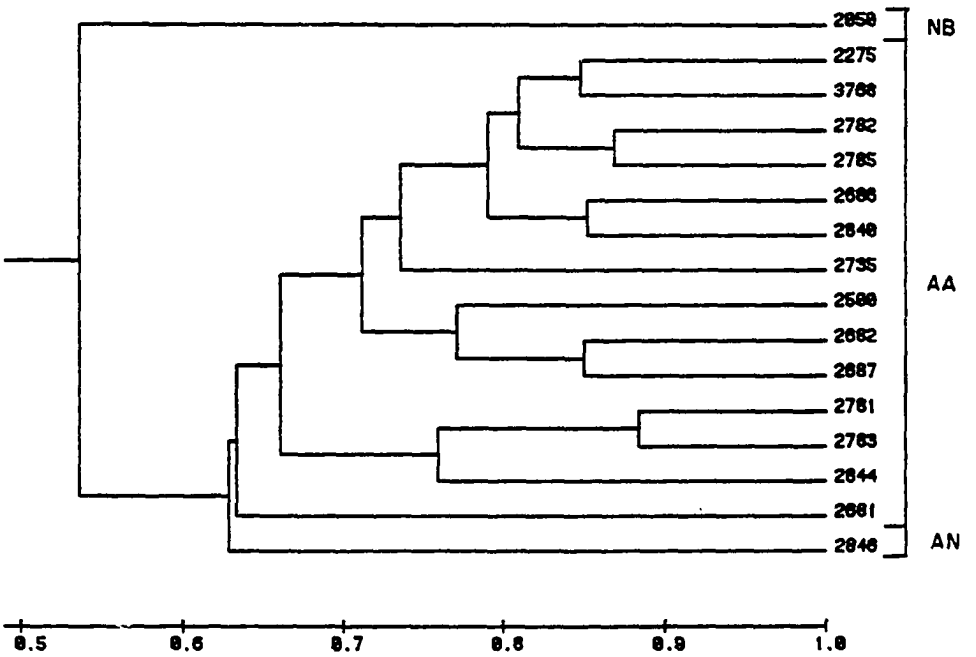
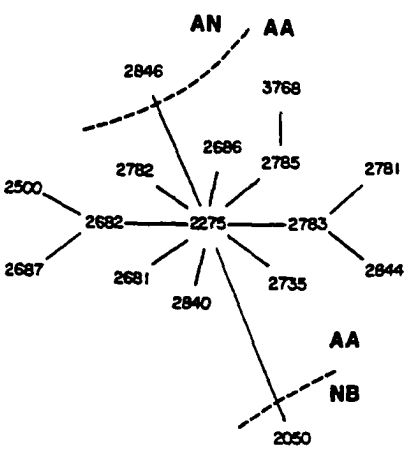

AA
4084
431
2491
2492
3467
2836
2688
80
2684
433
2786
432
2274
434
2843
2798
2356

Fig. C.23. Phenogram and MST of *Veronica* section *Beccabunga* in region EE (CCC .849).


2850
2275
3768
2782
2785
2686
2840
2735
2500
2682
2687
2681
2783
2844
2846
NB
AA
AN
0.5
0.6
0.7
0.8
0.9
1.0


AN
AA
2846
3768
2686
2782
2785
2781
2500
2682
2275
2783
2687
2681
2840
2735
2844
AA
NB
2050

Appendix D

DISTRIBUTION OF TAXA OF VERONICA SECTION BECCABUNGA

Each population represented by a herbarium specimen of taxa of Veronica section Beccabunga is represented by a dot. V. anagallis-aquatica is represented in Australia and New Zealand by only two specimens; therefore, a map of this region is not included for this taxon. V. beccabunga ssp. beccabunga is represented in the vicinity of Puerto Mont, Chile by approximately ten specimens. However, these are the only collections of this taxon from South America; therefore, a map of this region for this taxon is not included.

Fig. D.26. African distribution of V. anagallis-aquatica.

Fig. D.27. Eurasian distribution of V. anagallis-aquatica.

Fig. D.28. North American distribution of *V. anagallis-aquatica*.

Fig. D.29. South American distribution of *V. anagallis-aquatica*.

Fig. D.30. Eurasian distribution of *V. anagalloides*.

Fig. D.31. Asian distribution of V. beccabunga ssp. americana.

Fig. D.32. North American distribution of *V. beccabunga* ssp. *americana*.

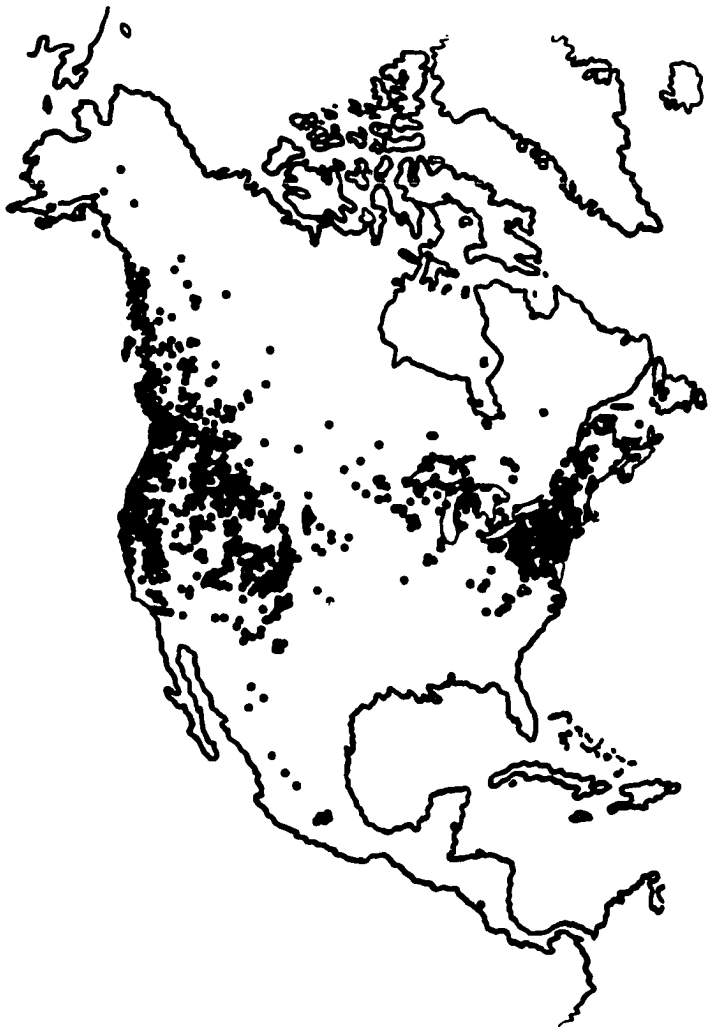


Fig. D.33. African distribution of V. beccabunga ssp. beccabunga.

Fig. D.34. Eurasian distribution of V. beccabunga ssp. beccabunga.

Fig. D.35. North American distribution of V. beccabunga ssp. beccabunga.

Fig. D.36. Eurasian distribution of V. scardica.