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A taximetric study of interspecific variation in Vitis

by

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Principal classifications of *Vitis* have been made by Planchon (1887), and Foex (1895) in France and by Munson (1909), and Bailey (1934) in the United States. These classifications are characterized by a wide disparity in the number and geographical origin of *Vitis* forms studied, in the recognition of species validity, and in the interpretation of species relationships.

The development of quantitative methods of measuring similarities between organisms and grouping these organisms into classes on the basis of similarities offers an additional means of reducing subjectivity in assessing affinity among species of *Vitis*. Details on the procedures and statistical techniques for these methods are described by Sokal and Sneath (1963).

The objectives of the present study were to quantify the degree of resemblance shown among various *Vitis* species based on a large number of characters, and to compare the phenetic relationships thus indicated with the classical systematic interpretations.

Materials and Methods

Twenty-one species of *Vitis* from the breeding collection growing on the Horticultural Farm of the University of Illinois were utilized for this study. Species included in the study, their code numbers, number of clones and origins are presented in Table 1. Average scores on 71 characters (see appendix) for from 2 to 20 clones of each species provided the data from which similarity coefficients were computed.

Three separate measures of phenetic similarity were computed for each species pair: the product-moment correlation coefficient (r), the distance coefficient (d) of Sokal (1961), and the divergence coefficient (D) of Clark (1952). When computing divergence coefficients a geometrical sequence of integers (eg: 1, 2, 4 . . .) was used for score values rather than the arithmetice sequence used in computing the correlation and distance coefficients. This geometrical sequence stabilizes the effects of the denominator in the divergence coefficient (Rhodes *et al.*, 1968). For the same reason scores were not standardized when computing divergence coefficients as was done before computing the correlation and distance coefficients. Phenograms, Figures 1—3, were constructed for all three types of similarity coefficients by the unweighted pair-group method of clustering using simple averages.

Because the magnitude of distance and divergence coefficients represents the degree of dissimilarity rather than similarity, the sign of each was reversed prior to cluster analysis. This was unnecessary in the case of the correlation coefficients, because they represent the degree of similarity. Computations were performed using University of Illinois Agronomy Statistical Laboratory programs on an IBM 7094 computer.

Results and Discussion

Differences exist between the three phenograms as shown in Figures 1—3. This would not be entirely unexpected since the r phenogram, which is based upon the

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Table 1

Vitis species and their geographical origin

Code number	No. of clones	Species	Origin
01	9	*V. riparia* Michaux	Illinois, Manitoba
02	15	*V. rupestris* Scheele	Missouri, Texas
03	3	*V. longii* Prince	Texas
04	5	*V. doaniana* Munson	Texas
05	20	*V. cinerea* Engelmann	Illinois, Indiana
06	12	*V. berlandieri* Planchon	Texas
07	18	*V. tiliaefolia* Humboldt & Bonpland	Puerto Rico
08	9	*V. cordifolia* Michaux	Illinois
09	10	*V. rubra* Michaux	Illinois
10	6	*V. monticola* Buckley	Texas
11	2	*V. baileyana* Munson	West Virginia
12	5	*V. bicolor* LeConte	Illinois
13	4	*V. aestivalis* Michaux	Virginia
14	5	*V. lincecumii* Buckley	Missouri, Kansas
15	5	*V. candicans* Engelmann	Texas
16	6	*V. champini* Planchon	Texas
17	2	*V. labrusca* Linnaeus	North Carolina
18	7	*V. vinifera* Linnaeus	Western Asia
19	2	*V. amurensis* Ruprecht	Northeastern Asia
20	4	*V. bourquiniana* Munson	South Carolina
21	16	*V. rotundifolia* Michaux	North Carolina, Arkansas

product-moment correlation coefficients, tends to emphasize shape while the d and D phenograms, which are based upon the distance and divergence coefficients, respectively, tend to emphasize both shape and size (Boyce, 1964; Rohlf and Sokal, 1965).

Primary affinity clusters

Although overall differences exist, certain congruities in primary affinity clustering are evident. These, arranged in approximate descending order of affinity and consistency, are as follows:

1. *V. aestivalis* and *V. lincecumii* have consistently formed clusters at quite high affinity levels in all phenograms.

2. *V. cinerea* and *V. tiliaefolia* show high affinity in the r and d phenograms but in the D phenogram *V. cinerea* and *V. berlandieri* have formed the primary cluster by a narrow margin over *V. tiliaefolia* which joins closely as a secondary cluster.

3. *V. longii* and *V. doaniana* show moderate affinity in all phenograms, exceeding the *V. cordifolia* and *V. rubra* primary cluster in affinity values by a slight margin in the d and D phenograms. In the r phenogram, however, *V. cordifolia* and *V. rubra* form a primary cluster at a moderately high value.

4. *V. candicans* and *V. champini* have formed primary clusters at moderate affinity levels in the r and D phenograms, but in the d phenogram *V. candicans* has only formed a primary cluster with *V. labrusca* at a low affinity level.

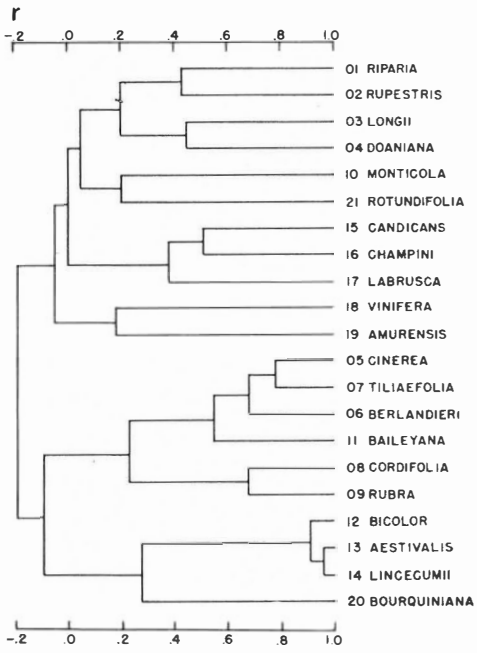

Fig. 1

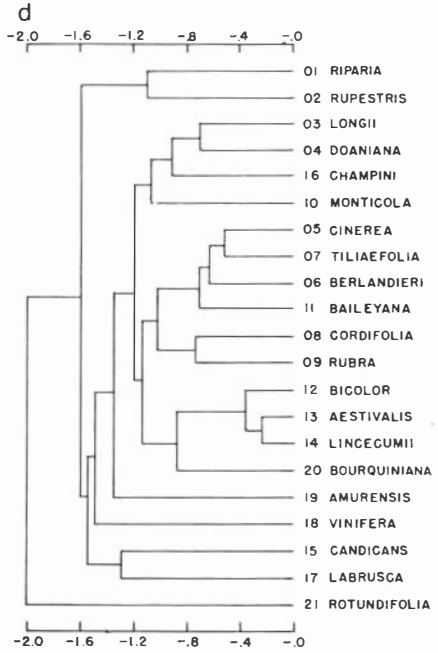

Fig. 2

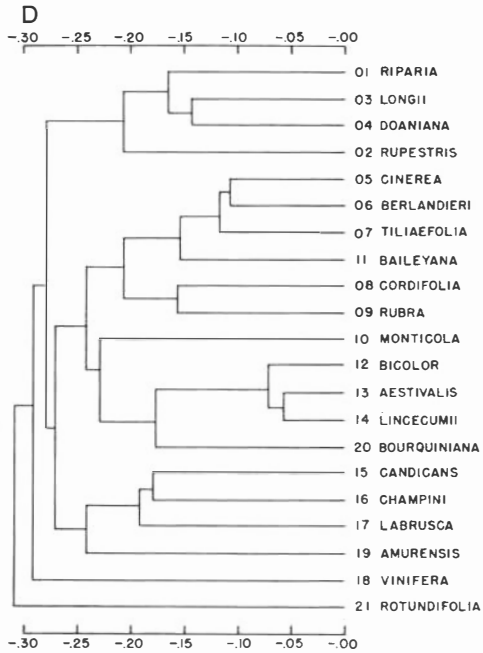

Fig. 3

Fig. 1: Correlation (r) phenogram obtained by the unweighted pair-group method of clustering using simple averages.
Fig. 2: Distance (d) phenogram. For explanation see Fig. 1.
Fig. 3: Divergence (D) phenogram. For explanation see Fig. 1.

5. *V. rupestris* and *V. riparia* have formed primary clusters in both the r and d phenograms at moderate to moderately low affinity levels respectively. In the D phenogram no primary cluster is formed at all, *V. rupestris* not joining an affinity group containing *V. riparia* until a low affinity value in reached and then only as a component of a tertiary affinity cluster.

6. Each of the species *V. amurensis, V. monticola, V. rotundifolia,* and *V. vinifera* has shown generally low affinity values when first joining with an affinity group; these species have shown no apparent congruities in their affinity relationships with other *Vitis* species.

Pattern of clustering sequence

Some definite congruities are also shown in the sequence with which the various species join the primary affinity clusters. The clustering sequence group *V. aestivalis — V. lincecumii; V. bicolor; V. bourquiniana* holds true in all phenograms. The clustering sequence group *V. cinerea — V. tiliaefolia; V. berlandieri; V. baileyana* is found in both the r and d phenograms and in the D phenogram with the minor exception that *V. berlandieri* and *V. tiliaefolia* are transposed in sequence order.

A further congruity found in both of these clustering sequence groups is that the level of affinity values at which each species joins its respective clustering sequence group is relatively constant in all phenograms. In the first named group clustering begins at a quite high value, closely joined by the secondary cluster, but the last species to join, *V. bourquiniana,* only completes the clustering sequence at a considerably lower value level. In the second group clustering begins at a high value, each succeeding species joining at a rather constant interval until clustering is completed with *V. baileyana* at a moderately high value. The pattern in the first group is one of three species quite close in affinity with the fourth species in a more remote affinity relationship. The pattern in the second group is one of four species fairly close in affinity but all separated in the sequence by rather uniform steps in relationship.

The *V. cordifolia — V. rubra* primary affinity cluster has shown a consistent pattern in all phenograms in that it joins the clustering sequence group *V. cinerea — V. tiliaefolia; V. berlandieri; V. baileyana* at a moderately low affinity level. The remaining species that form affinity clusters beyond the primaries at moderate affinity values are too erratic in their secondary associations to derive any consistent patterns of clustering sequence.

Congruence of phenograms

It is not possible to draw a straight line representing any level of affinity to obtain complete congruence of species-group among the phenograms. Maximum congruence of the three phenograms may be obtained by drawing a phenon line (line representing an equal similarity level) at the .44 value in the r phenogram, at the —.93 value in the d phenogram, and at the —.181 value in the D phenogram. At these similarity levels, the species will be arranged in the following affinity groups (arbitrarily numbered and arranged for convenience only):

Affinity Group 1. *V. rupestris.*
Affinity Group 2. *V. cinerea, V. tiliaefolia, V. berlandieri, V. baileyana.*
Affinity Group 3. *V. cordifolia, V. rubra.*
Affinity Group 4. *V. monticola.*
Affinity Group 5. *V. labrusca.*
Affinity Group 6. *V. amurensis.*

Affinity Group 7. *V. vinifera.*
Affinity Group 8. *V. rotundifolia.*
Affinity Group 9. *V. bicolor, V. aestivalis, V. lincecumii, V. bourquiniana.*
Affinity Group 10. *V. candicans, V. champini.*
Affinity Group 11. *V. riparia.*
Affinity Group 12. *V. longii, V. doaniana.*

It will be noted that *V. bourquiniana* in Affinity Group 9 is congruent in phenograms d and D; *V. champini* in Affinity Group 10 is congruent in phenograms r and D; *V. riparia* in Affinity Group 11 is congruent in phenograms r and d; *V. longii* and *V. doaniana* in Affinity Group 12 are not congruent with any other species in any phenogram although both are components of a primary affinity cluster in all phenograms. In the r phenogram both are the only members of their group but in the d phenogram *V. champini* joins the clustering group; *V. riparia* joining the group in the D phenogram.

Congruence of phenograms and classical classifications

As noted previously there are wide differences among the classifications of PLANCHON, FOEX, MUNSON, and BAILEY. It is impossible to state unequivocally which of these classifications, if any, is the "correct" interpretation of the genus. A comparison of these classifications with the phenograms may be useful in estimating the degree of congruence between them. For these comparisons the same levels of similarity (phenon lines) used to obtain maximum phenogram congruence will be employed, i. e. the .44 value for r, —.93 value for d and —.181 value for D phenograms.

An affinity group in a phenogram was rated congruent with a corresponding group in a classical classification if all species common to both were present in the corresponding groups. If a species common to both was present in other than its corresponding group the rating was incongruent. For example, PLANCHON places *V. aestivalis* and *V. lincecumii* in his group (Series) III. Phenogram r at the .44 affinity level places *V. aestivalis* and *V. lincecumii* as well as *V. bicolor* (not included with the species in PLANCHON) in the group and thus would be given a rating of congruent.

PLANCHON's classification contains *V. cinerea, V. berlandieri,* and *V. tiliaefolia (V. caribaea)* which are common to the species in the present study. The r phenogram at the .44 level places these three species plus *V. baileyana* in the same affinity group. PLANCHON places *V. cinerea* and *V. berlandieri* in his Group (Series) IV but places *V. tiliaefolia (V. caribaea)* in a separate Series II and thus the rating would be incongruent. The congruency ratings for the three phenograms and the four classical classifications are presented in Table 2.

The classifications of PLANCHON and FOEX both show the same congruency value with each of the phenograms but the degree of congruency is higher with the classification of FOEX (7 of 16 or 44%) than with PLANCHON (6 of 17 or 35%). MUNSON's classification is only slightly higher in congruency with the r phenogram (9 of 20 or 45%) but lower in both the d and D phenograms than FOEX's (6 of 20 or 30%). BAILEY's classification is very low in congruency with the r phenogram (1 of 18 or 6%) and slightly lower than MUNSON's in both d and D phenograms (5 or 18 or 28%).

The classification of FOEX shows the best overall congruency with all phenograms but there is no way to distinguish which of the phenograms, r, d, and D is the best. Looking at the problem the other way around, the d and D phenograms are slightly better than the r phenogram in overall congruency with all classifications but there is no way to distinguish which of the phenograms d and D is the

Table 2

Congruence of phenograms and classifications

Phenogram	Phenon value	Classification							
		Planchon		Foex		Munson		Bailey	
		No. of species congruent	No. of species in common[1])	No. of species congruent	No. of species in common[2])	No. of species congruent	No. of species in common[3])	No. of species congruent	No. of species in common[4])
r	.44	6	17	7	16	9	20	1	18
d	.93	6	17	7	16	6	20	5	18
D	.181	6	17	7	16	6	20	5	18

[1]) *V. aestivalis, amurensis, berlandieri, candicans, caribaea (tiliaefolia), champini, cinerea, cordifolia, labrusca, lincecumii, monticola, riparia, rotundifolia, rubra, rupestris, solonis (longii), vinifera.*

[2]) *V. aestivalis, amurensis, berlandieri, bicolor, candicans, caribaea (tiliaefolia), cinerea, cordifolia, labrusca, linsecomii (lincecumii), monticola, riparia, rotundifolia, rubra, rupestris, vinifera.*

[3]) *V. aestivalis, baileyana, berlandieri, bicolor, bourquiniana, candicans, caribaea (tiliaefolia), champini, cinerea, cordifolia, doaniana, labrusca, lincecumii, longii, monticola, rotundifolia, rubra, rupestris, vinifera, vulpina (riparia).*

[4]) *V. aestivalis, argentifolia (bicolor), baileyana, berlandieri, bourquina (bourquiniana), candicans, champini, cinerea, cordifolia, doaniana, labrusca, lincecumii, longii, monticola, palmata (rubra), rotundifolia, rupestris, vulpina (riparia).*

better. Thus no conclusive inference of relative merit may be drawn from the comparison of phenograms and classifications.

Congruence of phenograms and authors' concept of species relationship

Traditional methods of discrimination between species have been based upon morphological and anatomical data plus geographical origin. Biological factors which have proved useful in species discrimination are chromosome data, cross compatibility, and ecological adaption in the broader concept of gene pools and breeding barriers.

Several examples may be cited to illustrate discrimination criteria in *Vitis*. *V. rotundifolia*, a 40 chromosome species, is readily separated from the other 38 chromosome species in the present study, all of which form fully fertile hybrids with each other. The Eurasian species, *V. vinifera* and *V. amurensis*, are widely separated geographically from the North American species as well as between themselves.

Hermaphroditic flower types that breed true for this character have never been reported in natural populations of 38 chromosome *Vitis;* only *V. vinifera* and its hybrids of the *Euvitis* section of *Vitis* are known to be genetic sources for this trait. Thus most forms of *V. bourquiniana*, despite many characters similar to the Aestivales affinity group have hermaphroditic flowers and must have derived this trait from a *V. vinifera* ancestor. An examination of the three similarity matrices (not shown) used to construct the r, d, and D phenograms, respectively, lend support to this because in all three matrices *V. vinifera* has its highest affinity with *V. bourquiniana*.

Many American grape varieties with hermaphroditic flowers have also been erroneously cited as examples of pure *V. labrusca* despite preponderent evidence that *V. labrusca* is dioecious.

V. riparia, *V. cordifolia*, and *V. cinerea* are sympatric species commonly found growing in alluvial soil in close proximity but because of wide differences in blossoming period effective breeding barriers exist between them.

Although we may discriminate between the species cited in the preceding examples with reasonable confidence, the problems of species hybrids and subspecies is not so readily resolved by either traditional or taximetric methods. With present clustering techniques it is obvious that a supposed hybrid can join an affinity group containing only one of its putative parents, assuming the parents are in different clusters. If other obscuring factors such as introgression have intervened, the hybrid could conceivable join with a hybrid of similar parentage but with a differing level of intermediate characters to form an affinity group that contained neither parent. At the best we shall only discover one of the two putative parental species---at the worst we shall discover neither of the putative parents and perhaps obtain a misleading interpretation through construction of a hybrid--hybrid cluster in place of a parent-hybrid cluster. For an example of this in *Solanum* see Heiser, Soria, and Burton (1965).

In the authors' concept of species relationships there is a lack of convincing evidence that *V. longii*, *V. doaniana*, and *V. champini* are true species in the modern concept. Some doubt will perhaps persist as to the status of *V. baileyana* until more extensive field studies and collections are made. *V. aestivalis*, *V. bicolor*, and *V. lincecumii* differ by such relatively slight degree that some authorities have expressed the view that separate specific status may not be justified. (Steyermark, 1963).

Although our study has been as objective as possible we are still faced with a value judgement in deciding what phenogram is the "best" to use in expressing species affinity. The D phenogram is the most congruent with the authors' concept of species affinity relationships with a phenon line drawn at the —.181 value level. The authors would, however, make a further value judgement with respect to the interpretation of the status of hybrids. This interpretation would produce a tentative outline of affinity relationship among the 21 forms of *Vitis* studied in the following manner:

1. *V. riparia, V. longii* (Hybrid), *V. doaniana* (Hybrid).
2. *V. rupestris.*
3. *V. cinerea, V. berlandieri, V. tiliaefolia, V. baileyana.*
4. *V. cordifolia, V. rubra.*
5. *V. monticola.*
6. *V. aestivalis, V. bicolor, V. lincecumii, V. bourquiniana* (Hybrid).
7. *V. candicans, V. champini* (Hybrid).
8. *V. labrusca.*
9. *V. amurensis.*
10. *V. vinifera.*
11. *V. rotundifolia.*

It is perhaps somewhat fortuitous that the taximetric study reported herein was in general agreement with our own concept of species affinity. Our primary objection, which we view as a very serious one, is that the techniques thus far developed cannot discriminate true species hybrids. In *Vitis*, the inability of taxonomists to agree on interpretation of the hybridity problem has been one of the major underlying causes for discrepancies between classifications.

The classical studies of introgressive hybridization by Anderson (1949) point to a more precise approach to the hybridity question. Detailed studies of controlled introgressive levels might well elucidate what refinements in the way of choice and scoring of characters are necessary to adequately sample variation in species hybrids. If taximetrics has not measured up to all of its alleged attributes it has been instrumental in stimulating new interest and thought on more objective methods of discrimination between plants forms.

Summary

A taximetric study, utilizing 71 plant characters for 21 species of *Vitis* has been completed. Phenetic similarities among the species were estimated by product-moment (r), distance (d) and divergence (D) coefficients.

The unweighted pair-group method of clustering was used to graphically summarize the results in three phenograms. Congruency among the phenograms was examined by comparisons of primary affinity clusters and patterns of clustering sequence among phenograms and four classical classifications of *Vitis;* the classification of Foex showed the best overall congruency with the phenograms. The phenograms were also compared with the authors' concept of species affinity relationship; the divergence phenogram showed the greatest congruency. A tentative scheme of relationships based upon a modification of the divergence phenogram was devised.

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Appendix

List of characters, character states, and arithmetic code used for classification of *Vitis* spp.

1. Bud burst. (1) early, (2) midseason, (3) late.
2. Growing tip of immature cane. (1) leafy, (2) intermediate, (3) naked.
3. Color of growing tip of immature cane. (1) green or grey, (2) copper, (3) bronze.
4. Pubescence of growing tip on immature cane. (1) no pubescence, (2) slightly floccose, (3) tomentose, (4) densely tomentose.
5. Color of pubescence of growing tip at bud burst. (1) not red, (2) trace of red, (3) carmine, (4) carmine with reddish hair-like strands.
6. Pubescence on immature cane. (1) none to slight, (2) floccose, (3) dense.
7. Color of immature cane. (1) not green, (2) green.
8. Relative size of stipules on immature cane. (1) large, (2) medium, (3) small.
9. Density of glandular spines on immature cane. (1) none, (2) moderate, (3) dense.
10. Cross section of immature cane. (1) mostly rounded, (2) slightly angled, (3) distinclty angled.
11. Pubescence of internodes on mature canes. (1) none to slight, (2) moderate, (3) dense.
12. Lenticels on mature cane. (1) obscure, (2) prominent.
13. Striation on mature cane. (1) none to slight, (2) fine, (3) coarse.
14. Bloom on nodes of mature cane. (1) none to slight, (2) little, (3) much.
15. Diaphragm at node of mature cane. (1) none, (2) thin, (3) thick.
16. Rooting ability of dormant canes. (1) readily, (2) moderate, (3) very difficult.
17. Aspect of leaf blade. (1) distinctly folded upward, (2) slightly upfolded, (3) nearly flat, (4) down curved.
18. Texture of leaf blade. (1) soft, (2) leathery.
19. Aspect of leaf blade surface. (1) rugose, (2) smooth.
20. Presence of leaf blade tissue on petiolar sinus side of veins at junction of veins and petiole. (1) yes, (2) no.
21. Leaf margin. (1) serrate, (2) slightly serrate, (3) nearly entire.

22. Grooving of upper side of petiole. (1) slight, (2) moderate (3) deep.
23. Pubescence on lower surface of leaf blade. (1) absent, (2) present.
24. Relative length of pubescence on lower surface of leaf blade. (1) short, (2) medium, (3) long.
25. Bloom on lower surface of leaf blade. (1) absent, (2) present.
26. Pubescence on upper surface of young leaf blade. (1) none, (2) slight, (3) moderate, (4) heavy.
27. Pubescence on upper surface of mature leaf blade. (1) none, (2) slight.
28. Relative color density of upper leaf surface. (1) light, (2) medium, (3) dark.
29. Gloss of upper leaf blade surface. (1) dull, (2) intermediate, (3) shining.
30. Autumnal color of leaf. (1) yellow, (2) red.
31. Length/width ratio of mature leaf. (1) under 175, (2) .75 — 1.00, (3) over 1.00.
32. Ratio of petiole length to total leaf length. (1) under .32, (2) .32 to .41, (3) over .41.
33. Length ratio of lower lateral sinus to lower lateral lobe of mature leaf. (1) under, .70, (2) .71 to .89, (3) .90 to 1.00, (4) over 1.00.
34. Length ratio of upper lateral sinus to upper lateral lobe of mature leaf. (1) under, .60, (2) .60 to 1.00, (3) over 1.00.
35. Angle between midrib and primary vein of lower lateral lobe. (1) acute, (2) about 90^0, (3) slightly obtuse, (4) obtuse.
36. Angle between primary vein of lower lateral lobe and its secondary nerve (relative shape of petiolar sinus). (1) under 50^0, (2) 51 to 56^0, (3) 57 to 63^0, (4) over 63^0.
37. Continuous tendrils. (1) no, (2) yes.
38. Tendrils forked. (1) yes, (2) no.
39. Persistence of tendrils. (1) no, (2) slight, (3) yes.
40. Relative time of anthesis. (1) early, (2) midseason, (3) late.
41. Relative fragrance of staminate flower cluster. (1) high, (2) low.
42. Relative size of inflorescence. (1) small, (2) large.
43. Relative size of ovary. (1) large, (2) medium, (3) small.
43. Relative length of cluster peduncle. (1) short, (2) medium, (3) long.
45. Relative time of fruit maturity, (1) early, (2) midseason, (3) late.
46. Density of fruit in cluster, (1) compact, (2) intermediate, (3) loose.
47. Relative compoundness of fruit cluster. (1) simple, (2) moderate, (3) compound.
48. Terminal of fruit cluster. (1) not fasciated, (2) fasciated.
49. Relative number of berries per cluster. (1) small, (2) large.
50. Relative uniformity of maturity of berries on cluster. (1) even, (2) uneven.
51. Relative persistence of mature berry to cluster. (1) persistent, (2) non-persistent.
52. Relative size of individual berry. (1) small, (2) medium, (3) large.
53. Relative abundance of bloom on berries at maturity. (1) none, (2) moderate, (3) abundant.
54. Presence of spots on mature berries. (1) absent, (2) present.
55. Prominent lenticels on mature berries. (1) no, (2) yes.
56. Skin separates from pulp. (1) yes, (2) no.
57. Relative thickness of skin on berry. (1) moderately thin, (2) thick.
58. Presence of pungency in skin. (1) none or slight, (2) pungent.
59. Relative texture of skin of fruit. (1) tender, (2) intermediate, (3) tough.
60. Relative texture of flesh of berry. (1) tender, (2) intermediate, (3) tough.
61. Musky odor of fruit. (1) none, (2) moderate, (3) strong.
62. Relative soluble solids content of juice. (1) high, (2) intermediate, (3) low.
63. Presence of sucrose in juice. (1) absent or low, (2) high.

64. Relative acidity of juice. (1) high, (2) intermediate, (3) low.
65. Relative pigment concentration in juice. (1) high, (2) low.
66. Seed width/length ratio. (1) under .59, (2) .59 to .66, (3) .67 to .84, (4) over .84.
67. Relative resistance to lime chlorosis. (1) not resistant, (2) resistant.
68. Relative resistance of roots to phylloxera. (1) very high, (2) moderate, (3) low.
69. Resistance of foliage to gall formation by phylloxera. (1) susceptible, (2) resistant.
70. Chromosome number (somatic). (1) 38, (2) 40.
71. Flower sex. (1) basically dioecious, (2) basically dioecious, rarely hermaphroditic, (3) generally hermaphroditic or pistillate.