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Patterns of phenotypic variation in *Viola etrusca* Erben (Violaceae)

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RÉSUMÉ

SELVI, F., B. FOGGI & L. DI FAZIO (1995). Modèle de variation phénotypique chez *Viola etrusca* Erben (Violaceae). *Candollea* 50: 309-319. En anglais, résumés français et anglais.

Une étude sur la variation phénotypique interpopulationnelle de *Viola etrusca* Erben, un endémisme de la Toscane méridionale, est présentée. Neuf populations de la partie septentrionale de sa distribution et cinq de la partie méridionale ont été comparées sur la base de 40 caractères morphologiques. L'analyse numérique a montré l'existence d'une différenciation entre les deux groupes de populations. Plusieurs caractères sont différents aussi entre populations de différents habitats. L'origine de cette discontinuité est discutée en relation avec des aspects écochorologiques et historiques de la Toscane méridionale, qui fournissent des arguments indirects pour la variabilité génétique de cet endémisme non-conservatif.

ABSTRACT

SELVI, F., B. FOGGI & L. DI FAZIO (1995). Patterns of phenotypic variation in *Viola etrusca* Erben (Violaceae). *Candollea* 50: 309-319. In English, French and English abstracts.

Infraspecific phenotypical variation of *Viola etrusca* Erben, an endemism of mountains of Southern Tuscany, was investigated. Nine populations from the northern distribution area and five from the southern one were compared on the basis of 40 morphological characters. The numerical analysis showed the existence of a phenotypical discontinuity between the two groups of populations. Several characters gave a weak discrimination also between populations growing under different ecological conditions. The origin of this infraspecific differentiation is discussed in relation to eco-chorological and historical aspects of Southern Tuscany; they provide indirect evidence for the genetical variability of this non-conservative endemism.

KEY WORDS: *Viola etrusca* — Phenotypic variation — Numerical analysis — Southern Tuscany.

Introduction

As TERRACCIANO noticed (1889), the *Viola calcarata* L. complex of the sect. *Melanium* Ging. is one of the most interesting groups of the Southern European flora for its biogeographical and evolutionary aspects. According to MERXMÜLLER (1982), the group has a tertiary origin but it underwent a rapid evolution and differentiation only in glacial and postglacial ages, most probably in connection with the spread of human land-use activities. In Tuscany (Central Italy) the group is represented by four taxa with a distinct distribution: *Viola calcarata* L. subsp. *cavillieri* (Becker) Merxm. & Lippert ($2n = 40$, MERXMÜLLER & LIPPERT, 1977) and *Viola eugeniae* Parl. subsp. *eugeniae* ($2n = 34$, SCHMIDT, 1961, 1964) are orophytic species occurring respectively on the northern and central section of the Apenninic chain; *Viola corsica* Nyman subsp. *ilvensis* (Becker) Merxm. ($2n = 52$, MERXMÜLLER, 1974) is instead an endemism of the Island of Elba,

belonging to a thyrrenian taxon localized on mountains of Northern Sardinia (*Viola corsica* Nyman subsp. *limbariae* Merxm.) and Northern Corsica (*V. corsica* Nyman subsp. *corsica*).

Viola etrusca Erben is a recently described endemism of Southern Tuscany (ERBEN, 1986), with a distribution intermediate between the thyrrenian and the apenninic taxa. A recent chorological and karyological research (FOGGI & al., 1993) has pointed out that its distribution area includes two separated groups of populations with the same chromosomal number ($2n = 40$): a northern one on the Colline Metallifere and a southern one on Monte Amiata and Monte Labbro (see Fig. 1). Whatever the causes of this distribution type, it is possible that the reciprocal isolation of the two groups of gamodemes has caused the start of a slow process of differentiation, given the genecological variability of the whole sect. *Melanium* (CLAUSEN, 1931). Indeed, some morphological differences between southern and northern populations were indistinctly noticed during field researches of the previous work (FOGGI & al., 1993). These preliminary observations have induced us to test the existence of a phenotypical discontinuity between these populations by means of a numerical approach. At the same time, we compared southern populations growing under different environmental conditions, to evaluate in an empirical way the role of some environmental factors on phenotypes.

Materials and methods

1) Field sampling

This research is based on an intensive field sampling of wild populations, an approach which should provide a reliable basis to detect any morphological discontinuities among groups of populations. The northern distribution area of Montieri-Gerfalco was sampled through five populations (pop. L-P = NP) whereas the wider Amiata-Labbro southern one through nine populations (pop. A-I = SP). Geographical distribution of samples is shown in Fig. 1. Two populations (Q and R) of *V. calcarata* subsp. *cavillieri* from Monte Prado and one (S) of *V. eugeniae* subsp. *eugeniae* from Monte Falco were also sampled to compare the degree of morphological similarity occurring between the above two species with that between SP and NP of *V. etrusca*.

Forty morphological characters (Tab. 1) were measured in the field on twenty individuals per population. Two groups of individuals distanced at least 2 km apart were considered distinct populations. Individuals were mostly grouped in dense clumps, due to entomophilous pollination and propagation by means of rhizomes; there were no difficulties in the spatial delimitation of populations. Care was taken in considering real individuals and not different flowering stems from the same rhizome. Selection of characters was based on preliminary observations as well as on diagnosis and descriptions (BERTOLONI, 1810, 1835; PARLATORE, 1890; ERBEN, 1986), revisions (BECKER, 1910; MERXMÜLLER & LIPPERT, 1977) and main european floras (VALENTINE & al., 1968; FIORI, 1923; MERXMÜLLER, 1982). Characters were taken from all parts of the plant, from basal leaves to flowers; the majority were quantitative, both continuous and discrete; qualitative descriptions were converted to multistate characters by ranking them in numerical scales. The use of ratios has raised fundamental criticism (ATCHLEY & al., 1976), so they have been excluded from an initial list (CLAUSER & al., 1992).

2) Data analysis

Mean values and standard errors of all characters were first calculated for each population (Statgraphics.6); a Multifactor Analysis of Variance (MANOVA) was then performed to detect statistically significant differences between characters of NP, SP, Q-R and S. Populations from summer-dry scrubs and pastures of the Monte Amiata calcareous basement (pop. E-I = SP1) were then compared with those from mesic habitats on volcanic trachytes (pop. A-D = SP2) by means of a two-sided t-test analysis.

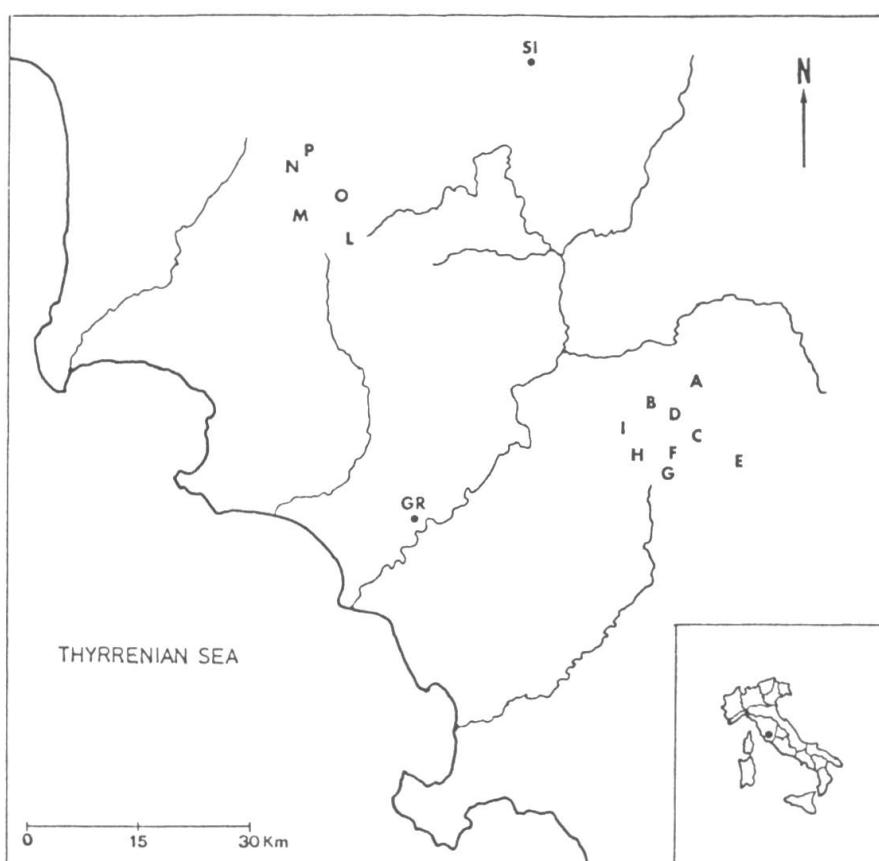


Fig. 1. — Geographical localization of sampled populations in Southern Tuscany (Central-Western Italy). **A-I** = Southern Populations, **L-P** = Northern Populations; **SI** Siena, **GR** Grosseto.

Agglomerative cluster analysis was then performed on the Euclidean Distance dissimilarity matrix, after the linear standardization by range of each variable of the raw matrix characters (mean values)/populations. The strict consensus index (SOKAL & ROHLF, 1982, cited in ROHLF, 1991) was used to compare average-linkage and complete-linkage dendograms.

A Principal Component Analysis (PCA) was performed on the correlation matrix to summarise the correlational structure among the variables and to display it in a non-hierarchical way. The use of PCA with mixed character types has been discussed by HILL & SMITH (1976). Both cluster and PCA analysis were performed by means of the program package NTSYS (ROHLF, 1991).

Results

1) Variation of characters in *V. etrusca*, *V. cavillieri* and *V. eugeniae*

The means and standard errors of characters of SP, NP, QR and S are presented in Tab. 2. MANOVA analysis showed that characters had a different significance between SP, NP and the other two violets, some giving a discrimination ($P < 0.05$) while others being statistically non significant. Of the 22 characters discriminating between SP and NP (of which 7 showed significant differences also between the other two violets), 19 were dimensional: plant height, length of the stem between the upper leaves and the flower and between the bracteoles and the flower, length of the spur, breadth of the lower petal, length of sepals and of their appendices, length and breadth of upper petals, length and breadth of upper leaves, length of upper leaves petioles, breadth of

HAAL	—	plant height (cm)
HASC	—	length of the stem between the upper leaves and the flower (cm)
HAFB	—	length of the stem between the bracteoles and the flower (cm)
HPSE	—	pubescence of sepals: 2 absent, 3 present (even if sparse)
CSLU	—	length of lateral sepals (mm)
CSLA	—	breadth of lateral sepals (mm)
HPEL	—	pubescence of stipules and leaves: 2 absent, 3 few hairs on margins, 4 few hairs on margins and on blades, 5 sparse hairs, 6 diffused hairs
CAPL	—	length of appendices of lateral sepals (mm)
CSAP	—	apical notching of lateral sepals: 2 acuminate, 3 semiacuminate, 4 rounded
CAAP	—	apical notching of appendices of lateral sepals: 2 triangular, 3 rounded, 4 truncated, 5 emarginated
CASU	—	apical notching of the upper sepal appendix: 2 acuminate, 3 semiacuminate, 4 rounded, 5 emarginated
KSFO	—	shape of the spur: 2 curved, 3 straight, 4 straight with hooked apex
KLPS	—	length of the lower petal (mm)
KPSL	—	breadth of the lower petal (mm)
KSLU	—	length of the spur (mm)
KSLA	—	breadth of the spur (mm)
KASU	—	apical notching of upper petals: 2 rounded, 3 truncate
KSOV	—	overlapping of upper petals: 2 absent, 3 slight, 4 marked
KPLU	—	length of upper petals (mm)
KPLA	—	breadth of upper petals (mm)
FPLU	—	length of petioles of upper leaves (mean of 2), (mm)
IPLU	—	length of petioles of lower leaves (mean of 2), (mm)
FLLU	—	length of upper leaves (mean of 2), (mm)
ILLU	—	length of lower leaves (mean of 2), (mm)
FLLA	—	breadth of upper leaves (mean of 2), (mm)
ILLA	—	breadth of lower leaves (mean of 2), (mm)
FCRE	—	notching of margins of upper leaves: 2 absent, 3 slight, 4 marked (more than 1/4 of leaf semibreadth)
ICRE	—	notching of margins of lower leaves: 2 absent, 3 slight, 4 marked (more than 1/4 of leaf semibreadth)
FINC	—	number of notches per side of upper leaves (mean of 2)
IINC	—	number of notches per side of lower leaves (mean of 2)
FPOS	—	position of maximum breadth of upper leaves (mean of 2) (mm)
IPOS	—	position of maximum breadth of lower leaves (mean of 2) (mm)
FBAS	—	shape of the base of the blade of upper leaves: 2 attenuate, 3 cuneate, 4 truncate, 5 cordate
IBAS	—	shape of the base of the blade of lower leaves: 2 attenuate, 3 cuneate, 4 truncate, 5 cordate
FSLU	—	length of the longest segment of the stipules of upper leaves (mean of 2), (mm)
ISLU	—	length of the longest segment of the stipules of lower leaves (mean of 2), (mm)
FSLA	—	breadth of the largest segment of the stipules of upper leaves (mean of 2), (mm)
ISLA	—	breadth of the largest segment of the stipules of lower leaves (mean of 2), (mm)
FLAC	—	number of segments of stipules of upper leaves
ILAC	—	number of segments of stipules of lower leaves

Table 1. — List of characters.

CHAR	SP	NP	Q-R	S
HAAL	21.9(0.4)	A	17.6(0.5)	B
HASC	13.2(0.2)	A	10.1(0.3)	B
HAFB	2.8(0.1)	A	2.3(0.1)	B
HPSE	2.2(0.3)	A	2.1(0.04)	AB
CSLU	9.0(0.1)	A	7.9(0.2)	B
CSLA	2.0(0.03)	A	2.0(0.05)	A
HPEL	3.7(0.07)	A	3.6(0.09)	A
CAPL	3.0(0.05)	A	2.7(0.08)	B
CSAP	2.0(0.01)	A	2.0(0.02)	A
CAAP	3.7(0.03)	A	3.6(0.05)	A
CASU	3.7(0.05)	A	3.6(0.07)	A
KSFO	2.6(0.05)	A	2.8(0.07)	B
KLPS	12.4(0.2)	A	11.9(0.2)	AB
KPSL	13.6(0.2)	A	12.6(0.2)	B
KSLU	11.0(0.1)	A	10.5(0.2)	B
KSLA	1.8(0.03)	A	1.7(0.04)	A
KASU	2.4(0.03)	A	2.7(0.05)	B
KSOV	2.8(0.05)	A	3.0(0.07)	B
KPLU	15.4(0.2)	A	13.4(0.3)	B
KPLA	12.1(0.2)	A	11.1(0.2)	B
FPLU	16.1(0.4)	A	14.5(0.5)	B
IPLU	17.5(0.6)	A	16.0(0.8)	AB
FLLU	22.5(0.4)	A	20.9(0.5)	B
ILLU	11.3(0.3)	A	10.5(0.4)	A
FLLA	5.8(0.1)	A	4.3(0.2)	B
ILLA	8.7(0.2)	A	8.0(0.3)	B
FCRE	3.0(0.03)	A	3.0(0.04)	A
ICRE	3.0(0.02)	A	3.0(0.02)	A
FINC	2.9(0.08)	A	2.6(0.1)	A
IINC	3.1(0.08)	A	2.8(0.1)	A
FPOS	11.6(0.2)	A	11.0(0.3)	A
IPOS	4.3(0.1)	A	3.8(0.2)	AC
FBAS	2.0(0.02)	A	2.1(0.03)	A
IBAS	3.7(0.05)	A	3.5(0.07)	A
FSLU	21.7(0.4)	A	17.8(0.5)	B
ISLU	7.2(0.2)	A	5.2(0.3)	B
FSLA	2.2(0.05)	A	1.6(0.07)	B
ISLA	1.2(0.05)	A	0.8(0.07)	B
FLAC	5.5(0.1)	A	5.1(0.2)	B
ILAC	2.0(0.09)	A	1.5(0.1)	B

Table 2. — Means and standard errors (in brackets) of characters (see Tab. 1) of southern (SP) and northern (NP) populations of *V. etrusca*, *V. calcarata* subsp. *cavillieri* (Q-R) and *V. eugeniae* subsp. *eugeniae* (S); A, B, C, D are statistically different groups ($P < 0.05$; confidence level 95%).

lower leaves, length and breadth of the major segment of the stipules (both upper and lower) and number of segments of stipules (upper and lower). These measurements reached all higher values in southern populations. Only three variables of qualitative nature showed significant differences: the shape of the spur tended to be slightly more curved in SP, the apical notching of upper petals tended to a rounded shape in SP and to a truncate one in NP and overlapping of petals was slightly more marked in NP. Sixteen dimensional characters and eight qualitative gave also statistical differences between *V. cavillieri* and *V. eugeniae* and in most of the cases dimensional differences were sharper than those occurring within *V. etrusca* (see Tab. 2).

In *V. etrusca* the most variable characters concerned length of petioles, breadth and number of notches of leaves, size and number of segments of stipules (with coefficients of variation ranging from 35% to 56%). Despite the lower number of individuals examined for the other two violets, it can be said that the overall level of infraspecific morphological variability was slightly lower in *V. etrusca* (mean coefficient of variation of characters in SP and NP = 27%), than in *V. cavillieri* (32%) and *V. eugeniae* (28%).

2) Variation of characters in SP1 and SP2

Nine characters were different for $P < 0.01$ (Tab. 3); the 6 quantitative had all higher values in populations of the trachytic area: length and breadth of the spur, length and breadth of the lower petal, length of upper petals and number of notches of lower leaves. Other 8 measurements reached statistically higher values ($P < 0.05$) in SP2, whereas the number of upper stipules segments was higher in SP1. Finally, pubescence was slightly more marked in SP1, apical notching of upper petals tended to be truncate in SP1 and rounded in SP2 and overlapping of petals was slightly stronger in SP1.

Twelve characters showed a statistical significance in both the SP-NP and SP1-SP2 comparison. The interpopulational variation of four of them with $P < 0.01$ in the SP1-SP2 comparison (Fig. 2), showed however that sharp discontinuities could not be detected due to the occurrence of broad and variable ranges (standard errors) of intrapopulational variation.

3) Multivariate analysis

Complete and average-linkage dendograms had rather consistent structures, the strict consensus index between them having resulted to be 0.866. The complete-linkage tree is shown in Fig. 3. Despite the lower number of examined populations of *V. eugeniae* and *V. cavillieri*, it can be said that the sharp splitting of the three violets confirmed their overall morphological differentiation. *V. etrusca* was split into two main clusters at an Euclidean Distance of 2.87, a level slightly lower than that (3.27) separating *V. cavillieri* and *V. eugeniae*. The first group included populations A-H, namely all those from the southern area except for I, which was clustered within the second group (L-P) from the northern area. Within SP, populations from dry calcareous pastures (E-G), except for pop. H, were separated from those of the volcanic area at a dissimilarity level of 2.5.

The two PCA axes, accounting for the 59.2 % of the total variation, produced a scattergram (Fig. 4) mostly fitting the cluster analysis picture. The three violets were sharply separated even though the "phenetic" distance between *V. eugeniae* and *V. cavillieri* was comparable with that between southern and northern populations of *V. etrusca*. These were gathered on the positive part of the first axis, with SP on the negative part of the second axis and NP on the positive one. The similarity of I to NP was also evidenced, whereas an SP1-SP2 differentiation was here scarcely detectable.

On the whole, multivariate analysis confirmed the sharp morphological discontinuity between the three violet species, but also the good correspondance between geographical distribution of *V. etrusca* and its infraspecific pattern of phenetic variation.

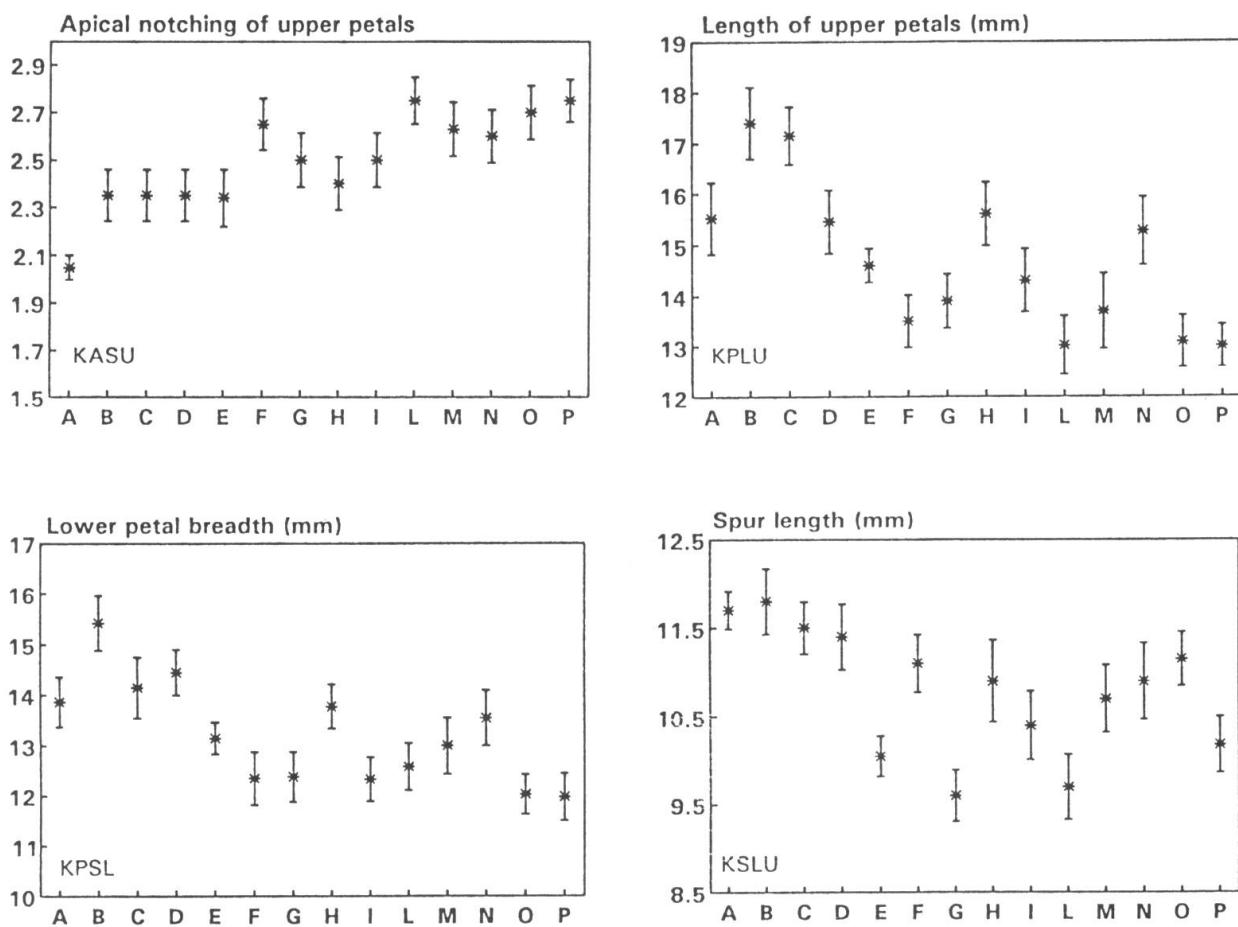


Fig. 2. — Variation of four significant characters through 14 *V. etrusca* populations (letters on the X axis: A-I = Southern Populations, L-P = Northern Populations). **KPSL**: breadth of the lower petal (mm); **KSLU**: length of the spur (mm); **KASU**: apical notching of the upper petals (2 rounded, 3 truncate); **KPLU**: length of upper petals (mm).

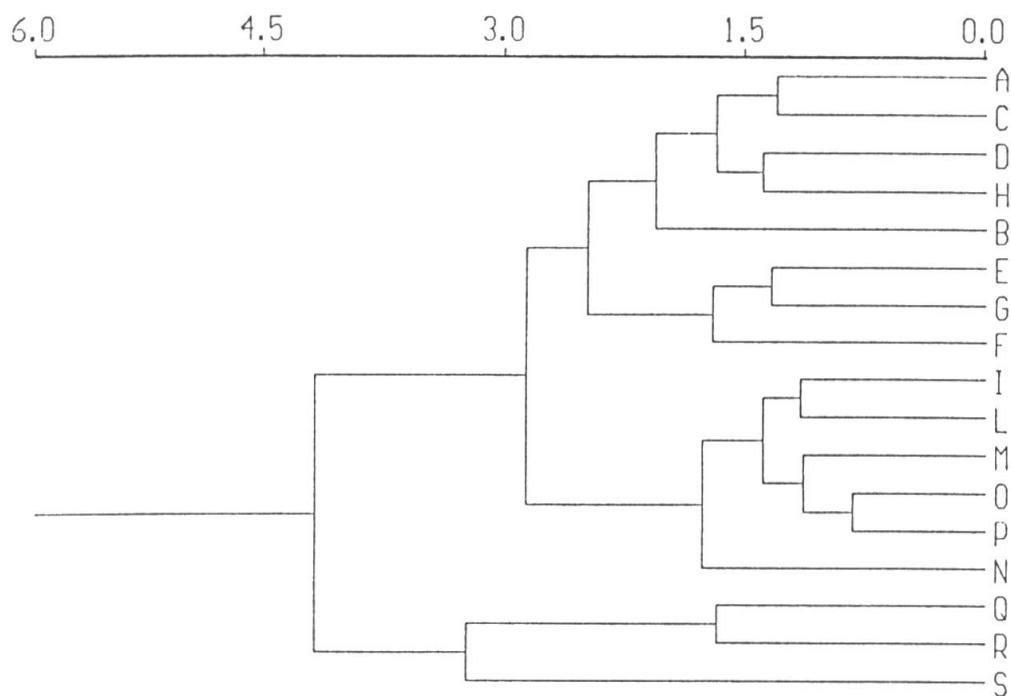


Fig. 3. — Complete-linkage dendrogram of populations of *V. etrusca* (letters on the X axis: **A-I** = Southern Populations, **L-P** = Northern Populations), *V. calcarata* subsp. *cavillieri* (**Q,R**) and *V. eugeniae* (**S**) with the Euclidean Distance dissimilarity Index (on the Y axis).

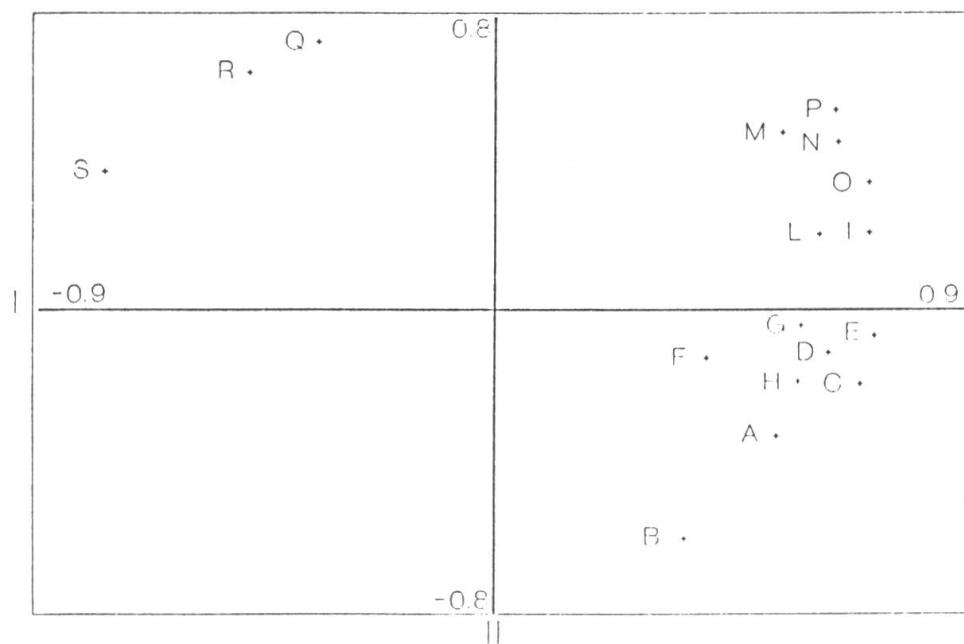


Fig. 4. — Non-hierarchical PCA scattergram of populations of *V. etrusca* (**A-P**), *V. calcarata* subsp. *cavillieri* (**Q-R**) and *V. eugeniae* (**S**).

CHAR	SP2 (A-D)	SP1 (E-I)	P
HAAL	21.47(0.62)	22.3(0.56)	ns
HASC	13.27(0.41)	13.04(0.37)	*
HAFB	3.07(0.16)	2.58(0.14)	*
HPSE	2.07(0.04)	2.28(0.04)	**
CSLU	9.25(0.19)	8.73(0.17)	*
CSLA	2.06(0.05)	1.95(0.04)	ns
HPEL	3.87(0.11)	3.58(0.1)	ns
CAPL	2.97(0.09)	3.07(0.08)	ns
CSAP	2.0	2.0	ns
CAAP	3.72(0.05)	3.73(0.04)	ns
CASU	3.68(0.07)	3.73(0.06)	ns
KSFO	2.67(0.08)	2.6(0.07)	ns
KLPS	12.96(0.21)	11.93(0.19)	**
KPSL	14.47(0.24)	12.79(0.22)	**
KSLU	11.61(0.17)	10.42(0.15)	**
KSLA	1.9(0.05)	1.62(0.04)	**
KASU	2.27(0.05)	2.49(0.05)	**
KSOV	2.61(0.07)	2.91(0.07)	**
KPLU	16.38(0.3)	14.38(0.27)	**
KPLA	12.49(0.26)	11.73(0.24)	*
FPLU	17.07(0.65)	15.09(0.57)	*
IPLU	16.59(1.04)	18.33(0.91)	ns
FLLU	23.55(0.56)	21.35(0.64)	*
ILLU	10.98(0.39)	11.65(0.34)	ns
FLLA	5.84(0.23)	5.67(0.2)	ns
ILLA	8.75(0.31)	8.72(0.27)	ns
FCRE	2.97(0.05)	3.01(0.04)	ns
ICRE	2.99(0.02)	2.99(0.02)	ns
FINC	3.09(0.12)	2.75(0.11)	*
INC	3.28(0.10)	2.91(0.09)	**
FPOS	11.17(0.42)	12.08(0.37)	ns
IPOS	4.29(0.21)	4.41(0.18)	ns
FBAS	2.0(0.02)	2.04(0.01)	ns
IBAS	3.72(0.08)	3.6(0.07)	ns
FSLU	22.41(0.64)	20.92(0.57)	ns
ISLU	7.06(0.38)	7.3(0.33)	ns
FSLA	2.36(0.09)	2.11(0.08)	*
ISLA	1.27(0.09)	1.22(0.08)	ns
FLAC	5.08(0.2)	5.9(0.17)	*
ILAC	2.07(0.14)	1.91(0.12)	ns

Table 3. — Means and standard errors (in brackets) of characters of southern populations of *Viola etrusca* from volcanic trachytes (SP2) and from calcareous scrubs (SP1); *: $P < 0.5$; **: $P < 0.01$; ns: non significant.

Discussion

Numerical analysis of phenotypical variation in *V. etrusca* fits the hypothesis of the existence of a consistent differentiation between populations from Monte Amiata-Monte Labbro and Poggio di Montieri-Cornate di Gerfalco. Southern populations proved to be formed on the average of slightly larger individuals; within this group several characters reached their maximum dimensions in populations from trachytic lavas of Amiata volcanic cone. The morphological discontinuity found between SP and NP, as well as between SP1 and SP2, is largely caused by numerous "slight" quantitative differences concerning vegetative structures and flowers, rather than sharp characters. The biosystematic value of this differentiation is consequently weak and, taken also into account the same chromosomal number (FOGGI & al., 1993), there is no sufficient basis for infraspecific taxonomical discriminations.

The key point is: what is the nature of such a phenetic differentiation? Indirect evidence is provided by correlations with chorological, ecological and paleogeographical data. SP and NP are today separated by about 60 Km of fluvial plains and lowlands; a distance which is likely to cause a genetical isolation in gamodemes pollinated by Hymenoptera such as *Apis*, *Bombus* and *Bombylius* (pers. observ., see also BEATTIE, 1978; PESSON & LOUVEAUX, 1984) and with vegetative propagation by means of rhizomes. According to BEATTIE (1976, 1978) the activities of pollen and seed vectors in most *Melanium* violets tend to establish neighbourhoods of small size and area and levels of within-neighbourhood gene exchange are much greater than levels of between-neighbourhoods gene exchange; under this regime, subdivision and differentiation among breeding units may occur on a local scale. Poggio di Montieri (NP) and Amiata (SP) populations grow under rather similar environmental conditions (edges of chestnut and beech forests on siliceous rocks) as do Cornate (NP) and Labbro (SP) populations (summer-dry scrubs and pastures on calcareous rocks); indeed, if ecological factors had induced phenetical convergence then we probably would have had the above "crossed" similarity rather than a geographical differentiation. These considerations suggest the hypothesis that SP and NP are in the midst of a slow schizogenetic differentiation process, made possible by genetical isolation. Schizogenesis followed by hybridization and diploidy is considered a major mechanism of speciation in *Viola* sect. *Melanium* (CLAUSEN, 1931; KÜPFER, 1971). On the contrary, the smaller size and the presence of few short hairs in populations of summer-dry calcareous scrubs (SP1) as compared to those of edges of mesic woods on trachytic rocks (SP2) can be supposed to be environment-induced "eco-morphosis". The causes of the bipolar distribution of *V. etrusca* are possibly correlated to the pliocenic marine ingression of Southern Tuscany (FOGGI & al., 1993). Nevertheless, its actual diffusion in non-natural habitats would indicate that the differentiation has a secondary origin, having probably started with its spread from natural sites as rocky outcrops, screes and cliffs. Evidence for this hypothesis is provided by the Monte Amiata geological history, where today *V. etrusca* is widespread at the margins of tracks, roads and in cultivated chestnut woods. This volcanic mountain has an age of 290.000-180.000 m.y. (BIGAZZI & al., 1981) and since its origin it was covered by dense woods (BERTOLANI MARCHETTI & JACOPI, 1962; BERTOLANI MARCHETTI & SOLETTI, 1972); therefore the spread upward on this mountain must have occurred when local human populations started to clear the natural vegetation, namely in the neolithic age. These considerations would fit the hypothesis of MERXMÜLLER (1982) of a certain increase of evolutionary rate in the sect. *Melanium* in connection with human modifications of original habitats. This kind of phenomena are considered to have played a rather important role in the evolution of many genera of the Mediterranean flora (PIGNATTI, 1979). Indeed the thriving of *V. etrusca* in non-conservative habitats with a wide range of microclimates and rocks as well as its derivated chromosomal number, are evidences for its genetical variability and therefore for its evolutionary potential.

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