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A morphometric study of the *Quercus crenata* species complex (Fagaceae)

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Abstract

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Plants ascribed to the complex *Quercus crenata* – *Q. pseudosuber*, supposed to be hybrids *Q. cerris* x *Q. suber*, grow sympatric with both parental species in peninsular Italy and Sicily, but they also occur in the Alpes Maritimes, in northern Italy, in Slovenia and Istra, where *Q. suber* is absent. To test whether northern and southern plants of this complex should be regarded as different taxa, a morphometric survey was done on 91 specimens. Based on 36 morphological characters of the leaf and fruit, the northern and southern specimens did not form distinct aggregates in a principal components analysis (PCA), but they could be segregated in a discriminant analysis. PCA ordination plots further indicated that the southern specimens are morphologically more variable. Indeed, when tested individually, the means of six characters differed significantly between the two parts of the distribution range, and 12 characters were significantly more variable in southern plants. Based on our results, we propose that the two sets of plants are taxonomically distinct. The "southern" plants are hybrids *inter parentes*, for which we propose to maintain the name *Quercus* x *pseudosuber* Santi. The "northern" plants with reduced variability are possibly relicts of ancient hybridization and to them properly applies the name *Quercus crenata* Lam.

Key words: Biometry, hybrids, Italian flora, *Quercus pseudosuber*, *Quercus fontanesii*, semi-evergreen oaks, taxonomy.

Introduction

Hybridization and introgression play a major role in determining variation in the genus *Quercus*, often challenging the concept of species (Howard et al. 1997). Although much recent research on hybrids has privileged molecular markers (Samuel 1999), morphological analysis can still be useful to elucidate relationships among presumed

hybrids and putative parental species (Bruschi et al. 2000; Gonzáles-Rodriguez et al. 2004).

A case study is offered by *Quercus crenata* Lamarck (1785), a semi-evergreen species of *Quercus* L. subgen. *Cerris* (Spach) Örsted. Its leaves, coriaceous as those of *Q. suber* L., persist throughout the winter and fall in spring, shortly before the new leaves develop. The cupules resemble very much those of *Q. cerris* L., whereas the general shape of the leaves is intermediate between *Q. suber* and *Q. cerris*. The bark is moderately corky, but very variable within the species. *Quercus crenata* is commonly thought to be a hybrid between *Q. suber* and *Q. cerris* (Pignatti 1982; Schwarz 1993) but its hybrid nature, as well as its taxonomic status, is still debated.

Besides the unresolved hybrid origin of this species, taxonomic and nomenclatural ambiguity results from the fact that Santi (1795) described a plant of Tuscany closely resembling the plant of Lamarck ("*foliis lanceolatis, sinuatis, subtus incanis, cortice rimoso-fungoso*") under the name *Quercus pseudosuber*, and Gussone (1825, 1844) published the name *Q. fontanesii* for a plant of Sicily, also morphologically similar to *Q. crenata*.

The distribution range of the species (assuming the three names are synonyms; Schwarz 1993; Jalas and Suominen 1976), stretches from southern France (Alpes Maritimes) to all continental Italy (without Apulia) and Sicily, western Slovenia and western Croatia (Istra). Further indications concerning Albania and Greece (Greuter et al. 1986; Schwarz 1993) are not accepted by Jalas and Suominen (1976), nor by recent Albanian floras (Demiri 1983; Paparisto 1988), and probably refer to hybrids between other species. Altogether, only a few hundred individuals of this species are known, no more than a hundred of which are recorded in the north.

The hybrid nature of *Q. crenata* s.l. was supported by Bellarosa et al. (1996), who used a molecular marker (rRNA) to prove that some specimens growing in a stand side-by-side with *Q. cerris* and *Q. suber* were genetically intermediate between the putative parental species, and by Schicchi et al. (2000), on the base of micro-morphological observations on the leaf epidermis of *Q. fontanesii* in Sicily. However, if we assume *Q. crenata* to be a hybrid, its presence in northern Italy, Alpes Maritimes and Slovenia is puzzling, since *Q. suber* does not grow in these regions, and long distance pollen dispersal from the nearest stands of *Q. suber* (on the Tyrrhenian coast) is highly unlikely. As a possible explanation for this paradox, Goiran (1897, 1899) stated that *Q. suber* was cultivated in northern Italy until the beginning of the XVIII century. In his opinion, the specimens of *Q. crenata* surviving at his time were the offspring of hybridization prior to local extinction of *Q. suber*.

Circumstantial evidence suggests that there may be an ecological (and possibly taxonomic) differentiation between northern and southern plants, so that Barbero et al. (1972) suggested that the name *Q. crenata* might cover two different entities, i.e. a "good" species, growing in the northern part of the distribution range, and a swarm of hybrids *inter parentes* in the southern part.

Lastly, *Q. crenata* in the north is found as isolated individuals, mostly in open places, in meadows, close to old farms and barns, or even in front of a church. More rarely it is found in woods, usually *Quercus cerris* coppice: in these cases, *Q. crenata* is always present with single, monocormic trees, obviously not periodically cut (pers. obs.). We never observed natural regeneration. These circumstances, beside the fact that trees of this species are sometimes regarded as sacred trees, suggest that *Q. crenata* in the northern part of its range might have been actively protected and preserved by humans during the last centuries.

The present study was designed to investigate (i) if the plants growing in the northern part of the distribution range (southern France, northern Italy, Slovenia) can be distinguished from those growing in peninsular Italy and Sicily, sympatric with both presumed parental species, and, consequently, (ii) if the species described by Lamarck as *Q. crenata* is the same as the species described as *Q. pseudosuber* by Santi in central Italy and as *Q. fontanesii* by Gussone in Sicily.

Methods

The distribution of the species was deduced by direct observations in the field and from the relevant literature (Alessandrini and Branchetti 1997; Armiraglio et al. 2004; Brus 1996; Cresta and Salvidio 1991; De Carli et al. 1999; Mondino 1986).

Twigs and acorns were collected in natural stands. Sampling was enhanced by exsiccata kindly loaned by the herbaria BOLO, FI-HCI, HBBS, LJU, NICE, P, RO, TO-HPE, TSB, VER (Appendix 1). The morphometric study covered 91 specimens. Namely, 62 specimens were collected in northern Italy, southern France and Slovenia, and represented the large majority of the specimens known in this part of the distribution range; 29 samples were collected in peninsular Italy and Sicily. Sampling included: the type of *Q. crenata* Lam. (PO-0238993); a specimen collected by Webb at the *locus classicus* of *Q. pseudosuber* Santi, presumably from the very specimen described in the protologue (RO-CAME-11); a specimen of *Q. fontanesii* Guss. collected at the *locus classicus* (RO-HG104). Besides, four samples of *Q. suber* and four samples of *Q. cerris* were used as outgroup in UPGMA.

For the sake of data processing, the specimens were preliminarily divided in two subsets: subset "North" to include specimens collected in the northern regions, where *Q. suber* is absent, and subset "South", including the specimens of peninsular Italy, where both *Q. suber* and *Q. cerris* are present.

The characters used in numerical analyses were chosen considering previous relevant literature (Moggi and Poli 1972; Filippello and Vittadini 1975; Milletti et al. 1982; Romero et al. 2000). Thirty-six morphological characters were found to be variable and potentially discriminant within *Q. crenata* (Tab. 1), 23 of them describing the leaves and twigs, and 13 describing the fruits. For each character, five measures were taken on each specimen, and averaged. Leaves were collected from the middle part of the twigs. Vegetative characters were recorded on the entire set of 91 specimens, whereas reproductive characters could only be determined on 29 specimens, since many exsiccata were sterile, or the fruits were unripe or incomplete. The geographic distribution of the specimens measured is given in Figure 1.

Qualitative characters were coded by dummy (0–1) variables, while all quantitative characters were normalised to fit to a 0–1 range. The complete matrix (not presented) is available from the authors upon request.

Clustering by unweighted pair group method with arithmetic mean (UPGMA) based on Euclidean distance, principal components analysis (PCA), and discriminant analysis (DA) were conducted using the software PAST version 1.32 (2004; Ryan et al. 1995). Operational taxonomic units were individual plants. In addition, means and variances of individual characters were assessed at the level of the species and of the two subsets "North" and "South". The significance of differences in means between the subsets was tested with Student's t-test and the significance of the differences in variances with Fisher's F-test.

Tab. 1. List and coding of the characters recorded.

A. Vegetative characters	
1. LL	Leaf total length from the base (petiole insertion) to the apex (mm).
2. LW	Leaf maximum width (mm)
3. LL / LW	
4. DL	Distance from the leaf apex to the point on the main rib corresponding to the maximum width (i.e.: the point where LL crosses with LW) (mm)
5. LL / DL	
6. DL / LW	
7. LOB	Distance from the mid rib to the apex of the lobe corresponding to the maximum width, measured on the right half of the leaf (mm)
8. SIN	Distance from the mid rib to the sinus immediately proximal with respect to the lobe of LOB (mm)
9. LOB / SIN	
10. PET	Petiole length (mm)
11. LL / PET	
12. LV	Number of main lateral veins, counted on the right half of the leaf. 'Main veins' are those that originate from the mid rib and end at the apex of a lobe
13. BB	Base of the blade: auriculate, subcordate, truncate, cuneate (four states)
14. SLO	Shape of the lobes: rounded or acute (two states)
15. SIHVU	Presence of simple hairs along the veins, on the upper side of the leaf, coded in four classes, from 0 (absent) to 1 (very dense)
16. STHVU	Presence of stellate hairs along the veins on the upper side of the leaf, observed and coded as above
17. STHBU	Presence of stellate hairs on the blade on the upper side of the leaf, observed and coded as above
18. SIHVL	Presence of simple hairs along the veins on the lower side of the leaf, observed and coded as above
19. STHVL	Presence of stellate hairs along the veins on the lower side of the leaf, observed and coded as above
20. STHBL	Presence of stellate hairs on the blade on the lower side of the leaf, observed and coded as above
21. STIP	Linear stipules persistent: present or absent (two states)
22. HYT	Hairs on young twigs: absent, scarce or dense (three states)
23. LYT	Lenticels on young twigs: present or absent (two states)
B. Characters of the fruit	
24. PED	Peduncle length (mm)
25. ACW	Acorn maximum diameter (mm)
26. ACL	Acorn length (mm)
27. ACL/ACW	
28. INW	Involucre maximum diameter (mm)
29. INL	Involucre length (mm)
30. INL/INW	
31. ACL/INL	
32. ACU	Acorn umbonate or not umbonate at the base (two states)
33. INM	Margin of the involucre: smooth or irregularly emarginate (two states)
34. SCE	Scales emerging or not emerging beyond the involucre margin (two states)
35. SCSH	Scale shape: subulate or linear (two states)
36. SCL	Scales in the lower (proximal) part of the involucre: longer, equal, or shorter than the scales near the margin of the involucre (three states)

Fig. 1. *Quercus crenata* sensu lato: geographic distribution of the specimens seen. • Specimens attributed to the "Northern subset", growing where *Q. cerris* only is present. ■ Specimens attributed to the "Southern subset", sympatric with both presumed parental species (*Q. cerris* and *Q. suber*).

Results

In the UPGMA phenograms, plants from different geographic provenance and of the two subsets were intermixed, regardless of the presence or absence of outgroup (*Q. cerris* and *Q. suber*), and of the set of characters considered (vegetative or reproductive). No distinct and consistent clusters could be detected. Addition or subtraction of individual samples or of single characters caused substantial changes in the tree topology, confirming the absence of a well-defined structure. One of the phenograms is shown as example in Appendix 2.

PCA resulted in the extraction of 26 principal components, whose eigenvalues were rather evenly distributed (Tab. 2). The first component explained only 22.47% of the total variance, and as many as nine components were required to explain 90% cumulative variance. The variables that gave the highest contribution to the first principal components were those describing the indumentum, the shape of the leaf base, the shape of the fruit, and peduncle length.

Tab. 2. First nine components extracted by PCA, with their eigenvalues (λ), the percentages of variance explained (per component and cumulative), and the main characters contributing to them (with their loadings in brackets). Abbreviations of character names as in Table 1.

Nr.	λ	% variance	% cumulative	Main characters and loadings
1	0.16	22.47	22.47	STHVL (–0.42). BB (–0.40)
2	0.11	15.76	38.22	STHVU (–0.56). ACL/INL (–0.40)
3	0.09	13.27	51.49	SIHVL (0.51)
4	0.08	11.74	63.23	PED (–0.59). SIHVL (–0.40)
5	0.06	7.83	71.06	STHVL (0.58). BB (–0.47)
6	0.04	6.12	77.18	DL/LW (0.41)
7	0.04	5.44	82.63	
8	0.03	4.39	87.01	
9	0.03	3.70	90.72	

All components caused a dispersion of the individuals along continuous gradients, without distinct clusters. However, the dispersion was uneven, in that the samples of subset "South" were dispersed in a space much broader than the samples of subset "North". As an example, Figure 2 shows their distribution on the second and third principal components, which are mainly determined by the indumentum and by the shape of the fruit.

Discriminant analysis conducted on the entire set of 91 specimens, based on vegetative characters only, correctly assigned 75.82% of the specimens to the "North" and to the "South" subsets respectively. Moreover, a second analysis on the 29 specimens for which both reproductive and vegetative characters were scored, allowed 100% of the specimens to be correctly assigned (Fig. 3). The main discriminant characters were related to the leaf indumentum (STHBL, SIHVU) and shape (DL/LW, LL/DL), to the petiole length (LL/PET), and to the shape of the fruit (ACL/INL; Appendix 3).

Six individual characters significantly differed in their mean values between the two subsets (Tab. 3). In particular, the northern subset differs from the southern one mainly for having leaves narrower (LL/LW), with the maximum width toward the apex (DL/LW), less deeply lobed (LOB/SIN), with a longer petiole (PET, LL/PET). Moreover, the variance of 12 characters proved to be significantly larger in the "southern" subset than in the "northern" one (Tab. 3). Altogether, 16 out of 36 characters revealed a significant difference between subsets, confirming the results obtained in multivariate analyses.

Discussion

Morphological variation within the *Quercus crenata* complex, as detected by PCA and by DA, was mainly determined by characters of the indumentum (stellate and simple hairs on the leaves), and by the shape of the leaves and of the fruit. However, the wide range of variation of such characters prevented them from being used as single diagnostic criteria. Consequently, UPGMA as well as PCA did not allow us to divide the set of specimens into discrete clusters. However, means of six characters differ significantly between the two subset. Accordingly, the discriminant analysis effectively discriminated the two subsets, even in the absence of diagnostic characters.

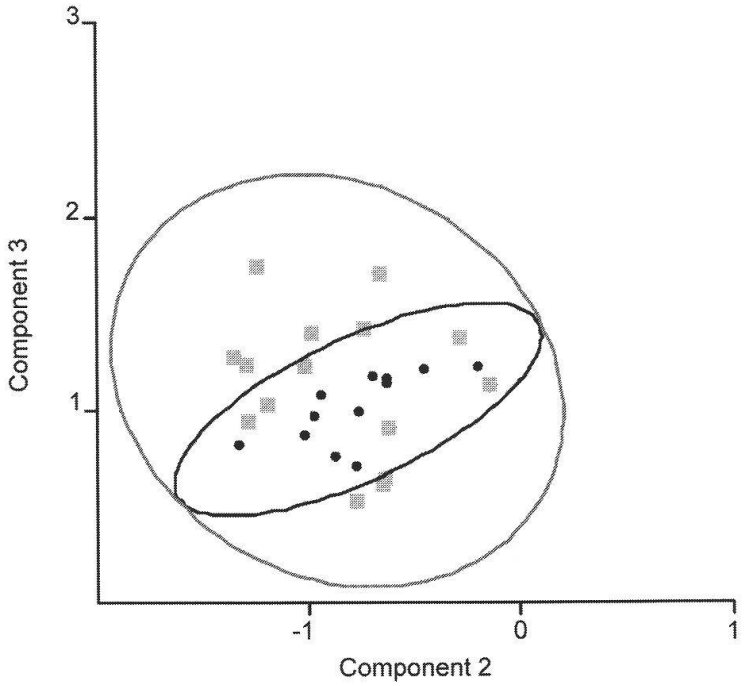

Fig 2. Principal components analysis: dispersion of the specimens along the second and third principal components. Ellipses delimit the space that includes, with $P_{0.95}$, the samples of subset "North" (circles, black ellipse), and the samples of subset "South" (squares, grey ellipse).

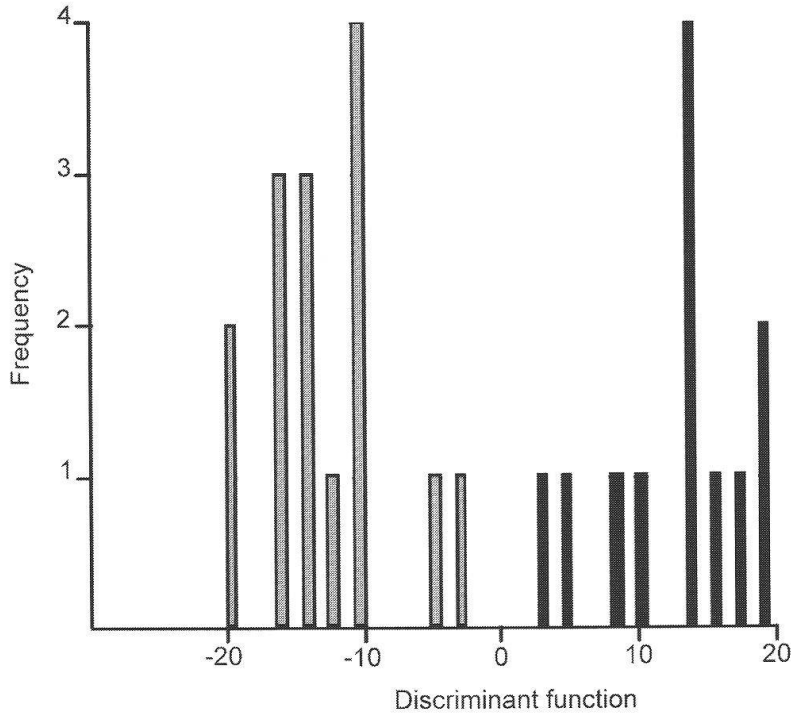

Fig. 3. Discriminant analysis of 27 samples, based on vegetative and reproductive characters. Bars show the number of individuals for each value of the discriminant function (subset "North": black bars; subset "South": grey bars).

Tab. 3. Means and variation of potentially discriminant characters (labeled as in Table 1) for the whole sample ("Overall"), and for the two subsets of "northern" and "southern" plants. At the bottom of the table, Student's *t*-values for differences between the means of the two subsets and Fisher's *F*-values for the difference between variances of the two subsets are given, with significant values in given bold (*: $p < 0.05$; ** : $p < 0.01$). Only characters with significant values of t or F are reported.

	LW	LL/LW	DL/LW	SIN	LOB/SIN	PET	LL/PET	LV	BB	SIHVU	STHVU	HYT	ACW	INL	ACW	SCL
Overall mean	31.41	1.97	1.00	11.82	1.38	9.55	7.55	6.27	0.69	0.02	0.61	0.88	0.68	0.61	14.92	0.86
Overall variance	43.49	0.04	0.02	9.55	0.25	13.47	14.02	0.85	0.04	0.01	0.06	0.06	0.01	0.02	4.23	0.05
Overall standard error	0.69	0.02	0.02	0.33	0.05	0.387	0.39	0.10	0.02	0.01	0.03	0.03	0.11	0.14	0.77	0.08
Northern subset																
Mean	31.61	1.95	1.00	12.32	1.29	9.74	7.34	6.35	0.68	0.02	0.63	0.90	0.70	0.65	15.00	0.95
Variance	38.93	0.03	0.02	9.01	0.04	11.80	14.16	0.79	0.03	0.01	0.05	0.05	0.02	0.01	2.12	0.02
Standard error	0.79	0.02	0.02	0.38	0.02	0.44	0.48	0.11	0.00	0.01	0.03	0.03	0.14	0.10	0.38	0.04
Southern subset																
Mean	30.97	2.03	1.02	10.76	1.57	9.14	8.01	6.10	0.70	0.03	0.56	0.84	0.67	0.58	14.87	0.80
Variance	54.68	0.07	0.04	9.33	0.67	17.34	13.88	0.95	0.07	0.02	0.08	0.09	0.01	0.03	7.60	0.06
Standard error	1.37	0.05	0.04	0.57	0.15	0.77	0.69	0.18	0.01	0.02	0.05	0.06	0.07	0.19	0.83	0.06
t	0.93	**3.45****	1.14	**8.44****	**3.68****	**2.99****	**3.28****	**2.49**	0.64	0.52	1.35	1.11	0.34	0.46	0.17	1.94
F	**1.40***	**2.41****	**2.20****	1.04	**18.22****	1.47	0.98	1.21	**2.04****	**2.10****	**1.60***	**1.90**	**4.16****	**2.70***	**3.58***	**2.83**

The greater variability of the "southern" plants is compatible with the hypothesis that they represent the offspring of current hybridization between the two parental species (and, in the case of Sicily, between slightly different local races). This result is consistent with their distribution (always in the presence of the parental species) and with the existing molecular evidence (Bellarosa et al., 1996).

On the contrary, the plants of Alpes Maritimes, northern Italy and Slovenia present low morphological diversity. Our findings are consistent with the historical reconstruction by Goiran (1897, 1899), in that the very few existing individuals – about one hundred, dispersed over a wide geographic range, and possibly derived from few ancestors – might have survived, at least in part, because they had been protected by humans. The hybrid origin is very likely, but not yet proved. A molecular study is currently in progress to elucidate their biological and genetic diversity.

In the presence of the morphological differences mentioned above, we adhere to the taxonomic hypothesis suggested by Barbero et al. (1972), and propose to use two different binomials for the two sets of plants: namely, we propose to reserve the name *Quercus crenata* Lam. to the northern, relict plants, whose hybrid origin is likely but not proved, and to maintain the name *Quercus* x *pseudosuber* Santi for the hybrids *inter parentes* of peninsular Italy and Sicily.

The distinction between the two taxa has a major bearing on conservation issues. *Quercus* x *pseudosuber*, rather common from Tuscany to Sicily, and currently generated where the parental species are sympatric, does not seem to require special protection. On the contrary, *Quercus crenata* is very rare and apparently severely endangered in all of its range.

Nomenclature

Quercus crenata Lam., Encycl. Méth. Bot. 1: 724 (1783)
• LECTOTYPE: Herb. Mus. Paris PO-0238993 . "*Quercus crenata* enc./ je croi qu'il perd ses feuilles / le chene le Comble des angl. / espece nouv. Son écorce est subéreuse" (designated by Brullo et al., 1999).
• DISTRIBUTION: *France*: Alpes Maritimes; *Italy*: Southern and western Piemonte (Provinces Torino, Cuneo, Asti, Alessandria); Liguria (Apennine in the province Savona); Lombardia (Pre-Alps in the provinces Bergamo and Brescia); Trentino (very rare); Veneto (Pre-Alps in the provinces Verona and Vicenza); Emilia (Appenine, in the provinces Parma, Reggio, Modena, Bologna, Forlì, Ravenna); *Slovenia*; *Croatia*: Istra.

Quercus* x *pseudosuber G. Santi, Viaggio al Montamiata:156 (1795)
• LECTOTYPE: G. Santi, Viaggio al Montamiata, tav. III (designated here by A. Chiarucci, G. Cristofolini and S. Crema). The original material by Santi, searched in several Italian herbaria (BOLO, FI, PI, RO, SI), could not be traced. The plant at the *locus classicus* (see below) is no more extant. Fortunately, Santi's diagnosis is accompanied by an excellent plate (Fig. 4) that we select as lectotype, in the absence of original exsiccata.
• EPITYPE: Arcidosso (Grosseto), dopo il colle Poggio della Madonna, vicino alla chiesina dei Fabbrazzoni, 21/12/1852, *Webb* (RO and FI) (designated here by A. Chiarucci, G. Cristofolini and S. Crema). Webb collected at the *locus classicus*, presumably from the type specimen, in 1852. His collection, preserved in RO and in FI, is designated here as epitype of the name ex Cod. Bot. Nomencl. art 9.7.

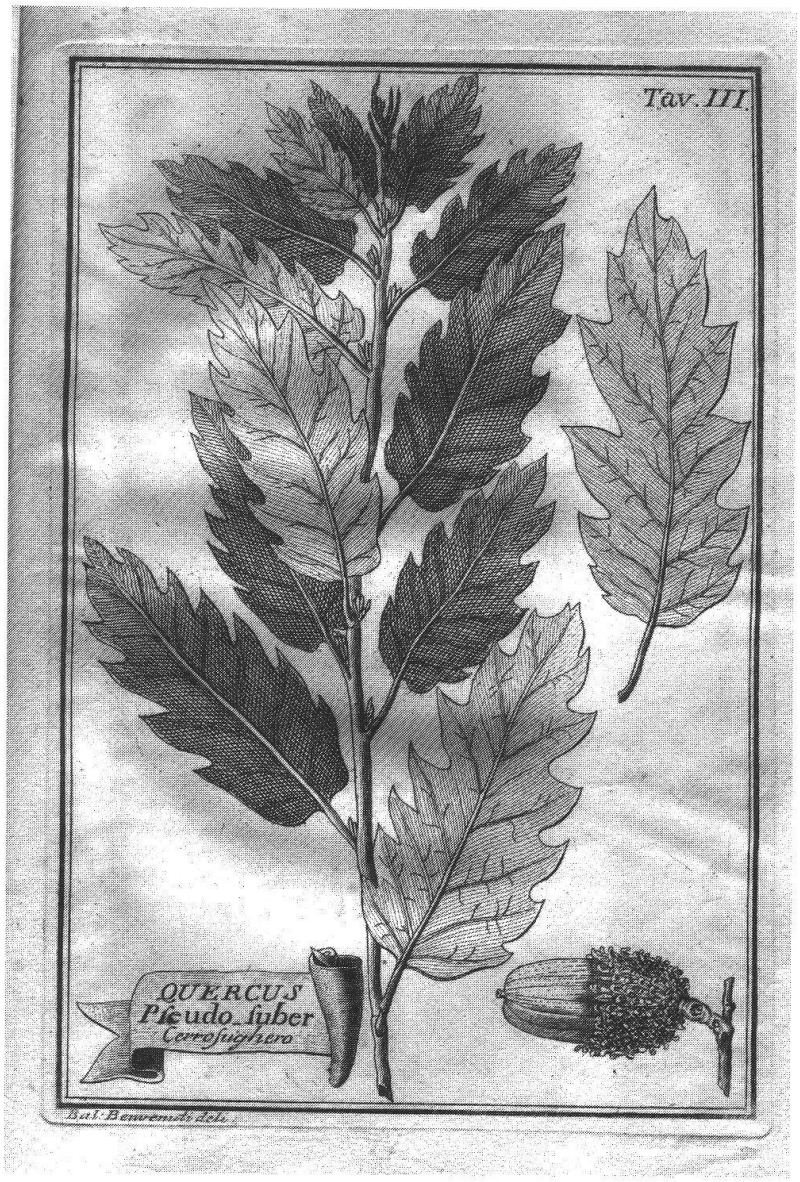

Fig. 4. Lectotype of the name *Quercus pseudosuber* Santi: Viaggio al Montamiata, tav. III.

• LOCUS CLASSICUS: Montamiata, Arcidosso, al poggio della Madonna, vicino alla chiesina dei Fabbrazzoni.
• SYNONIMS: *Q. fontanesii* Guss., Index Seminum Horti Boccadifalco an.1823 (1825); Florae siculae synopsis 2 :605 (1844).
• DISTRIBUTION: *Italy*: Scattered in all peninsula except Puglia; Sicilia.

Riassunto

Quercus crenata Lam. sensu lato (inclusiva di *Q. pseudosuber* Santi), supposto ibrido *Quercus cerris* x *Q. suber*, cresce nell'Italia peninsulare ed in Sicilia, simpatrica con i due presunti parentali, ma anche in Provenza, Italia settentrionale, Slovenia ed Istria,

dove *Q. suber* non è segnalata. Abbiamo condotto uno studio morfometrico su foglie e frutti di campioni raccolti attraverso tutto l'areale, per determinare se vi siano differenze fra le piante del settore settentrionale e quelle del settore centro-meridionale. Abbiamo rilevato 36 caratteri morfologici, che sono risultati potenzialmente discriminanti, su 91 piante, comprendenti la maggioranza degli individui noti nella parte settentrionale dell'areale ed un'ampia rappresentanza delle piante crescenti nell'Italia peninsulare ed in Sicilia. L'analisi delle componenti principali ha dimostrato che le piante settentrionali e quelle meridionali non formano due aggregati indipendenti; tuttavia, la dispersione delle piante meridionali nello spazio definito dalle componenti principali è molto maggiore della dispersione delle piante settentrionali. L'analisi statistica ha dimostrato che la varianza di 12 dei caratteri misurati è significativamente maggiore nelle piante meridionali in confronto a quelle settentrionali, e che i valori medi di 6 caratteri differiscono, fra le due parti dell'areale, più di quanto atteso per una distribuzione casuale. Nessun carattere è però risultato diacritico, a causa della alta variabilità. L'analisi discriminante ha dimostrato che i campioni provenienti dalla parte settentrionale dell'areale possono essere distinti da quelli dell'Italia peninsulare e della Sicilia. Si conclude che, pur in assenza di caratteri diacritici, il complesso *Quercus crenata – Q. pseudosuber* è eterogeneo. Per le piante della porzione meridionale dell'areale, che sono ibridi inter parentes, proponiamo di mantenere il nome *Quercus* x *pseudosuber* Santi. Le piante della parte settentrionale dell'areale, caratterizzate da ridotta variabilità, sono forse relitto di antica ibridazione, derivate da pochi progenitori. A queste si applica propriamente il nome *Quercus crenata* Lam., specie che appare gravemente minacciata di estinzione.

This article is dedicated to the memory of the late Dr. Gianfranco Paravidino from Rocca Grimalda, who valuably helped with field work in Piedmont.

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Electronic supplementary material

Appendix 1. Specimens seen, with the accession numbers of the specimens selected for the numerical analysis in square brackets.

Appendix 2. Clustering by UPGMA of 91 specimens, using a matrix of Euclidean distances based on quantitative vegetative characters. Individuals are identified by the accession number followed by the abbreviation of the province of origin (see Appendix 1).

Appendix 3. Main morphological characters discriminating between northern and southern specimens.

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