Vitis ×*sullivaniana* (Vitaceae), a name for the hybrid between *V. acerifolia* and *V. riparia*

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Abstract - A name, *Vitis* ×*sullivaniana*, is assigned to the cultigen hybrid between North American *V. acerifolia* and *V. riparia*, selected in France as a grape phylloxera-resistant rootstock in 1881 and currently naturalized in different European countries. A detailed morphological description of the nothospecies, accompanied by original and historical illustrations, is provided, along with a comparison with similar taxa and nothotaxa found in the wild in Europe. The history of the most widespread rootstock belonging to this nothospecies, 'Couderc 1616', is reconstructed in the context of the vineyard reconstitution of the 19th and 20th centuries.

Key words: alien species, Couderc 1616, flora, taxonomy, viticulture.

Riassunto - *Vitis* ×*sullivaniana* (Vitaceae), un nome per l'ibrido tra *V. acerifolia* e *V. riparia.*

Nel presente contributo è assegnato un nome, *Vitis* ×*sullivaniana*, all'ibrido cultigeno tra le nordamericane *V. acerifolia* e *V. riparia*, selezionato nel 1881 in Francia come portinnesto resistente alla fillossera della vite e attualmente naturalizzato in diversi paesi europei. Viene fornita una descrizione morfologica dettagliata della notospecie, accompagnata da illustrazioni originali e storiche, oltre a un raffronto con taxa e nototaxa affini diffusi allo stato spontaneo in Europa. È inoltre ricostruita, nell'ambito della ricostituzione dei vigneti del XIX e XX secolo, la storia del portinnesto più diffuso appartenente a questo ibrido, 'Couderc 1616'.

Parole chiave: Couderc 1616, flora, specie aliene, tassonomia, viticoltura.

INTRODUCTION

European taxonomists and flora researchers ascertained the occurrence of alien *Vitis* hybrids in natural and semi-natural environments since the early 2000's (see, e.g., Laguna, 2005). They originated from hybrid rootstocks and direct producers introduced en masse since the second half of the 19th century to recover the cultivation of *V. vinifera* L. from the plague of grape phylloxera [*Daktulosphaira vitifoliae* (Fitch, 1855)] (Gale, 2011). As evidenced by many floristic repertoires (e.g., Laguna, 2005; Ardenghi *et al.*, 2017; André *et al*., 2020; Galasso *et al.*, 2024; Ardenghi, 2025a), most of the alien *Vitis* naturalized or invasive in the European and Mediterranean countries are hybrids involving two or more American species and sometimes also Eurasian *V. vinifera*. Due to the status of invasiveness of some hybrids and their frequency in the wild, Ardenghi *et al.* (2014: 164) expressed the need of assigning a nothospecific binomial to these, both to underly their biological autonomy and to replace the use of some lengthy hybrid formulas commonly employed in agronomic and ampelographic literature, that are almost impractical in floristic, vegetation and ecological fields. Their approach was in line with Moore (1991), who accepted nothospecific binomials for spontaneous hybrids of native *Vitis* in North America (such as *V.* ×*novae-angliae* Fernald). Additional nothospecific binomials were subsequently published by Ardenghi *et al.* (2015a) and Vázquez & García (2017).

The occurrence in the wild of the hybrid between *V. acerifolia* Raf. and *V. riparia* Michx. was recorded for the first time in Europe by Laguna Lumbreras (2004) in Spain; its presence as a naturalized alien was subsequently evidenced in France (André, 2022). In Italy, it was collected for the first time in Tuscany in 2007 but was misidentified with *V.* ×*instabilis* Ardenghi, Galasso, Banfi & Lastrucci; its correct identity was ascertained only years later by Ardenghi (2025a). This hybrid seems to be quite widespread in central and northern Italy, where it forms stands not so dissimilar from those of invasive *V. riparia*, *V.* ×*koberi* Ardenghi, Galasso, Banfi & Lastrucci and *V.* ×*instabilis* (Ardenghi 2025a, 2025b).

With the aim to better circumscribe the identity of *V. acerifolia* × *V. riparia* and to avoid further misidentification with consequential underestimation of its real distribution in the wild, in this paper a new nothospecific binomial is proposed, in line with the philosophy expressed in previous contributions (Ardenghi *et al.*, 2014, 2015a, 2015b).

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Received for publication: 26 October 2025
Accepted for publication: 29 April 2026
Early access: 18 September 2026
Online publication: 5 November 2026

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MATERIALS AND METHODS

The present paper is based on the study of populations sampled in Italy, integrated with data acquired from herbarium specimens (herbarium codes are mentioned according to Index Herbariorum: Thiers, 2014 onwards), ampelographic, taxonomic and floristic literature.

The morphological description of the new nothospecies refers to individuals sampled in the field by the author, with special reference to the *locus classicus* population. Surface of the herbaceous stems, habit, texture and shine of the leaves and colours were evaluated on live specimens only.

Terminology regarding *Vitis* morphology is according to Boursiquot & Lacombe (2023), except for the definitions of "arachnoid" and "hirtellous" pubescence (used instead of "prostrate" and "erect" hairs), that follows Ardenghi *et al.* (2014), and the use of "folded" as a substitute to "keeled" for conduplicately folded leaf baldes.

Cultivar names follow Röckel *et al.* (2025), while syntaxa names Chytrý *et al.* (2024).

RESULTS AND DISCUSSION

Taxonomic treatment

Vitis* ×*sullivaniana Ardenghi, nothosp. nov. Figs. 1-6

Hybrid formula: *Vitis acerifolia* Raf. × *V. riparia* Michx.

Diagnosis: *Planta hybrida, a* V. riparia *pubescentia araneosa in iuvenibus sarmentis, foliis et paniculis, sarmentis herbaceis striatis, foliorum principalibus dentibus uncinatis et marginalis plerumque longioribus quam latis, foliis lucidioribus differt; a* V. acerifolia *pubescentia araneosa rariora, foliorum laminis longioribus, raro plicatis, cuneiformis differt.*

Hybrid plant, distinguished from *V. riparia* by the arachnoid pubescence on young shoots, leaves and inflorescences, the striated herbaceous stems, the uncinate teeth at the end of the two main lateral veins, the marginal leaf teeth usually longer than wide and the more lustrous leaves; from *V. acerifolia* by the scarcer arachnoid pubescence, and the longer, cuneiform and rarely folded leaf blades.

Type: ITALY. **Lombardy. Prov. Pavia**: Stradella, Via G. Di Vittorio, a lato dell'ex fabbrica di legnami "Guglielmo Massoni & C." (WGS84: 45.071270°N, 9.305632°E), 82 m, piazzale (con *Elymus repens*, *Rubus* sect. *Corylifolii*, *Lepidium draba*, *Cirsium arvense*), recinzione e muri di fabbricato abbandonato (con *Rubus* sect. *Corylifolii*, *Ailanthus altissima*, *Humulus lupulus*), tappezzante, 02.05.2025, *N.M.G. Ardenghi* (*holotypus* MSNM barcodes MSNM54968, MSNM54969, Figs. 5-6, *isotypus* FI).

Eponimy: the epithet is dedicated to Chicago pianist Joseph Michael O'Sullivan, better known as Joe Sullivan (1906-1971), the author's favourite jazz artist. Ninth child of Irish immigrants, Sullivan, who received twelve years of training in classical music, developed a style strongly influenced by Afro-American jazz pianists, mainly Earl Hines, Fats Waller and Jelly Roll Morton. An unpredictable improviser, he was provided with a powerful rhythmic left hand and a deep sense of the blues, that, matched with the bravura of classical pianists, made him one of the most appreciated white jazzmen of the 1930's-1950's. Sullivan impressed his talents in many recordings of his most popular compositions: *Gin Mill Blues*, *Little Rock Getaway*, *Just Strolling* and *In A Minor Mood*. During his lengthy career, he played both as a soloist and in association with artists like Eddie Condon, Red Nichols, Russ Columbo, Roger Wolfe Kahn, Bob and Bing Crosby, Jack Teagarden and Louis Armstrong. Sullivan contributed in many occasions to break down racial barriers in jazz since the 1920's, for instance by taking part to, according to jazz historian and journalist Dan Morgenstern, the first real integrated jazz recording session (Eddie's Hot Shots, in New York, on 8 February 1929) and leading, by October 1939 at New York's Cafe Society Downtown, one the earliest interracial groups performing live (Keepnews, 1949; Condon, 1962; Hadlock, 1982; Morgenstern & Meyer, 2004: 159). Jazz developed as an art form benefiting of a multicultural background; similarly, modern viticulture emerged as the result of a successful encounter of plants and minds from multiple nations.

Morphological description

Vines woody, deciduous, climbing or creeping-prostrate, reaching at least 3 m of height in presence of a support. ***Bark*** of one-year-old stems not exfoliating, slightly and finely striated, yellowish- to orange-brown, covered with grey-purplish pruine especially at the nodes; bark of stems older than one year exfoliating in narrow plates, dark greyish-brown. ***Tendrils*** bifurcate, reddish-green, glabrous, a tendril or inflorescence present at only 2 consecutive nodes. ***Stipules*** 6-7 mm long, white-translucent. ***Young shoots*** with ***growing tips*** enveloped by unfolding leaves ("closed"), curved, green, sometimes tinged with bronze, with hirtellous and sparse arachnoid pubescence. ***First three young unfolded leaves*** plane, usually cuneiform, with truncate to very widely U-shaped base; adaxial leaf surface lustrous, green, sometimes tinged with bronze, sinuses between teeth usually pink, with dense hirtellous and scattered arachnoid pubescence on the veins, that are pink at the base; abaxial leaf surface with both hirtellous and arachnoid pubescence on the veins, the latter concentrated near the insertion of the petiole, and white tuft of hairs at vein axils; leaf margin teeth hirtellous, acuminate to cuspidate, sometimes curved, those at the end of central the two lateral nerves very long, caudate; petiole reddish on the adaxial side, with scattered arachnoid hairs and a line of hirtellous pubescence on the adaxial side (petiolar channel). ***Herbaceous stem*** striated at least in the distal internodes, purplish-red on one side and glaucous green on the other, pruinose, glabrous to sparsely arachnoid. ***Adult leaves*** with blades undulated, occasionally conduplicately folded, 13-25 cm long, usually cuneiform, 3-shouldered, usually bearing phylloxera galls, yellow in autumn; ***leaf base*** widely U-shaped to bracket-shaped; ***adaxial surface***

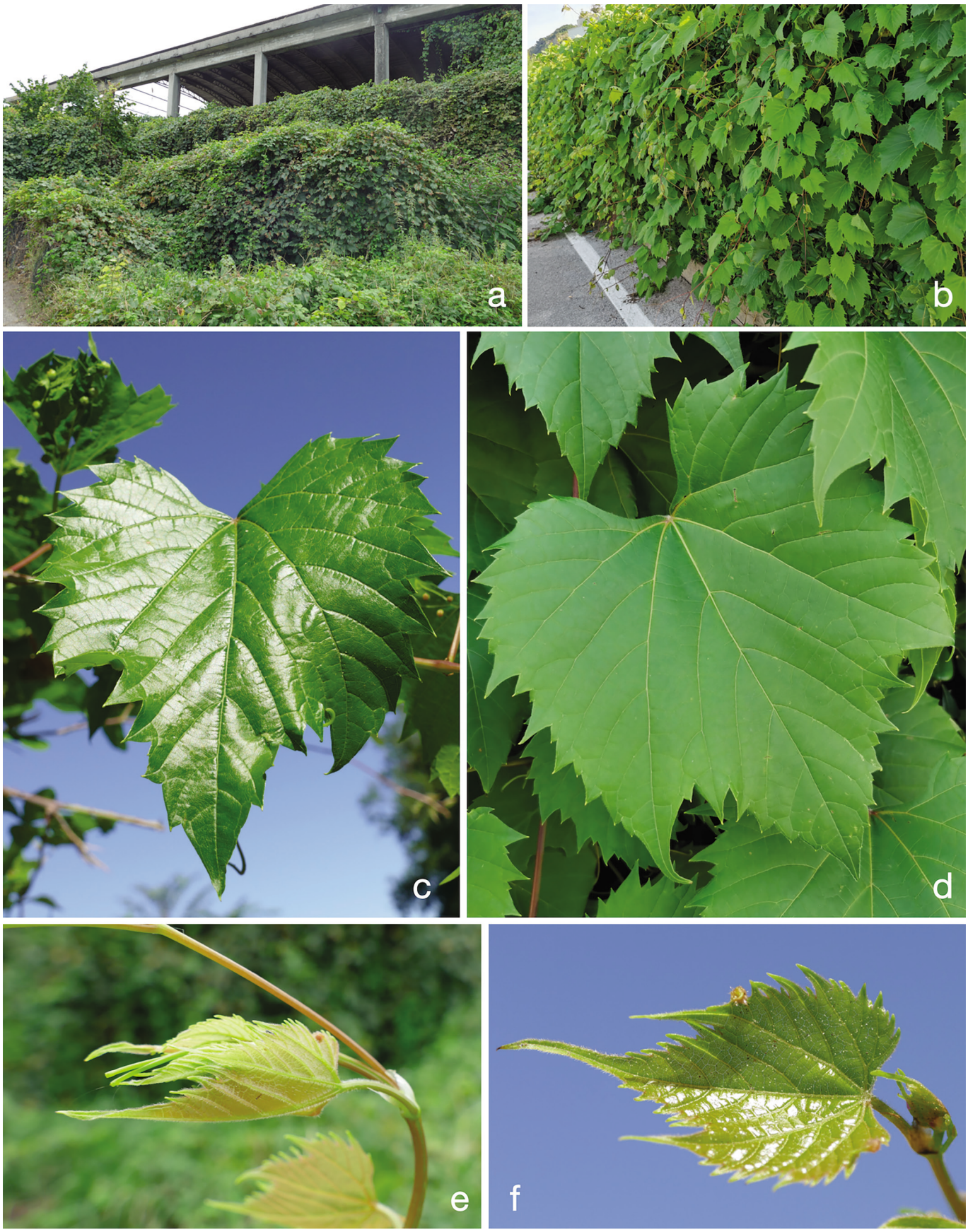


Fig. 1 - *Vitis* ×*sullivaniana*: a, b) naturalized stands; c, d) adult leaves; e) tip of a young shoot; f) young leaf; a, c, e, f) Stradella (Pavia, Italy), Via Di Vittorio, 14.09 and 05.10.2025; b, d) Pesaro (Pesaro e Urbino, Italy; 43.904515°N, 12.930941°E), 25.08.2025. (Photos / Foto: Nicola M. G. Ardenghi).

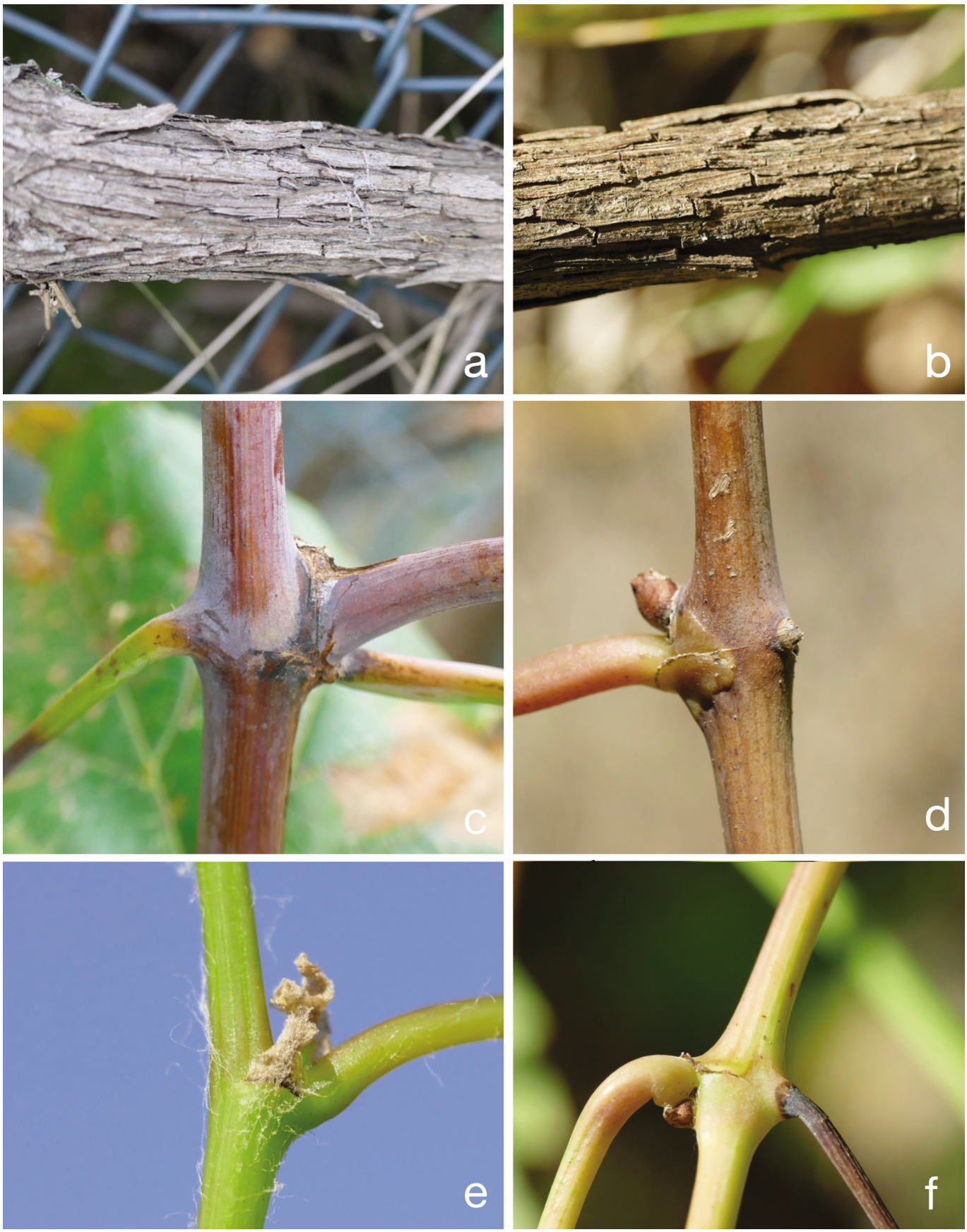


Fig. 2 - *Vitis* ×*sullivaniana*: a, b) bark on stems older than one year; c, d) bark on one-year-old stems; e, f) herbaceous stems; a, c, e) Stradella (Pavia, Italy), Via Di Vittorio, 14.09 and 05.10.2025; b, d, f) *ibidem*, between Torre Sacchetti and Solinga, 05.10.2025. (Photos / Foto: Nicola M. G. Ardenghi).

dark green, lustrous, slightly blistered; veins pinkish to reddish at the base, with short hirtellous pubescence and scattered arachnoid hairs; ***abaxial surface*** paler than the adaxial, dull; ***veins*** with hirtellous pubescence and scattered arachnoid hairs over the surface; primary and secondary veins with white tuft of hairs at the axils; ***leaf margin*** with hirtellous pubescence, teeth prominent, much longer than wide (occasionally wider than long near the apex of the leaf), straight or falciform in springtime leaves, sides both concave or concave and convex (occasionally both convex); teeth at the end of the two main lateral veins usually uncinate, the one at the end of the central vein uncinate or cuspidate to caudate; ***petiole*** pale green or pinkish, occasionally red when exposed to sun, with scattered arachnoid hairs and a line of hirtellous pubescence on the adaxial side along the petiolar channel. ***Inflorescence*** 7.5-12.0 cm long; peduncle and axis with arachnoid pubescence; ***flowers*** male (but see also the next paragraph). ***Fruits*** not developed (but see also the next paragraph).

Identity of the hybrid

The investigated Italian populations correspond to 'Couderc 1616' (= '1616 C.', '1616 Couderc', 'Solonis Riparia 1616', 'Solonis × Riparia 1616', 'Solonis × Riparia 1616 C.', 'Solonis × Riparia 1616 Couderc'), a hybrid rootstock selected in France by Georges Couderc, by crossing *Vitis acerifolia* 'Solonis' with *V. riparia* 'Riparia Gloire de Montpellier' (Röckel *et al*., 2025).

As recently put together by Ardenghi (2025a), "Solonis" was originally described by Jules Émile Planchon (1875: 118-120) as *V. cordifolia* Michx. var. *solonis* Planch., on the basis of specimens cultivated at the Berlin Botanic

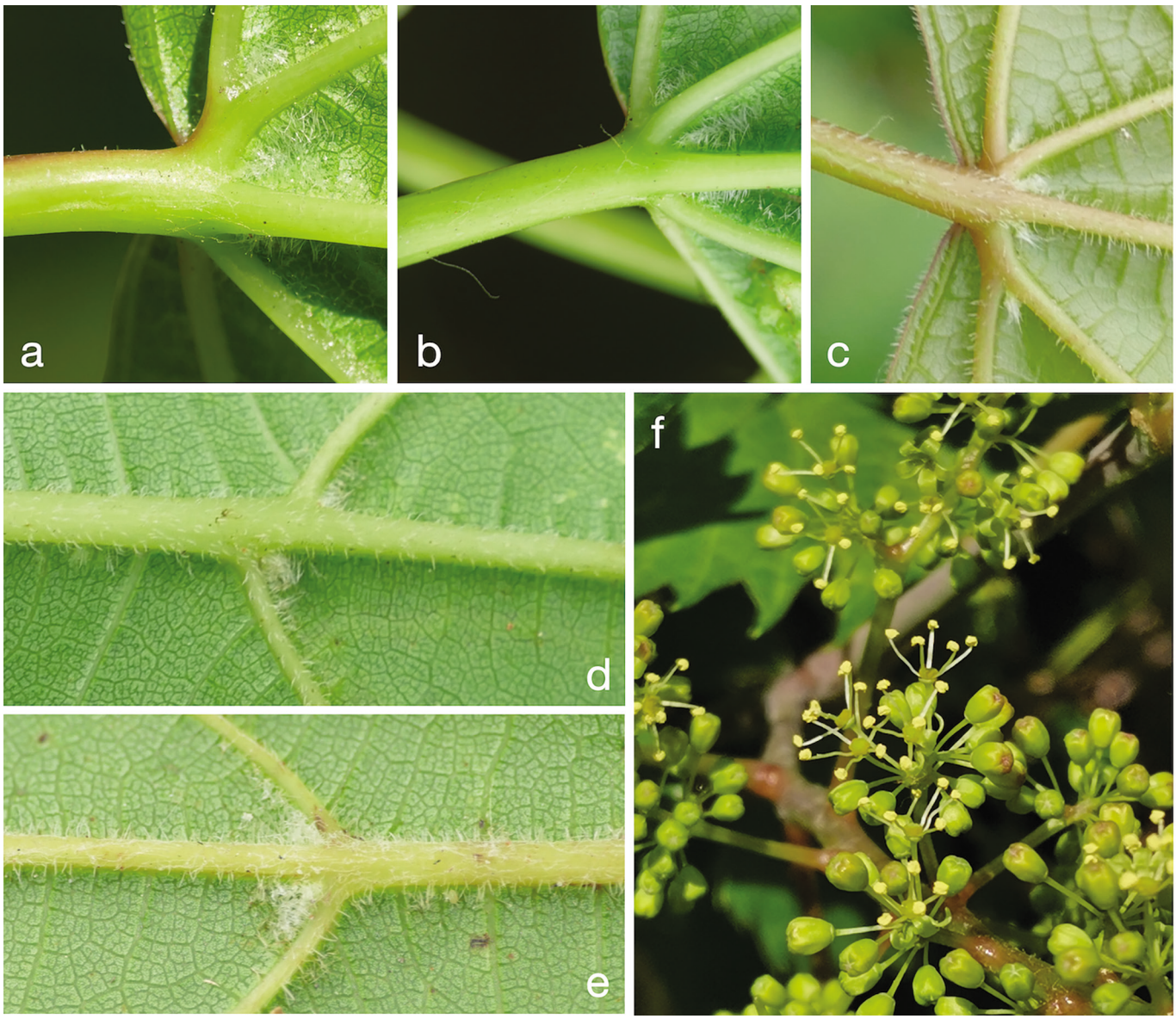


Fig. 3 - *Vitis* ×*sullivaniana*: a-c) hirtellous and arachnoid pubescence at the petiole insertion of adult (a, b) and young (c) leaves, abaxial surface; d, e) hirtellous and arachnoid pubescence on the abaxial surface of adult leaves; f) male flowers; a-e) Stradella (Pavia, Italy), Via Di Vittorio, 14.09 and 05.10.2025; f) *ibidem*, 02.05.2025. (Photos / Foto: Nicola M. G. Ardenghi).

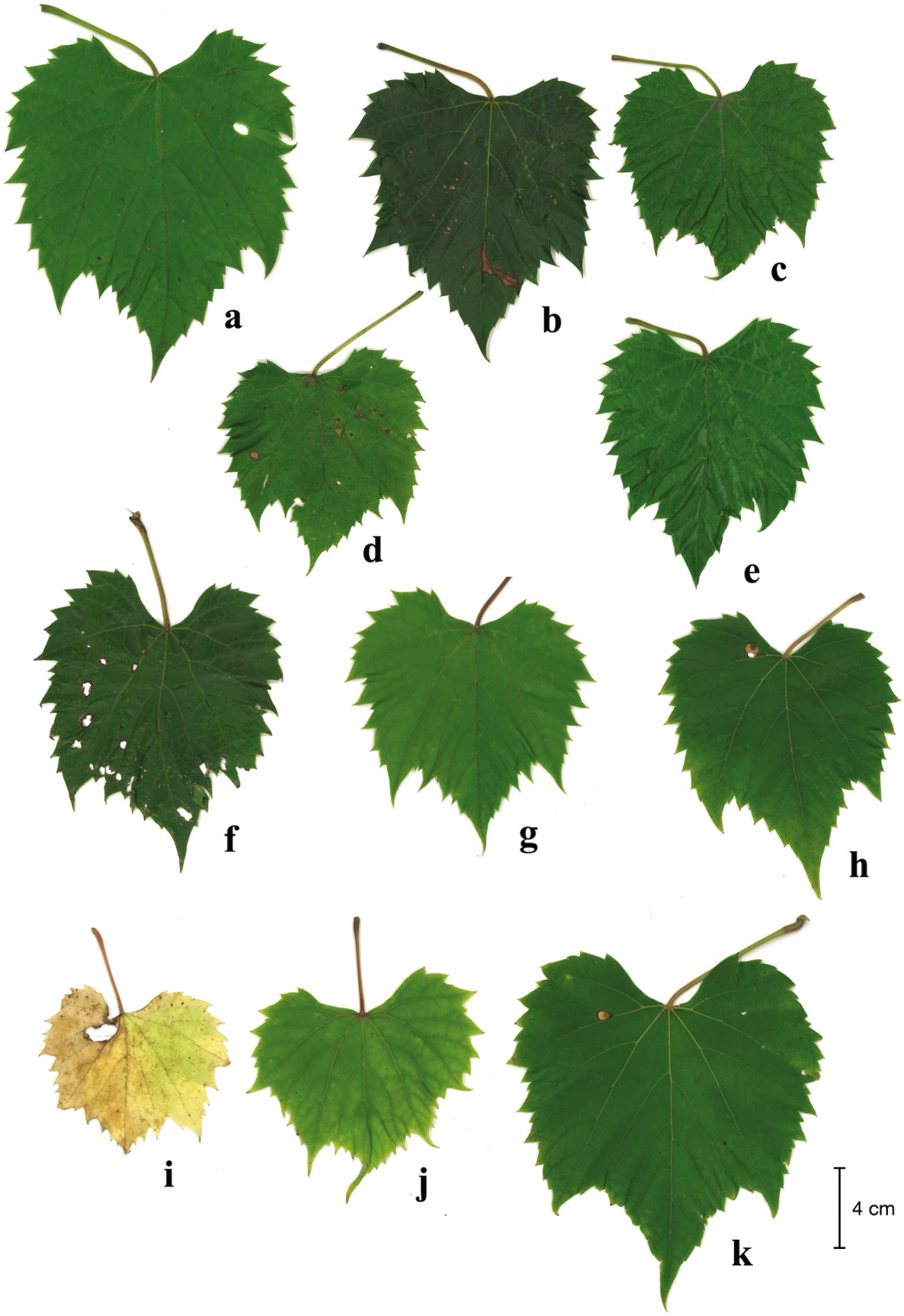


Fig. 4 - *Vitis* ×*sullivaniana*, variability of leaves; a-g) Stradella (Pavia, Italy), Via Di Vittorio, 05.10.2025; h-k) *ibidem*, between Torre Sacchetti and Solinga, 05.10.2025. Leaves i and j are yellow due to the autumn season; most of the holes are the consequence of mines produced by *Antispila oinophylla*, still visible in h and k. (Scans: Nicola M. G. Ardenghi).

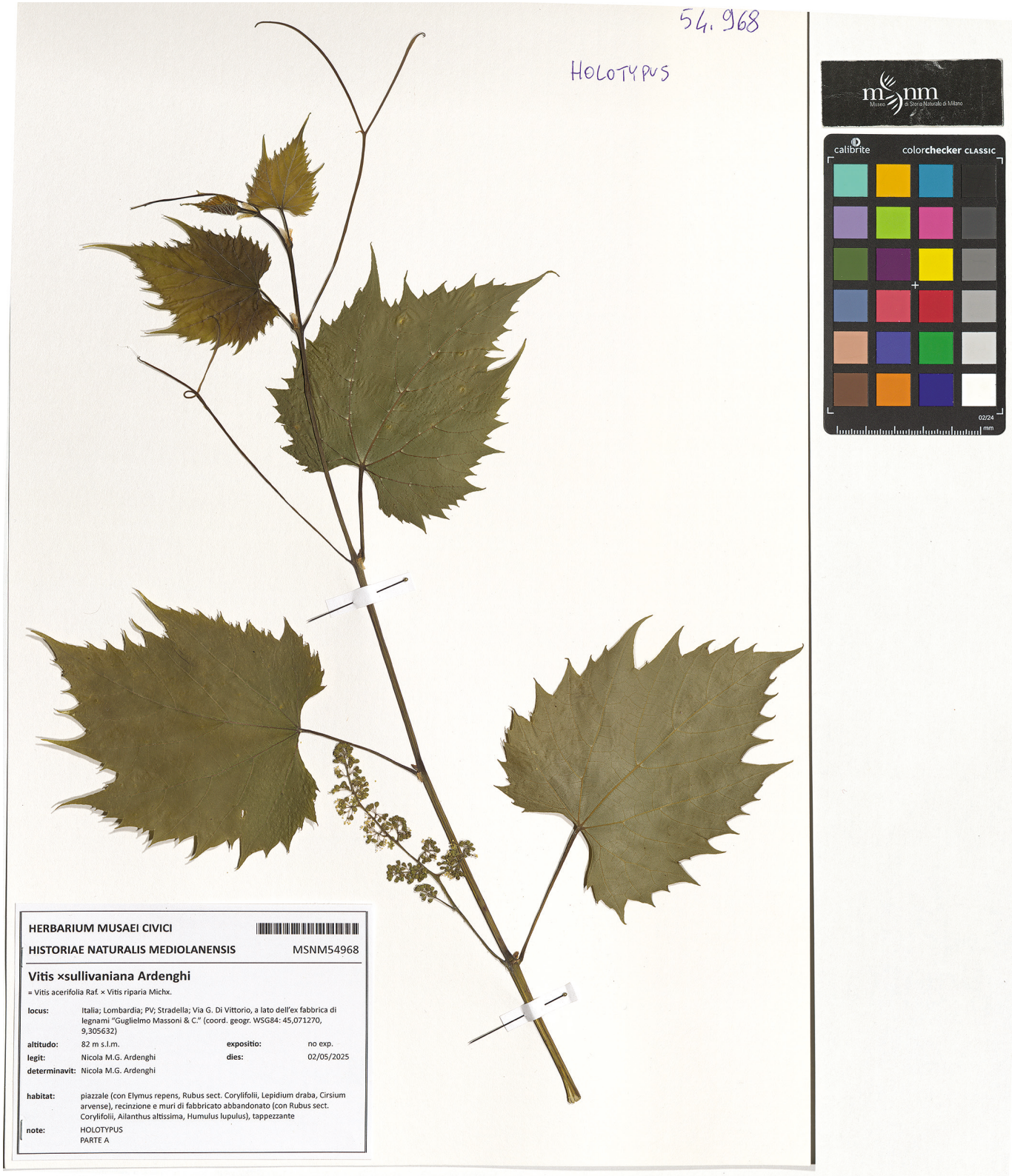


Fig. 5 - *Vitis ×sullivaniana*, holotype, part A (MSNM barcode MSNM54968). (Scan by Museo di Storia Naturale di Milano).



Fig. 6 - *Vitis ×sullivaniana*, holotype, part B (MSNM barcode MSNM54969) (Scan by Museo di Storia Naturale di Milano).

Garden (specimens collected by George Engelmann on 26.06.1868, MO-174715 [digital image!] and MO-174716 [digital image!]; see also Engelmann, 1883: 18) and at Léo Laliman's La Touratte estate in La Souys, Floirac, Gironde; the latter probably received the plant from nurserymen Louis and Prosper Berckmans of Augusta, Georgia, United States (Millardet, 1882: 25). Planchon subsequently observed an older specimen of "Solonis", collected in 1835 by Alexandre Louis Simon Lejeune, in a garden near Spa, Belgium, and preserved under the name of «Isabelle» at the herbarium of the Bruxelles Botanic Garden (Planchon in Engelmann, 1885: 30).

In the course of history, "Solonis" experienced conflicting taxonomic treatments, having been regarded as an independent species [*V. solonis* (Planch.) Engelm. ex Millardet] (Millardet, 1882: 23) or as a complex hybrid (cfr. Galet, 1988: 62). Currently, it is regarded as a synonym (Galet, 1988: 61; Moore, 1991: 359; Ardenghi *et al*., 2017) or as a cultivar (Laguna Lumbreras, 2004; André, 2022) of *V. acerifolia* (= *V. longii* W.R.Prince & Prince); the latter treatment is here followed. Conversely, Röckel *et al*. (2025), continue to consider "Solonis" as a hybrid between *V. acerifolia* and *V. riparia* (yet, without molecular evidence), adopting the rank of cultivar. Thus, 'Couderc 1616' can be regarded as a hybrid between *V. acerifolia* e *V. riparia*.

It seems that more than one clone of 'Couderc 1616' exists: plants cultivated in France are female and bear fruits (Galet, 1988: 334; André, 2022), while those propagated in Italy are male and do not set on fruit (Cosmo *et al.*, 1958: 116; Pecile & Zavaglia, 2025). Galet (1988: 335) and André (2022) describe a third clone from Alsace and Germany, named 'Couderc 1616 E', with marginal leaf teeth wider and less acute; according to one German source (Staatsmin. f. Wirtschaft, Abt. Landw., 1937, under «Typ E»), this clone is male. A fourth clone, named 'Couderc 1616 Davy', allegedly from France, is reported either as male by André (2022) or as female by Röckel *et al*. (2025). The Italian wild populations from Lombardy and Marche clearly belong to the male clone described by Cosmo *et al.* (1958).

Similar taxa and nothotaxa

Vitis ×*sullivaniana* can be easily mistaken with *V. riparia* and its cultivars, especially with those individuals bearing slightly uncinate teeth at the end of the three main nerves of the leaves. As summarized in the protologue of *V.* ×*sullivaniana* and in Tab. 1, *V. riparia* is distinguished for almost lacking arachnoid hairs on young shoots and leaves (vs. present), the terete herbaceous stems (vs. striated), leaf margin teeth more variable in shape, from wider than long to longer than wide (vs. usually longer than wide), and the adaxial leaf surface less lustrous to dull (vs. very lustrous) (Galet, 1988: 161; André *et al*., 2020: 38-45; Boursiquot & Lacombe, 2023; personal observations; Fig. 7, 8).

A very similar hybrid is *V. acerifolia* × *V. riparia* × *V. rupestris* Scheele 'Castel 216-3', a rootstock obtained by hybridist Pierre Castel in 1906 by crossing *V.* ×*sullivaniana* 'Couderc 1616' with *V. rupestris* 'Rupestris Du Lot', whose cultivation, concentrated in France only, almost stopped after 1975. It has been recorded in the wild only in Champagne (France). Its characters are strongly influenced by *V. rupestris*, thus it appears to be more similar to *V.* ×*instabilis*. It can be separated from *V.* ×*sullivaniana* by its non-climbing habit (vs. climbing), the half-open tips of young shoots (vs. closed), the reddish-brown woody stems (vs. yellowish- to orange-brown), the strongly folded leaves (vs. undulated), that are almost entire (vs. 3-shouldered), reniform in shape (vs. cuneiform), with a widely open basal sinus and tufts at vein axils absent or scarsely developed (Galet, 1988: 335; André *et al*., 2020: 63; Boursiquot & Lacombe, 2023; Röckel *et al*., 2025).

Less difficult is the distinction from parental *V. acerifolia* 'Solonis', although regularly provided with uncinate teeth like *V.* ×*sullivaniana*: the dense white-arachnoid pubescence on the tips of young shoots and on the young leaves, that in springtime appear glaucous and mat, make this cultivar unmistakable (Galet, 1988: 62-63, 331; André *et al*., 2020: 26-27; André, 2022).

Further confusion may arise from more-or-less climbing/creeping cultivars of *V.* ×*instabilis* (especially 'Millardet et Grasset 101-14' and 'Schwarzmann', the most widespread in the wild at least in Italy, according to author's observations) and *V. riparia* × *V. rupestris* × *V. vulpina* L. '106-8', particularly when these are provided with slightly uncinate teeth at the end of the main three nerves. As summarized in Tab. 1, *V. riparia* × *V. rupestris* × *V. vulpina* '106-8' has tips of young shoots and young leaves tinged with red copper (vs. green or bronze-tinged), leaf blades suborbicular and occasionally 3-lobed (vs. cuneiform and entire), the base of the leaf basal sinus directly bordered by the nerves (vs. not bordered) and the teeth usually wider than long, with sides both convex (vs. longer than wide, with sides only occasionally both convex). Climbing cultivars of *V.* ×*instabilis* are differentiated by the folded young and adult leaves (vs. plane and undulated, respectively), that varies from cuneiform to reniform in shape (vs. cuneiform), with marginal teeth wider than long or as wide as long (vs. usually longer than wide) (Cosmo *et al*., 1958: 64, 118; Galet, 1988: 225, 229, 344; Ardenghi *et al.*, 2014; André *et al.*, 2020: 120-121; Boursiquot & Lacombe, 2023; Röckel *et al*., 2025; Ardenghi, 2025a; personal observations).

In light of the new nothotaxa of alien *Vitis* recently discovered in Italy, the Author is preparing a new identification key relevant for the national flora.

Geographical distribution, ecology and habitat

Vitis ×*sullivaniana* has been recorded as naturalized in Spain (Laguna Lumbreras, 2004; Laguna, 2005), France (André, 2022: 184) and Italy (Ardenghi, 2025a); it was observed as a relic of cultivation in Hungary (Kiss, 1939; Facsar & Udvardy, 2008). All the recorded populations refer to 'Couderc 1616'.

This nothospecies has been collected and recorded mainly on marl- and calcareous-clay-based soils, sometimes in wet (at least temporarily so) and saline conditions near the sea, growing in semiruderal grasslands

Tab. 1 - Morphological comparison between diagnostic characters of *V.* ×*sullivaniana* and similar taxa and nothotaxa (based on: Ravaz, 1902; Cosmo *et al*., 1958; Galet, 1988; Ardenghi *et al.*, 2014; André *et al*., 2020; André, 2022; Boursiquot & Lacombe, 2023; Pecile & Zavaglia, 2025; Röckel *et al*., 2025; personal observations).

Notes: most modern ampelographic sources (Ravaz, 1902: 217-218; Cosmo *et al.*, 1958: 64; Galet, 1988: 225; André *et al*., 2020: 121; Boursiquot & Lacombe, 2023) do not admit the occurrence of arachnoid pubescence in *V.* ×*instabilis* 'Millardet et Grasset 101-14'. Yet, the breeders of this cultivar described the pubescence on the petiole as follows: «*couvert d'un velours assez serré de poils subulés courts, entremêlés de quelques poils laineux*» (Millardet & de Grasset, 1899: 205). The author encountered sparse arachnoid hairs on the petiole of 'Millardet & Grasset 101-14' and at its insertion on the leaf blade, as evidenced by figs. 6B, C in Ardenghi *et al.* (2014: 175), reproducing photographs taken on an individual of 'Millardet et Grasset 101-14' from a vineyard in Stradella (Pavia) (Ardenghi *et al.*, 2014: 198).

Cultivars of *V. riparia* referred to as "*tomenteux*" (Foëx, 1891: 88; Ravaz & Viala, 1896: 137) or "*pubescents*" (Ravaz, 1902: 79; André *et al.*, 2020: 45) are distinguished by their herbaceous stems covered with dense hirtellous pubescence (in opposition to glabrous-stemmed cultivars such as 'Riparia Gloire de Montpellier', 'Riparia Grand glabre', 'Riparia Baron Perrier' and 'Riparia Martin des Pallières'). The most used in the past were 'Riparia Scribner' and 'Riparia Géant de las Sorres' (Ravaz, 1902).

	***V.* ×*sullivaniana* 'Couderc 1616'**	***V. riparia*, incl. 'Riparia Gloire de Montpellier' (GM), 'Riparia Grand glabre' (GG) and "*tomenteux*" cultivars (T)**	***V. acerifolia* × *V. riparia* × *V. rupestris* 'Castel 216-3'**	***V. riparia* × *V. rupestris* × *V. vulpina* 'Millardet et Grasset 106-8'**	***V.* ×*instabilis* 'Millardet et Grasset 101-14' (M) and 'Schwarzmann' (S)**	***V. acerifolia* 'Solonis'**
Habit	climbing or creeping-prostrate	climbing or creeping-prostrate	caespitose	climbing or creeping-prostrate	caespitose, climbing or creeping-prostrate	caespitose, climbing or creeping-prostrate
Colour of one-year-old stems	yellowish- to orange-brown	yellowish- to reddish-brown	reddish-brown	chestnut-brown	yellowish- to purplish-brown	purplish-brown
Tips of young shoots	closed, curved, green, sometimes bronze-tinged, with hirtellous and sparse arachnoid pubescence	closed, curved, pale green, with almost only hirtellous pubescence (arachnoid hairs ephemeral and rare)	half-open, slightly bronze-tinged, with hirtellous and arachnoid pubescence	closed, curved, copper red, with hirtellous and sparse arachnoid pubescence	closed, curved, bronze-tinged, with hirtellous pubescence	half-open or almost closed, curved, with hirtellous and dense white-arachnoid pubescence
First three young leaves	plane, green, sometimes bronze-tinged; sinuses between teeth pink, with hirtellous and sparse arachnoid pubescence	plane, pale green or gold-tinged (GM); sinuses between teeth usually green, with hirtellous pubescence only	folded, pale green or slightly bronze-tinged; sinuses between teeth pink, with hirtellous and arachnoid pubescence	slightly folded, red copper-tinged; sinuses between teeth usually bright red, with hirtellous and arachnoid pubescence	folded, bronze-tinged; sinuses between teeth pink, with hirtellous pubescence	folded, bronze-tinged; sinuses between teeth pink, with dense and concealing white-arachnoid pubescence
Herbaceous stems	striated, glabrous to sparsely arachnoid	terete, glabrous (GG, GM) or densely hirtellous (T), arachnoid hairs ephemeral and very rare	striated, sparsely arachnoid	striated, glabrous to sparsely arachnoid	striated, glabrous (S) or sparsely hirtellous at the nodes (M)	striated, with dense arachnoid (then floccose) and sparse hirtellous pubescence
Adult leaves habit	undulated, occasionally folded	plane (GG) to undulated (GM)	strongly folded	undulated, slightly folded	slightly undulated and slightly folded	slightly folded
Adult leaves shape	usually cuneiform, 3-shouldered	cuneiform, 3-shouldered	reniform, almost entire	suborbicular, 3-shouldered or occasionally 3-lobed	cuneiform to suborbicular (M) or reniform (S), 3-shouldered	cuneo-reniform, 3-shouldered or occasionally the basal 3-lobed
Leaf base	widely U- to bracket-shaped	U-shaped (GM) to widely so, sometimes with the base directly bordered by the nerves (GG)	widely U- to bracket-shaped	U-shaped to widely so, usually with the base directly bordered by the nerves	widely U-shaped (M) or widely V- to bracket-shaped (S)	widely U- to V-shaped

	***V.* ×*sullivaniana* 'Couderc 1616'**	***V. riparia*, incl. 'Riparia Gloire de Montpellier' (GM), 'Riparia Grand glabre' (GG) and "*tomenteux*" cultivars (T)**	***V. acerifolia* × *V. riparia* × *V. rupestris* 'Castel 216-3'**	***V. riparia* × *V. rupestris* × *V. vulpina* 'Millardet et Grasset 106-8'**	***V.* ×*instabilis* 'Millardet et Grasset 101-14' (M) and 'Schwarzmann' (S)**	***V. acerifolia* 'Solonis'**
Adaxial surface	dark green, lustrous, slightly blistered	medium green, slightly lustrous to dull, slightly blistered (GM) or almost smooth (GG), sometimes goffered near the petiole (GG)	light green, lustrous, blistered	medium green, slightly lustrous, distinctly blistered, goffered near the petiole	yellowish-green (M) or dark green with bluish reflections (S), dull (M) or lustrous (S), smooth	glaucous-green and mat in springtime due to dense arachnoid pubescence, dark green and lustrous in summer, blistered
Abaxial leaf surface pubescence	hirtellous and scattered arachnoid hairs over the veins, tufts at vein axils	hirtellous, tufts at vein axils	hirtellous and scattered arachnoid hairs over the veins, tufts at vein axils absent or scarcely developed	densely hirtellous over the nerves and the leaf surface, tufts at vein axils	sparsely hirtellous over the nerves, sometimes arachnoid hairs at petiole insertion (M), with small tufts at vein axils	dense hirtellous and arachnoid, tufts at vein axils
Leaf margin teeth	much longer than wide, straight or falciform, sides both concave or concave and convex, occasionally both convex	from longer than wide to wider than long, straight, sometimes falciform, sides both concave, both straight or concave and convex	from wider than long to longer than wide, sides convex and concave	usually wider than long, straight, sides both convex or occasionally both straight	wider than long (M) or almost as wide as long (S), straight, sides both convex (M), both straight or convex and concave (S)	much longer than wide, falciform, sides concave and convex or both concave
Teeth at the end of the three main veins	usually uncinate	acuminate to caudate, sometimes uncinate	acuminate to slightly uncinate	shortly acuminate to caudate, rarely slightly uncinate	shortly acuminate, rarely slightly uncinate	usually uncinate
Petiole pubescence	hirtellous pubescence on the adaxial side and scattered arachnoid pubescence	hirtellous pubescence on the adaxial side (GM) or all over the surface (GG, T)	hirtellous pubescence on the adaxial side	hirtellous pubescence on the adaxial side or occasionally all over the surface	hirtellous pubescence on the adaxial side mixed with arachnoid hairs (M) or glabrous (S)	dense arachnoid pubescence and scattered hirtellous hairs

(*Convolvulo arvensis-Agropyrion repentis* Görs 1967), spiny bramble scrub (*Pruno spinosae-Rubion ulmifolii* O. de Bolòs 1954) and anthropogenic *Robinia pseudoacacia* L. groves (*Chelidonio-Robinietalia pseudoacaciae* Jurko ex Hadač et Sofron 1980) (André *et al*., 2020; Ardenghi, 2025a; personal observations).

'Couderc 1616' is considered a rootstock moderately tolerant to iron chlorosis, resistant up to 11% of active limestone in the soil. It is fairly well adapted to sandy-clay soils and humidity, and it is tolerant to chlorides. 'Couderc 1616' is highly resistant to grape phylloxera (*Daktulosphaira vitifoliae*) and nematodes *Meloidogyne arenaria* (Neal, 1889) and *M. incognita* (Kofoid & White, 1919) (Cosmo *et al.*, 1958: 116; Galet, 1988: 334; Boursiquot & Lacombe, 2023). Leaves of Italian wild and cultivated (at the Botanic Garden of Pavia) individuals were damaged, besides grape phylloxera, by *Popillia japonica* Newman, 1838 (in Lombardy only) and North American leaf-miners *Antispila oinophylla* van Nieukerken & Wagner, 2012, *Erasmoneura vulnerata* (Fitch, 1851) and *Phyllocnistis vitifoliella* Chambers, 1871 (personal observations).

History of 'Couderc 1616'

Les Américains, en créant leur Hybrides, ne se sont préoccupés du phylloxéra: aussi, sur plus de trois cents Hybrides venus d'Amérique, un très petit nombre a-t-il ans resistance suffisante. Dans la creation des mes Hybrides, je me suis au contraire préoccupè avant tout de la résistance au phylloxéra.

With these words, one of the earliest and most influential French hybridists, Georges Couderc (1850-1928), prefaced, in February 1888, the second catalogue of the Poisard brothers' nursery in Anse (Rhône) dedicated to the hybrids of *Vitis* produced and sold by Couderc (reproduced in Morisson-Couderc & Morisson-Couderc, 2022: 76). He referred to *Vitis* hybrids previously introduced to France from North America that were selected without considering the resistance to grape phylloxera.

American grapevines took part in the fight against phylloxera almost immediately after the pest was discovered in Saint-Rémy-de-Provence, Bouches-du-Rhône, France, on 15 July 1868 by Félix Sahut, Jules-Émile Planchon and Gaston Bazille (Pouget, 1990: 11).

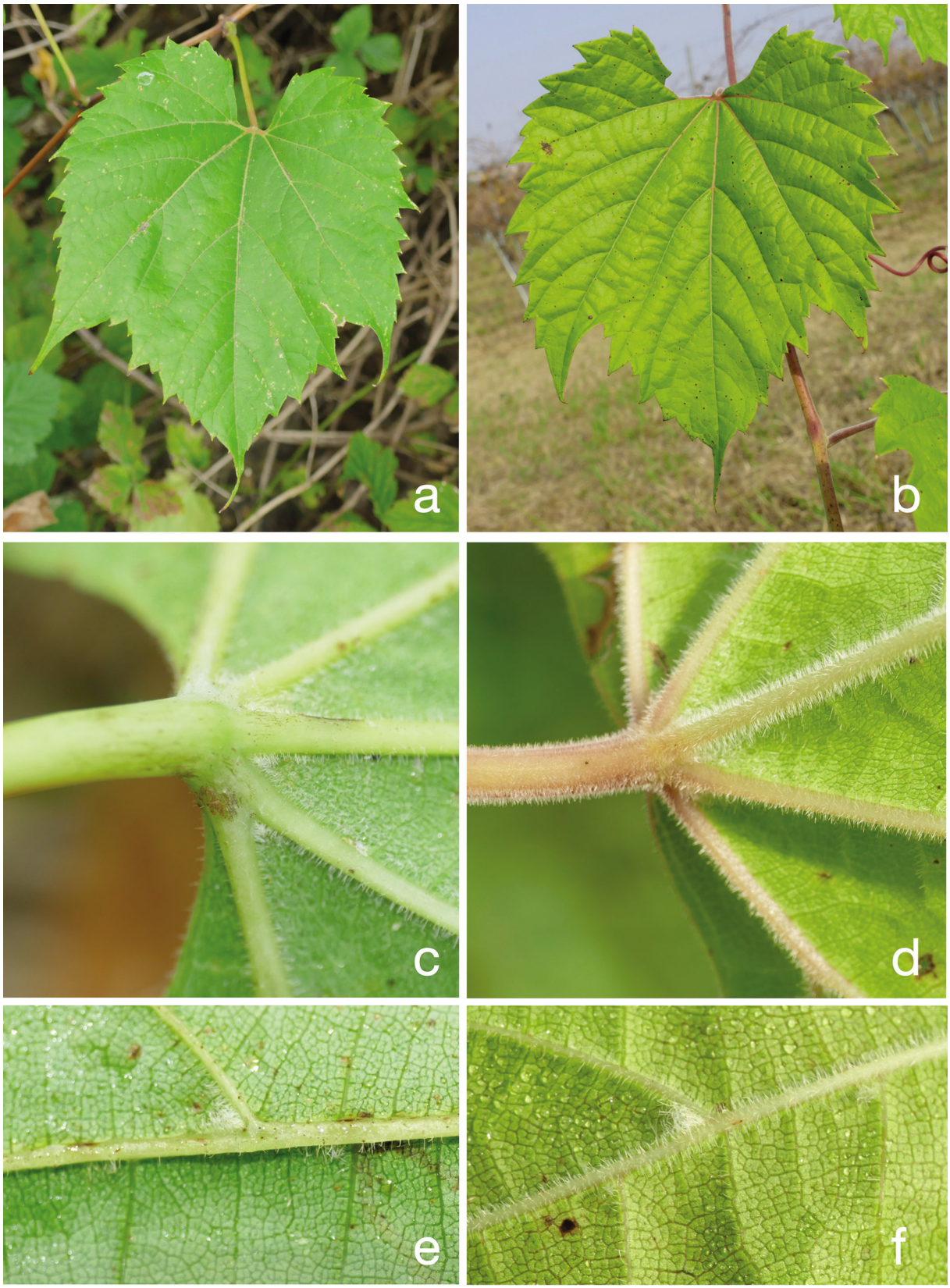


Fig. 7 - a, c, e) *Vitis riparia* 'Riparia Gloire de Montpellier', Montù Beccaria (Pavia, Italy; 45.05007°N, 9.30689°E), 12.10.2025; b, d, f) *V. riparia* cfr. 'Riparia Scribner', Montù Beccaria (45.04468° N, 9.30235°E), 12.10.2025; a, b) adult leaf blade; c, d) pubescence at the petiole insertion on the abaxial surface of adult leaves; e, f) pubescence on the abaxial surface of adult leaves. (Photos / Foto: Nicola M. G. Ardenghi).

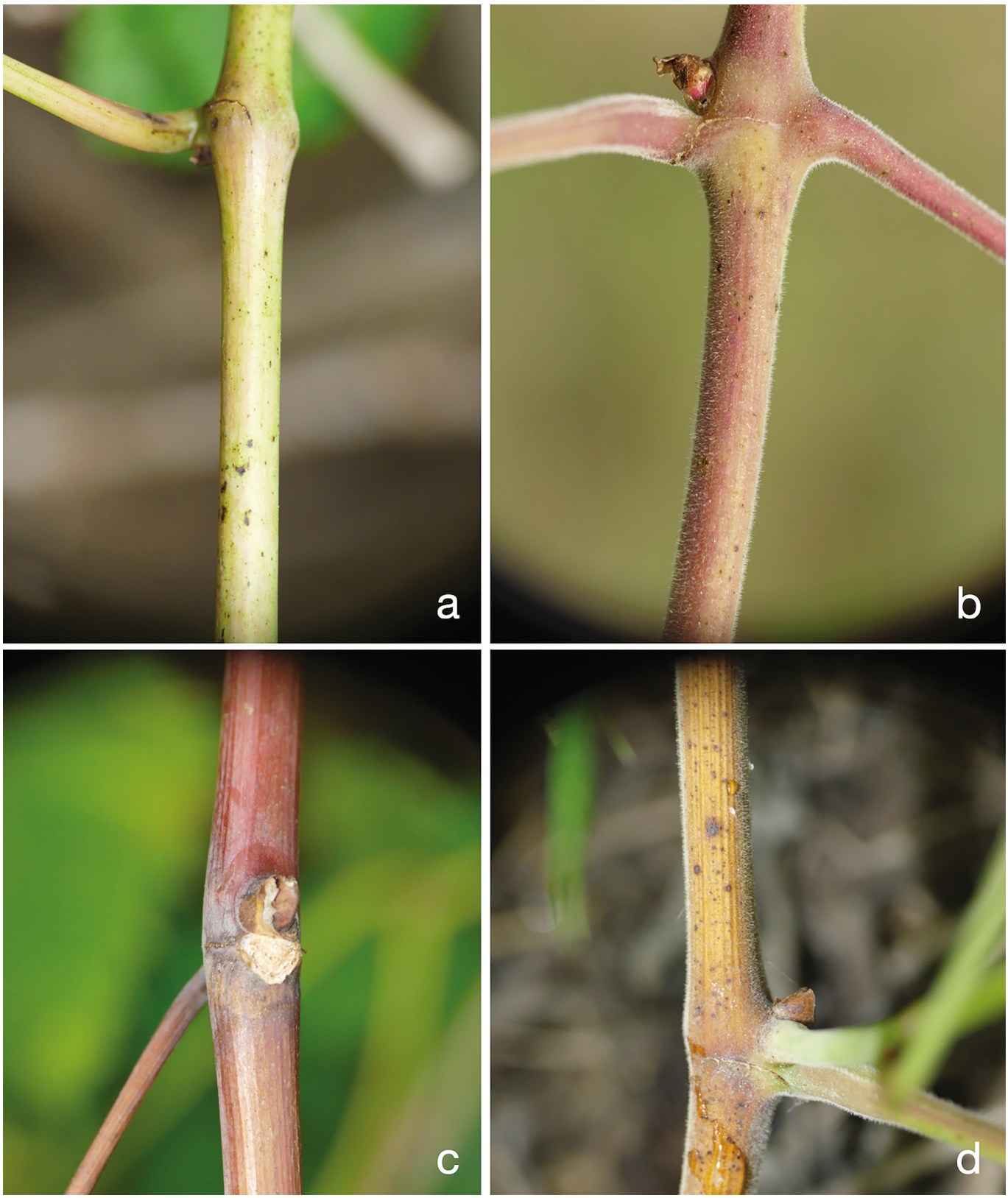


Fig. 8 - a, c) *Vitis riparia* 'Riparia Gloire de Montpellier', Montù Beccaria (Pavia, Italy; 45.05007°N, 9.30689°E), 12.10.2025; b, d) *V. riparia* cfr. 'Riparia Scribner', Montù Beccaria (45.04468° N, 9.30235°E), 12.10.2025; a, b) herbaceous stems; c, d) one-year-old stems (Photos / Foto: Nicola M. G. Ardenghi).

They acted along (or rather in opposition to) two other main strategies: the employment of insecticides and "direct producers", i.e., phylloxera-resistant American grapevines cultivated for wine production in substitution to *V. vinifera* cultivars (Gale, 2011). On 9 November 1869, Bordeaux vigneron Léo Laliman was the first to report, at the Congrès viticole de Beaune, the resistance of the American grapevines to the insect and to suggest their use as rootstocks for phylloxera-susceptible *V. vinifera* (Société des agriculteurs de France, 1869: 76-77; Planchon, 1875: IX-X). Yet, before reaching the status of definitive solution – still employed today worldwide (Forneck & Huber, 2009; Powell *et al.*, 2013) – against the feared pest, the practice of grafting *V. vinifera* on American-based rootstocks experienced many obstacles and different phases of development.

Between 1871 and 1874, and especially after the viticultural mission in the United States by Planchon (August-October 1873), the earliest rootstocks were directly imported from that country (mainly from Bush & Son & Meissner nursery in Bushberg, now Bushburg, Missouri); they were *V. rotundifolia* Michx. 'Scuppernong', *V. acerifolia* 'Solonis', and, above all, hybrids of *V. labrusca* L. (such as 'Concord', 'Ives Seedling', 'Clinton', 'Taylor') and *V. aestivalis* Michx. (e.g., 'Jacquez'), highly praised by Planchon. Yet, some years after their plantation, many of these resulted to be susceptible or poorly resistant to phylloxera, especially when planted in unsuitable soils (Planchon, 1875; Vialla & Planchon, 1875: 432-433; Sahut, 1887: 60; Pouget, 1990: 58; Muehl, 1999; Gale, 2011: 87, 127). After 1880, 'Scuppernong' and *V. labrusca* hybrids – apart from 'Clinton', 'Taylor' and 'Vialla', derived from hybridization with resistant *V. riparia*, and 'York Madeira', a hybrid with *V. vinifera* – were abandoned for grafting purposes; crossings of *V. aestivalis* ('Jacquez', 'Cunningham', 'Herbemont') were used as direct producers only (Cavazza, 1880: 86-87; Pouget, 1990: 64-65, 71-72). Botanist Alexis Millardet stated that early American hybrids were weakened because of traits inherited from susceptible species like *V. labrusca*; thus, it was necessary to go back to "pure" and more resistant wild American species, such as *V. riparia* and *V. rupestris*, that he started to cultivate from seeds by 1875 (Millardet, 1877: 10; Pouget, 1990: 63-64; Gale, 2011: 92-93). The two species later underwent to further selection, leading to more stable and performing cultivars such as 'Riparia Gloire de Montpellier' (1880) and 'Rupestris du Lot' (1879) (Galet, 1988: 214, 219; Gale, 2011: 151). To increase rootstocks' resistance, since 1876, different French hybridists obtained new binary hybrids by crossing two American species ("*américo-américains*") or an American species with a French cultivar of *V. vinifera* ("*franco-américains*"). By 1880-1881, after about a decade of adventurous experimentation, "*la reconstitution*", i.e. the planting of new *V. vinifera* vineyards grafted on American-based rootstocks, became established in France, with the reconstituted vineyard surface increased from 8,904 ha in 1881 to 299,801 ha in 1889 (Sahut, 1887: 61; Tisserand, 1890: 236; Pouget, 1990: 58, 68-69). Yet, a new obstacle emerged: many of the then available rootstocks, either species or hybrids, were not adapted to limestone soils and, after their plantation, succumbed to iron chlorosis similarly to the previous *V. labrusca* hybrids (Pouget, 1990: 71-73). Research, further experimentation and another viticultural mission in the United States (this time by Pierre Viala, in 1887) led to the solution: *V. berlandieri* Planch., a grapevine native to the limestone hills of Texas and Mexico (Moore, 1991). The crossings of this species, first with *V. vinifera* and then with *V. riparia* and *V. rupestris*, were already known since 1882 but spread only after 1888. They eventually paved the way to the reconstruction of calcareous vineyards in France (Pouget, 1990: 76-82) and other winegrowing countries of the world.

'Couderc 1616' belongs to the advanced "*américo-américains*" generation of rootstock hybrids originating from the crossing of phylloxera-resistant "pure" species, in this case, *V. acerifolia* 'Solonis' and *V. riparia* (Fig. 9). Georges Couderc obtained this hybrid from a sowing in 1881 at his property, Domaine de Champfleuri, in Aubenas (Ardèche). Here, in 1875, he started his collection of American grapevines and, in 1876, his activity of hybridist (Morisson-Couderc & Morisson-Couderc, 2022: 14, 40, 43, 77). Every year he sowed 8,000 to 10,000 grapevine seeds in soil contaminated by phylloxera; in 1882, the collection amounted to more than 100,000 hybrid rootstocks and direct producers, that he advertised and sold by means of annual catalogues. The property became an attractive and didactic destination for many personalities, coming either from France or foreign countries, interested in grapevine hybridization and reconstitution of vineyards damaged by phylloxera. Ercole Silva, director of the royal American grapevines nurseries in Asti (Italy), and Australian winegrower François de Castella were among these (Grandvoinnet, 1890: 428; Coutagne, 1893; Silva, 1900: 383; [De Castella], 1907). Couderc assigned to each seedling a number that expressed the row (hundreds) and the position of the plant in a row (tens, units); if the seedling survived and satisfied Couderc's agronomic needs (e.g., resistance to phylloxera and to limestone), the number became part of the cultivar's name (Morisson-Couderc & Morisson-Couderc, 2022: 54).

Apart from 'Couderc 1616', the best remembered rootstocks sold by Couderc are 'Couderc 3309' and 'Couderc 3306' (*V.* ×*instabilis*), 'Couderc 161-49' and its sibling 'Couderc 157-11' (both *V.* ×*koberi*), still propagated and popular today in France and Italy (Morisson-Couderc & Morisson-Couderc, 2022: 55-56; Boursiquot & Lacombe, 2023; Pecile & Zavaglia, 2025).

At the beginning of his experience as hybridist, Couderc was deeply disappointed by *V. acerifolia* 'Solonis', then one of the few American grapevines known to be adapted to limestone soils. Grafted with *V. vinifera*, it gave "*magnifiques espérances*" but after six or seven years, the roots became damaged by phylloxera. Couderc then tried to propagate 'Solonis' by seed, yet without any result. 'Solonis' became Couderc's «ennemi personnel». To solve his «maladie du Solonis», Couderc resorted to *V. riparia* pollen: brushed on 'Solonis' flowers, it gave origin to the hybrid 'Couderc 1616' (and siblings '1613', '1614' and '1615', later discarded), that combined the limestone adaptability of 'Solonis' with the strong root-

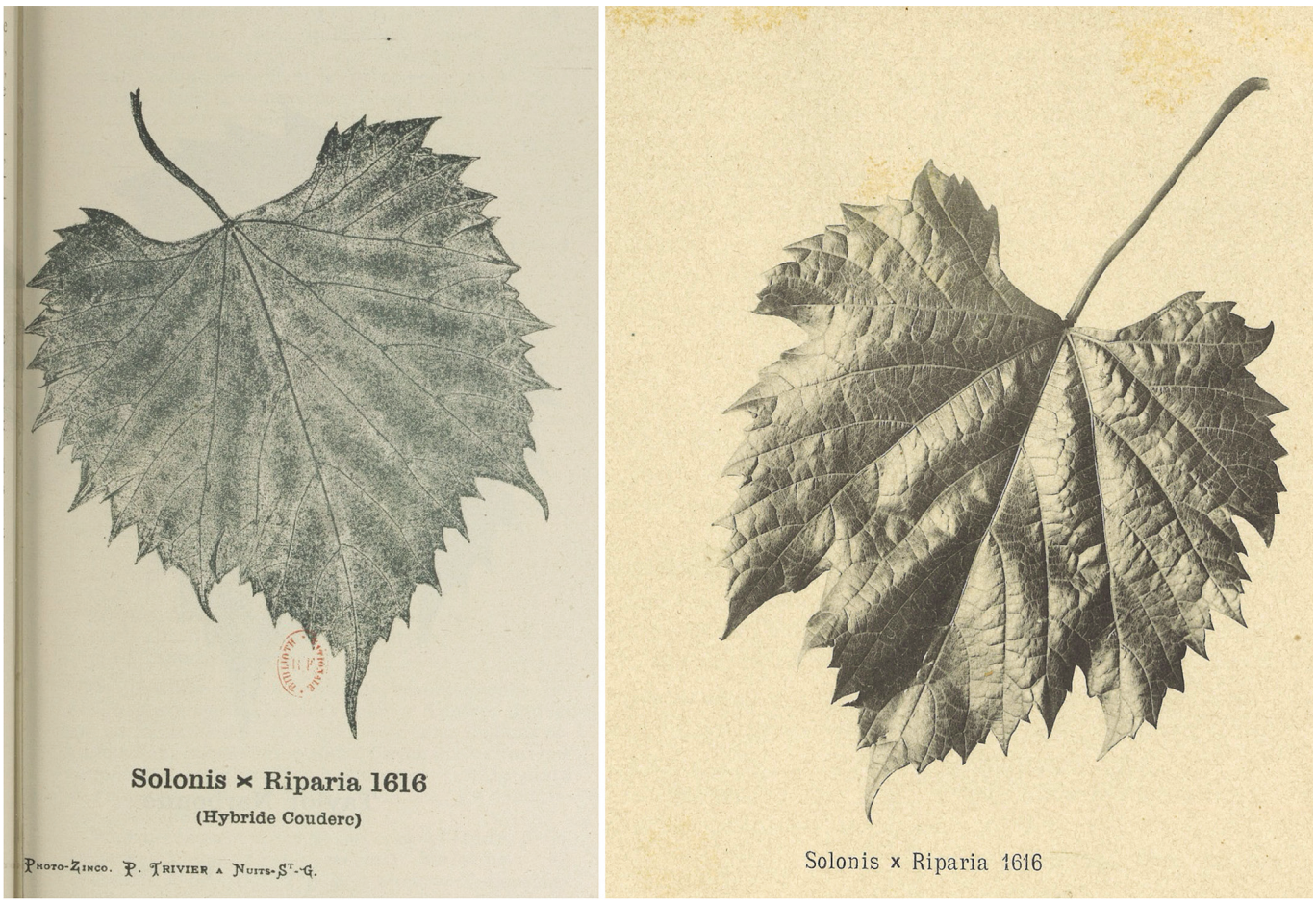


Fig. 9 - *Vitis* ×*sullivaniana* 'Couderc 1616', two early illustrations from Durand & Guicherd (1896; on the left) and F. Z. (1907; on the left). Reproduction courtesy of Bibliothèque nationale de France (BnF), département Sciences et techniques, and University of Pavia, Biblioteca della Scienza e della Tecnica (BST), Orto botanico, respectively.

resistance and vegetative vigour of *V. riparia* (susceptible to limestone). Couderc regarded 'Couderc 1616' as one of his most "flexible" («*souple*») hybrids and was defined by many as both an improved 'Solonis' and an improved *V. riparia* (Grandvoinnet, 1890; Couderc, 1891: 204; Labora, 1894; Gervais, 1900: 43-44; G. F., 1903; Viala & Vermorel, 1909: 464-465; Galet, 1988: 63). Before Couderc's 'Solonis'-*riparia* hybrids, there existed only one other hybrid with the same parentage, i.e., 'Solonis Feytel', obtained in 1877 or 1878 in Charentay (Rhône) by the noted abbot Fétél from Chessy-les-Mines, better known today for selecting the famous pear 'Abbé Fétél' (Vermorel, 1889).

Couderc started to sell 'Couderc 1616' in 1889, through his third catalogue; the cultivar and its siblings were advertised as «*indemnes* [to phylloxera] *et ne jaunissant pas dans les marnes et les calcaires blancs; vigeur égale à celle des meilleurs Riparia*». Cuttings of 60 cm long were sold at 0.30 French francs per hundred (Morisson-Couderc & Morisson-Couderc, 2022: 77, 80).

Since 1890, 'Couderc 1616' was planted with enthusiasm in many trial plots and vineyards across France and started to be distributed to winegrowers by various French agricultural societies. Thanks to the vigour and the leaves' green colour maintained in limestone, compact and humid soils, it was suggested among the rootstocks immune to chlorosis to be adopted in the reconstitution process. Couderc himself regarded it as the best new rootstock advertised in 1891 for resistance to phylloxera and declared that it tolerated up to 30-100% of calcium carbonate in the soil. Grafted *V. vinifera* cultivars – such as 'Pinot noir' and 'Chardonnay' in Bourgogne and 'Gamay noir' in Beaujolais – profited of major and advanced fruiting, and their must resulted in a higher content of sugar. In 1898, 'Couderc 1616' was widespread in Saône-et-Loire e in Côte-d'Or (De Mortlliet, 1890; Rousseau, 1891; F. C., 1892; Barbut, 1894; Gervais, 1898: 204, 206; Gervais, 1900: 43-44, 106-107; Carillon & Roy-Chevrier, 1903: 250). French nurseries started to sell 'Couderc 1616' at least by 1894 (Fig. 10).

After one decade of trials, 'Couderc 1616' resistance to limestone was downgraded to 22.5% of calcium carbonate in the soil, and, ironically, the hybrid was regarded as tolerant as the cultivars it had originally replaced, i.e., 'Solonis' and 'Jacquez' (Bonnet, 1902; Ravaz, 1902: 324). The percentage was furtherly reduced by Couderc himself in 1927 to 15-20% (Morisson-Couderc & Morisson-Couderc, 2022: 91). By 1963, it has been ascertained that 'Couderc 1616' resisted up to 11% of calcium carbonate in the soil (Mottard *et al.*, 1963; Boursiquot & Lacombe,



Fig. 10 - Commercial advertisements of French and Italian nurseries selling *Vitis* ×*sullivaniana* 'Couderc 1616' and other rootstocks and direct producers. Clockwise, from top left: Jacques Tibbal [*La Vigne américaine et la Viticulture en Europe* 19(1), 1895], Hyacinthe ("Giacinto") Raymond [*Bollettino quindicinale della Società degli Agricoltori Italiani* 6(19): III, 1901], C. Miédan [*La Vigne américaine et la Viticulture en Europe* 19(1), 1895], Edoardo and Guido Boschetti [*L'Italia Agricola. Giornale di Agricoltura*, 41(1): 1904], Edmond Coulet (*La Fabrication*, 24(622): [2], 1894). Reproduction courtesy of Bibliothèque nationale de France (BnF), département Sciences et techniques (French journals), and University of Pavia, Biblioteca della Scienza e della Tecnica (BST), Orto botanico (Italian journals).

2023). Ernest Vivet, professor of viticulture at the École Nationale d'Agriculture d'Alger, tested 'Couderc 1616' in Algeria, confirming its tolerance to chlorides; yet, like *V. riparia*, it was susceptible to compact and dry soils, making it unsuitable to Algerian vineyards. On the contrary, it was welcomed along the Gulf of Lion in France (Ravaz, 1915; Vivet, 1922; Agnel, 1945: 52-53). In 1919, it was considered «*passé de mode*» but was still appreciated in Champagne for its moderate tolerance to limestone and for positively contributing to the complete ripening of the fruits (Philipponat, 1919). In France, the surface planted with 'Couderc 1616' decreased from 8 ha in 1955 to 0.4 ha in 2015 (Boursiquot & Lacombe, 2023), mainly due to the replacement of viticulture along the Mediterranean coast with other crops or bathing establishments (Galet, 1988: 334).

Outside France, 'Couderc 1616' was introduced in most wine-producing countries. For instance, it was tested in Switzerland before 1900 (Gervais, 1900; Salomone, 1903) and in California and Peru since 1902 (Anonym, 1902; Dubosc, 1906: 78, 80), while in 1907, it was already in cultivation in Victoria, Australia ([De Castella], 1907). Since at least 1897, 'Couderc 1616' was cultivated in trial vineyards and government nurseries of American grapevines in Sicily, directly imported from France (Paulsen, 1897: 22-23; Sassino, 1899: 55; Ruggeri, 1901: 1280); subsequently, it was introduced in various government nurseries located in Sardinia (Maggioni, 1906: 1282), Apulia (Maggioni, 1916: 496-497) and Elba Island (Silva, 1905), before reaching, by at least 1906, North Italy, where it was tested in the Asti government nursery (Persi, 1907). Italian commercial nurseries started to sell this cultivar by 1904 (Fig. 10). By 1916, its cultivation was abandoned in Sicily (Maggioni, 1916: 496) but in 1918 it was gaining much popularity in the northern regions (Fabiani, 1918). After Second World War, 'Couderc 1616' started to be replaced in moderately brackish soils by Italian *V.* ×*ruggerii* Ardenghi, Galasso, Banfi & Lastrucci 'Paulsen 1103' (Lagard, 1946: 235; Cosmo *et al*., 1958: 116). The government production of rooted cuttings, stopped at least by 1989, was moderately revived in 2018 and 2020 (Pecile & Zavaglia, 2025).

Specimina visa

ITALY. Lombardy. Prov. Pavia: Stradella, Via Di Vittorio, a lato dell'ex fabbrica di legnami "Guglielmo Massoni & C." (45.071270°N, 9.305632°E), 82 m, piazzale (con *Elymus repens*, *Rubus* sect. *Corylifolii*, *Lepidium draba*, *Cirsium arvense*), recinzione e muri di fabbricato abbandonato (con *Rubus* sect. *Corylifolii*, *Ailanthus altissima*, *Humulus lupulus*), tappezzante, 02.05.2025, *N.M.G. Ardenghi* (*holotypus* MSNM barcodes MSNM54968, MSNM54969, *isotypus* FI; one specimen from this population is cultivated in the "Prohibited Vineyard" of the Botanic Garden of Pavia, code A496); *ibidem*, incolto con *Elymus repens*, *Rubus* sect. *Corylifolii*, *Humulus lupulus*, 2 piante isolate di *Ailanthus altissima* (juv.) e *Corylus avellana*; copertura del 90%; popolazione con foglie danneggiate da fillossera, *Popillia japonica*, *Antispila oinophylla*, *Phyllocnistis vitegenella*, *Erasmoneura vulnerata*, 14.09.2025, *N.M.G. Ardenghi* (MSNM barcodes MSNM54970, MSNM54971, MSNM54972, MSNM54973); Stradella, tra Torre Sacchetti e Solinga (45.057780°N, 9.295830°E), 162 m, E, arbusteto a *Prunus cerasus*, *Rubus ulmifolius* e *Clematis vitalba*, frammisto a *Cornus sanguinea*, *Ulmus minor*, *Ficus carica*, *Lathyrus latifolius*, *Elymus repens*, *Brachypodium rupestre*, su argilla calcarea, 05.10.2025, *N.M.G. Ardenghi* (*Herb. N. Ardenghi*). **Marche. Prov. Pesaro e Urbino**: Pesaro, strada ciclopedonale lungo il lato SW della ferrovia, ca. all'altezza dei Bagni Sole n. 47 (43.905319°N, 12.929801°E), 0 m, recinzione, con *Parthenocissus inserta*, 24.08.2025, *N.M.G. Ardenghi* (*Herb. N. Ardenghi*). **Tuscany. Prov. Firenze**: Valle del Santerno (Firenzuola, FI), sentiero dall'alveo del Santerno fino ai ruderi di Castiglioncello (44.175174°N, 11.481944°E), 230-350 m, vecchi ruderi, prati e margini boschivi; mix di argilliti e siltiti, 17.05.2019, *F. Roma-Marzio, M. D'Antraccoli, D. Dolci, M. Tiburtini & L. Peruzzi* (PI 038878 [digital image!] sub *V.* ×*instabilis* Ardenghi, Galasso, Banfi & Lastrucci). **Prov. Livorno**: Marciana, Procchio, strada tra Portoferraio e Procchio, poco prima del Km 7.5 (42.786855°N, 10.250458°E; staz. 03), 42 m, NW, margine boschivo, 26.06.2007, *A. Zoccola* (MSNM barcodes MSNM44778, MSNM44789 sub *V.* ×*instabilis* Ardenghi, Galasso, Banfi & Lastrucci).

Acknowledgements

The author is grateful to Anna Bendiscioli (Biblioteca della Scienza e della Tecnica, BST, University of Pavia, Italy) and to Bibliothèque nationale de France (BnF, France) for allowing the publication of the images reproduced in Fig. 9, 10. Eventually, Gabriele Galasso and an unknown reviewer are deeply thanked for critically reading the paper and their valuable suggestions.

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