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RESEARCH

Is *Genista anxantica* (Fabaceae, Genisteae) worth of taxonomic recognition? An integrative approach

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Abstract

Genista anxantica is an extremophile taxon described by Michele Tenore and strictly endemic to the mephitic fields in Ansanto Valley (Mefite, Rocca San Felice, province of Avellino, Campania region, SW Italy). Its taxonomic distinctness from the widespread *G. tinctoria* subsp. *tinctoria*, initially undoubted, has later been long debated. Recent population genetic evidence suggests that the Mefite population represents an ecotype within *G. tinctoria*, shaped by extreme ecological conditions. In this contribution, we integrate morphological data and ploidy estimation by flow cytometry with ecological and genetic information to reassess its taxonomical status. Our results highlight the distinctness of *G. anxantica* as a local, genetically established variant adapted to a peculiar ecology. Accordingly, we propose the subspecific rank. The name *G. anxantica* is typified on a specimen preserved in Tenore's herbarium (NAP, Botanical Garden of Naples).

Keywords Cold natural CO_2 springs · Ecotype · Extremophile · *Genista tinctoria* · Mediterranean flora · Mefite · Ploidy estimation

Introduction

In recent years, integrated taxonomy has become a key framework for resolving long-standing systematic problems in critical plant groups, thanks to the integration of multiple and complementary lines of evidence (Maltsev and Erst 2023). By jointly considering morphological, morphometric, molecular, cytogenetic, ecological and biogeographical data, this approach provides more robust and testable species delimitations, as the convergence of independent data sources increases the reliability of taxonomic hypotheses and reduces the subjectivity of single-evidence classifications (Pante et al. 2015). Although integrative

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taxonomy has proved particularly effective in clarifying complex species groups across the Mediterranean region (Colasante et al. 2021; Joffard et al. 2022; De Giorgi et al. 2022; Giacò et al. 2023; Tiburtini et al. 2023), and has been increasingly applied to Fabaceae worldwide (Chen et al. 2021; Karbalaei et al. 2025; Bocanegra González et al. 2025), it remains comparatively underused for Mediterranean Fabaceae (cf. De Castro et al. 2013), despite the high frequency of taxonomically critical Fabaceae genera and species complexes in the region.

Genista L. (Fabaceae, Genisteae) is a large genus of more than 140 species of shrubs or sub-shrubs (rarely trees) widespread throughout Europe and the Mediterranean Basin, eastward to the Caucasus and western Asia often with narrow endemic and critical taxa (Gibbs 1966; ILDIS 2010; De Castro et al. 2022; POWO 2026). The genus has undergone several morphological studies (e.g., Spach 1845; Gibbs 1966; Valsecchi 1993) and, more recently, has been molecularly investigated, in order to clarify phylogenetic relationships (De Castro et al. 2002; Pardo et al. 2004; Rega 2008) and population genetics (De Castro et al. 2015, 2022; Di Iorio et al. 2023).

Genista anxantica Ten. was discovered by Giovanni Gussone close to his birthplace during the first field surveys carried on for facilitating the monumental *Flora napolitana* of his mentor Michele Tenore (Tenore 1820). In fact, the species was first described by Tenore (1812) in the *Prodromus* to *Flora napolitana*. Tenore (1820) later provided an Italian description and a plate, and specified its classical and unique locality, i.e., the mephitic Anxanto Valley with Mefite lakelet, near Rocca San Felice (province of Avellino, Campania region, SW Italy). The taxon belongs to the autonym sect. *Genista*, whose generitype is *G. tinctoria* L., on account of the unarmed stems, the simple leaves, the glabrous corolla with standard broadly ovate and equalling both wings and keel, and the oblong legume (Gibbs 1968). According to its first descriptions, *G. anxantica* is characterized by shrubby habit, angulate and divergent woody branches, ovate and coriaceous leaves, and a general glabrescence (Candolle 1825; Tenore 1831; Spach 1845). For this latter character, Link (1822) considered *G. anxantica* as similar to *G. scariosa* Viv. (currently, *G. januensis* Viv.). Indeed, Sprengel (1826) synonymized it with *G. januensis*, an opinion followed by other German botanists (Koch 1837; Dietrich 1847), but not by Loudon (1869), who treated *G. scariosa* (= *G. januensis*) as a variety of *G. anxantica*. On the contrary, Candolle (1825), after examination of dried plants, accepted the distinctness of the species in his *Prodromus*. Tenore (1831), in reasserting the taxonomic value of *G. anxantica*, refused the synonymization with *G. scariosa* proposed by Sprengel (1826). The Tenorean species was accepted in the past by most authors (Brocchi 1820; Link 1822; Don 1832; Presl 1845; Bertoloni 1850; Boissier 1872; Cesati et al. 1883; Nyman 1878–1882; Arcangeli 1882; Jackson 1893), including the monographer Spach (1845), who relied on both specimens and cultivated plants. Koch (1837) at first included *G. anxantica* in *G. scariosa* (= *G. januensis*), following Sprengel (1826), but later accepted it as a different species (Koch 1847). It has to be noted that authors successive to Sprengel rather indicated a closer relationship of *G. anxantica* with *G. tinctoria* (Reichenbach 1869; Robinson 1903; Briquet 1908), from which it would be weakly differentiated (Bean 1919). More precisely, Reichenbach (1869) first proposed the varietal rank. His treatment was followed, for example, by Fiori (1900) and Briquet (1908). This latter author, in later reproposing the same rank (Fiori 1925), erroneously indicating the taxon as occurring also in Asia Minor, following Koch (1847). Ascherson and Graebner (1907) included *G. anxantica* in their *G. tinctoria* var. *elata* [unranked] *frutescens* (Schloss. & Vuk.) Asch. & Graebn. (= *G. tinctoria* subsp. *tinctoria*), whereas Brocchi (1820) regarded the species as related to "*Genista ovata* di Persoon", i.e., *G. tinctoria* subsp. *ovata* (Waldst. & Kit.) Arcang.

Despite its narrow range, *G. anxantica* was rather renowned for its very peculiar habitat and rarity (Pampanini 1911; Molinaro, 2015). The plant was also cultivated for its ornamental value (see e.g., Maund 1839–1840; Loudon 1869; Robinson 1903; Rehder 1917; Bean 1919; Silva Tarouca and Schneider 1922). Later, however, *G. anxantica* became a neglected taxon, possibly also because no more cultivated (the last traced indication about its cultivation is in Rehder 1949) and it was generally synonymized with *G. tinctoria* subsp. *tinctoria* (ILDIS 2010; POWO 2026) or included in it with some doubt (Zangheri 1976, sub *G. auxantica* [sic!]; Pignatti 1982, 2017). Gibbs (1968), who recognized within *G. tinctoria* only infraspecific "groups" worth of further study, listed *G. anxantica* in the first of these groups, that including the typical *G. tinctoria*.

More recently, *G. anxantica* has attracted renewed attention as an extremophile taxon, strictly confined to a cold natural carbon dioxide spring (CNCDS) in the Mefite area (Di Iorio et al. 2019), one of the most toxic CO_2-emitting habitats known (Chioini et al. 2010). Molinaro (2015) proposed a full reinstatement of the Tenorean species based on morphological and ecological considerations. Recent population-level genetic analyses subsequently confirmed the distinctiveness of the Mefite plants (Di Iorio et al. 2023). It is to be noted that currently no subspecies are accepted within *G. tinctoria* in Italy (ILDIS 2010; PFI 2026), although recorded in Pignatti (2017) and in global databases (e.g., POWO 2026). In this contribution, we reassess the taxonomic value of *G. anxantica* using an integrated approach that combines morphometric analyses, flow cytometric ploidy estimation, and ecological and genetic data (Di Iorio et al. 2023). This approach clarifies its distinctness from *G. tinctoria* and provides the basis for a coherent nomenclatural and taxonomic treatment, including lectotypification.

Materials and methods

Typification

For dating Tenore's works and the plates of his *Flora napolitana*, we follow respectively Sabato (1990) and Natale (2016, 2019). We checked for original material of the name in herbaria traditionally linked to Tenore (BOLO, FI, PAD, NAP, RO), but also in large European collections (CAT, G, LY, P, PAL, PI, WU, etc.) (herbarium codes according to Thiers 2026), and also inquiring online aggregators (e.g., GBIF 2026, JACQ 2004). We explored biographic literature to retrieve information about the first gatherings of *Genista anxantica* (Casale and Gussone 1811; Pasquale 1871; Trotter 1948).

The articles cited throughout the text follow Turland et al. (2025), hereafter *ICN*.

Morphometrics

To better assess the taxonomic distinctiveness of *Genista anxantica*, we examined a comprehensive set of diagnostic characters previously employed by various authors (e.g., Tenore 1831; Fiori 1900; Molinaro 2017). These included habitus, stem and leaf indumentum, flower length, angle between carina and standard, angle between main and lateral branches, stem cross-section shape, number of flowers per raceme, and legume dimensions. Additional characters considered relevant within the *G. tinctoria* complex (Pignatti 2017) were also employed, such as leaf shape and size, calyx and standard length, and hairiness of the calyx and legume. Furthermore, new traits were introduced, including calyx colour, further floral measurements, and seed number and diameter. The analysis was therefore based on a total of 28 characters, including 11 categorical (nominal or ordinal) and 17 scalar ones (see Table 1 for the complete list). When possible, three random measurements for each character were taken from a single individual, and their mean was used for representation. This strategy minimizes intra-individual variability and enhances consistency across the dataset, particularly for continuous variables such as floral dimensions and seed size (Del Guacchio and Caputo 2008; Del Guacchio et al. 2016, 2020).

Measurements were taken *in sicco* from 15 specimens collected at the locus classicus of *G. anxantica* and 13 from nearby populations of *G. tinctoria* subsp. *tinctoria* (voucher specimens kept at NAP). For broader comparison, we also examined additional specimens of *G. anxantica*, *G. tinctoria* subsp. *tinctoria*, and *G. tinctoria* subsp. *ovata* (preliminary treatment according to Pignatti (2017). These taxa have been reported from the area where *G. anxantica* occurs (Ferraris 1906). In total, we examined 44 specimens of *G. anxantica*, 85 of *G. tinctoria* subsp. *tinctoria*, and 22 of subsp. *ovata*.

Measurements were taken from digital herbarium images accessed via B, BM, BOLO, CAT, E, FI, K, LD, LY, MW, NAP, NL, P, PAL, PI, PILSL, PRC, RO, W, and WU (see Supplementary material S0). While structured sampling across populations is ideal, most specimens identified as *G. tinctoria* subsp. *tinctoria* and *G. tinctoria* subsp. *ovata* are single individuals from unique populations. Pooling such individual specimens into a single taxonomic unit is acceptable when, as in this case, identifications are reliable and the aim is to assess variation at the taxon level (Marhold 2011; Koutecký, 2015). This approach has already been adopted in multivariate morphometric taxonomy (Egan 2015; Finot et al. 2018; Kaplan and Marhold 2012; Christ et al. 2023), which aims at characterizing taxa in their entirety rather than testing them for population-level differentiation. In addition, assuming low morphological differentiation among populations, pooling individuals reduces bias in evaluating taxonomic boundaries (Marhold 2011).

To verify the assumption of low morphological differentiation among populations of the three taxa (hereafter indicated as 'Anxantica', 'Ovata', and 'Tinctoria'), we conducted two preliminary tests using Gower distance (Gower, 1971) on the cleaned matrix. The matrix was cleaned by imputing missing values using the mode for categorical variables and the mean for numerical variables, and by normalizing numerical variables using MinMax scaling. All analyses were performed in Python 3.12 (PSF, 2023), using the pandas, scikit-learn, and NumPy packages. First, within-group dispersion was calculated as the mean of pairwise Gower distances among individuals. The results were as follows: 'Anxantica' (0.1664), 'Tinctoria' (0.3337), and 'Ovata' (0.3772). These values indicate low internal variance in 'Anxantica', supporting homogeneity, while 'Tinctoria' and 'Ovata' show moderate dispersion. Second, a PERMANOVA-like test was performed to assess morphological differentiation among taxa (Zelditch et al. 2012). The test yielded a significant result ($F = 2.4091$, $p < 0.04$). Together, these findings justify the use of taxon-level grouping in subsequent statistical procedures.

Morphological data were compiled for the three taxa ('Anxantica', 'Ovata', and 'Tinctoria'). Scalar variables were standardized and visualized using boxplots grouped by taxon, generated in Python with Plotly (PTI, 2015). Categorical variables were visualized using grouped bar charts to illustrate frequency distributions across taxa. To quantify morphological variability, we calculated the standard deviation of group means for each numeric variable. Diversity in categorical traits was assessed by computing the mean standard deviation of category frequencies across taxa.

As in previous morphometric studies (Del Guacchio and Caputo 2008; Del Guacchio et al. 2016, 2020), we tested correlations among variables to minimize bias in statistical

Table 1 Characters employed for the morphometric analysis

Character	Code	Type	Approximation	Character status
Habitus	Hab	Nominal		(1) Ascending (2) Erect \ Virgate
Branch woodiness	Wood	Ordinal		(1) Herbaceous (2) Half-woody (3) Woody
Branch section	BraSct	Ordinal		(1) Terete or almost so (2) Striate (3) Angulate
Angle stem \ branches	BraAng	Scalar	± 5°	
Hairiness of the branches	BraHr	Ordinal		(1) Glabrous (2) Pubescent (3) Villose
Hairiness of the leaves	LeafHr	Ordinal		(1) Glabrous (2) Pubescent (3) Villose
Hairiness of the calyx	CalHr	Ordinal		(1) Glabrous (2) Pubescent (3) Villose
Hairiness of the legume	LegHr	Ordinal		(1) Glabrous (2) Pubescent (3) Villose
Leaf shape	LeafShp	Nominal		(1) Lanceolate-ovate (2) Linear-Lanceolate (3) Falcate
Apex of the leaf	LeafApx	Nominal		(0) Rounded (1) Apiculate (2) Acute
Leaf length	LeafLe	Scalar	± 1 mm	
Leaf width	LeafWi	Scalar	± 1 mm	
Ramification of the inflorescence	InfRam	Nominal		(1) Present (2) Absent
Flowers per raceme	FlRac	Scalar	Integer count	
Calyx colour	CalCol	Nominal		(1) Green (2) Stramineous (3) Reddish
Calyx tube length	TubLe	Scalar	± 0.5 mm	
Calyx lobe length	LobLe	Scalar	± 0.5 mm	
Standard length	StanLe	Scalar	± 0.5 mm	
Standard width	StanWi	Scalar	± 0.5 mm	
Wing length	WinLe	Scalar	± 0.5 mm	
Wing width	WinWi	Scalar	± 0.5 mm	
Carina length	CarLe	Scalar	± 0.5 mm	
Carina width	CarWi	Scalar	± 0.5 mm	
Flower length	FlLe	Scalar	± 0.5 mm	
Legume length	LegLe	Scalar	± 0.5 mm	
Legume width	LegWi	Scalar	± 0.5 mm	
Seed number per legume	SeedN	Scalar	Integer count	
Seed diameter	SeedD	Scalar	± 0.5 mm	

analyses. Correlation analysis is essential in morphometrics because it identifies redundant variables and helps prevent multicollinearity, reveals patterns of trait integration and modularity, and supports data reduction (Klingenberg 2009; Armbruster et al. 2014; Goswami and Polly 2017).

In detail, we conducted a comprehensive correlation analysis to assess associations among all morphometric variables, including categorical traits and continuous measurements. For numeric–numeric pairs, we applied Pearson's correlation coefficient. For categorical–categorical pairs—including ordinal variables treated as categorical—Cramér's V was used. For mixed-type associations between continuous variables and categorical traits, point-biserial correlation was applied only when the categorical variable was strictly binary; otherwise, associations were quantified using the correlation ratio (η). Missing data were addressed through pairwise deletion. Because Cramér's V and η are non-directional measures bounded in [0, 1], they were not artificially signed but incorporated into the association matrix in their native range. To reduce redundancy and mitigate multicollinearity, variables with an absolute association greater than 0.7 relative to any previously retained variable were excluded, yielding a reduced set of representative traits for subsequent multivariate analyses.

To explore overall morphological variation and assess the distinctiveness of the three groups ('Anxantica', 'Ovata', and 'Tinctoria'), we performed a Principal Coordinates Analysis (PCoA) based on Gower distance, which is suitable for datasets combining continuous and categorical variables. Prior to analysis, continuous traits were standardized to zero mean and unit variance, whereas categorical variables were treated as nominal factors. A Gower dissimilarity matrix was computed and subjected to PCoA to extract the principal axes summarizing overall morphological variation. The first two coordinates were visualized to inspect clustering patterns among taxa.

To formally test group separation among 'Anxantica', 'Ovata', and 'Tinctoria', we conducted a Linear Discriminant Analysis (LDA) using both categorical and metric variables. Categorical variables were encoded into numeric format using one-hot encoding and label encoding, depending on their structure. Continuous variables were standardized prior to analysis. The LDA was applied to the combined dataset to identify linear combinations of variables that best separate the three taxa. The analysis was performed using the scikit-learn implementation of LDA in Python, incorporating pandas, NumPy, and scikit-learn libraries (Harris et al. 2020). The first two linear discriminants were plotted to visualize group separation and assess classification performance.

Flow cytometric ploidy estimation

Leaf material was collected from 76 individuals of *G. tinctoria s.l.* for ploidy analysis: 12 from Torella (TB), 30 from Santa Felicita (SF) (both identified as *G. tinctoria* subsp. *tinctoria*), and 34 from the Mefite (M) (*Genista anxantica*). Sampling localities and codes follow Di Iorio et al. (2023), and the samples were collected in January 2024. Ploidy was determined by flow cytometry on silica gel-dried leaf tissue. *Secale cereale* L. (cultivar 'Dankovske'; $2C = 16.19$ pg; Doležel et al. 1998) was used as the internal standard. In a previous study, the genome size of a tetraploid *G. tinctoria* ($2n = 4x = 96$) from the Balkan Peninsula was estimated to be 3.34 pg (Siljak-Yakovlev et al. 2010). Therefore, the ratio between the fluorescence peak of tetraploid accessions of *G. tinctoria* and the peak of the internal standard are expected to be around 0.2.

However, no prior information was available on the cytotypes present in the investigated populations and the choice of the standard was made in order to avoid any possible overlap between the standard's and the samples' peaks.

For each measurement, c. 0.5–1.0 cm2 leaf tissue of the standard and leaf tissue from the dried samples were utilized. Nuclei were isolated in Otto I buffer (Otto 1992; Doležel & Göhde 1995), centrifuged for five minutes at 1,400 rpm and subsequently stained with 4',6-diamidino-2-phenylindole (DAPI) in a LB01 buffer (Doležel et al. 1989) modified by the addition of β-mercaptoethanol (0.015 mM). All analyses were performed on a CyFlow Ploidy Analyzer (Sysmex, Norderstedt, Germany), and the results were analysed using the software CUBE16 v.1.6 (Sysmex, Norderstedt, Germany). In general, we counted more than 5,000 nuclei for each measurement and only considered samples with CV values lower than 10. The relative fluorescence intensity of DAPI-stained nuclei was recorded, and the ratio between the relative fluorescence of the sample and the standard was used to estimate DNA content and infer ploidy.

Results

Typification

Tenore (1812) validly published the name *Genista anxantica* providing a Latin diagnosis ("Foliis ovato-ellipticis subcoriaceis glaberrimis venosis, ramis angulatis diffusis, leguminibus glabris, racemis terminalibus. Perennis"; transl.: "With ovate-elliptic leaves, almost leathery, perfectly hairless, with evident veins, angulate and spreading branches, glabrous legumes, terminal racemes. Perennial").

An illustration supervised by Tenore and bound with the first volume of *Flora napolitana* is available. In fact, the *G. anxantica* was depicted by Giuseppe Lettieri and published as the plate number LXVI (Fig. 1) within the second tome of the *Flora napolitana* (Tenore 1820, sub *G. amsanctica*). Although the plate was published after 1815 (Sabato 1990), its execution date is uncertain, likely between 1813 (date of the realization of the plate XLI) and 1816, when the relationships between Tenore and Lettieri broke up (Natale 2016, 2019). In any case, it cannot be regarded as original material.

Tenore (1812) did not indicate any locality; however, the chosen epithet clearly alludes to the Valley of the Ansanto river (Latin: Anxantum) (Tenore 1815).

Despite its rarity, *G. anxantica* is surprisingly represented in several herbaria, mostly sent by Gussone, Tenore or Gasparrini, and also by later authors (e.g., BOLO, G, L, LY [many], MPU, NAP, P, PAL, PI, RO, RSA, WU), especially because it was distributed by J. Briquet within the no. 864 of *Flora Italica Exsiccata* (cf. also Pampanini 1911, p. 177). However, material directly linked to Tenore has been traced only at BM (BM000750900), BOLO (not numbered), FI (barcode FI068578), G (barcode G00477338), NAP (various barcodes, see below), and RO (Herb. Cesati, not numbered).

The specimen at BOLO and G00477338 were sent by Tenore to Bertoloni and Candolle respectively in 1824; FI068578 was sent to Parlatore in 1842. Finally, the specimen at RO originated from NAP but was incorporated in his own herbarium and re-labelled by Cesati (cf. Böhnert and Del Guacchio 2023). As it is not possible to know from which collection the specimen at RO was curatorially "extracted", it is very difficult to identify it as original material for the name, albeit this cannot be excluded.

Fig. 1 Plate LXVI of *Flora napolitana* depicting "*Genista amxantica*" by Giuseppe Lettieri (engraved by Cotroneo). From the copy in the Library of the Botanical Garden of Naples (by permission of the Director)

BM000750900 was originally part of J. J. Roemer's herbarium but later incorporated in that of R. J. Shuttleworth. The original label, in Gussone's handwriting, reports "*Genista ampsantica* Nob.: | Ten". In this case, Gussone employed an orthographical variant for the epithet, maybe more correct than that adopted by Tenore (cf. Brocchi 1820). However, it cannot be considered confidently an original element.

In the Collection "Tenore" (NAP), a specimen (NAP0002351) is preserved (Fig. 2) labelled by Gussone as "*Genista anxantica* Nob. | Valle di Ansanto in Principato Ultra". In this case, the presence of Gussone's handwriting (the very discoverer of the taxon) and the abbreviation "Nob." (i.e., authored by myself) would suggest this to be original material but this cannot be proved definitively. NAP0002351 includes two poor fragments, i.e., a flowering stem and a branch with immature fruits. Some diagnostic features of *G. anxantica* can be readily distinguished nonetheless: the woody and angulate branches, the ovate leaves, the glabrous legumes.

In the Collection "Gussone-Generale" at NAP, unless subsequent manumissions, the label-missing specimens are normally duplicates of the last preceding one with label (Santangelo et al. 1998). Therefore, the specimen with the "representative label" (see e.g., Santangelo et al. 2017; Erben et al. 2018; Böhnert et al. 2025), i.e., NAP0002392, as well as its probable duplicates lacking original labels, i.e., NAP0002387 (with a later label by G.A. Pasquale, "*Genista anxantica* Ten. | Principato Ultra | Valle anxantica"), NAP0002388, and NAP0002389 were collected on 20 May 1831; NAP0002390 was collected in the same year but in June. All these specimens are not original material. Finally, NAP0002391 lacks any date but it is labelled as "*Genista ampsantica* Ten. | P.to Ultra | alla Valle di Ansanto": the variant of the epithet ("*ampsantica*"), already discussed above, leads to the same considerations.

As noticed in other cases (Del Guacchio et al. 2021), it is possible that Tenore described the species based on non-preserved material. All things stated, we prefer to choose NAP0002351 as nomenclatural type but to indicate it as a neotype, lacking by now definitive proof that it may be regarded as original material.

Morphometrics

Summaries for metric and non-metric variables are provided in Supplementary Materials S1 and S2, respectively. Boxplots for metric variables are presented in Supplementary Material S3, while scarplots for non-metric (categorical) variables are shown in Supplementary Material S4.

The correlation analysis revealed strong positive associations among several size-related continuous traits, indicating coordinated variation in these morphological dimensions. Categorical variables showed mostly low to moderate associations, with the highest values occurring among vegetative robustness traits such as BraHr, LeafHr, CalHr, and LegHr. Mixed-type associations were generally weak to moderate. Applying a |0.7| threshold to reduce redundancy led to the exclusion of variables showing high association with previously retained traits — specifically LeafHr, LegHr, and FlLe — resulting in a final set of 25 variables retained for subsequent multivariate analyses.

In the Principal Coordinates Analysis (PCoA) based on Gower distance, the first two axes explained 30.8% and 8.9% of the total variation, respectively, together accounting for approximately 40% of the overall dissimilarity (see Supplementary material S5).

Correlation analysis between original morphological variables and PCoA axes revealed clear trait patterns driving the ordination (Supplementary material S6). Axis 1 is strongly associated with BraHr, CalHr, LeafShp, LeafApx, and Wood. Axis 2 is chiefly related to CarLe, CarWi, WinLe, WinWi, StanLe, StanWi, and FlRac (see also Fig. 3).

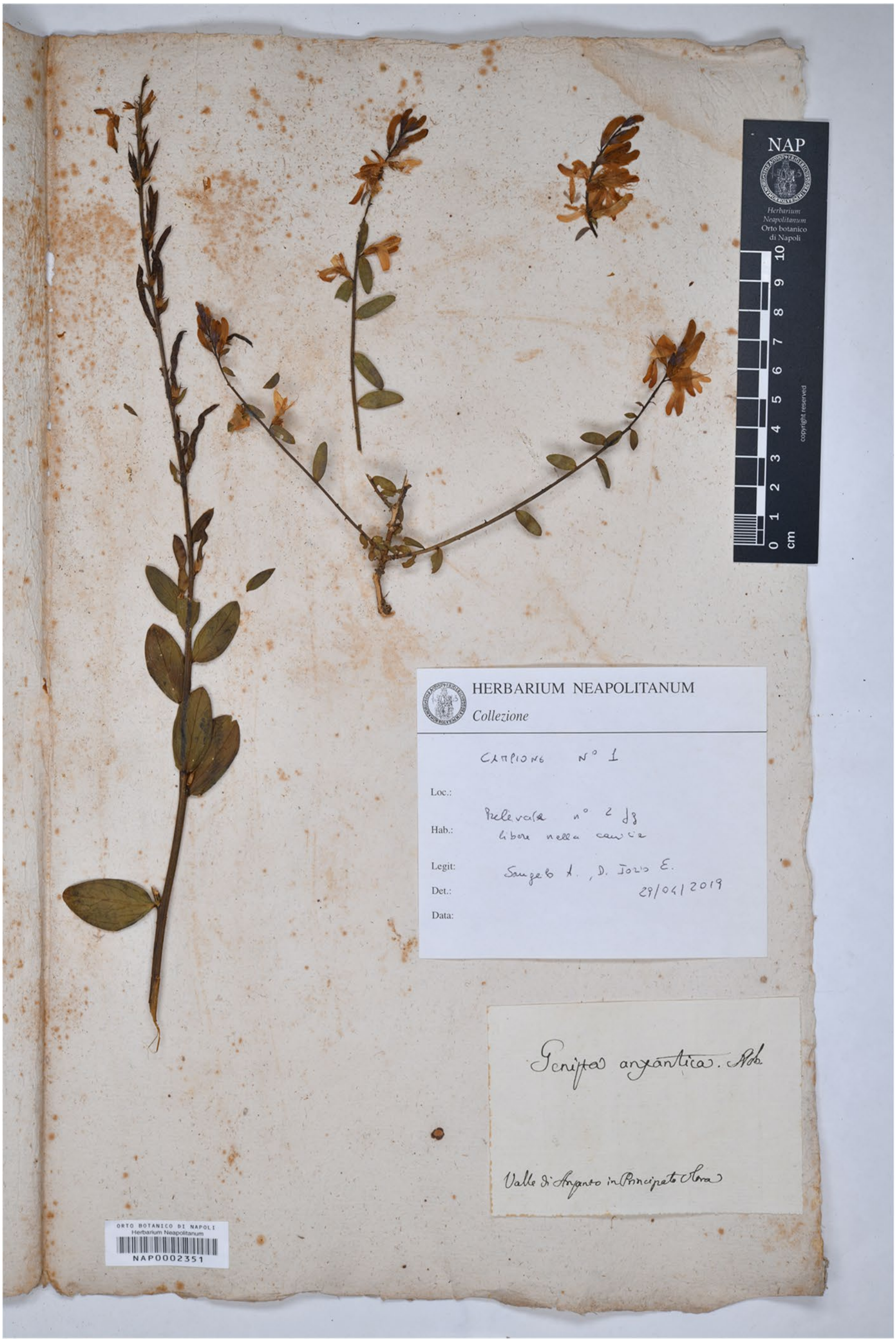

Fig. 2 NAP0002351, the proposed neotype of the name *Genista anxantica* (NAP, by permission of the Director)

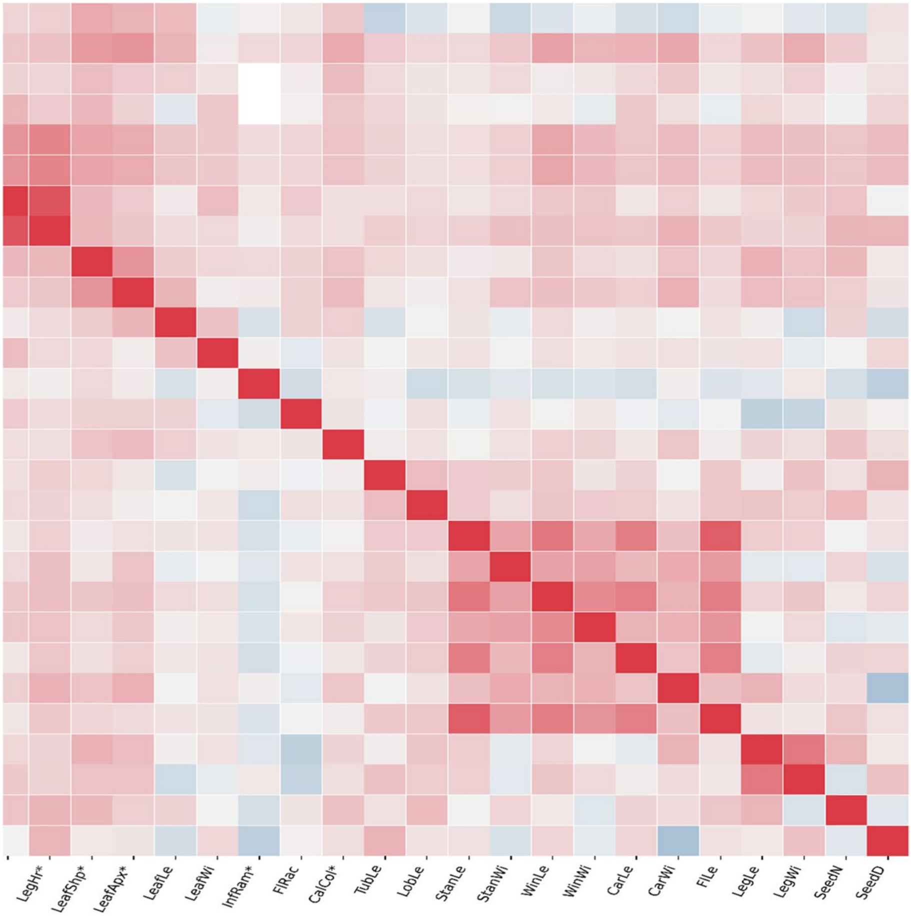

Fig. 3 Heatmap of pairwise associations among morphometric variables, with ordinal traits treated as categorical. Signed Pearson and point-biserial correlations range from − 1 to 1, whereas unsigned measures (Cramér's V and correlation ratio η) range from 0 to 1

The scatterplot (Fig. 4) shows a clear separation of 'Anxantica' from the other taxa along PCoA1. OTUs of this taxon form a compact cluster on the positive side of Axis 1, indicating morphological homogeneity and distinctiveness. In contrast, 'Tinctoria' and 'Ovata' display broader dispersion and partial overlap, reflecting their greater internal heterogeneity. Axis 2 contributes comparatively little to the overall separation.

Linear Discriminant Analysis (LDA) identified two discriminant functions (LD1 and LD2) that best separate the taxa. LD1 accounted for 79.16% of the variance and primarily distinguished 'Anxantica' from the other groups, whereas LD2 explained 20.84% and contributed to secondary differentiation. The ordination revealed a well-defined, discrete cluster for 'Anxantica'. In contrast, 'Tinctoria' and 'Ovata' showed partial overlap, indicating moderate but not complete discriminant separation between these two taxa. Cross-validated classification accuracy is 88.04% (Supplementary material S7), confirming that the combined use of categorical and metric traits provides strong predictive power (Fig. 5).

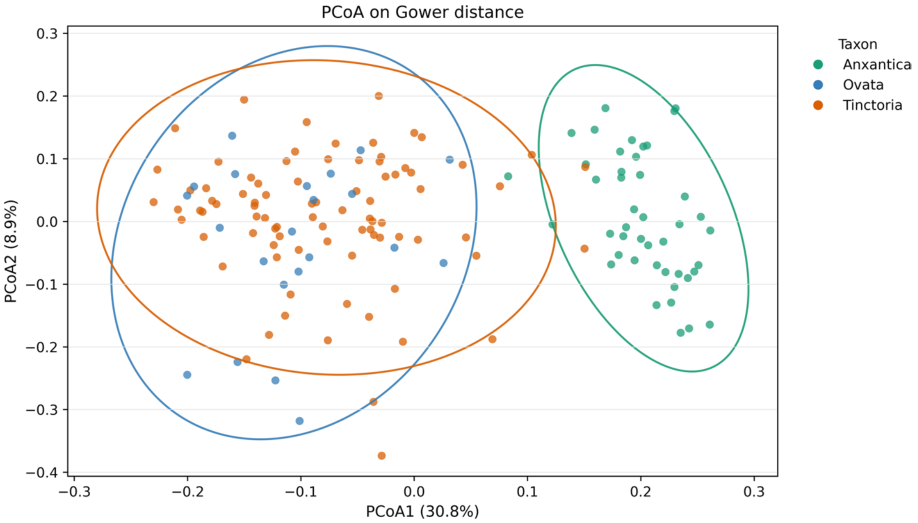

Fig. 4 Principal Coordinates Analysis (PCoA). Points represent individual samples, colored by taxon: green circles ('Anxantica'), blue circles ('Ovata'), and orange circles ('Tinctoria'). Ellipses indicate the 95% dispersion range for each group

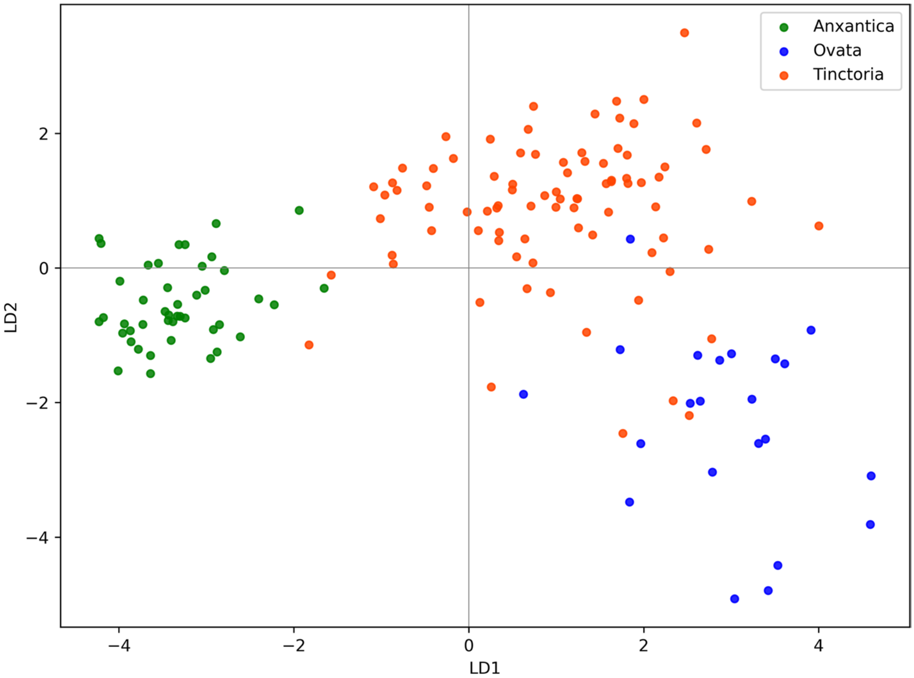

Fig. 5 Linear Discriminant Analysis (LDA) plot based on the reduced morphological matrix including mixed variables. Points represent individual samples, colored by taxon: blue circles ('Anxantica'), red circles ('Tinctoria'), and green circles ('Ovata'). The first two discriminant functions (LD1 and LD2) summarize the variation that best separates taxa

Flow cytometry ploidy estimation

Flow cytometric analyses of 76 samples from Torella (TB), the Mefite (M) and Santa Felicita (SF) gave a mean coefficient of variation (CV) was 4.1% for the internal standard (*Secale cereale*) and 6.3% for the *G. tinctoria* samples. The sample/standard ratio ranged from 0.19 to 0.23, with a single specimen collected at TB showing a fluorescence ratio of 0.32 (Fig. 6). According to these results and the previously reported genome size estimation for a tetraploid *G. tinctoria* (Siljak-Yakovlev et al. 2010), all samples measured here are found to be tetraploid, except for a single measurement from TB ('Tinctoria') with ratio > 0.3, which is most likely hexaploid.

Discussion

Morphometric results indicate that *G. anxantica* is morphologically distinct from plants identified as *G. tinctoria* subsp. *tinctoria* and *G. tinctoria* subsp. *ovata*, primarily because of its woody or partly woody branches. These latter in *G. anxantica* are consistently angulate, as opposed to the more variable terete or striate branches in *G. tinctoria s.l.* A diagnostic feature is also the indumentum, as *G. anxantica* typically has glabrous branches and leaves when mature, while *G. tinctoria* subsp. *tinctoria* is mostly pubescent and *G. tinctoria* subsp. *ovata* has either pubescent or even villose individuals. Calyx and legume are glabrous in *G. anxantica*, whereas *G. tinctoria* subsp. *tinctoria* shows moderate pubescence and *G. tinctoria* subsp. *ovata* is predominantly villose. Additionally, *G. anxantica*

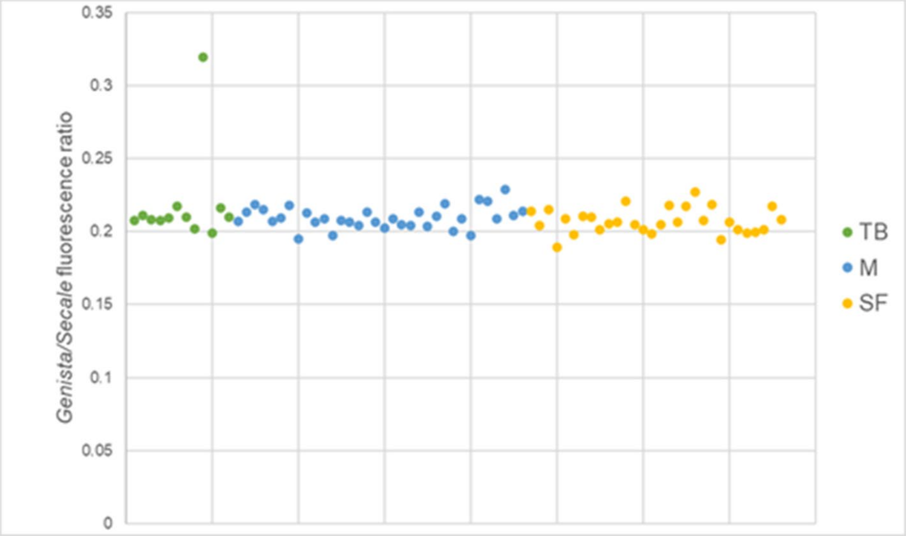

Fig. 6 Fluorescence ratios between *Genista tinctoria* samples and the internal standard (*Secale cereale*) obtained by flow cytometry. Each point represents an individual from the three analysed localities: Torella (TB, green), Mefite (M, blue) and Santa Felicita (SF, yellow). Ratios around 0.20–0.23 indicate tetraploid cytotypes. A single specimen from TB shows a higher ratio (approx. 0.32), consistent with a hexaploid genome size

displays wider branch angles compared to *G. tinctoria s.l.* (see Supplementary material S1 and S2 for further details).

According to our results, the groups representing *G. tinctoria* subsp. *ovata* and *G. tinctoria* subsp. *tinctoria* are largely overlapping (Figs. 5, 6) making the distinctness of the two taxa rather problematic. However, while a definitive assessment of the distinctness of *G. tinctoria* subsp. *ovata* would require a wider study ad hoc, the above-mentioned characters, especially when considered together, offer a robust framework for distinguishing *G. anxantica* from its close relatives in both field and herbarium settings. In the field, *G. anxantica* is readily distinguishable from typical *G. tinctoria* by its shrubby and patently branched habit, which is preserved even in cultivation (see e.g., L1959416 at https://medialib.naturalis.nl/file/id/L.1959416/format/large; cf. also P03121642), and only rarely occurs in the *G. tinctoria* group. Various authors, in fact, recognize the morphological distinctness of *G. anxantica* also after cultivation (e.g., Spach 1845; Loudon 1869; Weathers 1901; Robinson 1903; Webster 1908; Silva Tarouca and Schneider 1922). Briquet (1910), however, correctly observed that such a distinctness is well supported only when *G. anxantica* is compared with the typical *G. tinctoria*, whereas it becomes much less evident after considering the remarkable variability of the species. The latter author referred, in particular, to the variability of hairiness and habit. Actually, we verified that young plantlets are hairy along the leaf margins (EDG, pers. obs.). The variability within *G.tinctoria s.l.* is testified by the rich synonymy (POWO 2026), often related to small populations or groups thereof.

The weaker separation observed in the PCA, if based solely on metric variables (data not shown), underscores the predominant role of categorical traits, such as indumentum and branching morphology, in driving taxonomic differentiation. These qualitative characters likely reflect evolutionary adaptations that may be more stable than size-related measurements.

Flow cytometric ploidy estimation revealed no differences between *G. anxantica* and *G. tinctoria s.l.*, (Fig. 6). This indicates that ploidy variation does not contribute to the differentiation of the Mefite plants. In contrast, the population genetic investigation using uniparentally inherited plastid markers (cpDNA) and biparentally inherited nuclear microsatellites (nrDNA) carried out by Di Iorio et al. (2023) shows that *G. anxantica* represents an ecotype that has evolved under the exceptional environmental conditions of the Mefite area. The population exhibits a private haplotype, with only three peripheral individuals sharing the haplotype common in the adjacent *G. tinctoria* (Table 1 and Fig. 3D, Di Iorio et al. 2023). Despite this haplotypic similarity, they both individuals show nuclear microsatellite profiles that fall entirely within the Mefite genetic cluster (Fig. 3E, Di Iorio et al. 2023), confirming their belonging to the same lineage. The STRUCTURE analyses of nuclear microsatellites presented by Di Iorio et al. (2023) further emphasise this pattern. The plants of the Mefite area (i.e., *G. anxantica*) form a compact and clearly delimited genetic group, as shown by the red cluster in Fig. 3D of Di Iorio et al. (2023). In contrast, the three very nearby *G. tinctoria* populations, those located immediately around the Mefite site, display a marked admixture of the red and yellow genetic components. This admixture decreases progressively in the more distant *G. tinctoria* populations, which show more homogeneous genetic profiles (yellow cluster in Di Iorio et al. 2023). Consistently, the BARRIER analysis in Di Iorio et al. (2023) identifies clear discontinuities in gene flow between *G. anxantica* and *G. tinctoria* populations, indicating that the extreme ecological conditions of the Mefite act as an effective barrier to seed and pollen dispersal. This contrast reinforces the view that the toxic gas emitting environment of the Mefite promotes the isolation of the local ecotype and limits gene flow. Although plastid data revealed admixture only in three peripheral individuals, their nuclear microsatellite profiles fall entirely within the *G. anxantica* genetic cluster, suggesting occasional seed mediated contact rather than persistent introgression. This pattern is consistent with the known dispersal biology of *Genista*, which combines ballochory with myrmecochory mediated by elaiosome bearing seeds (Pemberton and Irving 1990; Stroh 2015). In the Mefite, however, soil fauna shows reduced diversity (Battaglini and Carbone 1981), and the ant communities potentially involved in myrmecochory are likely filtered by the extreme conditions, while the steep slopes of the valley may further constrain the escape of diaspores from the gas plume. In addition, historical and recent observations describe massive insect mortality around the gas vents (Santoli 1783; Reclus 1883; Gambino 1991, ODC pers. obs.). It is therefore plausible that pollinators experience reduced or irregular access to the Mefite population, potentially restricting pollen transfer and contributing to the slight mismatch between plastid and nuclear signals observed. Specific studies on both seed dispersal and pollination ecology would be valuable to clarify these dynamics. The combination of strong genetic homogeneity in *G. anxantica* and admixture in neighbouring *G. tinctoria* populations points to an advanced stage of divergence. Although Di Iorio et al. (2023) did not formally address the taxonomic rank of the entity, they clearly identified the *G. anxantica* population as an ecotype indicating an incipient evolutionary divergence and deserving appropriate taxonomic assessment of *G. anxantica* (Di Iorio et al. 2023).

The integrative approach clarifies therefore that *G. anxantica* matches the concept of an ecological subspecies, according to which populations are genetically distinct but not yet fully separated (Thompson et al. 2005) and supports the treatment of *G. anxantica* at subspecific rank within *G. tinctoria*. Several Mediterranean taxa provide comparable cases of habitat-driven differentiation. Within the Italian flora, the closest example is *Agrostis canina* L. subsp. *monteluccii* Selvi, a taxon strictly associated with geothermal marshes as well, although its taxonomic value remains highly debated (Selvi 1994; cf. PFI 2026). Along the Tyrrhenian coast, *Solidago virgaurea* L. subsp. *litoralis* (Savi) Burnat is confined to sandy dune systems, where it exhibits clear ecological and morphological divergence from inland *S. virgaurea* (Nardi et al., 2018). In Sardinia, *Helichrysum saxatile* Moris subsp. *morisianum* Bacch., Brullo & Mossa occurs on acidic or ultramafic rocky habitats and differs morphologically from the more widespread subsp. *saxatile* (Bacchetta et al. 2003). Likewise, *Mcneillia rosanoi* subsp. *moraldoi* is restricted to granitic rocky slopes of Mt. Sacro (Campania), showing clear differentiation from the calciphilous typical subspecies (De Luca et al. 2022).

Taxonomic treatment

***Genista tinctoria subsp. anxantica* (Ten.) Del Guacchio & De Castro, comb. nov. et st. nov.** ≡ *G. anxantica* Ten., Fl. Napol. 1(3) [Prodr.]: XLI. 1812 (basionym) ≡ *G. tinctoria* var. *anxantica* (Ten.) Rchb.f. in H. G. Reichenbach & G. Beck von Mannagetta, *Icon. Fl. Germ. Helv.* 22: 24. 1869 [Jan] ≡ *Corniola anxantica* (Ten.) C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 3: 567. 1845 ["1843–1844"] [Jul–Dec]

– "*Genista amsanctica* Ten.", Fl. Nap. 2: 127. 1820, var. orth. (Art. 61.1 of *ICN*).

Neotype (**here designated**): [ITALY.] "Valle di Ansanto in Principato Ultra", s. d., *[G. Gussone] s. n.* (NAP, Collection "Tenore", barcode NAP0002351!) (see Figure 2 for an image of the type).

Nomenclatural notes. The presumed illegitimate name "*Genista anxantica* Griseb.", Spic. Fl. Rumel. 1: 3. 1843 does not exist (cf. POWO 2026). In fact, it is only a misapplication of the Tenorean name to a Balkan plant. Tenore (1831) explicitly apologized for the inconsistency in the orthography of the epithet throughout his works, plates and specimens ("anxantica", "anxanthica", "amsantica"); according to him, such uncertainty, already noted by Candolle (1825), was due to the difficulties of translating the ancient Oscan name "Amsanctus" into modern Latin. See also the variant "ampsantica" discussed above. In any case, the original spelling by Tenore (1812) must be retained (Art. 60.1 of *ICN*; Briquet 1908). For the correct citation of the combination by Presl, see Stafleu & Cowan (1983). The combination *G. tinctoria* var. *anxantica* cannot be attributed to Fiori (cf. Schneider 1907; Bean 1919; POWO 2026). Fiori (1900) usually did not provide the authorship of recombined names, but only that of the basionym (the same choice occurs in Fiori 1925). This is clear in the few cases in which he added "nobis" after the basionym's author to indicate a new combination by him, for example for "*Medicago minima* [var.] *hirsuta* (L.) Nobis". Therefore, in reporting "var *anxantica* (Ten.)", as well as in listing "var. *ovata* (W. et K.)" or "var. *virgata* (W.)" in the same page (Fiori 1900: 18), he did not publish any isonym (cf. Art. 6.3, Note 2 of the *ICN*). Finally, the combination by Loudon (1869), i.e., "*G. anxantica* var. *scariosa*", is incorrect under Art. 11.4 of Turland et al. (2025).

At the present state of knowledge, a comprehensive assessment of the morphological variability of *Genista tinctoria s.l.* in Italy is still not feasible. This is due both to persistent nomenclatural uncertainty (cf. Pignatti 2017) and to the presence of numerous, geographically restricted variants, sometimes to some extent related to non-Italian taxa (Bernardo and Peruzzi 2016).

Here we provide an updated identification key including *G. januensis* and all Italian subspecies currently attributable to *G. tinctoria*. The key is based on Feoli Chiapella, Brullo & Guarino in Pignatti (2017) and was revised following Gibbs (1966, 1968), Pignatti (1973), Bernardo and Peruzzi (2016), and our own results.

The aim of this key is to stimulate further research on this complex group, particularly at molecular level. Names placed in quotation marks are provisional and reported at subspecific rank for consistency purposes. The combination of characters distinguishing these taxa from the remaining Italian species of *Genista* includes: plants unarmed; leaves simple and longer than the internodes; flowers arranged in racemes; standards glabrous.

1. Leaf margin narrowly hyaline and obscurely denticulate; stems usually triangular in cross-section and winged; plants heterophyllous

→ *G. januensis.*

1'. Leaf margin entire, without hyaline borders; stems usually terete or angular; plants homophyllous.

→ *G. tinctoria s.l.*

2. Shrubs with woody and angulate branches; leaves glabrous or nearly so, subcoriaceous

→ *G. tinctoria* subsp. *anxantica* (mephitic fields, Campania).

2. Subshrubs with branches not woody, terete or striate; leaves usually ciliate, membranaceous.

3. Plants usually > 20 cm; leaves > 10 mm; flowers numerous, in simple or branched racemes.

4. Leaves, calyces and legumes glabrescent.

→ *G. tinctoria* subsp. *tinctoria* (sub-Mediterranean woods and shrublands; widespread).

4'. Leaves, calyces and legumes villose.

→ *G. tinctoria* subsp. *ovata* (as above).

3'. Plants prostrate, rarely > 20 cm; leaves < 10 mm; flowers few, apical.

6. Calyces and fruits glabrescent; leaves glabrescent with conspicuous lateral veins →"*G. tinctoria* subsp. *alpestris*" (mountain grasslands, N-C Apennines and possibly elsewhere).

6'. Calyces and fruits hairy; leaves hairy, lacking conspicuous lateral veins.
→"*G. tinctoria* subsp. *tenorei*" (high-altitude grasslands, Pollino massif).

The provisional names "*G. tinctoria* subsp. *alpestris*" and "*G. tinctoria* subsp. *tenorei*" correspond respectively to *G. tinctoria* var. *alpestris* Bertol. (Pignatti 1973) and *G. tenorei* G.Don (Bernardo and Peruzzi 2016).

The presumed subspecies *Genista tinctoria* subsp. *tenuifolia* (Loisel.) Pignatti and *G. tinctoria* subsp. *scariosa* (Viv.) Pignatti (Pignatti, 1973, 1982, 2017), which would chiefly be distinguishable by their reduced flowers, are critical and their nomenclature problematic. Under the name *G. tinctoria* subsp. *scariosa*, Pignatti (1973) referred to a wetland plant occurring in Tuscany, especially characterized by shorter standards, very narrow leaves and frequently winged stems (Pignatti 2017). This last feature is typical of *G. januensis*, but it may represent an ecological adaptation of *G. tinctoria* to marshy environments rather than a link to *G. januensis*. The combination is based on *G. scariosa*, a younger synonym of *G. januensis*, and cannot be used for the taxon circumscribed by Pignatti (1973) (Art. 41.8 of *ICN*).

Regarding the combination *G. tinctoria* subsp. *tenuifolia*, it was not published by Pignatti (1973) (cf. ILDIS 2010). In this latter work, he actually proposed the name *G. tinctoria* subsp. *insubrica* (Brügger) Pignatti for the same taxon that he later informally indicated as *G. tinctoria* subsp. *tenuifolia* (Pignatti 1982, 2017). The distinctness of this taxon is unclear. Brügger (1882) interpreted *G. insubrica* as a hybrid between *G. tinctoria* and *G. germanica* L. In any case, the name *G. tenuifolia* Loisel. – and therefore, its combination *G. tinctoria* subsp. *tenuifolia* – is not a synonym of *G. tinctoria* subsp. *oligosperma* (Andrae) Soó (Novikov 2023) (cf. POWO 2026).

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Author contributions EDG and ODC conceived the study and coordinated it. EDI and ODC collected the field material. RV and EDI located the specimens and performed the morphological measurements. EDG carried out the morphometric analyses, typification and prepared the first draft of the manuscript. ODC handled the previous molecular results. ST conducted the cytological investigations. All authors contributed to the final revision and approved the submitted version.

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Data availability All data used in this study are provided in the supplementary files. Morphometric matrices are available from the corresponding author.

Declarations

Competing interests The authors declare no competing interests.

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