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RESEARCH ARTICLE

# A revision of the genus *Armeria* (Plumbaginaceae) in peninsular Italy and Sicily through an integrative taxonomic approach

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**Abstract** The genus *Armeria* in peninsular Italy has been affected by taxonomic ambiguity for more than a century due to high morphological variability. We present a comprehensive revision of peninsular Italian and Sicilian *Armeria* species, using an integrated taxonomic approach that combines molecular phylogeny, plant and seed morphometrics, and cytogenetics, taking advantage of species delimitation and data integration methods. Nuclear (ITS) and chloroplast (*trnF-trnL*, *trnH-psbA*, *trnL-rpl32*, *trnQ-rps16*) markers were sequenced to construct phylogenetic trees and conduct species delimitation using assemble species by automatic partitioning (ASAP), while seed and plant morphometric data were analysed using dimensionality reduction techniques and Gaussian mixture models (GMMs) for conducting Bayesian inference on species boundaries. The results support the hypothesis of 10 species endemic to the Italian peninsula. *Armeria gracilis* subsp. *majellensis* is no longer recognised as a distinct subspecies due to insufficient differentiation from *A. gracilis* s.str., while the occurrence of *A. canescens* in Italy is definitively excluded. On the contrary, we propose to raise *A. gracilis* var. *pollinensis* to species level, with its name lectotypified herein. A new identification key is provided. The findings confirm Italy as a second biodiversity hotspot for the genus, emphasizing the value of integrated data and methods to resolve taxonomically challenging groups, providing also a framework for future genus-wide revisions.

**Keywords** Gaussian mixture models; integrative taxonomy; karyology; morphometry; phylogeny; systematics

**Supporting Information** may be found online in the Supporting Information section at the end of the article.

## ■ INTRODUCTION

Over the past three centuries, taxonomic research has established a framework for understanding plant diversity through the description and classification of species. Traditionally, this work has relied on alpha-taxonomy (Turrill, 1938) – the discovery, description, and naming of species based primarily on morphological features. While this method has significantly contributed to our understanding of plant diversity, especially in regions with high biodiversity and limited resources, it has limitations. Notably, alpha-taxonomy may lack accuracy and replicability, often due to brief or absent methodological descriptions and a reliance on subjective interpretations (Turrill, 1938; Henderson, 2005). Integrative taxonomy, as proposed by Dayrat (2005), is a comprehensive framework for species delimitation that integrates multiple lines of evidence – such as molecular, morphological, cytological, ecological, and behavioural data – to formulate robust species hypotheses. This approach moves beyond reliance on morphological discontinuities alone, aiming instead to incorporate all available information to accurately delineate species boundaries. By doing so, integrative taxonomy addresses the limitations of traditional methods and enhances the reliability and reproducibility of taxonomic classifications.

Defining species boundaries in plants is complicated by factors like hybridisation, polyploidy, dysploidy, and reticulate speciation, which often hamper a traditional taxonomy based solely on qualitative morphological observations. This has already been extensively demonstrated by other studies

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in *Ficus* (Wang & al., 2024), *Pulmonaria* (Liu & al., 2022), and *Santolina* (Giacò & al., 2023).

Within this broader context, *Armeria* Willd. is infamously known for its complexity. It is a genus within Plumbaginaceae, comprising approximately 108 species, mainly distributed across the Mediterranean region, western Europe, and Macaronesia, with some taxa extending into temperate regions of Asia and North Africa (Malekmohammadi & al., 2024). This genus is characterised by a high level of endemism and ecological specialisation, particularly in mountainous and coastal habitats. Currently, there is no published genus-wide resolved phylogeny, apart from that published by Fuertes Aguilar & Nieto Feliner (2003), which analysed 71 taxa using ITS sequences and revealed extensive reticulation and additive polymorphisms, resulting in largely unresolved relationships with numerous polytomies. Members of *Armeria* typically exhibit cushion-like or tufted growth forms, with linear to lanceolate leaves arranged in basal rosettes, and inflorescences forming globose to hemispherical heads (Kubitzki, 1993). These morphological traits, combined with minor interspecific variation, have historically posed significant challenges to species delimitation, thus making *Armeria* an emblematic case study for integrative taxonomy and biosystematic research (Arrigoni, 2015; Villa-Machío & al., 2023 and citations therein) aimed to disentangle complex taxonomic scenarios. The Italian peninsula constitutes the second major global hotspot of biodiversity for the genus, with 17 endemic taxa currently recognised (POWO, 2017–; Bartolucci & al., 2024) (Fig. 1). Regarding peninsular Italy and Sicily, the most recent revision was conducted by Arrigoni (2015), who adopted an alpha-taxonomic approach. However, several of the taxa he accepted for the Italian peninsula are considered taxonomically doubtful by Bartolucci & al. (2024) and the identification of these taxa is a non-trivial task, even for expert botanists.

For instance, *Armeria aspromontana* Brullo & al. was formerly regarded as part of the intraspecific variability of *A. nebrodensis* (Guss.) Boiss. (Bianchini, 1977, 1982), until it was formally described by Brullo & al. (1997) based on qualitative morphological differences. Among these, the alleged monomorphism in pollen-stigma traits is particularly contentious, since *Armeria* species are typically obligate outcrossers exhibiting a dimorphic incompatibility system with two pollen-stigma morphs (Type A and Type B) occurring in equal proportions within each population (Erdtman, 1940; Iversen, 1940; Dulberger, 1975; Costa & al., 2019). This is unusual, as monomorphism is observed only in taxa from extreme environments like the poles (Baker, 1948, 1966). Moving to *A. brutia* Brullo & al. (Brullo & al., 2004), its taxonomic status remains uncertain, as only a brief description in a phytosociological paper is available. However, the taxonomic "*nightmare*" for botanists is *A. gracilis* Ten., which is believed to be widely distributed across the Italian peninsula, from the Umbria/Marche regions to the Pollino Massif (Basilicata/Calabria regions). The populations from central Italy have been subjected to contrasting taxonomic interpretations, with classifications changing dramatically over time (Zangheri, 1976; Bianchini, 1982; Conti & al., 2005; Brullo & Guarino, 2017). In the past century, this variation was organized into two species, each with its own subspecies: *A. majellensis* Boiss. and *A. canescens* (Host) Ebel. The former included *A. majellensis* subsp. *majellensis* and *A. majellensis* subsp. *ausonia* Bianchini (Bianchini, 1977), while the latter comprised *A. canescens* subsp. *canescens* and *A. canescens* subsp. *gracilis* (Ten.) Bianchini (Zangheri, 1976; Bianchini, 1982; Brullo & Guarino, 2017). However, Bianchini's (1977) distinction into subspecies was questioned by Arrigoni (2015), who argued that these subspecies are not actually distinct, as their diagnostic features fall within the range of the variation observed in *A. gracilis*. In addition, Arrigoni highlighted that some specimens deposited at the herbarium FI (Natural History Museum of Florence) from "Monte Coccorello" (today named Mt. Cocurello, in the Velino-Sirente group, Abruzzo) – i.e., the type locality of *A. majellensis* subsp. *ausonia* – have been identified by Bianchini (1982) himself as *A. canescens* subsp. *gracilis*. Earlier, Zangheri (1976), following Pinto da Silva (1972), recognised *A. canescens* subsp. *canescens* and *A. canescens* subsp. *nebrodensis* (Guss.) P.Silva, considering *A. majellensis* as a heterotypic synonym of *A. canescens* subsp. *canescens* (Pinto da Silva, 1972), and including both Calabrian and Sicilian populations in *A. canescens* subsp. *nebrodensis*. *Armeria canescens* subsp. *canescens* was reported for both the Balkans and the Italian peninsula. However, Papanicolaou & Kokkini (1982) in a morphometric study concluded that leaf ciliation and pubescence, used to distinguish the two putative subspecies of *A. canescens*, are problematic and often coexist within the same population. More recently, the occurrence of *A. canescens* in Italy, while accepted by some authors (Conti & al., 2005; Scassellati, 2011; Brullo & Guarino, 2017), is rejected by others (Arrigoni, 2015; Bartolucci & al., 2024), claiming that this species does not occur in Italy and that all the Italian populations referred to *A. canescens* should be referred to *A. gracilis*. Eventually, Arrigoni (2015) recognised two subspecies: *A. gracilis* Ten. subsp. *gracilis* and *A. gracilis* subsp. *majellensis* (Boiss.) Arrigoni. This view, implying the exclusion from the Italian flora of *A. canescens*, is currently accepted by Bartolucci & al. (2024), with doubts concerning the taxonomic value of *A. gracilis* subsp. *majellensis*, doubts that were confirmed also after the typification of these names (Iamonico & al., 2024).

In this study, we aim to clarify the systematics and taxonomy of the Italian peninsular and Sicilian taxa of *Armeria*, by employing an integrative approach that combines plant and seed morphometrics with molecular phylogeny and karyology.

## ■ MATERIALS AND METHODS

**Sampling. —** In total, 21 populations including all the type localities (Brullo & al., 1997, 2004; Selvi, 2009; Scassellati & al., 2011; Arrigoni, 2015; Iamonico & al., 2024) and other populations selected among those listed by Arrigoni (2015) were sampled. Sampling included one population each for *Armeria aspromontana*, *A. brutia*, *A. garganica* Arrigoni,



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*A. gussonei* Boiss., *A. nebrodensis*, and *A. saviana* Selvi; two populations for *A. canescens* (from Croatia), *A. gracilis* subsp. *majellensis*, and *A. macropoda* Boiss.; three populations for *A. denticulata* (Bertol.) DC.; and six populations for *A. gracilis* subsp. *gracilis* (Fig. 2, Appendix 1). Population acronyms marked with asterisks (*) throughout the text indicate type localities. Taxa attribution provided by Arrigoni (2015) was considered as null hypothesis and named "current taxonomic hypothesis" (11 taxa, considering also the non-Italian *A. canescens*, described from Croatia). On average, roughly 20 individuals per population were sampled (Appendix 1) for a total of 409 herbarium specimens.

**Molecular systematics workflow. —** Three individuals were randomly selected from each population (for a total of 63 accessions), and their leaves were preserved in silica gel for subsequent DNA extraction. We followed the protocol used by Tiburtini & al. (2022) for DNA extraction, primer selection for the complete nuclear ribosomal DNA cistron (ITS1 + 5.8S + ITS2) and four plastid intergenic spacers (*psbA-trnH*, *trnF-trnL*, *trnL-rpl32*, and *trnQ-rps16* IGS), as well as their amplification, sequencing, and data analysis. GenBank accession numbers are indicated in Appendix 1. Some sequences could not be amplified for certain taxa. Specifically, we were unable to amplify: (1) the *trnF-trnL* intergenic spacer from one individual each of *Armeria canescens* from Mt. Kozjak (MK), *A. gracilis* from Piani di Pezza (VS*), and *A. gracilis* from Vado di Corno (VC); (2) the *trnL-rpl*32 intergenic spacer from one individual of *A. gussonei* from Rocca Busambra (RB*); (3) the *trnQ-rps16* intergenic spacer for all individuals of *A. garganica* (SL*) and *A. gracilis* from Mt. Cucco (SI).

Sequences were visually inspected and manipulated by using BioEdit v.7.2.5 (Hall, 1999), and then aligned (available at: https://doi.org/10.5281/zenodo.21296362) using the ClustalW algorithm (Thompson & al., 1994), as implemented in the same software, with default values. Given the comparatively reduced number of sequences involved, when visually inspecting sequences by using BioEdit v.7.2.5 (Hall, 1999), we reverse-complemented the individual sequences and electropherograms obtained with the reverse primer (in the case

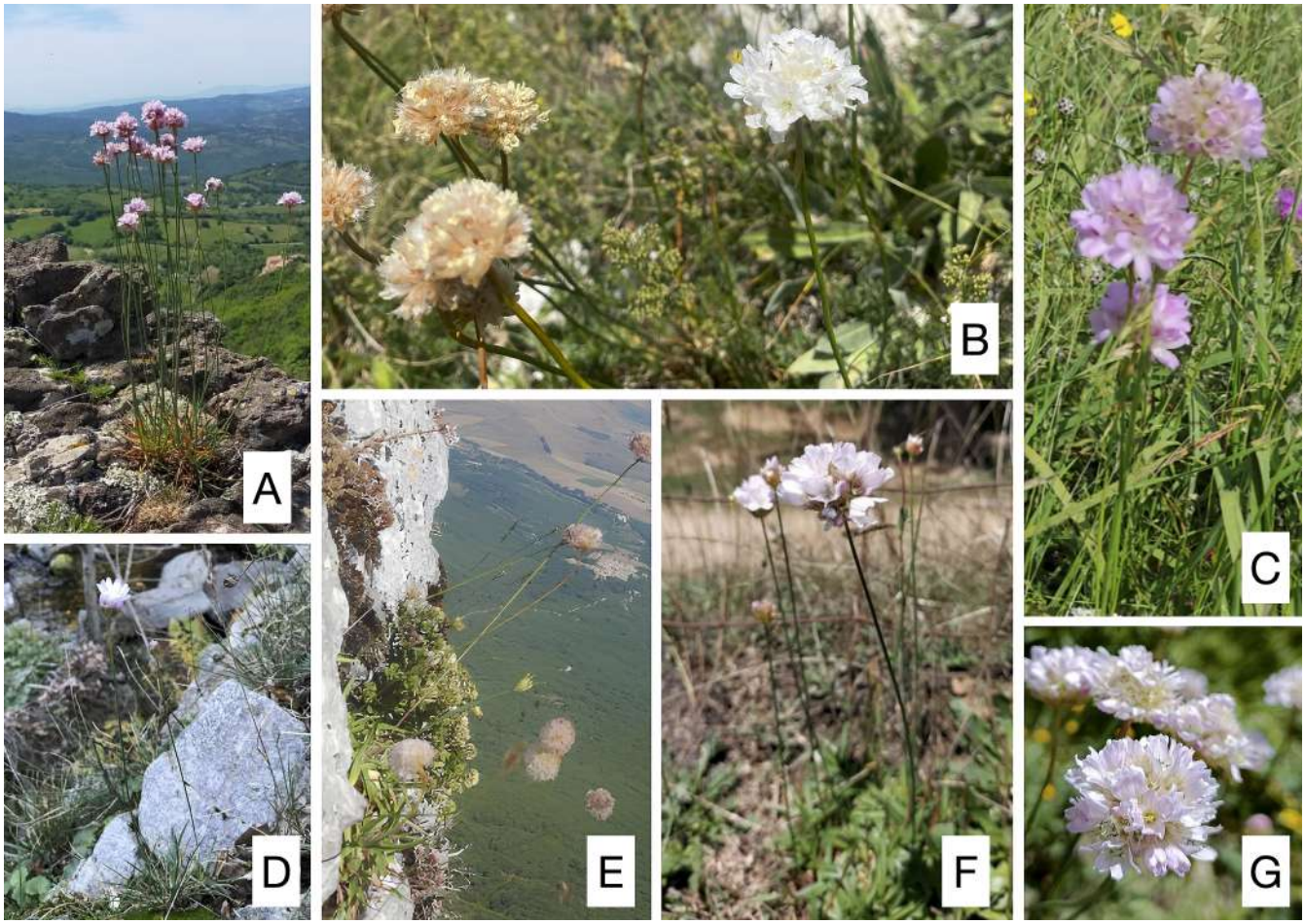


**Fig. 1.** Selected pictures of *Armeria* taxa endemic to peninsular Italy and Sicily. **A**, *A. denticulata* (Photo Credits: Luca Sandroni); **B**, *A. gracilis* (Photo Credits: Manuel Tiburtini) from the Central Apennines; **C**, *A. macropoda* (Photo Credits: Silvia Fruzzetti); **D**, *A. aspromontana* (Photo Credits: Valentina Lucia Astrid Laface); **E**, *A. gussonei* (Photo Credits: Gianniantonio Domina); **F**, *A. brutia* (Photo Credits: Liliana Bernardo); **G**, *A. gracilis* from Pollino (Photo Credits: Lorenzo Peruzzi).



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of ITS, primer JK12) and observed both the forward and the reverse strands simultaneously, nucleotide by nucleotide, editing divergent positions into paralogous ones when necessary. We did find paralogous positions in seven nucleotides, for a total of ten sequences. Multiple peaks and/or discrepancies between forward and reverse ITS sequences were resolved using ambiguous IUPAC codes. A nucleotide evolution model was computed for each of the five sequenced regions using jModelTest v.2.1.10 (Darriba & al., 2012), and the best-fitting model was chosen using the Bayesian information criterion (BIC) (Schwarz, 1978). Bayesian phylogenetic trees for nuclear and concatenated plastid markers were inferred in MrBayes v.3.2.6 (Huelsenbeck & Ronquist, 2001; Ling & al., 2016) in two simultaneous, independent runs with the following settings: 1,000,000 generations of MCMC sampling every 1000 generations and four chains (three cold and one heated). For the concatenated cpDNA dataset, convergence was reached in 3,000,000 generations and sampling was set every 3000 generations. Convergence and mixing were evaluated in Tracer v.1.7.2 (Rambaut & al., 2018) and the consensus Bayesian tree was visualised in FigTree v.1.4.2 (Rambaut, 2014). The best-fitting evolution models were HKY (Hasegawa & al., 1985) for ITS and the *trnH-psbA* IGS, GTR + I for the *trnF-trnL* IGS, and F81 + I (Felsenstein, 1981) for the other two plastid DNA markers.

The tree was rooted using homologous sequences from six individuals of *Armeria pungens* (Link) Hoffmanns. & Link. This species was selected as outgroup on both phylogenetic and morphological-geographical grounds. Genomic data place *A. pungens* as sister to a clade comprising *A. maritima* (Mill.) Willd. and *A. arenaria* (Pers.) F.Dietr. (Baker & al., 2022) both traditionally belonging to *A.* sect. *Armeria* (Boissier, 1848), providing a well-supported phylogenetic basis for rooting. Morphologically, *A. pungens* is a well-differentiated western Mediterranean species, traditionally referred to *A.* sect. *Macrocentron* Boiss., clearly distinct from the Italian peninsular and Sicilian taxa under investigation, all traditionally assigned to *A.* sect. *Armeria*. We note that sectional classification in *Armeria* has not been consistently supported by molecular phylogenetic analyses (Fuertes Aguilar & Nieto Feliner, 2003); however, the phylogenetic placement of *A. pungens* as confirmed by genomic data makes this concern less critical for the present study rooting choice. We acknowledge that any outgroup choice carries

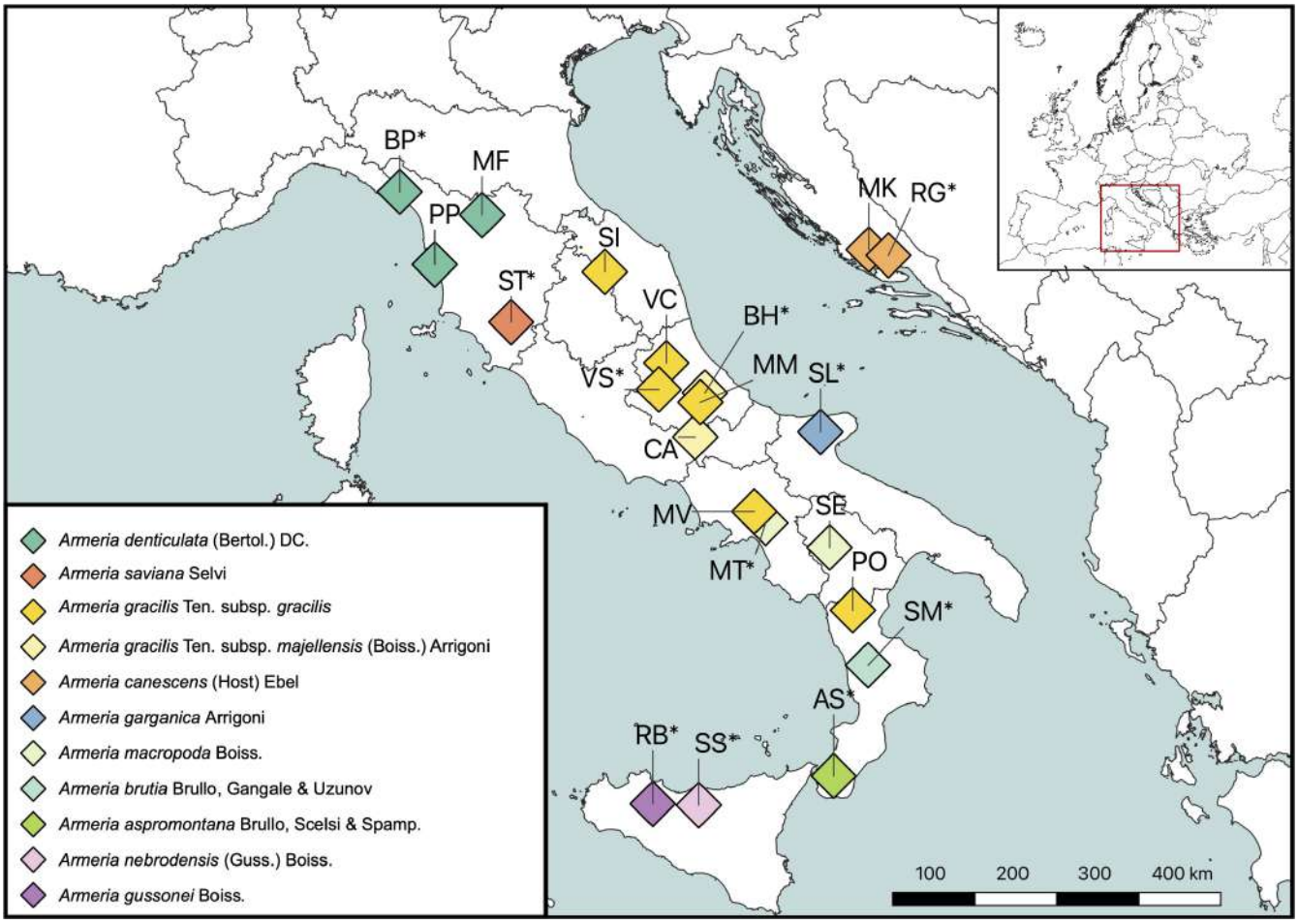


**Fig. 2.** Map of the 21 *Armeria* populations included in the study. Acronyms refer to the populations (see also Appendix 1 for further information). Asterisks indicate populations from type localities. Populations are coloured according to the taxonomic hypothesis proposed by Arrigoni (2015).



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limitations; however, we consider *A. pungens* the most reasonable option given current knowledge of *Armeria* phylogeny.

Species delimitation on genetic data was conducted using ASAP (Puillandre & al., 2021) – assemble species by automatic partitioning, a distance-based approach – that is the implementation of a modified hierarchical clustering algorithm that uses pairwise genetic distances and provides a ranked score for each defined partition. Although heuristic methods are generally less accurate (Yu & al., 2017), we chose a less demanding distance-based approach over a model-based one because the coalescent-based species delimitation method (e.g., Douglas & Bouckaert, 2022) failed to produce reliable parameter estimates in BEAST2 (Bouckaert & al., 2014). The lack of full convergence in the MC3 chains of the species delimitation process was likely due to the scarcity of informative sites required by such computationally demanding models, hindering accurate parameter estimation and, consequently, the reliability of the results. ASAP yields results somehow comparable with other simpler coalescent model-based methods (e.g., GMYC = generalized mixed Yule-coalescent model) (Puillandre & al., 2021). To run ASAP, population-wise consensus concatenated sequences of cpDNA and the consensus ITS sequence were separately obtained in Aliview v.1.28 (Larsson, 2014) and re-aligned using Clustal W (Thompson & al., 1994) run as daughter process of Aliview v.1.28 (Larsson, 2014). Then, the ASAP web app (https://spartexplorer.mnhn.fr/delimitation, accessed 4 Sep 2024) was used to run the species delimitation using simple p-distances. The best partition was selected based on the most reasonable and highest ranked asap-score and exported as spart files to be passed into LIMES (Ducasse & al., 2020) as daughter process of iTaxotools (Vences & al., 2021).

**Pollen-stigma dimorphism in *Armeria aspromontana* and *A. nebrodensis*. —** To determine whether *Armeria nebrodensis* can be truly differentiated from *A. aspromontana* based on pollen-stigma dimorphism vs. monomorphism – one of the key diagnostic traits reported by Brullo & al. (1997), 16 anthers were randomly selected from 16 individuals (one anther from each individual), 8 from *A. aspromontana* (AS* population, Fig. 2) and 8 from *A. nebrodensis* (SS* population). A chi-square test with Monte Carlo simulated *p*-value for correcting it due to small sample size was used to test for independence of the two morphs (A type / B type) (Iversen, 1940).

**Plant morphometry. —** For most populations, 20 pressed dry herbarium specimens were measured (Appendix 1). A total of 38 morphological characters were recorded; four qualitative variables were subsequently dropped, one invariant (papillose leaf cells), one of excessively high cardinality (shape of the leaf apex), and two found to be taxonomically meaningless (presence of hairs on the back of the bracts), resulting in a dataset of 409 individuals scored for 29 quantitative and 5 qualitative variables (shown in Table 1). For the graphical representation of calyx-related characters, see Tiburtini & al. (2022: fig. S1). A video is also publicly available to demonstrate how the morphological characters were measured (https://youtu.be/cSTTiK_UMoU?si=zZHaS_iPwByORqqy).

Macroscopic measurements were taken using a digital calliper (with an error margin of ±0.1 mm) under a stereomicroscope. Microscopic measurements were obtained from bar-scaled images in Fiji v.2.1.0 (Schindelin & al., 2012). To objectively count the number of leaf veins, free-hand transverse sections of leaves were made. A *vein* was defined as each fascicle composed by xylem and phloem surrounded by sclerenchyma. The anatomy of summer leaves was examined under a Leitz Diaplan light microscope at 40× magnification. We define *scales* as the series of bracts that protect the capitulum, which can be distinguished into inner, intermediate, and outer scales based on their position and morphology. *Bracts* refer to the larger structures subtending the spikelets that compose the inflorescence. Finally, *bracteoles* are defined as small, transparent bracts positioned between the paired flowers within a spikelet. All the data, excluding the molecular systematics if not differently specified, were analysed using R language v.4.3.2 and the RStudio IDE (Posit Team, 2022) on macOS. Continuous variables were used for dimensionality reduction and species delimitation, whereas categorical variables were utilized in feature selection and for descriptive statistics. We used the tidyverse v.2.0.0 meta-package (Wickham & al., 2019) for data exploration, preparation and description. We applied a standardized framework for data cleaning, preparation, visualisation and imputation of the few (4) missing values (Tiburtini & al., 2025a). Strong population-wise outliers greater than 4 interquartile ranges (IQR) were detected using the create_outlier_datatable function and checked twice upon herbarium material Tiburtini & al. (2025a). Dimensionality reduction and plotting via principal component analysis (PCA) was performed using the FactoMineR v.2.11 (Le & al., 2008) and factoextra v.1.0.7 (Kassambara & Mundt, 2020) R packages. A supervised manifold learning method (UMAP) (McInnes & al., 2018) – trained using tidymodels v.1.4.1 (Kuhn & Wickham, 2020) giving populations as groupings – was employed to better reveal inherent data groupings and plotted with plotly v.4.10.4 (Sievert, 2020) R package. Species delimitation was conducted under the Gaussian mixture models (GMMs) framework as described by Tiburtini & al. (2025a) using the mclust R package v.6.1.1 (Scrucca & al., 2016) to both implement the lumping-splitting algorithm and conduct Bayesian species circumscription on raw variables using the EDDA model (eigenvalue decomposition discriminant analysis, i.e., without assuming subgroups at population level) for decomposing the covariance matrix (Scrucca & al., 2023). The lumping-splitting algorithm is an iterative algorithm that lumps and splits pairs of populations, computes the relative support of such model using lnL, BIC and Bayes factors until it finds the maximum likelihood clustering solution achievable for such data.

Spatial morphometric admixture using predicted posterior probabilities from the fitted model was assessed using the mapmixture function in the mapmixture v.1.1.4 (Jenkins, 2024) R package. Admixture in GMMs arises from their probabilistic framework, wherein each observation is associated with posterior probabilities of belonging to each



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modelled component. Rather than being deterministically assigned to a single class, individuals are probabilistically assigned to multiple classes based on Bayes' theorem, which combines prior mixture proportions with the class-specific model parameters (means and covariance structures) to compute the likelihood of each herbarium specimen under the corresponding multivariate Gaussian density. Admixture thus reflects the presence of overlapping distributions in morphometric space: individuals or clusters situated near class boundaries – or in zones of morphospace intersection – exhibit non-negligible probabilities for more than one mixture component. Practically speaking, if a herbarium specimen shows an intermediate morphology between two taxa, the GMM might assign it a 50% probability of belonging to each of these two taxa, reflecting its intermediate morphology rather than forcing a fixed classification.

**Table 1.** List and description of the morphometric characters measured in the studied *Armeria* populations.

| Character | Description | Type | Tool |
|---|---|---|---|
| 1. AWN_LENG | Awn length (mm) | QC | Fiji (ImageJ) |
| 2. DIAM_CAP | Diameter of the capitulum (mm) | QC | Calliper |
| 3. LENG_CAL_PED | Length of the calyx pedicel (mm) | QC | Fiji (ImageJ) |
| 4. LENG_CAL_TUBE | Length of the calyx tube (mm) | QC | Fiji (ImageJ) |
| 5. LENG_INNER_SCAL | Length of the inner scale of the involucrum (mm) | QC | Calliper |
| 6. LENG_INNER_SPI_BRACLE | Length of the bracteole of an inner spikelet (mm) | QC | Calliper |
| 7. LENG_INNER_SPI_BRACT | Length of the bract of an inner spikelet (mm) | QC | Calliper |
| 8. LENG_INTER_SCAL | Length of the intermediate scale of the involucrum (mm) | QC | Calliper |
| 9. LENG_OUT_SCAL | Length of the outer scale of the involucrum (mm) | QC | Calliper |
| 10. LENG_OUTER_SPI_BRACLE | Length of the bracteole of an outer spikelet (mm) | QC | Calliper |
| 11. LENG_OUTER_SPI_BRACT | Length of the bract of an outer spikelet (mm) | QC | Calliper |
| 12. LENG_SUM_LEAF | Length of the summer leaf (mm) | QC | Ruler |
| 13. LIMB_LENG | Length of the limb (mm) | QC | Fiji (ImageJ) |
| 14. N_SCALES | Number of scales that form the involucrum | QD | – |
| 15. N_SUM_VEINS | Number of summer leaf veins with sclerenchyma in cross-section | QD | Microscope |
| 16. SCA_DIAM | Diameter of the scape at 1 cm from the base (mm) | QC | Calliper |
| 17. SCA_LENG | Length of the scape (mm) | QC | Ruler |
| 18. SCAP_NUM | Number of scapes | QD | – |
| 19. SHEATH_LENG | Length of the sheath (mm) | QC | Calliper |
| 20. WIDTH_CAL_TUBE | Width below the limb of the calyx tube (mm) | QC | Fiji (ImageJ) |
| 21. WIDTH_IAL_SUM | Width of the summer leaf hyaline margin (mm) | QC | Microscope |
| 22. WIDTH_INNER_SCAL | Width of the inner scale of the involucrum (mm) | QC | Calliper |
| 23. WIDTH_INNER_SPI_ BRACT | Width of the bract of an inner spikelet (mm) | QC | Calliper |
| 24. WIDTH_INNER_SPI_BRACLE | Width of the bracteole of an inner spikelet (mm) | QC | Calliper |
| 25. WIDTH_INTER_SCAL | Width of the intermediate scale of the involucrum (mm) | QC | Calliper |
| 26. WIDTH_OUT_SCAL | Width of the outer scale of the involucrum (mm) | QC | Calliper |
| 27. WIDTH_OUTER_SPI_ BRACT | Width of the bract of an outer spikelet (mm) | QC | Calliper |
| 28. WIDTH_OUTER_SPI_BRATLE | Width of the bracteole of an outer spikelet (mm) | QC | Calliper |
| 29. WIDTH_SUM_LEAF | Width in the middle of the summer leaf (mm) | QC | Calliper |
| 30. VEINS_HAIRS | Presence or absence of hairs underneath the leaves (YES/NO) | BI | – |
| 31. DIMORP | Presence or absence of dimorphic leaves (YES/NO) | BI | – |
| 32. WAVY | Presence or absence of denticulate leaves margin (YES/NO) | BI | – |
| 33. MAR_SUM_LEAF | Type of hyaline margin (smooth/denticulate) | BI | – |
| 34. COL_PET | Petal colour (PINK/WHITE) | BI | – |

BI = Binary; QC = quantitative continuous; QD = quantitative discrete. Fiji = the improved version of ImageJ.



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**Seed morphometry. —** Seeds were collected in the late season from the studied populations (Fig. 2, Appendix 1), then cleaned, selected and prepared for image analysis at both the Germplasm Bank in Pisa and the Sardinian Germplasm Bank (BG-SAR) in Cagliari, Italy, following established international protocols to reduce internal moisture content to 3%–5%, ensuring uniformity in seed size and weight and enabling effective long-term storage (Bacchetta & al., 2006). Digital images of seeds for each population were captured using a flatbed scanner (Epson Perfection V550 photo) at a resolution of 1200 dpi. Seeds were randomly arranged on the scanner tray without touching each other, using a light blue background to prevent environmental light interference. Images were processed with the software package ImageJ v.1.53v, and the Particles8 plugin was employed to measure 9 raw and 16 derived morphometric variables (suppl. Table S1). For a graphical representation of the seed morphometric variables, see De Giorgi & al. (2022: fig. S1). Overall, the raw data matrix comprised 2066 seeds with 26 variables. Initially, outliers potentially caused by scanning errors, were removed using the IQR method when values were greater than four times the IQR. This is justified given the fact that aborted seeds or error in the measurements may be present and must be removed. The final number of seeds used in the analyses are presented in Table S2. The conversion of Feret and Breadth (suppl. Tables S2, S3) from pixels to millimetres was achieved by dividing by a factor of 47 pixels per millimetre, then we followed the same statistical framework applied to plant morphometry. Three-dimensional seed volume was estimated from the two-dimensional morphometric data by modelling seeds as surfaces of revolution generated by circular arcs. The mean Feret diameter (length) and Breadth (maximum width) were used to parameterize a fusiform geometry, with seed volume calculated via numerical integration of the cross-sectional area along the longitudinal axis using R and the pracma v.2.4.4 package (Borchers, 2023).

**Karyology. —** Based on the protocol reported by Tiburtini & al. (2022), at least four metaphase plates for each population were selected and measured. To avoid possible artefacts induced by different observers (Peruzzi & al., 2024), all the chromosome measurements were collected by the first author. Chromosome number and karyological indices follow Peruzzi & Eroglu (2013). The following parameters were obtained from each plate using MATO v.4.2 (Liu & al., 2023) run on macOS: THL (total haploid length), $M_{CA}$ (mean centromeric asymmetry), $CV_{CL}$ (coefficient of variation of chromosome length), and $CV_{CI}$ (coefficient of variation of the centromeric index) (suppl. Table S4). Data engineering was carried out using the tidyverse metapackage v.2.0.0 (Wickham & al., 2019) and related styling functions. Finally, the games_howell_test from the rstatix v.0.7.2 package (Kassambara, 2023) was employed alongside the capabilities of the tidyverse functions to conduct population-pairwise comparisons of the four karyological indices for a total of 684 comparisons. To minimize the false discovery rate resulting from multiple comparisons, the built-in Tukey's method was applied. Results were considered significantly different when $\alpha < 0.01$ and noteworthy when $\alpha < 0.05$. Clustering was archived by fitting an unsupervised GMM through the mClust function (Scrucca & al., 2016) with default hyperparameters.

**Data integration. —** Lastly, data were integrated using LIMES (Lineage Identification and MEtadata-driven Species delimitation) (Ducasse & al., 2020) – as part of iTaxotools software for integrative taxonomy (Vences & al., 2021) – to produce species partition and display the species delimitation results from each line of evidence (ITS, cpDNA, seed and plant morphometrics). LIMES is a bioinformatic tool designed to qualitatively compare species partitions derived from various species delimitation methods, regardless of their theoretical frameworks or the presence of a reference topology (Ducasse & al., 2020). Partitions for genetic data were directly imported from ASAP as spart file, whereas morphological partitions were manually assembled and loaded into LIMES as csv.

**Identification key construction. —** We trained a machine learning supervised decision tree-based model to aid the construction of the identification key for the best-fitting species circumscription. This process was carried out in two main stages. First, we employed the recursive partitioning and regression trees (rpart) algorithm of the rpart v.4.1.23 R package (Therneau & al., 2012) or randomForest v.4.7-1.2 (Breiman & Cutler, 2022) to determine the optimal split values for structuring the identification key. This step ensured that the decision trees effectively select the threshold value that reduces the incorrect identification. In the second stage, we utilized the Boruta algorithm (Kursa & Rudnicki, 2010) with 1000 runs of importance source for resolving attributes left "Tentative" and ranking the best features. Boruta is a feature selection method, to identify and confirm the most relevant and significant variables that contribute to accurate species identification on morphology. Both quantitative and qualitative summary statistics of variables are reported in suppl. Tables S5, S6, and S7.

## ■ RESULTS

**Molecular systematics. —** The ITS matrix had a consensus length of 806 characters, while the plastid DNA dataset comprised 1557 characters (*trnF-trnL*: 311; *trnH-psbA*: 322; *trnL-rpl32*: 573; *trnQ-rps16*: 351), with the nuclear marker (ITS) showing only 14 phylogenetically informative positions (1.74%), and the plastid sequences having a total of 45 informative sites (2.89%), distributed as follows: *trnF-trnL*: 7; *trnH-psbA*: 10; *trnL-rpl32*: 21; *trnQ-rps16*: 7.

Both trees (Figs. 3, 4) are largely unresolved and depict different evolutionary histories. The nuclear tree (Fig. 3) shows few, rather robust clades: the ingroup includes a clade (posterior probability [pp] = 1.00) encompassing a collapse of all the individuals of *Armeria canescens* from the two populations (MK, RG*) under investigation and an inner group



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(pp = 1.00) with all the individuals from the three populations of *A. denticulata* (BP*, PP, MF). Within this latter monophyletic unit, the individuals from Brina di Ponzano (BP*), in turn, form a clade (pp = 1.00). All the other individuals fall into a different group (pp = 1), within which few subgroups can be distinguished. Specifically, the individuals of *A. brutia* (pp = 0.94) (SM*), two individuals of *A. gracilis* subsp. *gracilis* from Vado di Corno (VC) (pp = 0.99), as well as the individuals from Mt. Cucco (SI), *A. gracilis* subsp. *majellensis* from Mt. Meta (CA), and *A. saviana* from Piano dell'Olmo (ST) (pp = 0.99), all cluster within the same broader clade of central Italian taxa. These do not represent independent lineages, but rather weakly structured clusters within the unresolved backbone of *A. gracilis* sensu lato.

The plastid DNA tree (Fig. 4) is slightly more resolved than the ITS phylogram (Fig. 3). However, it shows a strong geographical signal in the phylogenetic reconstruction, providing a nuanced phylogenetic reconstruction. As an example, *Armeria aspromontana* (AS*), *A. garganica* (SL*), and *A. macropoda* (SE) form a clade (pp = 0.95), whereas individuals of *A. gracilis* from Montevergine (MV) and of *A. macropoda* from Mt. Terminio (MT*) (both localities are in nearby mountain areas in Campania) are included in different clades with high support (pp = 1.00). Overall, the tree shows several polytomies, but some pattern emerges.

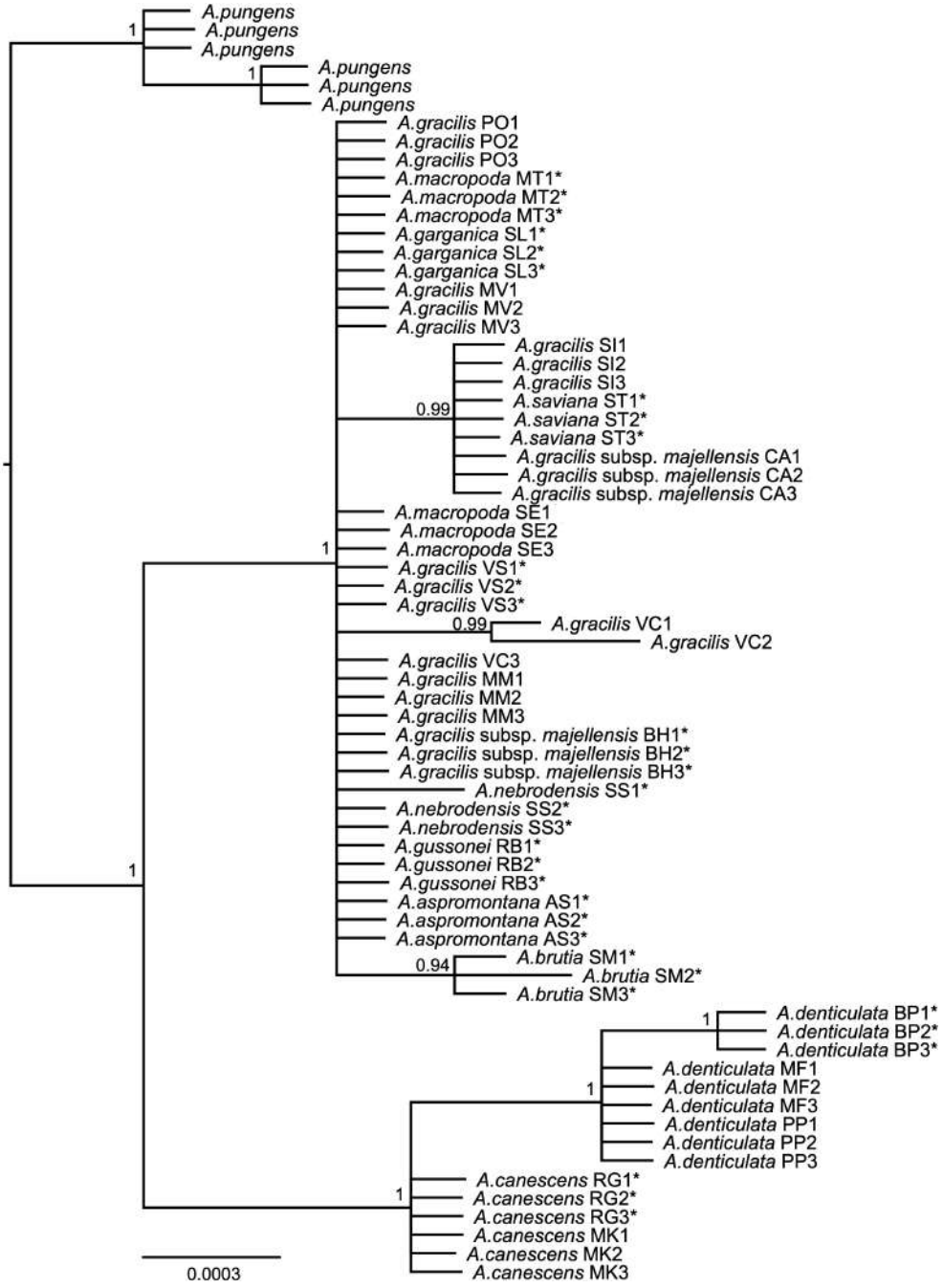


**Fig. 3.** Bayesian phylogenetic tree of Italian peninsular and Sicilian *Armeria* taxa based on the nuclear ITS dataset. Population acronyms as in Fig. 2 and Appendix 1. Asterisks indicate populations from type localities. Numbers at nodes indicate posterior probability. *Armeria pungens* used as outgroup.



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Species delimitation in ASAP, based on the concatenated population-wise consensus cpDNA, identified nine distinct genetic partitions, obtaining an asap score of 6.50 and a threshold distance of $1.696 \times 10^{-3}$ whereas for the ITS, the asap score was 2.50 with five partitions and a threshold distance of $6.21 \times 10^{-4}$.

**Pollen-stigma dimorphism in *Armeria aspromontana* and *A. nebrodensis*. —** In *Armeria aspromontana*, a total of two type-A pollen grains and six type-B pollen grains were found. In contrast, in *A. nebrodensis*, four pollen grains of each type were identified. All of them were found fully formed. The test yielded a chi-square value of 1.0667 with a $p = 0.6332$. Thus, the result was not statistically significant, suggesting that there is no significant difference in the distribution of pollen grain morphs between *A. aspromontana* and *A. nebrodensis*. As expected, the two style morphs were observed (COB-type / PAP-type) always associated with their respective pollen type.

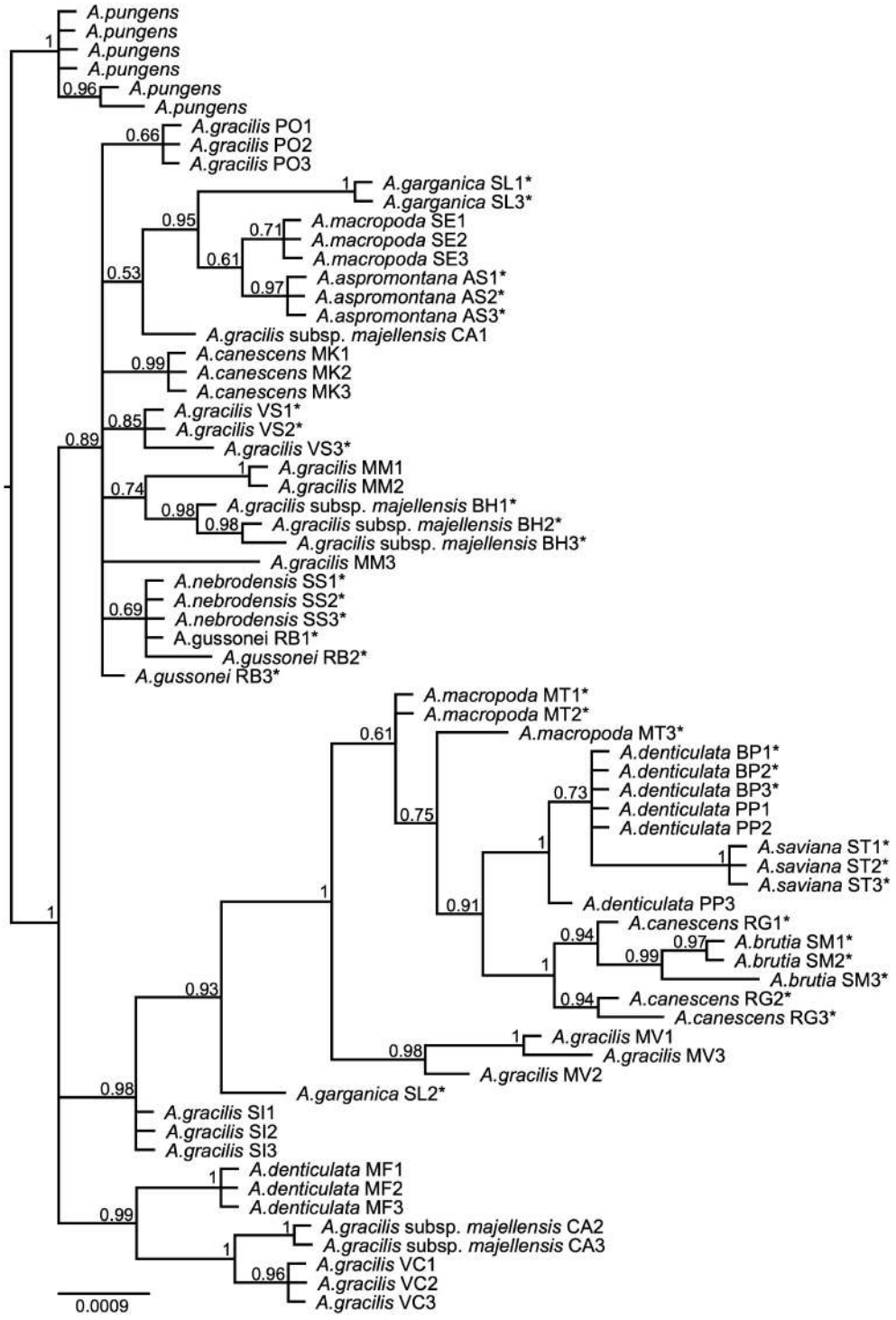


**Fig. 4.** Bayesian phylogenetic tree of Italian peninsular and Sicilian *Armeria* taxa based on the concatenated dataset of the plastid markers (*trnF-trnL*, *trnH-psbA*, *trnL-rpl32*, *trnQ-rps16*). Population acronyms as in Fig. 2 and Appendix 1. Asterisks indicate populations from type localities. Numbers at nodes indicate posterior probability. *Armeria pungens* used as outgroup.



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**Plant morphometry. —** The PCA biplot (Fig. 5) provides a graphical representation of the morphological variation among different species of *Armeria*. The first two principal components explain 35.8% of the total variance, with PC1 accounting for 22.1% and PC2 for 13.7% of the variance. Most of the reproductive characters are strongly correlated with the first principal component. Overall, floral morphological traits are the primary drivers of variation among *Armeria* species, particularly size-related traits such as scape length (SCA_LENG), pseudocapitulum diameter (DIAM_CAP), and bracts and scales length and width. Two distinct groups of species can be observed along PC1: those with larger, more developed reproductive structures (PCA scores >0), and those with smaller (PCA scores <0), less pronounced features. In particular, *A. denticulata* shows the smallest pseudocapitula, whereas *A. gussonei* has the widest, as well as *A. macropoda* from the type locality (MT*). The two other populations currently referred to this latter taxon are far apart in the ordination, with SE placed closer to other species and sharing much shorter leaves than MT*. Interestingly, the MT* population shows overall large sizes in morphological features with *A. garganica* (SL*) as the least distant population. The type localities of the two subspecies currently recognised under *A. gracilis* (VS*, BH*) appear morphologically close and both show overall intermediate traits. The two Sicilian endemic taxa, in contrast, are positioned in different regions of the biplot. *Armeria nebrodensis* (SS*) is located on the negative end of the size-related variables, including scape length (ca. 16 cm on average; see suppl. Tables S5 and S6). In contrast, *A. aspromontana* and *A. brutia* are positioned far from *A. nebrodensis* and are characterised by relatively smaller floral and bract structures compared to *A. gussonei*.

The third principal component raises the total explained variance to 47.6% (suppl. Fig. S1). As expected, *Armeria denticulata* is further separated due to its markedly elongated outer bracts, which average 10 mm in length – almost twice the average of *A. gracilis* (VS*, BH*), which shows an average length around 5.5 mm. The broadest leaves are observed in *A. gussonei* (RB*) (3.98 ± 0.97 mm) and *A. macropoda* (from type locality MT*) (3.53 ± 2.02 mm), while *A. garganica* (SL*) exhibits the longest calyx limbs (3.46 ± 0.51 mm) compared to the other taxa. The UMAP results are presented in suppl. Fig. S2 and provide more insights on the clustering structure of the morphometric data. The

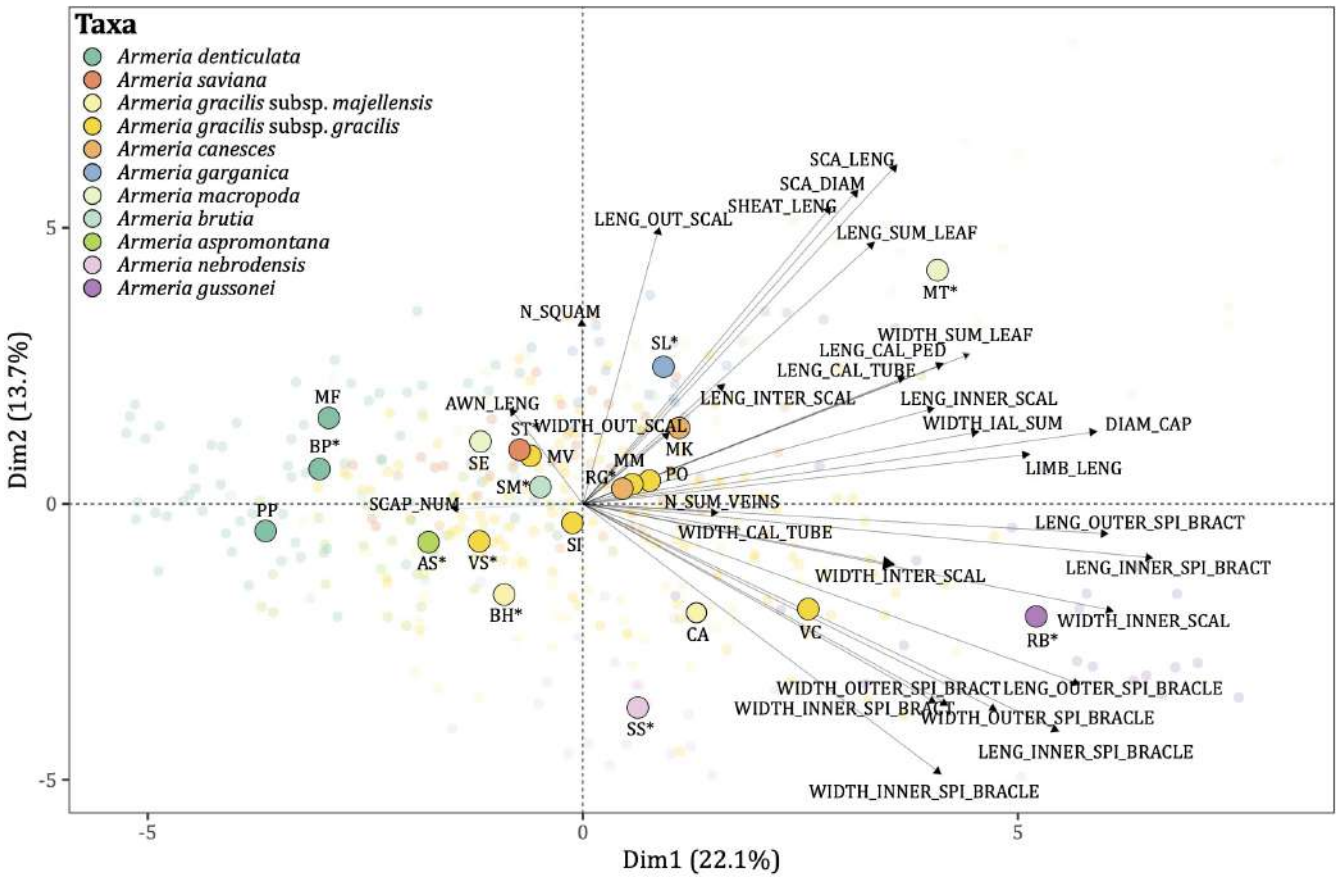


**Fig. 5.** PCA biplot of the first and second axes based on the plant morphometric matrix for Italian peninsular and Sicilian *Armeria* taxa, displaying the 15 most important morphometric variables. Points are coloured by taxon according to the current taxonomic hypothesis proposed by Arrigoni (2015). Population acronyms are placed closer to the sample centroids of each population. Population acronyms as in Fig. 2 and Appendix 1. Asterisks indicate populations from type localities. Character acronyms as in Table 1.



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lumping-splitting algorithm applied to the morphometric dataset supported a five-cluster solution. This configuration grouped together all the populations from the southernmost part of peninsular Italy (AS*, PO, SM*) and retained two distinct clusters comprising all the "graciloid" populations: the first including BH*, MV, SI, SE, MT*, and SL*; the second composed of CA, VC, MK, RG*, MM, and VS*. These were kept separate from the *A. denticulata* complex as a whole (BP*, PP, ST*, MF) and from a fifth group uniting the two Sicilian endemics (RB*, SS*). The log-likelihood of this solution is −15,262.38, with a BIC of −34,505.83. For comparison, the current taxonomic hypothesis resulted in a higher BIC of −39,616 and a log-likelihood of −16,627.

**Seed morphometry. —** Seeds exhibit a fusiform morphology, with mean length of 2.48 mm, mean width of 1.01 mm, and a mean seed volume of 1.11 $mm^3$.

The first two principal components account for 80% of the total variance. The PCA biplot (Fig. 6) reveals three main groups of correlated morphometric variables: size-related traits (Area, Perimeter, Feret, etc.), shape compactness traits (Circularity, Roundness, Sphericity, etc.), and elongation/irregularity traits (AspRatio, Shape, Concavity). Based on seeds, *Armeria aspromontana* and the MF and BP populations of *A. denticulata* have slightly higher compactness values, indicating that their seeds are more circular or square-like. A low compactness value suggests that the seed is more elongated or irregularly shaped, with a large Feret dimension compared to its area. Conversely, the Shape variable (that is Perimeter$^2$ / Area, see suppl. Table S1 for all the definitions) is negatively correlated with compactness and its influence is positioned at the opposite side on the PCA biplot. Higher values of "Shape" indicate seeds that are more elongated or have a more irregular outline.

Species or populations that align with the Shape vector (e.g., VS*, CA) tend to have seeds that are less compact, with a greater perimeter relative to their area, suggesting an elongated form. Lastly, "graciloid" plants (i.e., *Armeria gracilis* subsp. *gracilis*, *A. gracilis* subsp. *majellensis*, and *A. canescens* from Croatia) consistently show positive values on the first axis and they are correlated with higher values of Feret, Breadth, ArBBox, and Area indicating bigger seeds, with some population exhibiting markedly elongated seeds (BH*, SI), in contrast to the more compact seeds observed in other groups (e.g., *A. denticulata*), consistently having

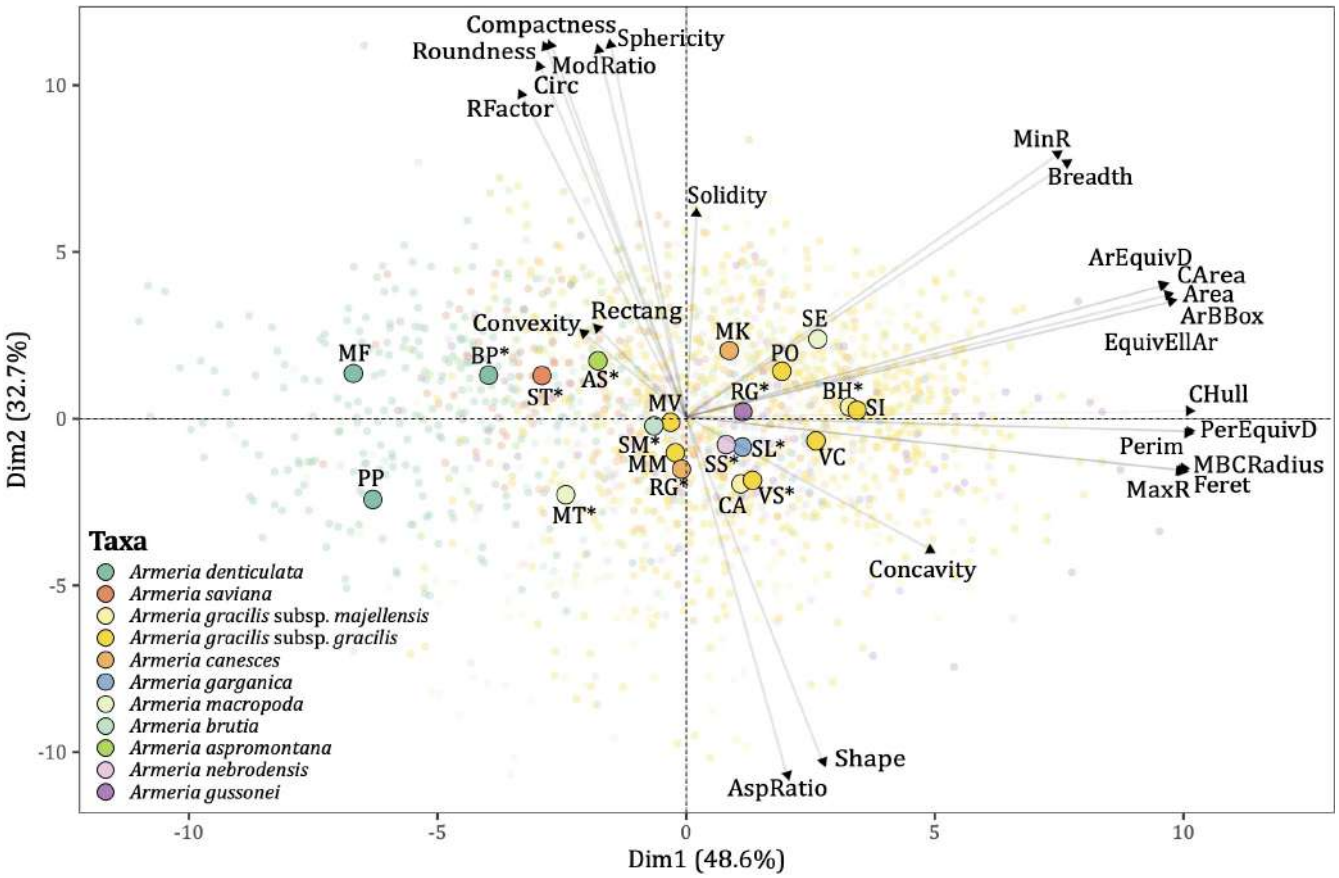


**Fig. 6.** PCA biplot of the first and second axes based on the seed morphometric matrix for Italian peninsular and Sicilian *Armeria* taxa. Points are coloured by taxon according to the current taxonomic hypothesis proposed by Arrigoni (2015). Population acronyms are placed closer to the sample centroids of each population. Population acronyms as in Fig. 2 and Appendix 1. Asterisks indicate populations from type localities. Character acronyms as in Table 1.



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negative values along PC1. Indeed, seeds from BH* and SI are, on average, approximatively 2.75 mm long, whereas those from MF and PP are on average 2 mm long (suppl. Table S2). Lastly, the SE population shows the seeds with largest width (1.13 mm). Conversely, *A. macropoda* (MT*) shows the thinnest seeds (0.90 mm). The lumping-splitting algorithm on the raw variables shows a BIC of −49,800 and indicates that 5 clusters can be recognised (AS*-MT*-VS* | BH*-SI-MV-SM*-SL*-SS* | BP*-ST*-MF-PP | CA-RB*-MM | MK-VC-PO-RG*-SE) even though neither geographical nor ecological structure emerges. The log-likelihood (lnL) of the model is −23,865.46 and the obtained value represents the best clustering solution for such data.

**Karyology. —** All the populations investigated confirmed to have $2n = 2x = 18$ chromosomes, with mostly median (54.1%), submedian (45.14%) or rarely subterminal (0.76%) centromeres (suppl. Figs. S3, S4; suppl. Table S4).

Secondary constrictions were rarely observed and, when detectable, were localized on the short arms. The average chromosome length is 4.69 ± 0.79 µm. Unfortunately, VS* and MV seeds did not germinate making impossible retrieving karyological information for these two populations. Pairwise Games-Howell tests revealed almost no significant differences for the four considered karyological parameters among the populations, except for a few cases. A significant difference was observed between AS* and SS* for the THL variable ($p < 0.001$). Slightly significant differences were found between MF and PO ($p = 0.03$) and MF and ST* for $CV_{CL}$ ($p \approx 0.04$), whereas $CV_{CI}$ slightly differed between AS* and VC ($p \approx 0.02$). The $M_{CA}$–$CV_{CL}$ scatterplot (Fig. 7) illustrates the relationship between intrachromosomal ($M_{CA}$) and interchromosomal ($CV_{CL}$) asymmetry across taxa, revealing a continuous pattern of karyotype variation without clear clustering, although some populations (e.g., BP, SL, RB*) occupy a more distinct peripheral position, indicating lower intrachromosomal and higher interchromosomal asymmetry.

Overall, no substantial differences were found, since a single multivariate Gaussian distribution adequately fits the data (Equal volume, Equal shape, Equal orientation [EEE], BIC = −2481.9), meaning the populations are considered homogeneous with no distinct subgroups or clusters.

**Data integration. —** The ITS and cpDNA data show a marked disagreement regarding the number of species inferred by ASAP, with ITS suggesting five "species" and cpDNA suggesting nine. In contrast, morphological data (both seed and plant) generated by the lumping-splitting algorithm support the presence of five "morphospecies", although differently circumscribed (Table 2). Plant morphology groups the three populations AS*, SM*, and PO from the extreme south of peninsular Italy together, and within this morphological group *Armeria brutia* and the PO population are distinguished by both cpDNA and seed morphometric analyses. The *A. denticulata* complex, which includes *A. denticulata* and *A. saviana*, is consistently recognised as a distinct group

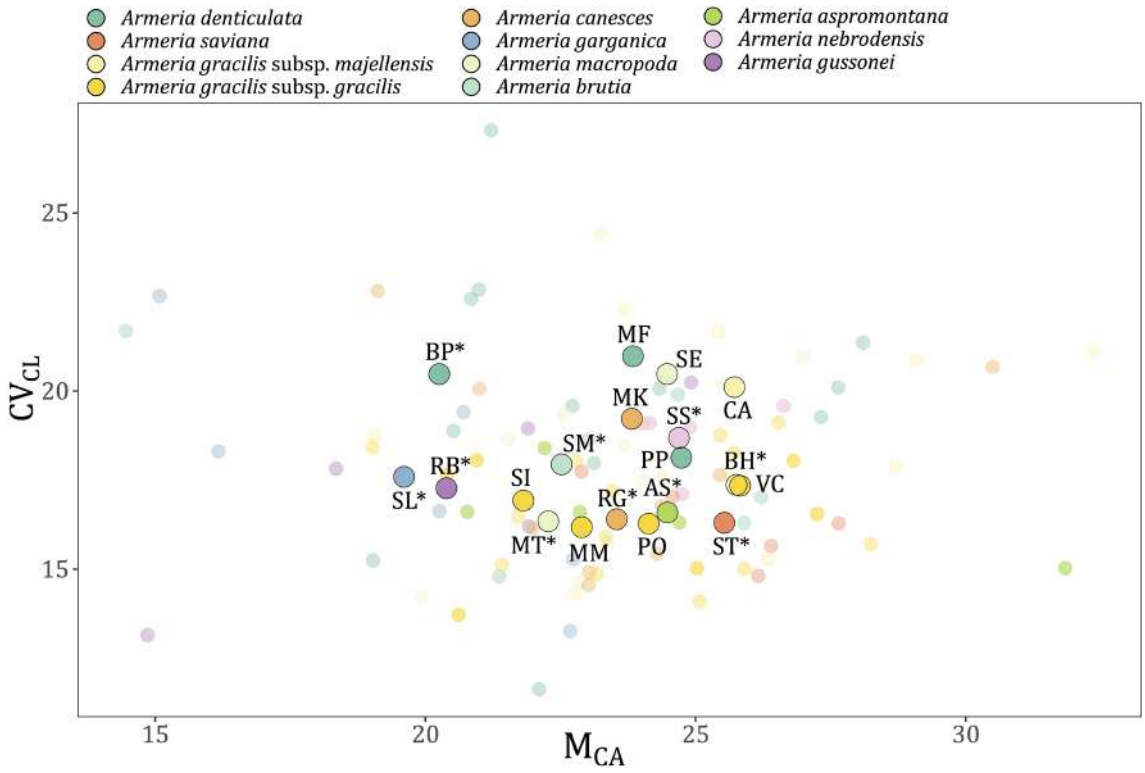


**Fig. 7.** Scatterplot of the two karyotype asymmetry indices $M_{CA}$ vs. $CV_{CL}$ for Italian peninsular and Sicilian *Armeria* taxa, according to the current taxonomic hypothesis. Population acronyms as in Fig. 2 and Appendix 1. Asterisks indicate populations from type localities.



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across multiple lines of evidence, while phylogenetic data reveal a finer structure supporting the independence of *A. saviana*. Sicilian taxa (*A. gussonei*, *A. nebrodensis*) are grouped together by plant morphometry, but *A. nebrodensis* is well distinct by seed data based on the lumping-splitting algorithm. *Armeria macropoda* is non-monophyletic in the cpDNA tree with its two populations placed in two distinct, divergent clades (i.e., each population exhibits a different cpDNA haplotype). Accordingly, the application of this name should be restricted to the population from the type locality. The cpDNA also supports the recognition of *A. garganica* as a distinct unit. Both populations of *A. canescens* from Croatia show ITS patterns that do not occur in the Italian peninsula, supporting their status as a species separate from *A. gracilis*, and the exclusion of *A. canescens* from the Italian flora. Lastly, the type localities (BH*, VS*) of the two subspecies under *A. gracilis* are genetically grouped as belonging to the same group based on both cpDNA and ITS. Interestingly, cpDNA reveals haplotype differentiation between northern (SI) and southern (MV) extremes of *A. gracilis* distribution (Fig. 4), but seed morphometry and plant morphology place these haplotypes in the same morpho-group. The overall pattern of variation in *A. gracilis* is fairly complex according to Table 2, but the existence of two subspecies within *A. gracilis* is not supported by our data. Karyotype analyses revealed a largely homogeneous structure among all studied populations, suggesting that karyotype data alone do not provide evidence for subdivision into multiple groups due to karyological stability of the genus *Armeria*.

Based on the above integration process, we can elaborate a taxonomic hypothesis with 11 taxa (10 from Italy plus the Balkan *Armeria canescens*), confirming most of the species

**Table 2.** Visualisation of the data integration process among the 5 different lines of evidence produced in this study for peninsular Italian and Sicilian *Armeria* taxa (plus the Croatian *A. canescens*).

| Pop. | PM | SM | cp | nr | K | IH | NT | AH |
|---|---|---|---|---|---|---|---|---|
| AS* | 1 | 1 | 1 | 1 | 1 | 1;1;1;1;1 | *A. aspromontana* | *A. aspromontana* |
| SM* | 1 | 2 | 2 | 1 | 1 | 1;2;2;1;1 | *A. brutia* | *A. brutia* |
| MK | 2 | 5 | 1 | 2 | 1 | 2;5;(1,2);2;1 | *A. canescens* | *A. canescens* |
| RG* | 2 | 5 | 2 | 2 | 1 | | *A. canescens* | *A. canescens* |
| BP* | 3 | 3 | 3 | 3 | 1 | 3;3;(3,4);(3,4);1 | *A. denticulata* | *A. denticulata* |
| MF | 3 | 3 | 4 | 4 | 1 | | *A. denticulata* | *A. denticulata* |
| PP | 3 | 3 | 3 | 4 | 1 | | *A. denticulata* | *A. denticulata* |
| SE | 4 | 5 | 1 | 1 | 1 | 4;(2,5);(1,5);1;1 | *A. garganica* | *A. macropoda* |
| SL* | 4 | 2 | 5 | 1 | 1 | | *A. garganica* | *A. garganica* |
| BH* | 4 | 2 | 1 | 1 | 1 | (2,4);(1,2,4,5);(1,6,7);(1,5);1 | *A. gracilis* | *A. majellensis* |
| CA | 2 | 4 | 1 | 5 | 1 | | *A. gracilis* | *A. majellensis* |
| MM | 2 | 4 | 1 | 1 | 1 | | *A. gracilis* | *A. gracilis* |
| MV | 4 | 2 | 6 | 1 | 1 | | *A. gracilis* | *A. gracilis* |
| SI | 4 | 2 | 7 | 5 | 1 | | *A. gracilis* | *A. gracilis* |
| VC | 2 | 5 | 1 | 1 | 1 | | *A. gracilis* | *A. gracilis* |
| VS* | 2 | 1 | 1 | 1 | 1 | | *A. gracilis* | *A. gracilis* |
| RB* | 5 | 4 | 1 | 1 | 1 | 5;4;1;1;1 | *A. gussonei* | *A. gussonei* |
| MT* | 4 | 1 | 8 | 1 | 1 | 4;1;8;1;1 | *A. macropoda* | *A. macropoda* |
| SS* | 5 | 2 | 1 | 1 | 1 | 5;2;1;1;1 | *A. nebrodensis* | *A. nebrodensis* |
| PO* | 1 | 5 | 1 | 1 | 1 | 1;5;1;1;1 | *A. pollinensis* | *A. gracilis* |
| ST* | 3 | 3 | 9 | 5 | 1 | 3;3;9;5;1 | *A. saviana* | *A. saviana* |
| | 5 | 5 | 9 | 5 | 1 | 11 | 11 | 11 |

Pop. = Population; PM = Plant morphology; SM = Seed morphology; cp = cpDNA; nr = ITS; K = Karyology; IH = Integration hypothesis; NT = Taxon attribution in this study; AH = Arrigoni (2015) hypothesis.
Different shades of colour indicate different partitions suggested by each single line of evidence. Row-wise identical colour/number does not indicate that the populations belong to the same partition: they have to be read only vertically. The column "Integration hypothesis" summarizes the different lines of evidence, adopting the numbers used in the previous columns and following the same order from left to right, each separated by a semicolon. It highlights the unicity of each species as defined by the integration of the data, as well as – in brackets – the internal variability of species such as *A. canescens* (cpDNA), *A. denticulata* (cpDNA and ITS), *A. garganica* (seed morphometry and cpDNA), *A. gracilis* (all the lines of evidence with the exception of karyology). Asterisks indicate populations from type localities.



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according to the current taxonomic hypothesis with three major exceptions: the synonymisation of the two subspecies of *A. gracilis*, the separation of the population from Mt. Pollino as a distinct species, and a new circumscription of *A. garganica* with respect to *A. macropoda*. Since morphological diagnosability is essential for species identification, we then tested the new scenario on morphological data and compared it with the current species circumscription. The first model fit, named "current taxonomic hypothesis", strictly adheres to the species circumscription proposed by Arrigoni (2015), by recognising 11 taxa distributed as follows: *A. denticulata* (BP*, MF, PP) and *A. saviana* (ST*) within the *A. denticulata* complex; *A. macropoda* broadly circumscribed as including SE and MT* regions; *A. canescens* from Croatia (MK, RG*); *A. gracilis* split into the two subspecies *A. gracilis* subsp. *majellensis* (BH*, CA) and *A. gracilis* subsp. *gracilis* (VS*, SU, SI, MM, MV, VC, PO); *A. garganica* (SL*) restricted to Puglia. The second model fit, named "alternative taxonomic hypothesis" emerged by the integration process and introduces the idea of considering the PO population as a distinct species named *A. pollinensis* comb. & stat. nov., not recognising instead the subspecies within *A. gracilis*. The independence of *A. canescens* (restricted to the Balkans), *A. denticulata*, *A. gussonei*, *A. nebrodensis*, and *A. saviana* is retained, in line with current taxonomic understanding. In contrast, the application of the name *A. macropoda* is here limited to its type locality (MT*), while *A. garganica* is expanded to include the SE population, previously referred to *A. macropoda*. The results of this comparison are presented in Tables 3 and 4.

The results indicate that the current species circumscription is less supported by the data than the new alternative taxonomic hypothesis, that is more in line with the newly produced data. Given the importance of morphology for species identification, an admixture analysis was performed on the morphometric data to validate the findings. This analysis reveals an overall low level of plant morphological admixture among species under the newly proposed taxonomic framework. No admixture is detected in *Armeria canescens*, *A. nebrodensis* (Fig. 8), *A. denticulata* (particularly from its

**Table 3.** Plant morphometric species circumscription based on the newly proposed alternative integrated taxonomic hypothesis against the current taxonomic hypothesis proposed by Arrigoni (2015).

| Hypothesis | Taxonomic grouping | K | BIC | ΔBIC | BFs | Prior Mod | Post Mod |
|---|---|---|---|---|---|---|---|
| Newly proposed | ASPRO \| BRUTIA \| CANE \| DENT \| GARG2 \| GRAC \| GUSS \| MACRO2 \| NEBRO \| POLLINO \| SAVI | 11 | −37,259.07 | 0 | 1 | 0.5 | 1 |
| Current | ASPRO \| BRUTIA \| CANE \| DENT \| GARG1 \| GRAC_GRAC \| GRAC_MAJE \| GUSS \| MACRO1 \| NEBRO \| SAVI | 11 | −37,848.63 | 589.56 | ≈0 | 0.5 | ≈0 |

Models are sorted in decreasing order (the first is the better) based on Bayesian posterior model probabilities (PostMod) assuming equal priors (PriorMod) among models. K indicates the number of taxa, BIC (Bayesian information criterion) measures the model fit while penalizing model complexity; ΔBIC is the difference in BIC relative to the best model; BFs (Bayes factors) express the relative support for each model compared to the best model calculated as BF = exp(ΔBIC/2), with values close to 0 indicating negligible support relative to the best model. Vertical lines (|) indicate species boundaries.
ASPRO = *A. aspromontana*; BRUTIA = *A. brutia*; CANE = *A. canescens*; DENT = *A. denticulata*; GARG1 = *A. garganica* (restricted to SL); GARG2 = *A. garganica* (including SE); GRAC = *A. gracilis* (no subspecies); GRAC_GRAC = *A. gracilis* subsp. *gracilis*; GRAC_MAJE = *A. gracilis* subsp. *majellensis*; GUSS = *A. gussonei*; MACRO1 = *A. macropoda* (including SE); MACRO2 = *A. macropoda* (only type locality); NEBRO = *A. nebrodensis*; POLLINO = PO population; SAVI = *A. saviana*.

**Table 4.** Seed morphometric species circumscription based on two different models for delimiting *Armeria* based on seed features. In total, two taxonomic hypotheses were tested.

| Hypothesis | Taxonomic grouping | K | BIC | ΔBIC | BFs | Prior Mod | Post Mod |
|---|---|---|---|---|---|---|---|
| Newly proposed | ASPRO \| BRUTIA \| CANE \| DENT \| GARG2 \| GRAC \| GUSS \| MACRO2 \| NEBRO \| POLLINO \| SAVI | 11 | −52,301.14 | 0 | 1 | 0.5 | 1 |
| Current | ASPRO \| BRUTIA \| CANE \| DENT \| GARG1 \| GRAC_GRAC \| GRAC_MAJE \| GUSS \| MACRO1 \| NEBRO \| SAVI | 11 | −52,735.64 | 434.51 | | 0.5 | ≈0 |

Models are sorted in decreasing order (the first is the better) based on Bayesian posterior model probabilities (PostMod) assuming equal priors (PriorMod) among models. K indicates the number of taxa, BIC (Bayesian information criterion) measures the model fit while penalizing model complexity; ΔBIC is the difference in BIC relative to the best model; BFs (Bayes factors) express the relative support for each model compared to the best model calculated as BF = exp(ΔBIC/2), with values close to 0 indicating negligible support relative to the best model. Vertical lines (|) indicate species boundaries.
ASPRO = *A. aspromontana*; BRUTIA = *A. brutia*; CANE = *A. canescens*; DENT = *A. denticulata*; GARG1 = *A. garganica* (restricted to SL); GARG2 = *A. garganica* (including SE); GRAC = *A. gracilis* (no subspecies); GRAC_GRAC = *A. gracilis* subsp. *gracilis*; GRAC_MAJE = *A. gracilis* subsp. *majellensis*; GUSS = *A. gussonei*; MACRO1 = *A. macropoda* (including SE); MACRO2 = *A. macropoda* (only type locality); NEBRO = *A. nebrodensis*; POLLINO = PO population; SAVI = *A. saviana*.



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type locality), or in the central Italian populations of *A. gracilis*. In contrast, southern Italian populations show higher levels of admixture, especially between *A. gracilis* and *A. garganica*.

The analysis also indicates minimal admixture in *Armeria macropoda* from the type locality, further supporting its independence. This pattern of low admixture is also observed in the three taxa from the extreme south of the Italian peninsula (*A. aspromontana*, *A. brutia*, *A. pollinensis*). In particular, the low level of admixture reinforces the status of the population from the Pollino Massif as an independent species. As shown in suppl. Table S5, the PO population shows larger inner scales (the bracts that subtend the inflorescence) compared to *A. aspromontana* (AS*) and *A. brutia* (SM*), along with longer leaves and a generally larger plant size. Both Sicilian endemic taxa also display low levels of admixture, supporting their distinction as separate species.

## ■ DISCUSSION

In this paper, we aimed to revise and update the peninsular Italian and Sicilian *Armeria* taxa using an integrative taxonomic approach (Dayrat, 2005) under the "consilience principle" derived from cpDNA and nrDNA phylogenies, as well as seed morphometric, plant morphometric and karyological lines of evidence. Starting from the phylogenetic data, the nrDNA tree exhibits a high level of polytomy, making the reconstruction of evolutionary history challenging and, overall, partially unresolved. This pattern agrees with previous studies on central Mediterranean *Armeria* from surrounding areas (Tiburtini & al., 2022, 2023) and at genus level (Fuertes Aguilar & Nieto Feliner, 2003). This is potentially due to a limited number of ITS polymorphic sites (14), which is likely the result of a combination of extensive gene flow, concerted evolution and geographical patterns of variation (Fuertes Aguilar & al., 1999; Nieto Feliner & al., 2001, 2004). As for the maternally inherited plastid DNA (Nieto Feliner & al., 2002), frequent haplotype sharing across species is common, particularly when populations of closely related species are geographically close and isolated from others (Gutierrez Larena & al., 2002), with a low-level genetic diversity ($G_{ST}$ = 0.43) of plastid markers, as found by Scassellati (2011). This explains why species delimitation based on ITS and cpDNA yields different results. Regardless, cpDNA data show unique values for both *A. saviana* (ST*) and *A. macropoda* (MT*), indicating no agreement between this marker and the other lines of evidence for these taxa, whereas

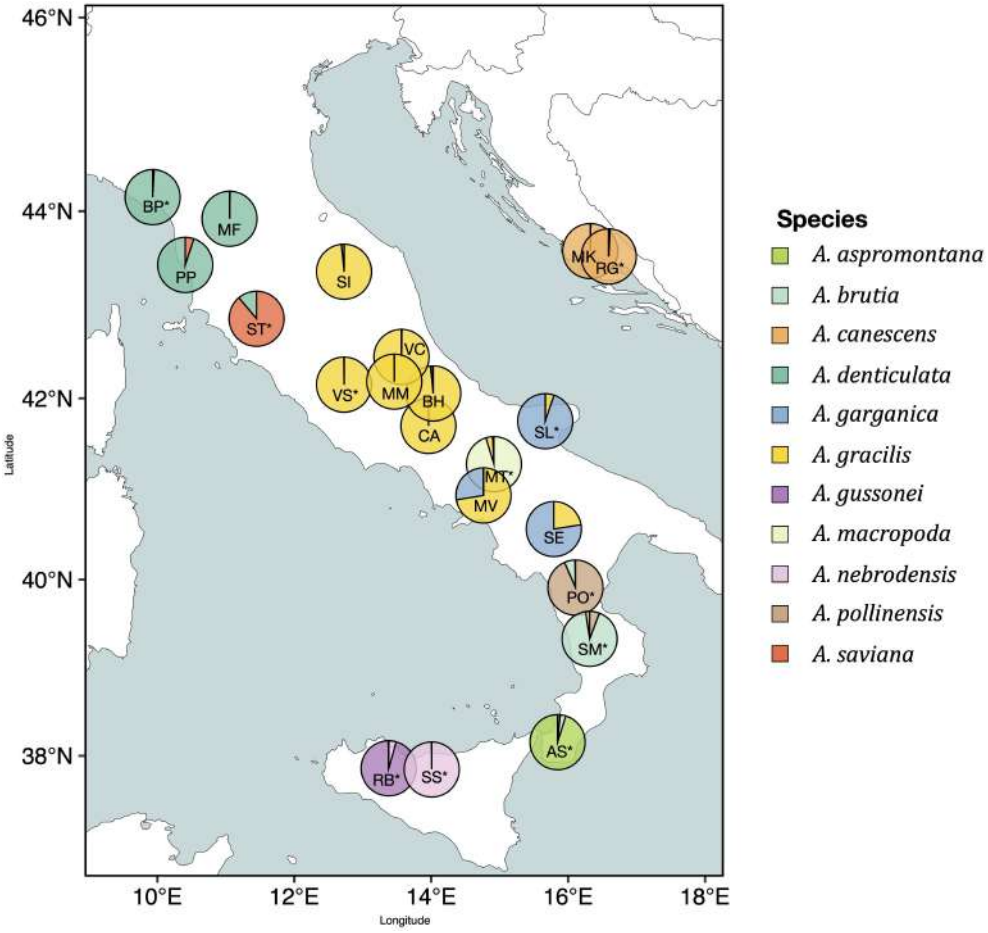


**Fig. 8.** Spatial morphometric admixture among the species according to the newly proposed taxonomic hypothesis for *Armeria*. Population acronyms as in Fig. 2 and Appendix 1. Asterisks indicate populations from type localities. The placement of some pie charts was slightly adjusted to avoid excessive overlap.



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ITS data exclusively place *A. canescens* (MK, RG*) in its own partition.

We refute the previously reported differences in pollen-stigma dimorphism between *Armeria nebrodensis* and *A. aspromontana* as described by Brullo & al. (1997). Additionally, our observations indicate that *A. nebrodensis* possesses inner scales measuring 7.53 ± 0.92 mm in length and 4.84 ± 0.77 mm in width, which contrasts with the earlier reported dimensions of 4–5 mm in length (Brullo & al., 1997).

Morphological data proved several times to be highly informative in *Armeria* (Nieto Feliner & al., 2001; Larena & al., 2004; Baumel & al., 2009; Villa-Machío & al., 2023).

The morphological variation in peninsular Italian and Sicilian *Armeria* is structured geographically and many narrowly distributed endemic taxa are supported by the new data produced in this study. The *Armeria denticulata* complex (Brullo & Guarino, 2017), composed by *A. denticulata* (MF-PP-BP*) and *A. saviana* (ST*), is consistently supported and retrieved by both runs of the lumping-splitting algorithm on seed and plant morphometry, and by phylogeny. Within *A. denticulata*, the MF population behaves oddly, especially in the cpDNA, that ASAP decided to split it into a single-standing taxon. This is only partially supported by morphological data, but there are insights that higher diversity of these populations could have originated through introgressive events with other taxa from northern Italy (Tiburtini & al., 2025b). The recently described *A. saviana* (Selvi, 2009) is supported as a distinct species, which, according to incongruences between cpDNA and ITS data, could be considered of homoploid hybrid origin between *A. denticulata* and *A. gracilis* (Tiburtini & al., 2025b). The most taxonomically relevant character is the width of the hyaline margin of the leaves, almost negligible in *A. denticulata*, but conspicuous in *A. saviana* and *A. gracilis* (suppl. Table S6, suppl. Fig. S6).

Both *Armeria saviana* and *A. denticulata* are easily recognisable based on the overall appearance, due to the high frequency of short, dentate (wavy) leaves (suppl. Table S7), the small pseudocapitula with long scales (see PCA in Fig. 5 and suppl. Fig. S1) and the habitat, with the former preferring jasper at high altitudes and the latter growing on serpentine substrates (Selvi, 2007, 2009). *Armeria canescens* and *A. gracilis*, not separated in the past (Scassellati & al., 2011, 2013), are instead confirmed in our study as distinct species, with the former not occurring in Italy. Following our revision, however, no subspecies can be recognised within *A. gracilis*, which contrasts with the opinion expressed by Arrigoni (2015). As such, here we consider *A. gracilis* subsp. *majellensis* as a heterotypic synonym of *A. gracilis*. On phylogenetic grounds, our study independently supports the findings of Scassellati (2011) about the ribotype and haplotype variation within *A. canescens* and its absence from Italy. Thus, we can conclude that *A. canescens* is a Balkan species (Mitić & Hruševar, 2015), occurring in Croatia (Milović & al., 2021), Serbia (Buzurović & al., 2015), Bosnia-Herzegovina (Mitić & Hruševar, 2015), Greece (Papanicolaou & Kokkini, 1982), Montenegro (pers. obs.), North Macedonia (PI!), and Albania (Fanelli & al., 2018). This species shows no close connection with the Italian endemic *A. gracilis*, to which all the previous records for Italy of *A. canescens* should be referred. It is noteworthy that some populations of *A. canescens* in Serbia occasionally act as serpentinophytes (Buzurović & al., 2015; Tomović & al., 2018), a feature not observed in the Italian *A. gracilis* populations.

*Armeria gracilis* can often show white flowers (suppl. Table S7). Completely white-flowered populations of *A. gracilis* have been observed in many localities of the Central Apennines (e.g., Monte San Vicino [PI!], Monte Castel Manardo [PI!], Campo Imperatore, etc.) but still expressing the overall features of this species. Hairiness at the base of the scapes was observed in a specimen from M. Carpegna (FI!) and in many plants of the VC population, and this character may occur scattered in other populations (Lefèbvre & Kakes, 1978; Richards & al., 1989).

The Apulian population of *Armeria* (SL*) is supported as an independent species, as hypothesized by Arrigoni (2015) when he described *A. garganica*. Indeed, both cpDNA and morphology (Figs. 4, 5, Table 2) support the independence of this species. Notably, one character that is difficult to measure, but was observed in this species, is the strongly campanulate – hawk-feet-like shape of the mature calyces. This feature is highly distinctive and is not observed in other taxa. A broader sampling effort is needed to clarify the precise distribution of this species, which, under our revised circumscription, now reaches the Basilicata region.

*Armeria macropoda* shows distinctive features that make this species easily recognisable among other plants of the Italian peninsula, particularly due to its large pseudocapitula, thick scapes and usually long leaves (Fig. 5, suppl. Fig. S6). The independence of this taxon is supported by both cpDNA and morphology (Figs. 4, 5, Table 2) in its type locality (MT*). On the contrary, the Serranetta population (SE) is better attributed to *A. garganica*, according to our results. A further population that fully pertains to *A. macropoda* occurs, at least, in the Monti Alburni, according to a herbarium specimen conserved in PI (PI066835). More in-depth herbarium revision is needed to update the distribution of this species, which is however seemingly limited to Campania. Interestingly, in southern Italy (Basilicata and surroundings) there is the highest degree of morphological admixture (Fig. 8), leaving space for further investigation. Regarding the populations from the extreme south of peninsular Italy (AS*-SM*-PO), these are kept separated by the lumping splitting algorithm on morphological grounds, and no admixture with other "graciloid" plants is observed, supporting the recognition of an *A. aspromontana* complex. Within this complex, we confirm the species level for the two taxa already described by Brullo & al. (1997, 2004), one endemic to Aspromonte (*A. aspromontana*) and one to Sila (*A. brutia*), as evidenced in Fig. 8. *Armeria brutia* is further supported by ASAP based on cpDNA (Table 2).

The PO population, so far classified as falling within the variability of either *Ameria canescens* (Scassellati



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& al., 2013) or *A. gracilis* (Arrigoni, 2015), displays distinct morphological traits (>13 scales, bracteoles >1.5 mm wide, calyx lobes >2.3 mm, see identification key) and shows almost no admixture with other taxa on morphological grounds. In Table 2, *A. pollinensis* is the only species combining plant morphology "1" (shared with *A. aspromontana* and *A. brutia*), seed morphology "5" (shared with *A. canescens* from Croatia, one *A. gracilis* population and the *A. garganica* from SE population), and cpDNA haplotype "1" simultaneously – a combination not observed in any other population. In addition, albeit with low support, *A. pollinensis* also forms a separate clade in the cpDNA analysis. Based on these findings, we propose elevating *Armeria gracilis* var. *pollinensis* N.Terracc., originally described by Terracciano (1891), to species rank, having *A. brutia* as the morphologically closest related taxon. The existence of an *Armeria* species endemic to the Pollino area is not particularly surprising on biogeographical grounds, given that these mountains are well known to host several narrow endemics also in other angiosperm genera, as for instance *Carduus affinis* subsp. *brutius* (Fiori) Kazmi (Peruzzi & al., 2015), *Cynanchica aristata* subsp. *calabra* (Fiori) P.Caputo & Del Guacchio (Del Guacchio & al., 2017), *Gagea peruzzii* J.-M.Tison (Tison & al., 2013), *Genista sericea* subsp. *pollinensis* F.Conti & al. (Conti & al., 2014), *Genista tenorei* G.Don (Peruzzi & al., 2017), *Linum katiae* Peruzzi (Peruzzi, 2011), *Plantago media* subsp. *brutia* (Ten.) Arcang. (Palermo & al., 2010), *Silene oenotriae* Brullo (Peruzzi & al., 2007), and *Taraxacum pollinense* Aquaro & al. (Aquaro & al., 2009).

For a long time, these southern peninsular populations were speculated to be closely related to *Ameria nebrodensis* by Boissier (1848) who stated: "forsan etian in Calabriae montibus". Then, this relationship seems to have been accepted as a fact up to recent times (Bianchini, 1982; Brullo & al., 1997; Brullo & Guarino, 2017), with Brullo & Guarino (2017) proposing to name the group as "*Armeria nebrodensis* complex". However, neither the lumping-splitting algorithm nor the spatial admixture analysis (Fig. 8) support the recognition of an *A. nebrodensis* complex, since there is no admixture at all between the Sicilian (RB*, SS*) and the Calabrian populations (AS*, PO, SM*). For these reasons, our morphological and cpDNA phylogenetic results (Table 2) do not support an *A. nebrodensis* complex but rather an *A. aspromontana* complex, endemic to southern Basilicata and Calabria.

The Sicilian taxa *Armeria gussonei* and *A. nebrodensis*, both show well distinct phenotypes whose identity can be assessed easily on herbarium material. Indeed, they do not show admixture with other populations (Fig. 8). Phylogenetically they are closely placed in the cpDNA tree (Fig. 4) and considered in the same group by ASAP for both cpDNA and ITS data (Table 2). Based on their morphological distinctiveness and isolated ranges, we support their independence as two species. Interestingly, *A. gussonei* was placed taxonomically close to the Sardinian endemic *A. morisii* Boiss. by several authors (Zangheri, 1976; Bianchini, 1982; Brullo & Guarino, 2017), or even considered a heterotypic synonym of the latter (POWO, 2017–), since these two species share the broad rosulate leaves, the habitat (cliffs) and the overall appearance. We also observed that the characters used in the currently available identification keys do not allow a reliable identification (e.g., Brullo & Guarino, 2017); nonetheless, we consider that these two species deserve to be kept separated, as they can be easily distinguished by examining the epidermal cells of the leaves (suppl. Fig. S5), a character previously not considered in the taxonomy of *Armeria*.

It is worth noting that, even though most of the species currently accepted are still supported after this study, many of the previously reported diagnostic characters were not confirmed by us. The same has been reported by several other authors (Scassellati, 2011; Scassellati & al., 2013; Brullo & Guarino, 2017).

For *Armeria aspromontana* we found inner scales 6.32 ± 1.12 mm long × 3.44 ± 0.59 mm wide, while a range of 3.5–5 mm long × 3–3.5 mm wide has been reported by Brullo & al. (1997). Similar discrepancies were observed for *A. brutia* (see suppl. Table S6 vs. Brullo & al., 2004). Lastly, the values reported in the diagnostic table of the taxa investigated by Selvi (2009) for *A. saviana* against *A. denticulata* do not agree with our results as well. Specifically, awns in *A. saviana* never reach 2 mm in our sampling (suppl. Table S6, suppl. Fig. S6), sheaths in *A. denticulata* are often more than 15 mm long and plants are shorter than 35 cm. The same can be said about *A. garganica* (Arrigoni, 2015), that shows awns shorter than 1 mm long (suppl. Table S6). We would like to stress that *Armeria* species have many taxonomically informative characters hidden within the pseudocapitulum, whereas vegetative characters usually bring less information, when dealing with closely resembling taxa. Indeed, among the 15 most important loadings on first two axes of the PCA (Fig. 5, suppl. Fig. S1), 4 are vegetative characters, while 11 are reproductive. In accordance with ecological theory, the seed size observed in *Armeria* (Fig. 6) may be explained by the findings of Baker & al. (1994) for *A. maritima* (Mill.) Willd.: individuals growing in resource-rich environments tend to produce larger seeds compared to those growing in poor soils, such as serpentine soils, as seen in species of the *A. denticulata* complex.

Karyologically, the stability and uniformity of this species, already highlighted by Buzurović & al. (2019) and Tiburtini & al. (2023), are further confirmed here, since all the populations investigated showed chromosomes with centromeres roughly in a median position and exhibited ranges of karyological parameters (THL, $M_{CA}$, $CV_{CL}$, $CV_{CI}$) comparable to those found in other taxa from Sardinia and Corsica or within the *Armeria arenaria* complex (see Tiburtini & al., 2022, 2023).

One limitation of our study is the fact that selected molecular markers (complete nuclear ribosomal DNA cistron and four plastid intergenic spacers) resulted in only partially resolved phylogenetic reconstructions (Tiburtini & al., 2022, 2023) due to potential incomplete lineage sorting, hybridisation and concerted evolution, gene flow and geographical patterns (Fuertes Aguilar & al., 1999; Nieto Feliner & al., 2004).



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Our findings provide a robust framework for the taxonomy of *Armeria* in peninsular Italy and Sicily, also underscoring the importance of rigorous methodological approaches in taxonomy and systematics, particularly in complex, multispecies integrative taxonomic revisions. Furthermore, we confirm the Italian peninsula and Sicily as a hotspot of *Armeria* diversity, with 10 taxa endemic to the study area and an updated total of 15 endemic taxa in Italy (Tiburtini & al., 2022, 2023).

While previous morphometric studies, such as that of Scassellati & al. (2013), conducted on the same populations and species, concluded that the *Armeria canescens–A. majellensis* complex lacked distinct morphological separation – mainly based on overlapping distributions in PCA morphospaces – our study highlights that the choice of analytical methods significantly influences taxonomic interpretations. Although our PCA (Fig. 5) also shows overlapping morphospaces among taxa similarly to the results obtained by Scassellati & al. (2013), the adoption of powerful methods like population-wise supervised dimensionality reduction techniques (UMAP, suppl. Fig. S2) and model-based clustering (GMM) enabled us to detect subtle but significant morphological structures that PCA cannot uncover, since it is not intended to do so: PCA preserves directions of maximum variance without regard to group separability, and, as demonstrated by Chang (1983), components with the highest variance (i.e., largest eigenvalues) do not necessarily contain the most relevant information for distinguishing subgroups, making PCA inherently unsuitable for inferring taxonomic structure in genus-wide revisions.

This demonstrates that integrative approaches, combining multiple lines of evidence and sophisticated statistical methods, can resolve longstanding taxonomic uncertainties. Thus, our study not only advances the systematics of *Armeria* but also reinforces the broader need for the integration of genomics, morphometrics, and data-driven modelling in the taxonomic revision of other Mediterranean and temperate plant groups characterised by complex morphological variability.

**Identification key to the Italian *Armeria* taxa from the Apennines and Sicily. —** Note for usage: all scape length measurements were taken from the base of the scape to the base of the capitulum, with the scape pulled from the base for accurate measurement. The key refers to summer leaves and their width should be measured around the middle of the leaf, while the width of the outer scale is measured at its base, and the width of the inner scale at its middle. In this key, we consistently use the same terminology as in our previous identification keys (Tiburtini & al., 2022, 2023). *Scales* refers to the series of involucral bracts that subtend the capitulum. These are classified as inner, intermediate, or outer scales based on their position and morphology. Although their size may vary – inner scales may be larger or smaller than the outer ones – their relative position within the pseudocapitulum remains a reliable criterion for their recognition.

*Bracts* denote the larger structures subtending the spikelets that compose the inflorescence. We differentiate them based on their position within the capitulum: *inner bracts* subtend the spikelets situated centrally, typically erect, while *outer bracts* are associated with the peripheral spikelets, which are often slightly knelt.

Finally, *bracteoles* are defined as small, transparent bracts located between the paired flowers within a spikelet. For measurement purposes, the bracteole to be considered is the larger one, which typically corresponds to the most developed flower positioned facing the centre of the pseudocapitulum. We measured its size both in the inner in the outer spikelets.

All measurements were taken from dry herbarium specimens, and pseudocapitulum width refers to measurements on pressed specimens. For measurements on the calyx (tube, limb, awns, etc), see the drawing in supplementary material in Tiburtini & al. (2022). The key includes also *Armeria arenaria* (occurring in the extreme north of peninsular Italy) and provides tips for the identification of *A. morisii* (see Tiburtini & al., 2023) from Sardinia, erroneously considered a synonym of *A. gussonei* (POWO, 2017–). The key for identifying subspecies within *A. arenaria* can be found in Tiburtini & al. (2022). The most important characters for *Armeria* identification are shown in suppl. Fig. S6.

1. Leaves often undulate and dentate along the margins, with the inner leaves always short (5.1 ± 1.5 cm long); pseudocapitula small (1.1 ± 0.2 cm wide) with broad (3.10 ± 0.72 mm) and long (9.87 ± 2.31 mm) triangular-shaped outer scales, forming a cup-shaped "crown" around it; inner spikelet bracts <6 mm long; seeds 2.1 ± 0.18 mm long..... ..... 2 (*A. denticulata* complex)
1. Leaves neither undulate nor dentate and leaf size variable; pseudocapitula often >1.3 cm wide with outer scales of variable size, that do not form a distinct cup-shaped "crown"; inner spikelet bracts >6 mm long; seeds 2.6 ± 0.24 mm long.....3
2. Leaf margin usually translucent (microscope!) often >0.05 mm wide; calyx limbs of inner flowers >2.15 mm long; outer spikelet bract >5.9 mm long; plants from jasper or limestone at high elevation (more than 800 m) ..... ..... ***A. saviana***
2. Leaf margin not translucent (microscope!) <0.05 mm wide; calyx limbs of inner flowers <2.15 mm long; outer spikelet bract <5.9 mm long; plants from ophiolitic outcrops at lower elevation (less than 800 m) ..... .....***A. denticulata***
3. Scapes <20 cm (16.5 ± 3.13 cm) long and <1 mm (0.77 ± 0.11 mm) wide at the base; pseudocapitula often ≤17 mm wide; inner spikelet bracteole width <2.2 mm; rosettes with short and narrow leaves (42.15 ± 15.76 mm × 0.95 ± 0.24 mm), very densely packed ... ***A. nebrodensis***
3. Scapes >20 cm (36.07 ± 10.72 cm) long and >1 mm (1.37 ± 0.33) wide at the base; pseudocapitula >17 mm wide; inner spikelet bracteole width ≥2.2 mm; rosettes variable in size, but always not so dense.....4
4. Scapes >1.8 mm wide at the base, if ≤1.8 mm, then scapes >50 cm long and calyx tube >3.5 mm;



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pseudocapitula often >2 cm (2.28 ± 0.33 cm) wide; leaves 14.1 ± 4.6 cm long, if <10 cm, then bract of the outer spikelet ≥6 mm wide..... ***A. macropoda***

4. Scapes ≤1.8 mm wide at base, if >1.8 mm, then scapes usually <50 cm long and calyx tube ≤3.5 mm; pseudocapitula often <2 cm wide; leaves <10 cm long, if ≥10 cm, then bract of the outer spikelet <6 mm wide.....5
5. Leaves <1.75 mm (1.33 ± 0.45 mm) wide; inner spikelet bract <1.66 mm (1.40 ± 0.43 mm) wide; intermediate scale <5.65 mm (5.19 ± 1.05 mm) long..... .....6 (*A. aspromontana* complex)
5. Leaves usually >1.75 mm (2.61 ± 1.22 mm) wide; inner spikelet bract >1.66 mm (2.25 ± 0.69 mm) wide; intermediate scale >5.65 mm (6.53 ± 1.45 mm) long .....8
6. Scapes <32 cm (24.1 ± 7 cm) long; intermediate scale >5.3 mm (6.00 ± 0.83 mm) long; calyx pedicel of the most developed inner flower <1.75 mm (1.37 ± 0.51 mm) long..... ***A. aspromontana***
6. Scapes usually >32 cm (37.3 ± 6 cm) long; intermediate scale <5.3 mm (4.70 ± 0.86 mm) long; calyx pedicel of the most developed inner flower >1.75 mm (2.42 ± 0.57 mm) long.....7
7. Pseudocapitulum with more than 13 scales; inner scales >4 mm wide; inner spikelet bracteole >1.5 mm wide; leaves 9.7 ± 1.9 cm long ..... ***A. pollinensis***
7. Pseudocapitulum with less than 13 scales; inner scales <4 mm wide; inner spikelet bracteole <1.5 mm wide; leaves 7.1 ± 2.4 cm long ..... ***A. brutia***
8. Plant with a campanulate-hawk feet-like calyx when ripen; leaves 2.18 ± 0.77 mm wide and length of inner spikelet's bracteole <3.9 mm..... ***A. garganica***
8. Plants without a campanulate-hawk feet-like calyces when ripen; leaves ≥3mm wide; if leaves <3 mm wide, then the length of inner spikelet's bracteole ≥3.9 mm..... 9
9. Calyx limb ≥2.8 mm (3.14 ± 0.33 mm) long; leaves >3 mm (3.98 ± 0.97 mm) wide, sheaths <18 mm (15.10 ± 3.09 mm) long ..... ***A. gussonei***
   [Note: The Sardinian endemic *Armeria morisii* can be easily distinguished from *A. gussonei* by the rounded, protruding cells covering the leaves vs. rectangular cells with a smooth surface in the latter (suppl. Fig. S5).]
9. Calyx limb <2.8 mm long; leaves <3 mm wide, if >3mm then sheath >18 mm long.....10
10. Leaves <2.2 mm wide, if ≥2.2 mm, then scale number <12 and width of the pseudocapitulum >18.6 mm.... ***A. gracilis***
10. Leaves >2.2 mm wide, if ≤2.2 mm, then scale number ≥12 and width of the pseudocapitulum ≤18.6 mm .....***A. arenaria***

## ■ TAXONOMIC TREATMENT

***Armeria aspromontana*** Brullo, Scelsi & Spamp. in Edinburgh J. Bot. 54(1): 91. 1997 – Holotype: ITALY. Aspromonte, Bocca del Lupo, 18 Jul 1992, *Brullo, Scelsi & Spampinato s.n*. (CAT n.v.; isotype: FI barcode FI002424!).

*Other specimens seen.* – ITALY. Calabria: Contrada Nardello, Aspromonte. Habitat: Pascoli a 1750 m s.l.m, [WGS84: 38.156663°N 015.871213°E], 27 Jun 2019, *L. Bernardo s.n*. (PI066770–PI066794).

*Distribution.* – Aspromonte (southern Calabria, southern Italy).

*Ecology.* – Mountain meadows and pastures, rocky areas on siliceous substrates.

*Conservation status.* – LC (Orsenigo & al., 2018).

***Armeria brutia*** Brullo, Gangale & Uzunov in Bot. Jahrb. Syst. 125(4): 465. 2004 – Holotype: ITALY. Sila, Silvana Mansio, 20 Aug 1998, *Bartolo, Brullo & Gangale s.n*. (CAT n.v.).

*Other specimens seen.* – ITALY. Calabria: Silvana Mansio, Sila. Habitat: Pascoli a 1360 m s.l.m. [WGS84: 39.3152510°N 16.540388°E], 18 Jun 2019, *L. Bernardo s.n*. (PI066749–PI066769).

*Distribution.* – Sila (central Calabria, southern Italy).

*Ecology.* – Shrubby vegetation on siliceous substrates, at 1300–1800 m a.s.l.

*Conservation status.* – LC (Orsenigo & al., 2018).

***Armeria canescens*** (Host) Ebel, Armeriae: 28. 1840 ≡ *Statice canescens* Host, Fl. Austriac. 1: 407. 1827 – Lectotype (designated by Scassellati & al. in Ann. Bot. Fenn. 48: 456. 2011): CROATIA. Dalmatia, s.d., *Portenschlag-Ledermayer s.n*. (W No. W0023451!).

*Other specimens seen.* – CROATIA. Dalmatia: M. Mosor, presso il rifugio Umberto Girometta [WGS84: 43.522726°N, 016.619126°E], 19 Jun 2022, *F. Conti & A. Stinca s.n*. (PI066892–PI066911); M. Kozjak, pendii rupestri, 564 m [WGS84: 43.579128°N, 016.348802°E], 21 Jun 2021, *F. Conti & A. Stinca s.n*. (PI066682–PI066687). NORTH MACEDONIA. Polog: Monte Madenica, Parco Nazionale del Mavrovo. Habitat: praterie aride su calcare [WGS84: 41.621728°N, 020.664287°E], 22 Aug 2023, *M. Tiburtini & F. Caramuscio s.n*. (PI).

*Distribution.* – Balkan peninsula: Croatia, Serbia, Montenegro, Albania, North Macedonia, Greece. Not occurring in Italy.

*Ecology.* – Mountain dry pastures, in various substrates, even in serpentines.

*Conservation status.* – NE (Not Evaluated), possibly not threatened since it is widespread across the Balkans.

***Armeria denticulata*** (Bertol.) DC., Cat. Pl. Horti Monsp.: 7. 1813 ≡ *Statice denticulata* Bertol., Rar. Lig. [Ital.] Pl. 2: 34. 1806 – Lectotype (designated by Selvi in Nordic J. Bot. 27: 132. 2009): ITALY. Liguria, prope Sarzanam in montibus Brina et Nuda di Ponzano, in rupibus serpentinis, 1805, *Bertoloni s.n*. (BOLO!).

*Other specimens seen.* – ITALY. Liguria: Nei pressi del castello della Brina (Sarzana, La Spezia) [WGS84: 44.14732°N, 009.95068°E], 11 Jun 2021, *L. Sandroni s.n*. (PI049856–PI049876). Tuscany: Monte Pelato (Rosignano M.mo, Livorno), verso la cima. Habitat: Gariga su suolo



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ofiolitico, 345 m [WGS84: 43.43780°N, 010.43188°E], 8 May 2017, *F. Roma-Marzio & L. Peruzzi 591* (PI063923!); Poggio Pelato (Rosignano M.mo, Livorno) [WGS84: 43.43525°N, 010.43103°E], 25 May 2021, *L. Sandroni & G. Astuti s.n*. (PI049924–PI049947); Monteferrato (Prato) [WGS84: 43.92042°N, 011.07572°E], 9 Jun 2021, *L. Sandroni s.n*. (PI049902–PI049923).

*Distribution.* – Tuscany and eastern Liguria (central Italy).

*Ecology.* – Obligate to serpentine outcrops.

*Conservation status.* – LC (Orsenigo & al., 2018).

***Armeria garganica*** Arrigoni in Fl. Medit. 25 (spec. iss.): 25. 2015 – Holotype: ITALY. Apulia, Gargano in herbidis apricis pr. S. Nicandro sol. calcar., 30 Jun 1874, *Porta & Rigo s.n*. (FI barcode FI007465!).

*Other specimens seen.* – ITALY. Basilicata: Pignola, Potenza, Monte Serranetta, prati-pascoli rocciosi a 1440 m s.l.m. [WGS84: 40.564678°N, 015.818625°E], 21 Jul 2021, *D. Iamonico s.n*. (PI066709–PI066728, RO); Apulia: San Marco in Lamis, Foggia. Habitat: prati mesofili a margine boschivo a 860 m s.l.m. [WGS84: 41.751227°N, 015.690502°E], 1 Jun 2022, *D. Iamonico s.n*. (PI066688–PI066705, PI066707, PI066708, RO); SS 89, km 10,2, (rocky) garrigue a 590 m, UTM: 33T WG 0581/4617, Carta d'Italia (IGMI): 397/2, 3 Jun 1985, *W. Licht 553* (MJG023616); doline fields Le Chiancate, Xerograminetum a 820–880 m, UTM: 33T WG 05/46, Carta d'Italia (IGMI): 397/1, 6 Jun 1985, *W. Licht 2369* (MJG023626); SS 528 (km 30,2), Xerograminetum a 580 m, UTM: 33T WG 0581/4624, Carta d'Italia (IGMI): 397/2, 9 Jun 1987, *W. Licht 555* (MJG023618); Doline fields Le Chiancate. Habitat: Xerograminetum a 820–880 m, UTM: 33T WG 05/46, Carta d'Italia (IGMI): 397/1, 12 Jun 1987, *W. Licht 554* (MJG023625-1, MJG023625-2); Doline fields Le Chiancate. Habitat: Xerograminetum a 850–880 m, UTM: 33T WG 0559/4624, Carta d'Italia (IGMI): 397/1, 6 Jun 1990, *W. Licht 1313* (MJG023624); SS 528 (km 31,5), Xerograminetum a 580 m, UTM: 33T WG 0582/4623, Carta d'Italia (IGMI): 397/2, 31 May 1994, *W. Licht 2366* (MJG023621); *Stipa*-lawn east of S. Marco. Habitat: Xerograminetum, light forest/sparse tree cover a 670–770 m, UTM: 33T WG 0550/4620, Carta d'Italia (IGMI): 396/1, 3 Jun 1996, *W. Licht 2365* (MJG023623); SS 528 (km 31,5), Xerograminetum a 580 m, UTM: 33T WG 0582/4623, Carta d'Italia (IGMI): 397/2, 31 May 1998, *W. Licht 2920* (MJG023620); Monte Nero, plateau. Habitat: xeric, exposed terrain with sparse trees and/or shrubs a 920–1000 m, UTM: 33T WG 0557/4619, Carta d'Italia (IGMI): 397/1, 17 May 1999, *W. Licht 5490* (MJG023622); branch from the street Sannicandro–S. Marco (km 6,8) to Cagnano, km 11,2, grassland a 580 m, UTM: 33T WG 0553/4626, Carta d'Italia (IGMI): 397/2, 19 May 1999, *W. Licht 5491* (MJG023619).

*Distribution.* – Apulia and Basilicata (southern Italy).

*Ecology.* – Calcareous grassland or rocky places, at 580–1440 m a.s.l.

*Conservation status.* – DD (Orsenigo & al., 2018).

***Armeria gracilis*** Ten., Syll. Pl. Fl. Neapol.: 158. 1831 ≡ *Armeria vulgaris* var. *minor* Ten., Fl. Napol. 2(1) (= tomo 3): 353. 1824–1829 – Lectotype (designated by Iamonico & al. in Phytotaxa 665: 194. 2024): ITALY. Abruzzo, Velino, Mt Corno, s.d., *Tenore s.n*. (NAP barcode NAP0002550!).

= *Armeria gracilis* var. *humilis* Ten., Syll. Pl. Fl. Neapol.: 158. 1831 – Lectotype (designated by Iamonico & al. in Phytotaxa 665: 194. 2024): ITALY. Abruzzo, Corno, Velino, s.d., *Tenore s.n*. (NAP barcode NAP0003186!).

= *Armeria majellensis* Boiss. in DC., Prodr. 12: 685. 1848 ≡ *A. gracilis* subsp. *majellensis* (Boiss.) Arrigoni, Fl. Medit. 25 (spec. iss.): 22. 2015 – Lectotype (designated by Scassellati & al. in Ann. Bot. Fenn. 48. 456. 2011): ITALY. In rupibus et pascuis editioribus montis Majella in Aprutio Neapolitano, copiosissima, Aug 1844, *Leresche s.n*. (G barcode G00177568! [on 2 sheets] [image!]).

= *Armeria majellensis* subsp. *ausonia* Bianchini in Giorn. Bot. Ital. 111(1–2): 49. 1977 – Holotype: ITALY. In monte Coccorello, 13 Aug 1875, *Levier s.n*. (FI barcode FI001253 [image!]).

*Other specimens seen.* – ITALY. Marche: Arquata del Tronto, M. Comunitore, 14 Jun 2007, *F. Conti s.n*. (APP33890); Monte Castel Manardo (Montefortino, Fermo), praterie calcaree a 1650 m s.l.m. [WGS84: 42.963417°N, 013.242722°E], 4 Jul 2022, *M. Tiburtini & S. Quitarrà s.n*. (PI066839–PI066842); Vetta del Monte San Vicino (Apiro, Macerata), praterie calcaree a 1470 m s.l.m. [WGS84: 43.331402°N, 013.059779°E], 5 Jul 2022, *M. Tiburtini s.n*. (PI066851–PI066858). Umbria: Monte Cucco, Pian di Monte, Sigillo (Perugia), 1220 m s.l.m., prati pascoli [WGS84: 43.359939°N, 012.749166°E], 15 Jun 2022, *D. Iamonico s.n*. (PI066729–PI066748, RO); Codice Stazione C, settori sommitali del Monte Pennino, 1400–1571 m s.l.m., stazione di *Genista radiata* e faggeta, 27 Jun 2021, *C.M. Musarella s.n*. (PI066870); Codice Stazione A, Monte Pennino (Perugia), versante sud-occidentale, 1000–1300 m s.l.m., 26 Jun 2021, *V.L.A. Laface & C.M. Musarella s.n*. (PI066871); Pascolo a *Bromus erectus*, Stazione D1 [Escursione Floristica Sistematica ed Evoluzione M. Pennino 2021], 26 Jun 2021, *s. coll*. (PI066869); Monte Pennino, Escursione FSE 2021, 28 Jun 2021, *L. Pinzani s.n*. (PI066868); Codice Stazione D, settori sommitali del Monte Pennino, 1400–1571 m s.l.m. Habitat: stazione di *Genista radiata* e faggeta [coordinates not provided], 27 Jun 2021, *V.L.A. Laface s.n*. (PI066865); Provincia di Perugia, Nocera Umbra, Gruppo del Monte Pennino, cima del Monte Acuto, prati aridi su calcare, 1258–1300 m s.l.m., esposizione: ovest [WGS84: da 43.082278°N, 012.891760°E a 43.079326°N, 012.891188°E], 25 Jun 2021, *G. Galasso s.n*. (PI066866–PI066867); Nei dintorni di Castelluccio di Norcia, Pian Perduto, Monti Sibillini, prati calcarei, 4 Jul 2022, *M. Tiburtini & S. Quitarrá s.n*. (PI066859–PI066864); Nei dintorni del Colle San Ruffino, Monte Subasio, Assisi (Perugia), pascoli a 1050 m s.l.m. [WGS84: 43.069989°N, 012.651782°E], 19 Jun 2024,



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*L. Sandroni & V. Ursida s.n*. (PI); Monte Subasio (Assisi), parcheggio degli Stazzi. Substrato calcareo, praterie montane [WGS84: 43.072917°N, 012.654167°E], 3 Jun 2021, *M. Tiburtini & J. Sulpizi s.n*. (PI066330). Abruzzo: Fara San Martino, Monte Acquaviva. Habitat: pascoli sassosi, 2700 m s.l.m., 22 Sep 1991, *F. Conti s.n*. (APP10828); Cesacastina, località Fosso dell'Acero, limite superiore del bosco, 1660 m s.l.m. [WGS84: 42.59615°N, 013.41543°E], 16 Jun 2003, *F. Conti, D. Tinti, D. De Santis, A. Rutigliano, F. Ferroni, V. Viscosi, G. D'Orazio, M. Latini, G. Grossi, M. Barbo, A. Santoni, F. Morena, D. Uzunov, S. Peccenini s.n*. (APP7316–APP7314); Comune di Cesacastina, località Monti della Laga - Fosso dell'Acero, pascoli, 1660 m s.l.m. [WGS84: 42.59615°N, 013.41543°E], 9 Jul 2004, *F. Conti & D. Lakušić s.n*. (APP16932); Rocca S. Maria, Gruppo della Laga, Valle del Rio Castellano, dosso sinistro Cascata Regina, pascoli, praterie, limite inferiore della faggeta [WGS84: 42.50605°N, 013.36842°E], 18 May 2005, *S. Cecchetti s.n*. (APP21064); Abruzzo, Alena, Monte Secine (Polledrara), pascoli, 1700 m s.l.m. [WGS84: 41.73073°N, 013.15307°E], 24 May 2006, *F. Conti s.n*. (APP33932); Majella al Blockhaus, Caramanico Terme, Pescara, 2070 m s.l.m. Habitat: praterie [WGS84: 42.148431°N, 014.113218°E], 06 Jul 2020, *F. Bartolucci & F. Conti s.n*. (PI065401–PI065420); Monti della Meta in località Campitelli (Alfedena, L'Aquila), praterie, 1441 m s.l.m. [WGS84: 41.699966°N, 013.982889°E], 24 Jun 2020, *F. Bartolucci & F. Conti s.n*. (PI065482–PI065501); Gran Sasso a Vado di Corno (L'Aquila), praterie e pendii rupestri, 1845 m s.l.m. [WGS84: 42.447867°N, 013.588635°E], 26 Jun 2020, *F. Bartolucci & F. Conti s.n*. (PI065381–PI065400); gruppo Velino-Sirente in località Piani di Pezza (Rocca di Mezzo, L'Aquila), praterie e pendii rupestri, 1490 m s.l.m. [WGS84: 42.181080°N, 013.483870°E], 17 Jun 2020, *F. Bartolucci & F. Conti s.n*. (PI065421–PI065440); alle falde del Monte Morrone a Passo San Leonardo (Pacentro, L'Aquila), praterie e margine faggeta, 1298 m s.l.m. [WGS84: 42.053020°N, 014.053311°E], 19 Jun 2020, *F. Bartolucci & F. Conti s.n*. (PI065462–PI065481). Abruzzo: Rifugio del Falco (Pizzone, Isernia), prati, 1400 m, 7 Jul 1992, *F. Conti* (APP23586); Le Forme (Pizzone, Isernia), pascolo montano, 1400 m, 15 Jun 1993, *F. Conti s.n*. (APP23584); La Metuccia, Monte a Mare (Pizzone, Isernia), pascoli montani, 2000–2150 m, 8 Jul 1992, *F. Conti s.n*. (APP23582, APP 23583); tra Pizzone e Casone del medico (Pizzone, Isernia), pascolo montano, 1000 m, 26 May 1992, *F. Conti s.n*. (APP23580, APP 23581); Valle Fredda (Pizzone, Isernia), pascolo sommitale, 1800–2000 m, 16 Jun 1993, *F. Conti s.n*. (APP23575, APP 23576); M. Castelnuovo (Rocchetta a Volturno, Isernia), pascolo, 1200 m, 23 May 1994, *F. Conti s.n*. (APP23577). Campania: Monte Vergine, Ospedaletto d'Alpinolo, Avellino, Campo Maggiore, Rifugio CAI, 1340 m s.l.m. Habitat: prati pascoli sul fondo della dolina [WGS84: 40.936849°N, 014.713004°E], 8 Jul 2021, *D. Iamonico & E. Del Guacchio s.n*. (PI066815–PI066834, RO).

*Distribution.* – Central and Southern Apennines (central Italy): Marche, Umbria, Lazio, Abruzzo, Molise, Campania.

*Ecology.* – Mountain dry pastures, on calcareous substrates and rocky places at 1000–2700 m a.s.l.

*Conservation status.* – LC (Orsenigo & al., 2018).

***Armeria gussonei*** Boiss. in DC., Prodr. 12: 687. 1848 – Lectotype (designated by Brullo & al. in Peccenini & Domina [Soc. Bot. Ital., Gr. Florist.], Loci Classici, Taxa Critici e Monumenti Arborei della Flora d'Italia: 35. 2011): ITALY. Busambra in pascuis et rupibus umbrosis, May–Jun, *Gussone s.n*. (NAP-GUSS n.v.).

*Other specimens seen.* – ITALY. Sicilia: Rocca Busambra, Monti Sicani. Habitat: rupi carbonatiche esposte a nord [WGS84: 37.856170°N, 013.402200°E], 1 Jul 2019 / 5 Jul 2023, *G. Domina & G. Barone s.n*. (PI066418–PI066439).

*Distribution.* – Mount Busambra, north-western Sicily (Italy).

*Ecology.* – Mountain rupicolous vegetation on dolomite cliffs.

*Conservation status.* – NT (Orsenigo & al., 2018).

***Armeria macropoda*** Boiss. in DC., Prodr. 12: 688. 1848 – Lectotype (designated by Iamonico & al. in Phytotaxa 665: 196. 2024): ITALY. Campania, Montevergine et Monte Terminio in Principato Ultra s.d., *Gussone s.n*. (G barcode G00390387!).

*Other specimens seen.* – ITALY. Campania: Ripa della Falconara (Serino, Avellino), pendici del Monte Terminio, pendici boscate su calcari a 1300 m s.l.m. [WGS84: 40.818084°N, 014.941297°E], 30 Jun 2019, *L. Bernardo s.n*. (PI065441–PI065461); Monte Panormo [Alburni], Salerno, praterie rocciose, 29 Jun 2023, *S. Fruzzetti s.n*. (PI066835).

*Distribution.* – Southern Campania (Monte Terminio, Monti Alburni and possibly elsewhere) in southern Italy.

*Ecology.* – Calcareous grassland and rocky places.

*Conservation status.* – DD (Orsenigo & al., 2018).

***Armeria nebrodensis*** (Guss.) Boiss. in DC., Prodr. 12: 685. 1848 ≡ *Statice nebrodensis* Guss., Fl. Sicul. Syn. 1: 366. 1843 ≡ *A. canescens* subsp. *nebrodensis* (Guss.) P.Silva in Bot. J. Linn. Soc. 64(4): 376. 1971 – Lectotype (designated by Iamonico & al. in Phytotaxa 665: 197. 2024): ITALY. Sicily, s.d., *Gussone s.n*. (G barcode G00440380!).

*Other specimens seen.* – ITALY. Sicilia: Monte San Salvatore, Madonie, Piano Grande, pascoli rocciosi su silice [WGS84: 37.842780°N, 014.031291°E], 5 Jul 2019 / 4 Jul 2023, *G. Domina s.n*. (PI066440–PI066468).

*Distribution.* – Madonie (Sicily, Italy), "Nebrodi" in classical times.

*Ecology.* – Sunny cliffs and rocky grasslands.

*Conservation status.* – LC (Orsenigo & al., 2018).

***Armeria pollinensis*** (N.Terracc.) Tiburtini & Peruzzi, **comb. & stat. nov.** ≡ *Armeria gracilis* var. *pollinensis* N.Terracc. in Annuario Reale Ist. Bot. Roma 4: 121. 1891 –



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**Lectotype (designated here):** ITALY. Calabria, salendo al Pollinello, Jul 1885, *N. Terracciano s.n*. (RO!).

In the protologue, Terracciano describes this variety for Pollinello. We traced a herbarium sheet in RO that contains two different collections from the same site, in different dates (July 1885 and July 1889). Both specimens were collected and annotated by Terracciano and are original material for this name. They both match the original description, so that the older collection at the top of the herbarium sheet is here selected as the lectotype. Even though the specimen clearly shows a dwarf and not well-developed plant, the type fits well within the variability of plants from the Pollino Massif for the shape of the scales, the length of the sheaths and the width of the leaves. Accordingly, the type represents just an extreme dwarf or immature form of the plants found in the Pollino Massif, which are otherwise very variable in size, as we found in the studied specimens.

*Other specimens seen.* – ITALY. Basilicata: Pozze di Serra Scorsillo, Massiccio del Pollino, ambienti umidi, 7 Jun 2001, *L. Peruzzi, N.G. Passalacqua s.n*. (CLU15276); Piano Ruggio, Pollino. Habitat: prato-pascolo su calcare a 1550 m s.l.m. [WGS84: 39.9113802°N, 016.132727°E], 23 Jun 2019, *L. Bernardo s.n*. (PI066795–PI066814). Calabria: salendo al Pollinello. Jul 1889, *N. Terracciano s.n*. (RO); Timpa di Cassano, Cosenza (verso il nido dell'aquila), 16 Jun 1976, *G. Cesca, P. Mirabelli s.n*. (CLU16118); Pollinello - Castrovillari, 1700 m s.l.m., 3 Oct 1983, *M. Codogno, D. Puntillo s.n*. (CLU15269); Monte Mula, S. Donato di Ninea, 1900–1935 m s.l.m., 30 Jul 1992, *L. Bernardo, G. Cesca s.n*. (CLU16105); Dirupata di Morano, Cosenza, 722 m s.l.m., 24 May 1994, *P. Calvosa* (CLU16226); Cozzo Pellegrino, S. Donato di Ninea, prato in radura faggeta vicino a *P. alpina*, 1950–1970 m s.l.m., 13 Jul 1994, *L. Bernardo, N.G. Passalacqua s.n*. (CLU16114); Serra del Dolcedorme, Pollino Massif (a Nord di Castrovillari), prato sassoso gradonato calcareo, 2120 m s.l.m., 24 Jul 1996, *L. Bernardo, N. Passalacqua, M. Aversa, A. Beni s.n*. (CLU16124).

*Distribution.* – Pollino Massif (southern Italy, between southern Basilicata and northern Calabria).

*Ecology.* – Dry grasslands or rocky places at 722–2120 m a.s.l.

*Conservation status.* – NE, possibly not threatened since it is widespread across the Pollino Massif.

***Armeria saviana*** Selvi in Nordic J. Bot. 27(2): 126. 2009 – Holotype: ITALY. Tuscany, province of Grosseto, municipality of Arcidosso, loc. Poggio all'Olmo, 2 Jun 2008, *F. Selvi 3018* (FI barcode FI002195!).

*Other specimens seen.* – ITALY. Tuscany: Stribugliano, alla Pietra Sorbella (Arcidosso, Grosseto) [WGS84: 42.854980°N, 011.465530°E], 28 May 2021, *L. Sandroni & G. Astuti s.n*. (PI049877–PI049901).

*Distribution.* – Southern Tuscany (central Italy).

*Ecology.* – Mountain pastures and rocky slopes with sparse xerophilous vegetation at 900–1050 m a.s.l., on limestones or jasper.

*Conservation status.* – EN (Orsenigo & al., 2018).

## ■ CONCLUSIONS

Our integrative revision of the challenging genus *Armeria* – combining multilocus phylogenies, seed and vegetative morphometry, Gaussian-mixture species delimitation, and karyology – clarifies the long-standing taxonomic confusion surrounding its biodiversity in peninsular Italy and Sicily. The evidence supports 10 endemic species in the study area. We (1) confirm the independence of *A. denticulata*, *A. garganica* (in a new, extended, circumscription), *A. gussonei*, *A. macropoda* (restricted to its type locality), *A. nebrodensis*, and *A. saviana*; (2) demonstrate that the Balkan *A. canescens* is absent from Italy; (3) synonymise *A. gracilis* subsp. *majellensis* with *A. gracilis* s.str.; and (4) raise *A. gracilis* var. *pollinensis* to species rank as *A. pollinensis*. The revised taxonomy, updated identification key, and newly generated sequence data offer a solid foundation for future studies on biogeography, evolution, and conservation of *Armeria* in the Central Mediterranean, confirming its role as second hotspot for the genus worldwide, after the Iberian peninsula. These results also underscore the relevance of integrative taxonomic approaches for disentangling complex species groups in biodiversity-rich but taxonomically difficult taxa.

## ■ DATA AVAILABILITY

The newly generated nuclear ITS and chloroplast intergenic-spacer sequences have been deposited in the DDBJ/EMBL/GenBank databases and are publicly accessible upon publication. The complete plant- and seed-morphometric matrices and karyological measurements can be obtained from the corresponding author upon reasonable request. R scripts and workflow documentation supporting the findings of this study are included as a LaTeX file containing all the code used (suppl. Appendix S1).

## ■ AUTHOR CONTRIBUTIONS

Conceptualization, LPe; methodology, MT, LPe, and PC; validation, LPe; formal analysis, MT and PC; investigation, FB, FC, GD, LB, MI (field sampling), DI (field sampling and measurements), MS, GB (seed morphometry), LPa, EDI, PC (molecular systematics), LPe, DI, MI (nomenclature); data curation, MT and PC; writing – original draft preparation, MT; writing – review and editing, LPe; visualisation, MT and PC; supervision, LPe; funding acquisition, LPe. All authors have read and agreed to the published version of the manuscript.

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## ■ COMPETING INTERESTS

We declare no competing interest.

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**Appendix 1.** ID (acronym), taxon, locality, coordinates, voucher information and GenBank accession numbers for the 21 *Armeria* populations sampled along the Italian peninsula, Sicily and Croatia. Current taxonomic hypothesis according to Arrigoni (2015). Asterisk (*) = type locality; n = specimens used for plant morphometry.

| ID | Taxon | Locality | n | Voucher |
|---|---|---|---|---|
| AS* | ***Armeria aspromontana*** Brullo, Scelsi & Spamp. | Italy, Calabria, Bocca del Lupo, Aspromonte, Contrada Nardello (Santo Stefano in Aspromonte, Reggio Calabria); [38.156663°N, 015.871213°E] | 24 | *L. Bernardo s.n.*; 27 Jun 2019 (PI066770–PI066794); ITS LC861363–LC861365; *psbA-trnH* LC861426–LC861428; *trnF-trnL* LC861489–LC861491; *trnL-rpl32* LC861549–LC861551; *trnQ-rps16* LC861611–LC861613 |
| SM* | ***Armeria brutia*** Brullo, Gangale & Uzunov | Italy, Calabria, Sila, Silvana Mansio, close to Montescuro (Serra Pedace, Cosenza); [39.315251°N, 016.540388°E] | 20 | *L. Bernardo s.n.*; 18 Jun 2019 (PI066749–PI066769); ITS LC861366–LC861368; *psbA-trnH* LC861429–LC861431; *trnF-trnL* LC861492–LC861494; *trnL-rpl32* LC861552–LC861554; *trnQ-rps16* LC861614–LC861616 |
| MK | ***Armeria canescens*** (Host) Ebel | Croatia, Dalmatia, Mali Kozjak (Kaštela, Split); [43.57168°N, 016.40348°E] | 6 | *F. Conti & A. Stinca s.n.*; 21 Jun 2021 (PI066682–PI066687); ITS LC861369–LC861371; *psbA-trnH* LC861432–LC861434; *trnF-trnL* LC861495–LC861496; *trnL-rpl32* LC861555–LC861557; *trnQ-rps16* LC861617–LC861619 |
| RG* | ***Armeria canescens*** (Host) Ebel | Croatia, Dalmatia, Monte Mosor, Planinarski dom Girometta (Gornje Sitno, Mosor); [43.522726°N, 016.619126°E] | 20 | *F. Conti & A. Stinca s.n.*; 19 Jun 2021 (PI066892–PI066911); ITS LC861372–LC861374; *psbA-trnH* LC861435–LC861437; *trnF-trnL* LC861497–LC861499; *trnL-rpl32* LC861558–LC861560; *trnQ-rps16* LC861620–LC861622 |
| BP* | ***Armeria denticulata*** (Bertol.) DC. | Italy, Liguria, M. Nuda e Brina di Ponzano (Sarzana, La Spezia); [44.147630°N, 009.951430°E] | 20 | *L. Sandroni s.n.*; 11 Jun 2021 (PI049856–PI049876); ITS LC861375–LC861377; *psbA-trnH* LC861438–LC861440; *trnF-trnL* LC861500–LC861502; *trnL-rpl32* LC861561–LC861563; *trnQ-rps16* LC861623–LC861625 |
| MF | ***Armeria denticulata*** (Bertol.) DC. | Italy, Tuscany, Monte Ferrato (Prato); [43.920420°N, 011.075720°E] | 20 | *L. Sandroni s.n.*; 9 Jun 2021 (PI049902–PI049923); ITS LC861378–LC861380; *psbA-trnH* LC861441–LC861443; *trnF-trnL* LC861503–LC861505; *trnL-rpl32* LC861564–LC861566; *trnQ-rps16* LC861626–LC861628 |
| PP | ***Armeria denticulata*** (Bertol.) DC. | Italy, Tuscany, Poggio Pelato (Rosignano Marittimo, Livorno); [43.432316°N, 010.428041°E] | 20 | *L. Sandroni s.n.*; 25 May 2021 (PI049924–PI049947); ITS LC861381–LC861383; *psbA-trnH* LC861444–LC861446; *trnF-trnL* LC861506–LC861508; *trnL-rpl32* LC861567–LC861569; *trnQ-rps16* LC861629–LC861631 |
| SL* | ***Armeria garganica*** Arrigoni | Italy, Apulia, Gargano (San Marco in Lamis, Foggia); [41.750948°N, 015.690411°E] | 20 | *D. Iamonico s.n.*; 1 Jun 2022 (PI066688–PI066708); ITS LC861384–LC861386; *psbA-trnH* LC861447–LC861449; *trnF-trnL* LC861509–LC861511; *trnL-rpl32* LC861570–LC861572; *trnQ-rps16* LC861632–LC861633 |
| MM | ***Armeria gracilis*** Ten. subsp. ***gracilis*** | Italy, Abruzzo, Monte Morrone, Passo San Leonardo (Pacentro, L'Aquila); [42.053020°N, 014.053311°E] | 20 | *F. Bartolucci & F. Conti s.n.*; 19 Jun 2020 (PI065462–PI065481); ITS LC861390–LC861392; *psbA-trnH* LC861453–LC861455; *trnF-trnL* LC861514–LC861516; *trnL-rpl32* LC861576–LC861578; *trnQ-rps16* LC861637–LC861639 |

*(Continues)*



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**Appendix 1.** Continued.

| ID | Taxon | Locality | n | Voucher |
|---|---|---|---|---|
| MV | ***Armeria gracilis*** Ten. subsp. ***gracilis*** | Italy, Campania, Montevergine (Mercogliano, Avellino); [40.940697°N, 014.712487074°E] | 20 | *D. Iamonico & E. Del Guacchio s.n.*; 8 Jul 2021 (PI066815–PI066834); ITS LC861393–LC861395; *psbA-trnH* LC861456–LC861458; *trnF-trnL* LC861517–LC861519; *trnL-rpl32* LC861579–LC861581; *trnQ-rps16* LC861640–LC861642 |
| PO* | ***Armeria gracilis*** Ten. subsp. ***gracilis*** | Italy, Basilicata, Serra del Prete, Pollino Massif (Viggianello, Potenza); [39.911380°N, 016.132727°E] | 20 | *L. Bernardo s.n.*; 23 Jun 2019 (PI066795–PI066814); ITS LC861399–LC861401; *psbA-trnH* LC861462–LC861464; *trnF-trnL* LC861523–LC861525; *trnL-rpl32* LC861585–LC861587; *trnQ-rps16* LC861643–LC861645 |
| SI | ***Armeria gracilis*** Ten. subsp. ***gracilis*** | Italy, Umbria, Monte Cucco (Sigillo, Perugia); [43.359939°N, 012.749166°E] | 20 | *D. Iamonico s.n.*; 15 Jun 2022 (PI066729–PI066748); ITS LC861396–LC861398; *psbA-trnH* LC861459–LC861461; *trnF-trnL* LC861520–LC861522; *trnL-rpl32* LC861582–LC861584 |
| VC | ***Armeria gracilis*** Ten. subsp. ***gracilis*** | Italy, Abruzzo, Monte Corno, Vado di Corno (L'Aquila); [42.447867°N, 013.588635°E] | 20 | *F. Bartolucci & F. Conti s.n.*; 26 Jun 2020 (PI065381–PI065400); ITS LC861387–LC861389; *psbA-trnH* LC861450–LC861452; *trnF-trnL* LC861512–LC861513; *trnL-rpl32* LC861573–LC861575; *trnQ-rps16* LC861634–LC861636 |
| VS* | ***Armeria gracilis*** Ten. subsp. ***gracilis*** | Italy, Abruzzo, Monte Velino, Piani di Pezza (Rocca di Mezzo, L'Aquila); [42.181080°N, 013.483870°] | 20 | *F. Bartolucci & F. Conti s.n.*; 17 Jun 2020 (PI065421–PI065440); ITS LC861408–LC861410; *psbA-trnH* LC861471–LC861473; *trnF-trnL* LC861532–LC861533; *trnL-rpl32* LC861594–LC861596; *trnQ-rps16* LC861652–LC861654 |
| BH* | ***Armeria gracilis*** Ten. subsp. ***majellensis*** (Boiss.) Arrigoni | Italy, Abruzzo, Majella al Blockhaus (Caramanico Terme, Pescara); [42.148431°N, 014.113218°E] | 20 | *F. Bartolucci & F. Conti s.n.*; 06 Jul 2020 (PI065401–PI065420); ITS LC861402–LC861404; *psbA-trnH* LC861465–LC861467; *trnF-trnL* LC861526–LC861528; *trnL-rpl32* LC861588–LC861590; *trnQ-rps16* LC861646–LC861648 |
| CA | ***Armeria gracilis*** Ten. subsp. ***majellensis*** (Boiss.) Arrigoni | Italy, Abruzzo, Monti della Meta, loc. Campitelli (Alfedena, L'Aquila); [41.699966°N, 013.982889°E] | 20 | *F. Bartolucci & F. Conti s.n.*; 24 Jun 2020 (PI065482–PI065501); ITS LC861405–LC861407; *psbA-trnH* LC861468–LC861470; *trnF-trnL* LC861529–LC861531; *trnL-rpl32* LC861591–LC861593; *trnQ-rps16* LC861649–LC861651 |
| RB* | ***Armeria gussonei*** Boiss. | Italy, Sicily, Rocca Busambra (Corleone, Palermo); [37.856170°N, 013.402200°E] | 20 | *G. Domina & G. Barone s.n.*; 1 Jul 2019 / 5 Jul 2023 (PI066418–PI066439); ITS LC861411–LC861413; *psbA-trnH* LC861474–LC861476; *trnF-trnL* LC861534–LC861536; *trnL-rpl32* LC861597–LC861598; *trnQ-rps16* LC861655–LC861657 |
| MT* | ***Armeria macropoda*** Boiss. | Italy, Ripa della Falconara, pendici del Monte Terminio (Serino, Avellino); [40.818083°N, 014.941297°E] | 20 | *L. Bernardo s.n.*; 30 Jun 2019 (PI065441–PI065461); ITS LC861414–LC861416; *psbA-trnH* LC861477–LC861479; *trnF-trnL* LC861537–LC861539; *trnL-rpl32* LC861599–LC861601; *trnQ-rps16* LC861658–LC861660 |
| SE | ***Armeria macropoda*** Boiss. | Italy, Basilicata, Pignola, Serranetta (Pignola, Potenza); [40.564865°N, 015.815888°E] | 19 | *D. Iamonico s.n.*; 21 Jul 2021 (PI066709–PI066728); ITS LC861360–LC861362; *psbA-trnH* LC861423–LC861425; *trnF-trnL* LC861486–LC861488; *trnL-rpl32* LC861546–LC861548; *trnQ-rps16* LC861608–LC861610 |
| SS* | ***Armeria nebrodensis*** (Guss.) Boiss. | Italy, Sicily, Madonie sopra Petralia e al Cuozzo del Predicatore (Petralia Sottana, Palermo); [37.842780°N, 014.031291°E] | 20 | *G. Domina s.n.*; 5 Jul 2019 / 4 Jul 2023 (PI066440–PI066468); ITS LC861417–LC861419; *psbA-trnH* LC861480–LC861482; *trnF-trnL* LC861540–LC861542; *trnL-rpl32* LC861602–LC861604; *trnQ-rps16* LC861661–LC861663 |
| ST* | ***Armeria saviana*** Selvi | Italy, Tuscany, Poggio all'Olmo (Cinigiano, Grosseto); [42.858326°N, 011.471124°E] | 20 | *L. Sandroni s.n.*; 28 May 2021 (PI049877–PI049901); ITS LC861420–LC861422; *psbA-trnH* LC861483–LC861485; *trnF-trnL* LC861543–LC861545; *trnL-rpl32* LC861605–LC861607; *trnQ-rps16* LC861664–LC861666 |



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