

Cristina Salmeri

Plant morphology: outdated or advanced discipline in modern plant sciences?*

Abstract

Salmeri, C.: Plant morphology: outdated or advanced discipline in modern plant sciences? — Fl. Medit. 29: 163-180. 2019. — ISSN: 1120-4052 printed, 2240-4538 online.

In the last decades, with the increase of molecular studies, the study of plant forms has gone through a steady decline in interest, and researches on this topic are often neglected and underestimated. Notwithstanding, comparative morphology as integrative discipline still assumes a pivotal role in modern sciences, remaining fundamentally relevant to nearly all fields of plant biology, such as systematics, evolutionary biology, ecology, physiology, genetics, molecular biology, not to mention also agriculture, bioengineering, and forensic botany. Contrary to common belief, plant morphology is not a conservative finished science, but, like other sciences, it is open to constant innovations involving both concepts and methods. This contribution aims to promote a reflective discourse on the role of plant morphology in modern sciences and provides some examples of significant supports from plant morphology to different botanical issues.

Key words: Systematics, plant micromorphology, seed coat sculpturing, leaf anatomy, ecomorphology, climate adaptation.

Introduction

Despite the increasing societal awareness and sensitivity about the knowledge of biological diversity and ecosystem functioning as pivotal matters for nature conservation on which human health and well-being fundamentally depend, studies in morphology-based classical taxonomy have increasingly become marginalized and considered less significant than other scientific methods in plant biology. This has led to a progressive decline in attention both at research institutions and funding allocation, and nowadays most scientists and academic students think of plant morphology as just a classical and largely outdated field of research.

Plant morphology is a biological discipline that aims at understanding the biology of plant organisms on the basis of their structural appearance, so it essentially consists in the scientific investigation on the plant forms and/or structures.

*Extended and enriched version of the oral presentation given at the International Symposium "Botany at the intersection of Nature, Culture, Art and Science", Selinunte, 28-30 June 2018.

As a discipline, plant morphology can be intended in either a narrow or a broad sense. In narrow sense, plant morphology is the science of external forms and their relationships expressed at the whole plant down to the organ level of organization. In broad sense, plant morphology includes forms and structures at each level of organization, that is whole plant, organs, tissues, cells, cell organelles, etc.; in this respect plant morphology also involves micromorphology, anatomy and cell ultrastructure (Sattler 1978; Sattler & Rutishauser 1997).

Traditionally, the study of plant morphology takes its origin in the history of botany. From early times, great importance was made in the geometrical appearance of plant organs and consequently many taxonomic groups (especially genera and species) were named accordingly to their morphological characters. Similarly, also several plant families have had their taxonomic name based on characteristics of the shape of flowers or other morphological features (Betz 2006; Cervantes & de Diego 2010). Since the introduction of the term intended as a scientific discipline by Goethe (1790), modern plant morphology has resulted from an eventful history (Kaplan 2001; Claßen-Bockhoff 2001).

Contrary to a widespread misconception of being conceived as the science of static forms, plant morphology has showed an intrinsic dynamic essence. Firstly, it deals with the topological and sequential changes of plant forms and structures throughout the time, during ontogeny and phylogeny. In addition, it has dynamically changed over time and improved its theoretical and analytical approaches embracing new technologies and tools, without neglecting traditional methods (Sattler 1990; Liem 1991; Ledford 2018).

Progresses in plant morphology have influenced research in various disciplines of plant biology which fundamentally use or imply morphological concepts, such as systematics, evolutionary biology, ecology, physiology, genetics, molecular biology. Even in the current times of genomics (plus many other “omics” topics) and functional ecology, when trait-based approaches are essential for studying and understanding plant functions and species relationships, it is clear that plant morphology, used as comparative and integrative approach, still assumes a pivotal role, remaining fundamentally relevant to nearly all fields of plant science (Sattler & Rutishauser 1997; Kaplan 2001; Scotland & al. 2003; Pochynok 2012; Schönenberger & von Balthazar 2012; Schönenberger & al. 2016; Bucksch & al. 2017).

Lots of studies have demonstrated how vegetative and reproductive characters, and their anatomical and/or micro-morphological structures, can be informative for phylogenetic studies and helpful to solve systematic problems at various levels. Most phenotypic traits show adaptive variation and different range of plasticity which have proved to be of great ecological and physiological significance and useful, for instance, in reconstructing plant adaptation to past climatic conditions or establishing defence mechanisms and structural changes in response to stress, climate changes and plant invasions, which all are basic information for nature conservation. Meanwhile, understanding patterns and origins of such morphological modifications and how plant traits connect to gene activity across species is crucial to address main evo-devo questions. Not to mention the basic role of plant morphology in other applied sciences, such as agriculture, bioengineering, and forensic botany.

Notwithstanding, plant morphology and the strictly related descriptive taxonomy are often considered a lower form of science, not fashionable and very far from the biggest challenges facing humanity. If not associated to molecular and phylogenetic data, they are in general underappreciated in many highly visible journals and inadequacy of research

funding in these field is disproportionate relative to other disciplines in biology (Pyšek & al. 2013; Tahseen 2014; Coleman 2015), even though it seems that in the last decade taxonomic publications increased faster than those from other biological fields and reached high citation performances (Steiner & al. 2015).

This contribution intends to promote a reflective discourse aiming to change the current scientific culture towards a better acknowledgment and academic evaluation of research in plant morphology as the backbone of many other fields of plant biology and applied biosciences. Examples of fundamental interrelations between plant morphology and other biological disciplines are provided.

Material and Methods

Macromorphology

Studies on gross morphology were performed on both living wild plants collected from many localities of the Mediterranean area (exsiccates are preserved in CAT) and cultivated plants (10 to 30 individuals per species). Qualitative and quantitative morphological features were examined and recorded under a Zeiss Stemi SV11 Apo stereomicroscope at 6–66× magnification, on fresh samples when possible. Morphological comparison was also based on herbarium collections from various botanical museums and literature data. Both vegetative and reproductive characters were chosen according to their diagnostic value for discriminating among the investigated taxa and populations.

Micromorphology

Micromorphology was studied under a Zeiss EVO LS10 scanning electron microscope (SEM Zeiss, Oberkochen, Germany) using mature dehydrated samples set onto aluminium stubs with double adhesive tape and coated with gold prior to observation. Scanning electron micrographs were performed at an accelerating voltage of 10 kV and 18–1000× magnifications, depending on samples size. Terminology used for leaf surface and seed-coat sculpturing was based on Wilkinson (1979) and Barthlott (1981, 1984).

Leaf anatomy

Leaf blades of maximum size in their optimal vegetative development were used for the anatomical study. Cross sections 25 µm thick were made using a Leica CM 1900® cryostat (Leica, Wetzlar, Germany) at a temperature of -20 °C, then stained with 1% w/v aqueous Safranin. Vascular patterns were emphasized through leaf clarification based on the Fuchs' method (Fuchs 1963) modified by avoiding leaf tissue maceration in dried oven at 60°C. Semipermanent slides were mounted with glycerol/water 1:1 and sealed with transparent nail polish. Photographs were taken under Zeiss Axioskope 2 light microscope equipped with digital camera.

Statistical analyses

Micro-morphological and anatomical characters were measured from five to ten different samples for each investigated species/population. Measurements were done using the Zeiss AxioVision Rel. 4.8.2 image analysis software.

Statistical analyses were computed on both quantitative and qualitative morpho-anatomical parameters and performed using XLSTAT 2018.1.1 software (Addinsoft) on Microsoft Excel platform. Simple descriptive statistics of the intra- and inter-phenetic diversity (mean, standard deviation, range, median, and so on) were calculated from the data. The statistical effect of climate conditions on leaf traits among different populations was estimated by simple and multiple linear regression models. Mean annual precipitation (MAP) and mean annual temperature (MAT), from each population site, were used as the explanatory variables. De Martonne Aridity index (expressed by the formula $AI_{DM} = MAP/MAT + 10$) was also calculated and tested as potential predictor for climate influence on leaf structure. Multivariate analyses were performed in order to assess the similarity or dissimilarity among populations and the degree of separation of different groups. A step-wise discriminant factorial analysis (DFA) was employed on measured data (using the method of inclusion and removal at each step) The determination of the most discriminating variables was carried out by means of Fisher's coefficient at the significant threshold value of 0.05. The posterior probability of classification of each sample (cross validation) and the Wilks' lambda value of each variable were also calculated. Principal coordinates analysis (PCoA) was carried out on general dissimilarity matrix from 23 qualitative morphological characters.

Results

Descriptive morphology and taxonomic issues

The comparative study of plant structures, at both macro- and micromorphological level, has always been the backbone of plant Systematics. There exist lots of review summarising the main role of structural aspects in systematic botany at different taxonomic levels, where the comparative morphology appear to be still necessary and helpful, and reliable determination keys based on morphological characters continue to be a major information source for species identification and distinction (e.g. Greuter 1973; Ronse & al. 2010; Endress 2011; Kendorff & al. 2015; Mannino & al. 2015; Nardi 2015; Brullo & Erben 2016; Iamonico 2016; Brullo & al. 2018; Colasante 2018). It may help in areas and at levels of the tree of life where molecular studies are difficult for some reason.

This is the case of wide complicated genera, such as the genus *Allium* whose systematic arrangement in subgenera and sections is largely based on specific combination of discriminant morphological features (Fritsch 2001; Khassanov & al. 2011; Govaerts & al. 2018; Brullo & al. 2019), which was in many cases confirmed by molecular approaches (Friesen & al. 2006; Nguien & al. 2008; Hirschegger & al. 2010; Li & al. 2010). The role of comparative morphology in *Allium* taxonomy was also essential to clarify the systematic positions and relationships within several species' complexes, many of which have proven to include cryptic species. This is, for example, the case with the *Allium cupanii* Raf. group where a distinctive combination of morphological diagnostic features, i.e. fibrous and more or less markedly reticulate outer bulb tunics, basally adherent or detached, filiform leaves, with cylindrical to semicylindrical outline, subglabrous to densely hairy leaf indumentum, persistent spathe, with 1 or 2 valves basally connate, partially sheathing the flower pedicels, few-flowered inflorescence, usually fastigiate and unilateral, arranged in

2 or 4 bostryces when the spathe is 1-valved or 2-valved respectively, perigon cylindrical to urceolate, white-pinkish to pink-purplish, simple stamen filaments included into the perigon, ovary with well-developed nectariferous pores, covered by a membranous plica, and capsule included into the perigon, suggested a more appropriate inclusion of this group in the autonomous sect. *Cupanoscordum* Chesm., also confirmed by molecular investigations; the intrinsic variability in these morphological traits allows to identify five distinct series and many new species whose populations were all formerly identified sub *A. cupanii* (bulb coats basally attached) or sub *A. hirtovaginatam* Kunth (bulb coats basally detached) (Brullo & al. 1995; Brullo & al. 2015; Salmeri & al. 2015). Another investigated critical group in the genus *Allium* was the *Allium paniculatum* L. complex. Based on literature and many herbarium collections, *A. paniculatum* was frequently conceived as having an extremely wide geographic distribution (from West to East Europe, North Africa and Asia), both in synanthropic and wild habitats, and a large morphological variability. Detailed surveys on herbarium collections, including the type specimen of the species, and on living plants from lots of different territories of the Euro-Mediterranean and Irano-Turanian regions, actually revealed that many different taxa of *A. sect. Codonoprasum* Rchb., all characterized by big size, diffuse and densely flowered umbrella, very long spathe valves, long pedicels, and cylindrical-campanulate perigon, have been wrongly attributed to *A. paniculatum*, thus affecting records on the geographic distribution and morphological characterization of this species. Thus, while the true *A. paniculatum* resulted to be native and circumscribed to the far eastern European territories (Ukraine and Russia), many other allied but distinct taxa (previously treated as *A. paniculatum*) have been described and well discriminated on the basis of the combination of a few relevant morphological traits (Brullo & al. 2001; Brullo & al. 2008; Salmeri & al. 2015).

Then again, comparative morphological analyses concerning vegetative and reproductive structures, such as bulbs, leaves, inflorescence and seed, were crucial to assess the current systematics of the complex genus *Scilla* L. *sensu lato*, leading to its splitting in different closely related, but taxonomically well-differentiated natural genera within the *Hyacinthaceae* family, largely confirmed by molecular data (Speta 1998; Pfosser & Speta 1999, 2004). Most of these features are easily detectable also in the field and have proven very useful in discriminating among the Italian squills (Fig. 1), for which identification keys to the existing genera and species were also implemented (Brullo & al. 2007).

Other useful examples come from leaf morphology and anatomy, which provided relevant elements for characterizing and discriminating species of the genus *Dittrichia* Greuter. This genus is represented by five distinct taxa, all distributed in the Mediterranean area, from West (*D. viscosa*, *D. revoluta*, *D. maritima*) to East (*D. orientalis*), and partly extended into the Irano-Turanian region (*D. graveolens*). Despite a certain intraspecific variability (Brullo & al. 2004), clear and stable interspecific differences were found in the leaves (but not only), regarding their shape and size, types of margin, apex, venation, and hairs, plus some anatomical aspects of palisade and spongy tissues, which can be considered valuable characters supporting the distinction at specific level (Fig. 2).

Insights from comparative micromorphology

Plant micromorphology is the study of finer details of external features, based on micro-level analyses of leaves, pollens, seeds, petals and other plant organs. The diversity of plant

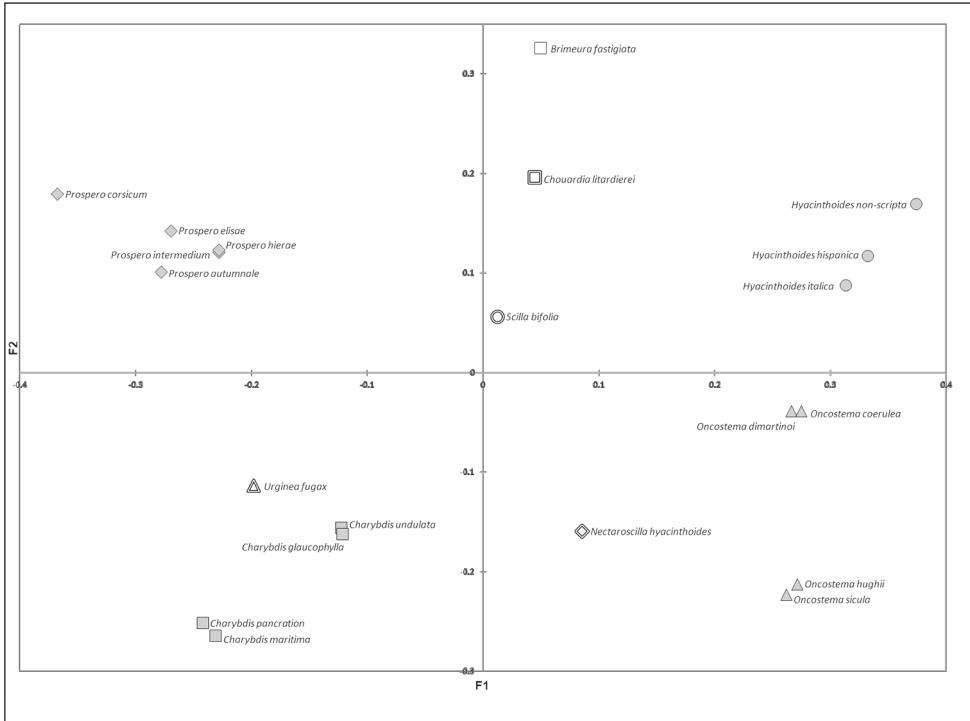


Fig. 1. Scatter plots resulting from principal coordinates analysis (PCoA) on *Scilla* s.l. species based on a data matrix of 23 morphological data.

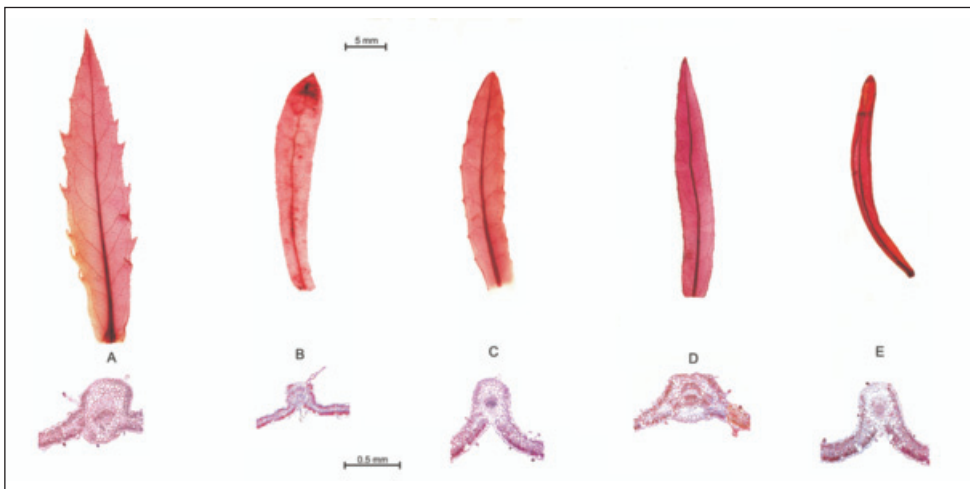


Fig. 2. Morpho-anatomical leaf variation in *Dittrichia* species: **a**, *D. viscosa*; **b**, *D. graveolens*; **c**, *D. maritima*; **d**, *D. orientalis*; **e**, *D. revoluta*.

surface structures arises from the variability of cell shape and size, and stratified microstructures of the cell surfaces, such as cuticle layers, epicuticular wax crystals, cuticular folds, hairs and glands. Almost unlimited different combinations of these cellular sculptures generate the high structural and functional diversity which characterizes land plants' surfaces (Barthlott & al. 2017).

The surface of plants is the critical interface for the interaction with the environment and fulfils many different functions (mechanical protection, attachment and particle adhesion, water loss reduction, light reflection, temperature control, air retention, wettability) related to ecological adaptation and/or reproductive strategies (Barthlott 1981, 1984; Bargał & al. 2004; Koch & Barthlott 2006). Furthermore, with exception of fossil pollens and spores, cuticles represent the most widespread unaltered fossil plant remains and are known from the Devonian to the recent times (Taylor & al. 1989). Thus, comparative studies of micromorphological features can provide significant insights into physiological properties and ecological responses of plants to environmental constraints and aid in systematic and evolutionary questions in extant and fossil plants, as highlighted by a vast existing literature (e.g. Stace 1965; Jones 1986; Kessler & al. 2007; Ickert-Bond & Rydin 2010; Albert & Sharma 2013; Anil Kumar & Murugan 2015; Arabi & al. 2017; Ickert-Bond & al. 2018; Sur & al. 2018; Scoppola & Magrini 2019).

Examples of micromorphological surveys include comparative analyses of seed coat sculpturing. The seed coat is the direct interface between embryo and external environment, acting as main modulator in the plant life cycle with key functions of regulation and protection. The taxonomic value of the macro- and micro-morphological characters of seeds and outer coats has been clearly demonstrated, being very conservative and stable features. In the genus *Brassica* L. sect. *Brassica*, with 20 taxa ten of which strictly endemic to Sicily, seed morphology and seed coat patterns provided useful information for discriminating among close taxa, especially those at subspecific level. Eighteen exomorphic parameters, including shape, size, color, surface texture, from 50 seeds for each accession (see Salmeri & al. 2011) were investigated. SEM analysis was carried out on 5-10 seeds from each sample, considering the arrangement and shape of epidermal cells, the architecture of anticlinal and periclinal cell walls (primary sculptures), their fine cuticular ornamentations (secondary sculptures).

Seed coat sculptures at low magnification (20×) showed a reticulate pattern, but higher magnifications (200-600×) revealed more complex networks, identifiable in 4 basic subtypes, i.e. simple reticulate, micro-reticulate, reticulate-foveate, reticulate-rugose, on account of their finer structuring. Significant differences were found in the overall cell shape (\pm polygonal or irregular) and the size, height and alignment of the meshes, which may be lax to compact, sharply angled to smooth, regular or irregular. Great variation among different taxa and populations was also observed in the anticlinal and periclinal cell walls and cell lumen, which can be straight to \pm undulate, depressed, concave, flat or convex, smooth to \pm markedly wrinkled, foveolate and / or papillose. Clear differences and very characteristic architectures were highlighted in most of the investigated species (Salmeri & al. 2011), with very close taxa such as the *B. villosa* and *B. rupestris* complexes (Fig. 3) characterized by well-defined sets of microsculptures valuable as discriminant features at specific and subspecific levels. In addition, seed coat microsculpturing can be helpful in the management of seed accessions in the seedbanks' collections.

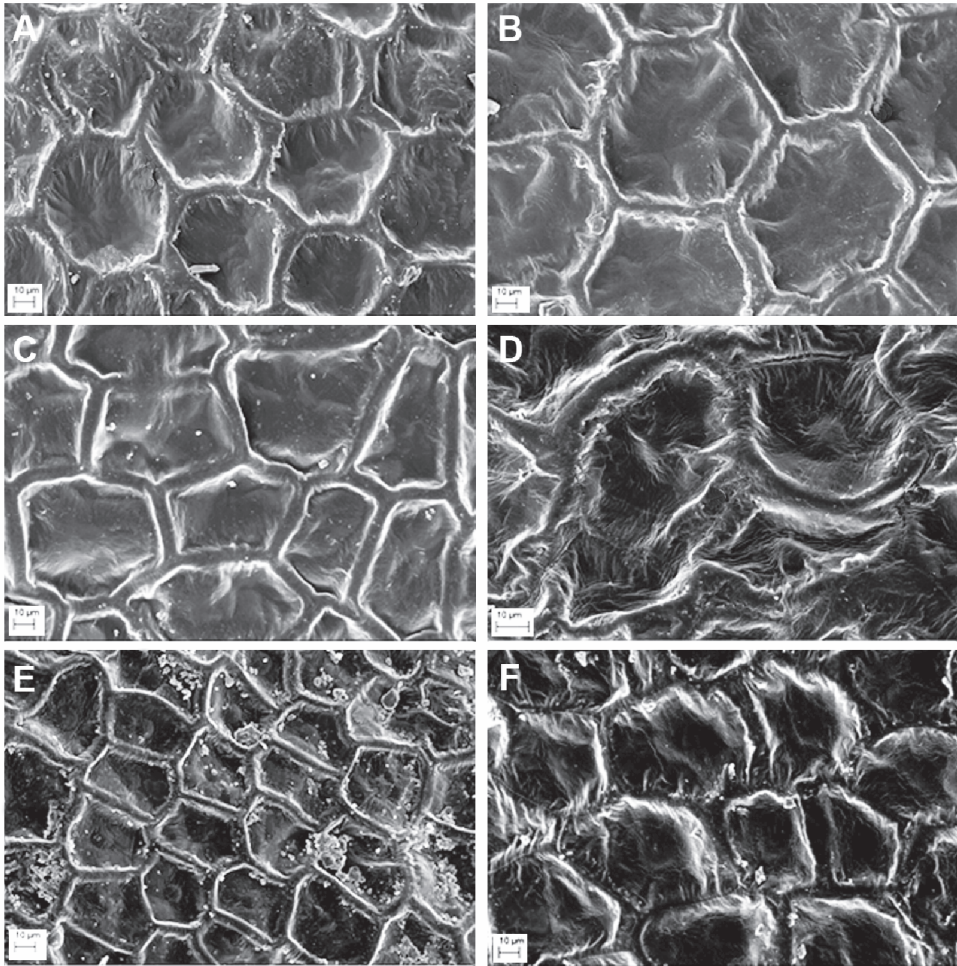


Fig. 3. Seed coat microsculpturing of some Sicilian taxa of *Brassica* sect. *Brassica* (500 \times): **a**, *B. villosa* subsp. *villosa*; **b**, *B. villosa* subsp. *bivoniana*; **c**, *B. villosa* subsp. *drepanensis*; **d**, *B. villosa* subsp. *tineoi*; **e**, *B. rupestris* subsp. *rupestris*; **f**, *B. rupestris* subsp. *hispida*

Comparative micromorphology of seed sculpturing is also relevant to assess dispersal strategies and infer potential and effective pathways of the gene flow within and among populations. A representative case is given by *Daucus carota* mericarps. Wild carrot fruits are oblong-ovoid schizocarps, 2-4 mm long, at maturity splitting into 2 small mericarps, with an outer convex surface provided with 5 primary short ciliate ridges and 4 secondary higher ridges with hooked prickles. Due to their shape, wild carrot diaspores can be transported by both wind and animals. Experiments revealed that especially spines decrease the fall of seeds in the air and that seeds were found to be scattered by wind over a distance on average not longer than 3 m (Lacey 1981; Manzano & Malo 2006), but they can reach

longer distances (rarely up 100 m away from the original area), especially when whole dry umbels, curled into a ball, are detached from the host plants (tumbleweed effect). Actually, the post-fertilization contraction of the umbels due to hygroscopic responses to air humidity can also act as regulator of seed dispersal (through retention or release) in local microsites (Lacey 1980; Heywood 1983). However, the commonest means of dispersal is by attachment to animal fur or human clothing. Manzano & Malo (2006) demonstrated that wild carrot mericarps attached to sheep fleece could be transported 400 km by transhumant flocks, with about 7% remaining adherent for up to 6 months so that seed dispersal continues for a greater length of time. Thus, barbs and prickles undoubtedly favour seed dispersal and the number and the distance over which propagules are scattered can differ depending on scattering medium. A preliminary survey on different Sicilian populations of wild carrot from internal and coastal sites revealed a great variation in the mass of pericarps (both size and shape), but especially in the length and density of prickles along the ridges and in the number (1 to 4-5) and orientation ($\leq/\approx/\geq 90^\circ$) of apical hooks (Fig. 4). These data, which still need further samplings, could provide useful information to interpret and predict gene flow among populations and hybridization patterns.

Ecomorphology and adaptive traits

Our current knowledge of biodiversity, adaptive strategies and ecosystem function is largely founded on descriptive comparative morphology, which enables our understanding of plant phenotypic plasticity and the related biological and ecological roles. The observation, description and documentation of variation in plasticity among and within populations allow to find adaptive explanations for specific forms and comprehend the ecological and evolutionary consequences of their diversity. Lots of publications discussed on the interaction of plant structures with environment or analysed how the environment conditions might modify the phenotypic expression of intrinsic features (Rotondi & al. 2003; Royer & al. 2005; Rozendaal 2003; Xu & al. 2009; Nicotra & al. 2010; Blonder & Enquist 2014; Angiolini & al. 2015; Yang & al. 2015; Mannino & Graziano 2016; Pilote & Donovan 2016; Saatkamp & al. 2018).

One investigated species showing significant levels of leaf morphometric variation across its populations was *Pancreatium maritimum* L. In this widespread Mediterranean coastal species different combinations of some key leaf traits, such as thickness of epidermis components, blade tissues, features and size of stomata apparatus, and leaf venation, provide special morphological patterns which ensure populations to have a plastic eco-physiological adaptation to the local microclimatic conditions (Perrone & al. 2015). In fact, despite a main and rather stable morpho-anatomical structure, leaves in *P. maritimum* populations revealed significant differences in the size, number, and/or type of several micro-morphological and histological features. Single and multiple linear regression analyses, conducted to clarify the statistical effects of different climate parameters (mean annual precipitation, mean annual temperature, mean maximum temperature, aridity index) on leaf traits of *P. maritimum*, indicated the existence of significant correlations, positive or negative, between leaf plasticity and local climate. Thus, intra-specific variability in functional leaf traits of *P. maritimum*, especially those related to stress tolerance (thickness of cuticle and epidermis cells, cell size of palisade and spongy tissue, size and density of stomata, size and number of intercostal areas with aerenchyma or mucilage)

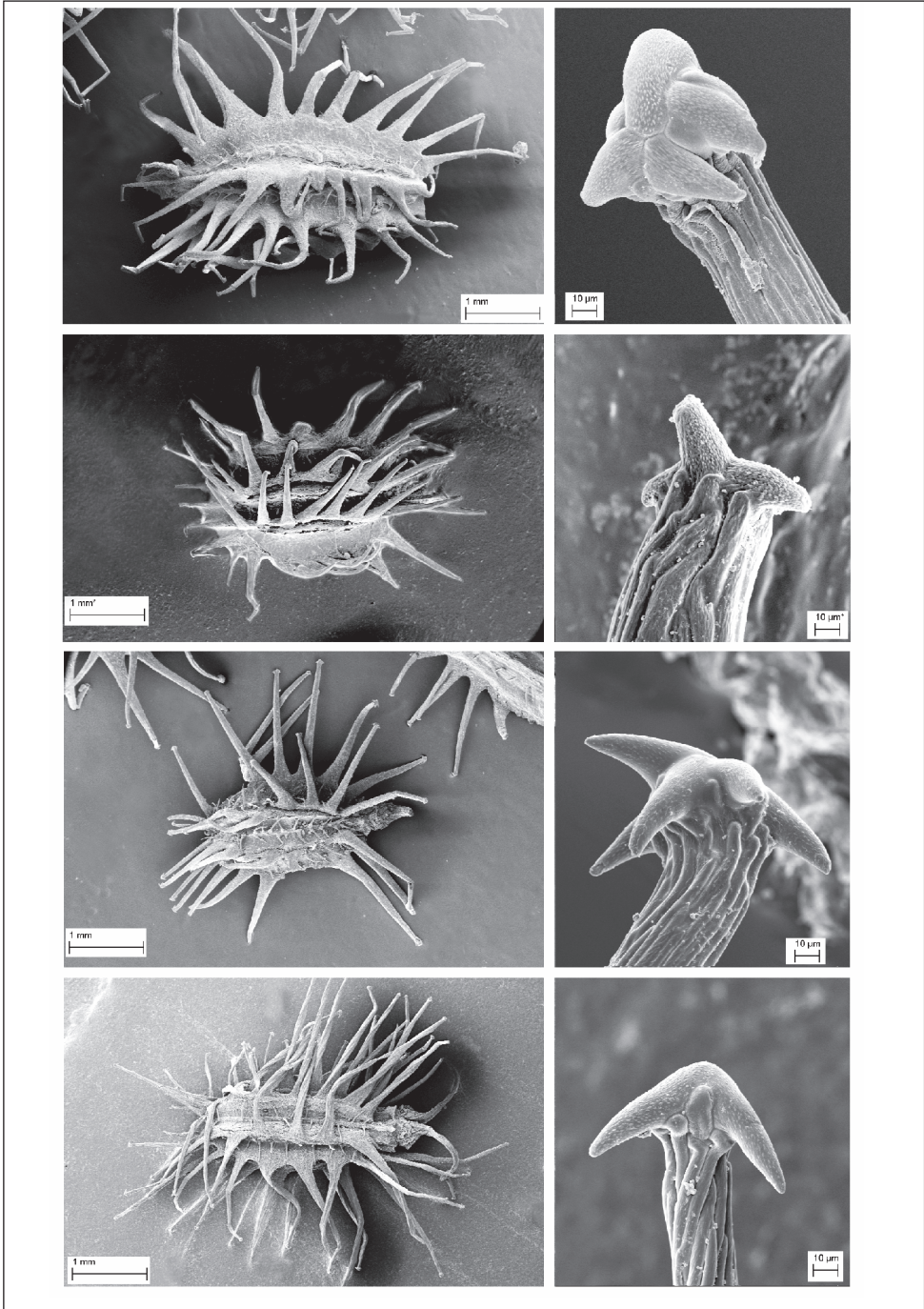


Fig. 4. Micromorphological fruit variation in some *Daucus carota* populations from Sicily: **a**, single mericarp with barbs and hooked hairs (18 \times); **b**, detail of the tip of hooked hairs (600 \times).

turned out to be a key aspect for long-term conservation, ensuring local adaptation to microsite conditions (insolation, drought, sandblasting) and increasing plant aptitude to adjust to climate changes.

Investigations on 6 different annual species of the genus *Salsola* sect. *Kali* Dumort, that is *S. kali* L., *S. tragus* L., *S. australis* R. Br., *S. squarrosa* Steven ex Moq. (formerly *S. tragus* L. subsp. *pontica* (Pall.) Rikle), and 2 taxa recently described within the genus *Kali* due to the previous taxonomic elevation of the homonymous section (i.e. *K. basalticum* Brullo & al. and *K. dodecanesicum* Brullo & al.), also revealed significant morpho-anatomical variations between species from maritime and inland areas, which clearly represent adaptations to survive under specific environmental conditions. Distinctive common features in this taxonomic group are stems rigid, not articulate, cortex green to greenish-red, with longitudinal chlorenchymatous striae, leaves linear-cylindrical, broadened at base, provided with apical spine, bracts similar to the leaves, but smaller, membranaceous perianth of 5 free segments, fruiting perianth usually winged, provided with unequal rudimentary abaxial appendices, membranaceous fruits, above flattened. Nevertheless, the species diverge in different combinations of morphological and anatomical characters, mainly related to the habit, stem, leaves and bracts, indumentum and salt glands, shape and size of flowers and fruits, which were proved to be directly involved in adaptive ecophysiological responses and/or reproductive strategies. As far as leaves are concerned, the investigated species show a cylindrical to semicylindrical outline, rather reflecting the same indumentum as the stem, no hypodermis, two concentric layers of chlorenchyma, typical of C4 Kranz anatomy, water storage tissue with mucilage in the central part, one central vascular bundle and 2 minor ones in the peripheral part, and 2 longitudinal colenchymatic ridges which interrupt palisade and Kranz cells. As showed in Fig. 5, main differences regarded the general leaf size (leaf area, leaf thickness), leaf indumentum, cell size and tissue thickness (complex cuticle-epidermis, palisade tissue, and collenchyma), which represent useful discriminant features among species (Fig. 6). Results from single and multiple linear regressions carried out on some leaf morphological characters (Fig. 7) suggested that climatic parameters have significant influence on leaf variability; in particular warming has positive relationships with leaf area and leaf thickness, while increased precipitations seem to affect negatively the leaf size. This can be explained by the fundamental role of a well-developed water storage tissue in drought conditions.

Discussion

The examples provided have demonstrated that plant morphology can and should contribute in a dynamic way to both basic and applied research, since today it has new and more opportunities than ever before, especially due to new techniques for structural research, such as SEM, confocal microscopy, microcomputer tomography and the modern morphometric analyses, which are opening possibilities for a better understanding of organisms' evolution and a further integration of comparative morphological studies and other biological disciplines.

Contrary to common belief, plant morphology is not a conservative finished science, but, like other sciences, it is open to constant innovations involving concepts and methods.

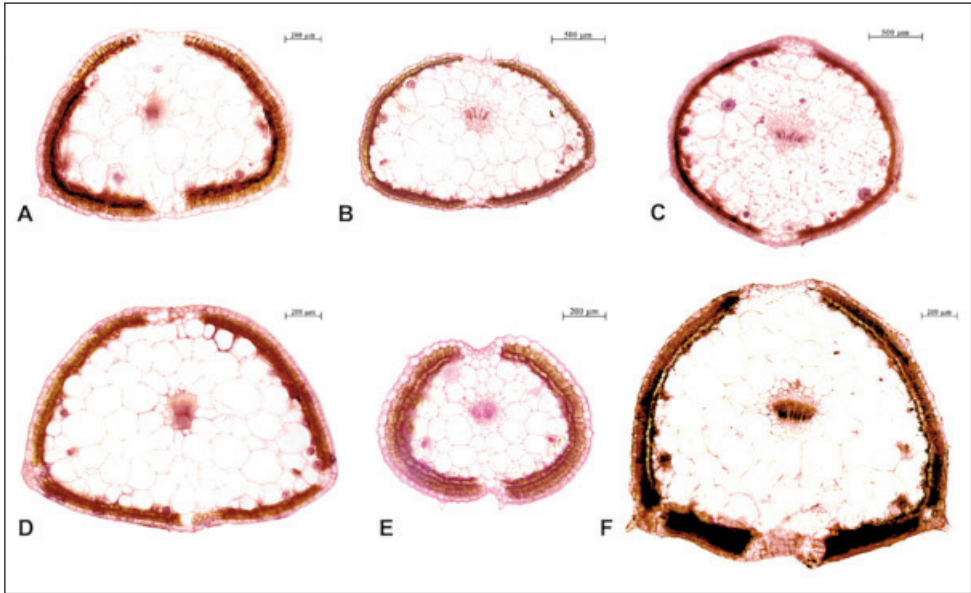


Fig. 5. Morpho-anatomical leaf variation in some annual *Salsola* species: **a**, *S. kali*; **b**, *S. tragus*; **c**, *S. dodecanesica* (*Kali dodecanesicum*); **d**, *S. squarrosa*; **e**, *S. basaltica* (*Kali basalticum*); **f**, *S. australis*.

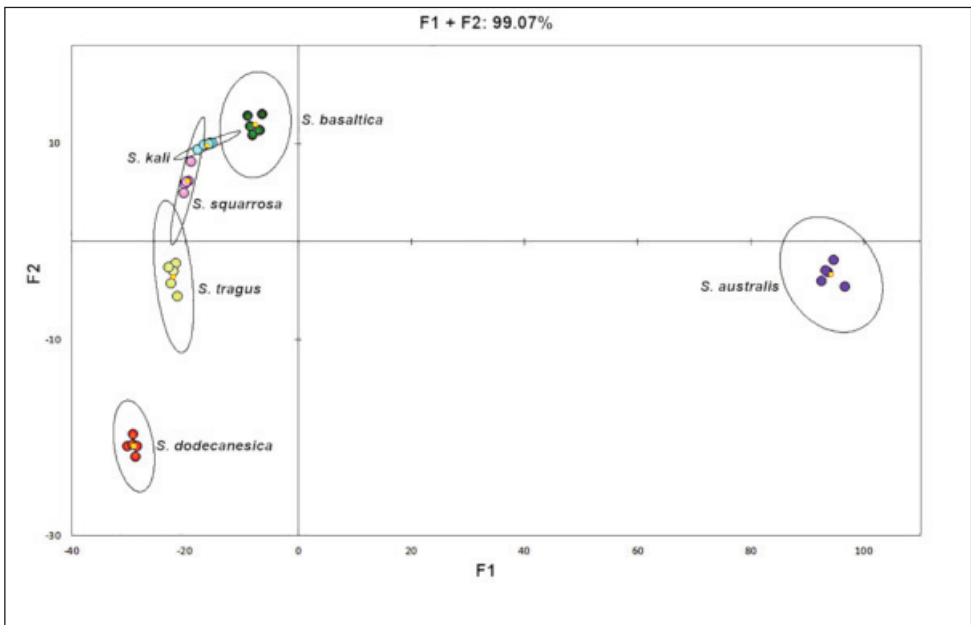


Fig. 6. Similarities among *Salsola* species resulting from discriminant factorial analysis among based on leaf parameters.

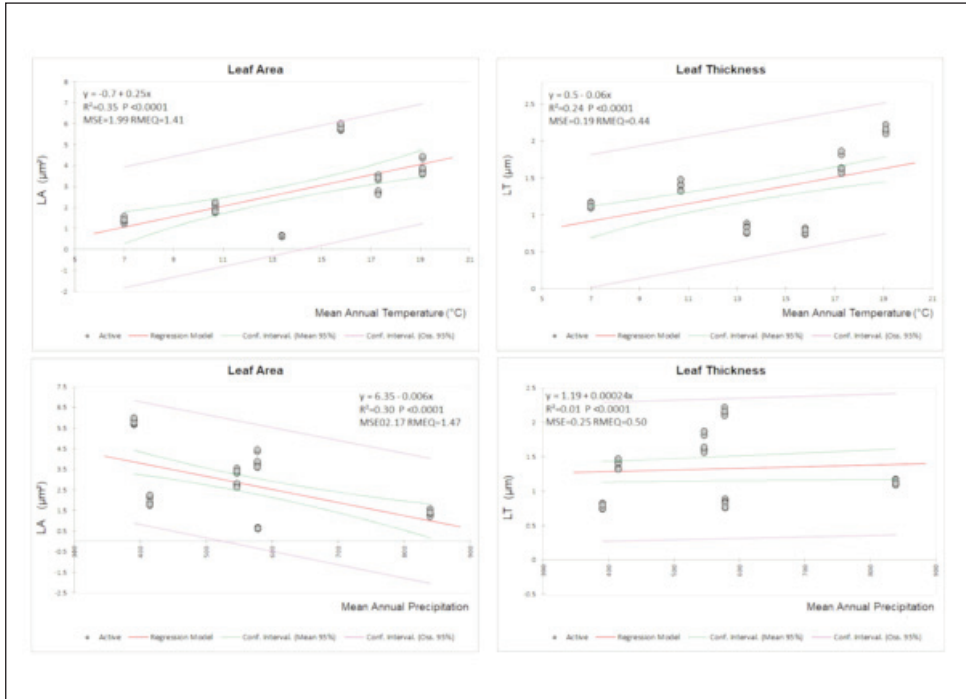


Fig. 7. Scatter plots and linear regressions indicating correlations between some leaf features and climatic parameters in *Salsola* species.

In fact, plant morphology has changed over time and improved its analytical approaches embracing new technologies and tools, without neglecting traditional methods.

Notwithstanding, morphological studies and their main related discipline, the classical alpha taxonomy, are still underestimated and somehow marginalized. Results from morphology-based research are often poorly cited in top-ranking journals, maybe because many authors tend to cite papers that support taxonomic treatments or reviews with molecular data, rather than papers only based on classical taxonomy (Pysek & al. 2013). The low number of specialists for particular limited groups further contribute to reducing the chances of plant morphology papers becoming highly cited (Krell 2002). This has progressively led to a worldwide decline in morphologists and taxonomists in general, which could have a broad impact on plant biology research and biodiversity conservation. Unfortunately, the simple assumption that biodiversity studies cannot advance without morphologists is unlikely to produce an adequate increase in public funding and broad support (Pearson & al. 2011). Thus, now it should be time to re-evaluate the contribution of plant morphology and contemporary plant morphologists at the level of modern botanical and evolutionary research in order to avoid the loss of a wide baseline expertise and favour the involvement of students and young researchers, especially through modern approaches and high technical tools, in this field of botany sciences.

References

- Albert, S. & Sharma, B. 2013: Comparative foliar micromorphological studies of some *Bauhinia* (*Leguminosae*) species. – Turk. J. Bot. **37**: 276-281. <https://doi.org/10.3906/bot-1201-37>
- Angiolini, C., Bonari, G., Frignani, F., Iiriti, G., Nannoni, F., Protano, G. & Landi, M. 2015: Ecological patterns of morphological variation in Italian populations of *Romulea bulbocodium* (*Iridaceae*). – Flora **214**: 1-10. <https://doi.org/10.1016/j.flora.2015.05.001>
- Anil Kumar, V. S. & Murugan, K. 2015: Taxonomic implications with special reference to stomatal variations in *Solanum* species using light and scanning electron microscope. – Int. J. Appl. Biol. Pharm. **6(2)**: 112-125.
- Arabi, Z., Ghahremaninejad, F., Rabeler, R. K., Heubl, G. & Zarre, S. 2017: Seed micromorphology and its systematic significance in tribe *Alsineae* (*Caryophyllaceae*). – Flora **234**: 41-59. <http://dx.doi.org/10.1016/j.flora.2017.07.004>
- Bargel, H., Barthlott, W., Koch, K., Schreiber, L. & Neinhuis, C. 2004: Plant cuticles: multifunctional interfaces between plant and environment. – Pp. 171-194 in: Hemsley, A. R. & Poole, I. (eds), The Evolution of Physiology. - London.
- Barthlott, W. 1981: Epidermal and seed surface characters of plants: Systematic applicability and some evolutionary aspects. – Nord. J. Bot. **1**: 345-355. <https://doi.org/10.1111/j.1756-1051.1981.tb00704.x>
- 1984: Microstructural features of seed surface. – Pp. 95-105 in: Heywood, V. H. & Moore, D. A. (eds): Current concepts in plant taxonomy. – London.
- , Mail, M., Bhushan, B. & Koch, K. 2017: Plant Surfaces: Structures and functions for biomimetic innovations. – Nano-Micro Lett. **9**: 23. <https://doi.org/10.3732/ajb.1600314>
- Betz, O. 2006: Ecomorphology: Integration of form, function, and ecology in the analysis of morphological structures. - Mitt. Dtsch. Ges. Allg. Angew. Ent. **15**: 409-416.
- Blonder, B. & Enquist, B. J. 2014: Inferring climate from angiosperm leaf venation networks. - New Phytol. **204(1)**: 116-126. <http://doi.org/10.1111/nph.12780>
- Brullo, S., Brullo, C., Cambria, S., Acar, Z., Salmeri, C. & Giusso Del Galdo, G. 2018: Taxonomic and phylogenetic investigations on *Psoralea acaulis* (*Psoraleae*: *Fabaceae*) with the description of a new genus *Kartalinea*. – Ann. Missouri Bot. Gard. **103(4)**: 604-627. <https://doi.org/10.3417/2018140>
- , Brullo, C., Cambria, S., Giusso Del Galdo, G. & Salmeri, C. 2019: *Allium albanicum* (*Amaryllidaceae*) a new species from Balkans and its relationships with *A. meteoricum* Heldr. & Hausskn. ex Halácsy. – Phytokeys **119**: 117-136. <http://dx.doi.org/10.3897/phytokeys.119.30790>
- , Campo, G., Colombo, P., Salmeri, C. & Venora, G. 2004: Morfologia, cariologia e anatomia fogliare nel genere *Dittrichia* Greuter (*Asteraceae*). – Inform. Bot. Ital. **36**: 489-496.
- & Erben, M. 2016: The genus *Limonium* (*Plumbaginaceae*) in Greece. – Phytotaxa **240(1)**: 1-212. <http://dx.doi.org/10.11646/phytotaxa.240.1.1>
- , Guglielmo, A., Pavone, P. & Salmeri, C. 2001: Osservazioni tassonomiche e cariologiche sulle specie del ciclo di *Allium paniculatum* L. in Italia. – Inform. Bot. Ital. **33(2)**: 536-542.
- , —, — & — 2007: Indagine biosistemica su *Scilla* s. l. in Italia e generi affini (*Hyacinthaceae*). - Inform. Bot. Ital. **39(1)**: 165-169.
- , —, — & — 2008: Taxonomical remarks on *Allium dentiferum* and its relationships with allied species. – Taxon **57**: 243-253. <https://doi.org/10.2307/25065965>
- , Pavone, P. & Salmeri, C. 1995: Considerazioni citotassonomiche e fitogeografiche su *Allium cupanii* Rafin. S. l., gruppo critico dell'area mediterranea. – Giorn. Bot. Ital. **129(1)**: 117-119.
- , — & — 2015: Biosystematic researches on *Allium cupanii* Raf. group (*Amaryllidaceae*) in the Mediterranean area. – Fl. Medit. **25 (Special issue)**: 209-255. <https://doi.org/10.7320/FIMedit25SI.209>

- Bucksch, A., Atta-Boateng, A., Azihou, A. F., Battogtokh, D., Baumgartner, A., Binder, B. M., Braybrook, S. A., Chang, C., Coneva, V., DeWitt, T. J., Fletcher, A. G., Gehan, M. A., Diaz-Martinez, D. H., Hong, L., Iyer-Pascuzzi, A. S., Klein, L. L., Leiboff, S., Li, M., Lynch, J. P., Maizel, A., Maloof, J. N., Markelz, R. J. C., Martinez, C. C., Miller, L. A., Mio, W., Palubicki, W., Poorter, H., Pradal, C., Price, C. A., Puttonen, E., Reese, J. B., Rellán-Álvarez, R., Spalding, E. P., Sparks, E. E., Topp, C. N., Williams, J. H. & Chitwood, D. H. 2017: Morphological Plant Modeling: Unleashing Geometric and Topological Potential within the Plant Sciences. – *Front. Pl. Sci.* **8**: 900. <https://doi.org/10.3389/fpls.2017.00900>
- Cervantes, E. & de Diego, J. G. 2010: Morphological description of plants. New perspectives in development and evolution. – *Int. J. Pl. Dev. Biol.* **4(1)**: 68-71.
- Claßen-Bockhoff, R. 2001. Plant Morphology: The Historic Concepts of Wilhelm Troll, Walter Zimmermann and Agnes Arber. – *Ann. Bot.* **88**: 1153-1172. <https://doi.org/10.1006/anbo.2001.1544>
- Colasante, M. 2018: *Iridaceae* presenti in Italia. – Roma.
- Coleman, C. O. 2015: Taxonomy in times of the taxonomic impediment – Examples from the Community of Experts on Amphipod Crustaceans. – *J. Crustace. Biol.* **35(6)**: 729-740. <https://doi.org/10.1163/1937240X-00002381>
- Eglinton, G. & Hamilton, R. J. 1967: Leaf epicuticular waxes. – *Science* **156**: 1322-1335.
- Endress, P.K. 2011: Evolutionary diversification of the flowers in Angiosperms. – *Amer. J. Bot.* **98(3)**: 370-396. <https://doi.org/10.3732/ajb.1000299>
- Friesen, N., Fritsch, R. M. & Blattner, F. R. 2006: Phylogeny and new intrageneric classification of *Allium* L. (*Alliaceae*) based on nuclear rDNA ITS sequences. – *Aliso* **22(1)**: 372-395. <https://doi.org/10.5642/aliso.20062201.31>
- Fritsch, R. M. 2001: Taxonomy of the genus *Allium*: Contribution from IPK Gatersleben. – *Herbetia* **56**: 19-50.
- & Friesen, N. 2002: Evolution, domestication, and taxonomy. – Pp. 5-30 in: Rabinowitch, H. D. & Currah, L. (eds): *Allium* Crop Science: Recent Advances. – Wallingford.
- Fuchs, C., 1963: Fuchsin staining with NaOH clearing for lignified elements of whole plants or plants organs. – *Stain Technol.* **38**: 41-144. <https://doi.org/10.3109/10520296309067156>
- Goethe, J. W. 1790: Versuch die Metamorphose der Pflanzen zu erklären. Gotha. Neuauflage 1960 mit Anmerkungen und Einleitung von Rudolf Steiner. – Stuttgart.
- Govaerts, R., Kington, S., Friesen, N., Fritsch, R. M., Snijman, D. A., Marcucci, R., Silverstone-Sopkin, P. A. & Brullo, S. 2018: World Checklist of *Amaryllidaceae*. – Facilitated by the Royal Botanic Gardens, Kew. <http://wcp.science.kew.org> [Last Accessed 1 August 2019].
- Greuter, W. 1973: Monographie der Gattung *Ptilostemon* (*Compositae*). – *Boissiera* **22**: 1-215.
- Heywood, V. H. 1983: Relationships and evolution in the *Daucus carota* complex. – *Isr. J. Pl. Sci.* **32(2)**: 51-65. <https://doi.org/10.1080/0021213X.1983.10676964>
- Hirschegger, P., Jakse, J., Trontelj, P. & Bohanec, B. 2010: Origins of *Allium ampeloprasum* horticultural groups and a molecular phylogeny of the section *Allium* (*Allium: Alliaceae*). – *Mol. Phylogenet. Evol.* **54(2)**: 488-497. <https://doi.org/10.1016/j.ympev.2009.08.030>
- Iamonico, D. 2015: Taxonomic revision of the genus *Amaranthus* (*Amaranthaceae*) in Italy. – *Phytotaxa* **199(1)**: 1-84. <http://dx.doi.org/10.11646/phytotaxa.199.1.1>
- Ickert-Bond, S. M., Harris, A., Lutz, S. & Wen, J. 2018: A detailed study of leaf micromorphology and anatomy of New World *Vitis* L. subgenus *Vitis* within a phylogenetic and ecological framework reveals evolutionary convergence. – *J. Syst. Evol.* **56(4)**: 309-330. <https://doi.org/10.1111/jse.12313>
- & Rydin, C. 2010: Micromorphology of the seed envelope of *Ephedra* L. (*Gnetales*) and its relevance for the timing of evolutionary events. – *Int. J. Pl. Sci.* **172(1)**: 36-48. <https://doi.org/10.1086/657299>

- Jones, J. H. 1986: Evolution of the *Fagaceae*: the implications of foliar features. – *Ann. Missouri Bot. Gard.* **73**: 228-275. <https://doi.org/10.2307/2399112>
- Kaplan, D. R. 2001: The science of plant morphology: definition, history, and role in modern biology. – *Amer. J. Bot.* **88**(10): 1711-1741. <https://doi.org/10.2307/3558347>
- Kerndorff, H., Pasche, E. & Harpke, D. 2015: The genus *Crocus* (*Liliiflorae*, *Iridaceae*): lifecycle, morphology, phenotypic characteristics, and taxonomical relevant parameters. – *Stapfia* **103**: 27-65.
- Khassanov, F. O., Shomuradov, H. F. & Kadyrov, G. U. 2011: Taxonomic revision of *Allium* L. sect. *Allium* s. l. in Central Asia. – *Stapfia* **95**: 171-174.
- Koch, K. & Barthlott, W. 2006: Plant Epicuticular Waxes: Chemistry, Form, Self-Assembly and Function. – *Nat. Prod. Commun.* **1**(11): 1067-1072. <https://doi.org/10.1177/1934578X0600101123>
- Krell, F. T. 2002: Why impact factors don't work for taxonomy. – *Nature* **415**: 957. <https://doi.org/10.1038/415957a>
- Lacey, E. P. 1980: The influence of hygroscopic movement on seed dispersal in *Daucus carota* (Apiaceae). – *Oecologia* **47**: 110-114. <https://doi.org/10.1007/BF00541784>
- 1981. Seed dispersal in wild carrot. – *Mich. Bot.* **20**: 15-20.
- Ledford, H. 2018: Botanical renaissance. Advances in genomics and imaging are reviving a fading discipline. – *Nature* **553**: 396-398.
- Li, Q. Q., Zhou, S. D., He, X. J., Yu, Y., Zhang, Y. C. & Wei, X. Q. 2010: Phylogeny and biogeography of *Allium* (*Amaryllidaceae*: *Allieae*) based on nuclear ribosomal internal transcribed spacer and chloroplast rps16 sequences, focusing on the inclusion of species endemic to China. – *Ann. Bot.* **106**(5): 709-733. <https://doi.org/10.1093/aob/mcq177>
- Mannino, A. M. & Graziano, M. G. 2016: Differences in the growth cycle of *Ruppia cirrhosa* (Petagna) Grande in a Mediterranean shallow system. – *Pl. Biosyst.* **150**(1): 54-61. <https://doi.org/10.1080/11263504.2014.906511>
- , Menéndez, M., Obrador, B., Sfriso, A. & Triest, L. 2015: The genus *Ruppia* L. (*Ruppiaceae*) in the Mediterranean region: An overview. – *Aquatic Bot.* **124**: 1-9. <https://doi.org/10.1016/j.aquabot.2015.02.005>
- Manzano, P. & Malo, J. E. 2006: Extreme long-distance seed dispersal via sheep. – *Front. Ecol. Environ.* **4**: 244-248. [https://doi.org/10.1890/1540-9295\(2006\)004\[0244:ELSDVS\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0244:ELSDVS]2.0.CO;2)
- Nardi, E. 2015: Il genere *Aquilegia* L. (*Ranunculaceae*) in Italia. – Firenze.
- Nguyen, N. H., Driscoll, H. E. & Specht, C. D. 2008: A molecular phylogeny of the wild onions (*Allium*; *Alliaceae*) with a focus on the western North American center of diversity. – *Mol. Phylogenet. Evol.* **47**: 1157-1172. <https://doi.org/10.1016/j.ympev.2007.12.006>
- Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F. & van Kleunen, M. 2010: Plant phenotypic plasticity in a changing climate. – *Trends Pl. Sci.* **15**: 684-692. <https://doi.org/10.1016/j.tplants.2010.09.008>
- Pearson, D. L., Hamilton, A. L. & Erwin, T. L. 2011: Recovery plan for the endangered taxonomy profession. – *BioScience* **61**: 58-63. <https://doi.org/10.1525/bio.2011.61.1.11>
- Perrone, R., Salmeri, C., Brullo, S., Colombo, P. & De Castro, O. 2015: What do leaf anatomy and micromorphology tell us about the psammophilous *Pancretium maritimum* L. (*Amaryllidaceae*) in response to sand dune conditions? – *Flora* **213**: 20-31. <https://doi.org/10.1016/j.flora.2015.03.001>
- Pfossor, M. & Speta, F. 1999: Phylogenetics of *Hyacinthaceae* based on plastid DNA sequences. – *Ann. Missouri Bot. Gard.* **86**: 852-875. <https://doi.org/10.2307/2666172>
- & — 2004: From *Scilla* to *Charybdis* – is our voyage safer now? – *Pl. Syst. Evol.* **246**: 245-263. <https://doi.org/10.1007/s00606-004-0153-z>

- Pilote, A. J. & Donovan, L. A. 2016: Evidence of correlated evolution and adaptive differentiation of stem and leaf functional traits in the herbaceous genus *Helianthus*. – *Amer. J. Bot.* **103**: 2096-2104. <https://doi.org/10.3732/ajb.1600314>
- Pochynok, T. 2012: Is there a place for Plant Morphology in the contemporary research? – *Modern Phytomorphol.* **2**: 13-16. <https://doi.org/10.5281/zenodo.162422>
- Pyšek, P., Hulme, P. E., Meyerson, L. A., Smith, G. F., Boatwright, J. S., Crouch, N. R., Figueiredo, E., Foxcroft, L. C., Jarošík, V., Richardson, D. M., Suda, J. & Wilson, J. R. U. 2013: Hitting the right target: taxonomic challenges for, and of plant invasions. – *AoB Plants* **5**: plt042. <https://doi.org/10.1093/aobpla/plt042>
- Ronse, A. C., Popper, Z. A. & Preston, J. C. 2010: Taxonomic revision of European *Apium* L. s.l.: *Helosciadium* W.D.J. Koch restored. – *Pl. Syst. Evol.* **287**: 1-17. <https://doi.org/10.1007/s00606-010-0284-3>
- Rotondi, A., Rossi, F., Asunis, C. & Cesaraccio, C. 2003: Leaf xeromorphic adaptations of some plants of a coastal Mediterranean macchia ecosystem. – *J. Mediterr. Ecol.* **4(3-4)**: 25-35.
- Royer, D. L., Wilf, P., Janesko, D. A., Kowalski, E. A. & Dilcher, D. L. 2005: Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. – *Amer. J. Bot.* **92**: 1141-1151. <https://doi.org/10.3732/ajb.92.7.1141>
- Rozendaal, D. M. A., Hurtado, V. H. & Poorter, L. 2006: Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. – *Funct. Ecol.* **20**: 207-216. <https://doi.org/10.1111/j.1365-2435.2006.01105.x>
- Saatkamp, A., Affre, L., Dutoit, T. & Poschlod, P. 2018: Plant traits and population characteristics predict extinctions in a long-term survey of Mediterranean annual plants. – *Biodivers. Conserv.* **27(10)**: 2527-2540. <https://doi.org/10.1007/s10531-018-1551-9>
- Salmeri, C., Brullo, C., Brullo, S., Giusso Del Galdo, G. & Moysiyenko, I. I. 2015: What is *Allium paniculatum* L.? Establishing taxonomic and molecular phylogenetic relationships within *A.* sect. *Codonoprasum* Rechb. – *J. Syst. Evol.* **54(2)**: 123-135. <https://doi.org/10.1111/jse.12170>
- , Brullo, S., Pavone, P. & Guglielmo, A. 2011: La morfologia ultrastrutturale dei semi come strumento per l'identificazione delle specie del genere *Brassica* L. (*Brassicaceae*). – Pp. 45-49 in: Peccenini, S. & Domina, G. (eds): Loci classici, taxa critici e monumenti arborei della flora d'Italia. – Palermo.
- Sattler, R. (ed.) 1978: *Theoretical Plant Morphology, Introduction*. – Leiden.
- 1990: Towards a more dynamic plant morphology. – *Acta Biotheor.* **38**: 303-315. <https://doi.org/10.1007/BF00047245>
- & Rutishauser, R. 1997: The Fundamental Relevance of Morphology and Morphogenesis to Plant Research. – *Ann. Bot.* **80**: 571-582. <https://doi.org/10.1006/anbo.1997.0474>
- Schönenberger, J. & von Balthazar, M. 2012: Modern plant morphological studies. – *Bot. J. Linn. Soc.* **169**: 565-568. <https://doi.org/10.1111/j.1095-8339.2012.01287.x>
- , Chartier, M. & Staedler, Y. 2016: Modern theoretical and technical approaches in plant morphology. – *Mod. Phytomorphol.* **9(Suppl.)**: 79. <http://doi.org/10.5281/zenodo.159706>
- Scoppola, A. & Magrini, S. 2019: Comparative palynology and seed morphology in annual pansies (*Viola* sect. *Melanium*, *Violaceae*): implications for species delimitation. – *Pl. Biosyst.* <https://doi.org/10.1080/11263504.2019.1610113>
- Scotland, R. W., Olmstead, R. G. & Bennett, J. R. 2003: Phylogeny reconstruction: the role of morphology. – *Syst. Biol.* **52**: 539-548. <https://doi.org/10.1080/10635150390223613>
- Speta, F. 1998: Systematische Analyse der Gattung *Scilla* L. (*Hyacinthaceae*). – *Phyton* (Horn, Austria) **38**: 1-141.
- Stace, C. A. 1965: The taxonomic importance of the leaf surface. Current concept of Plant Taxonomy. – London.

- Steiner, F. M., Pautasso, M., Zettel, H., Moder, K., Arthofer, W. & Schlick-Steiner, B. C. 2015: A falsification of the citation impediment in the taxonomic literature. – *Syst. Biol.* **64**: 860-868. <https://doi.org/10.1093/sysbio/syv026>
- Suda, J. & Wilson, J. R. U. 2013: Hitting the right target: taxonomic challenges for, and of, plant invasions. – *AoB Plants* **5**: plt042. <https://doi.org/10.1093/aobpla/plt042>
- Sur, G. L., Keating, R., Snow, N. & Stacy, E. A. 2018: Leaf micromorphology aids taxonomic delimitation within the hypervariable genus *Metrosideros* (Myrtaceae) on O'ahu. – *Pac. Sci.* **72(3)**: 345-361. <https://doi.org/10.2984/72.3.6>
- Tahseen, Q. 2014: Taxonomy - The Crucial yet misunderstood and disregarded tool for studying biodiversity. – *J. Biodiv. Endanger. Species* **2(3)**: 128. <https://doi.org/doi:10.4172/2332-2543>. <http://doi.org/10.4172/2332-2543.1000128>
- Taylor, W. A., Taylor, T. N. & Archangelsky, S. 1989: Comparative ultrastructure of fossil and living gymnosperm cuticles. – *Rev. Palaeobot. Palynol.* **59**: 145-151. [https://doi.org/10.1016/0034-6667\(89\)90013-4](https://doi.org/10.1016/0034-6667(89)90013-4)
- Wilkinson, H. P. 1979: The plant surface (mainly leaf). – Pp. 97-165 in: Metcalfe, C. R. & Chalk, L. (eds), *Anatomy of the Dicotyledons*, 2nd Ed, **1**. – Oxford.
- Xu, F., Guo, W., Xu, W., Wei, Y. & Wang, R. 2009: Leaf morphology correlates with water and light availability: What consequences for simple and compound leaves? – *Progr. Nat. Sci.-Mater.* **19**: 1789-1798. <https://doi.org/10.1016/j.pnsc.2009.10.001>
- Yang, J., Spicer, R. A., Spicer, T. E., Arens, N. C., Jacques, F., Su, T., Kennedy E. M., Herman A. B., Steart, D. C., Srivastava, G., Mehrotra, R. C., Paul, J. Valdes, P. J., Mehrotra, N. C., Zhou, Z.-K. & Lai, J.-S. 2015: Leaf form-climate relationships on the global stage: an ensemble of characters. – *Global Ecol. Biogeogr.* **24**: 1113-1125. <https://doi.org/10.1007/s40820-016-0125-1>

Address of the author:

Cristina Salmeri

Department of Biological, Chemical and Pharmaceutical Sciences and Technologies (STEBICEF), University of Palermo, Via Archirafi 38, 90123 Palermo, Italy. E-mail: cristinamaria.salmeri@unipa.it