

Let's pluck the daisy: dissection as a tool to explore the diversity of Asteraceae capitula

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Asteraceae, the daisy family, are one of the most diverse families of angiosperms and are predominant in many ecosystems, including grasslands, deserts, savannas and high-elevation mountains. They are characterized by a peculiar inflorescence, the capitulum, which mimics a flower, but is actually made up of many tightly grouped florets. The capitulum is considered a key character underpinning the impressive evolutionary success of the family, and it plays a pivotal role in the economic importance of the family, given that many species are cultivated for their capitulum for agricultural and horticultural purposes. However, to date, there is still no comprehensive understanding of the extent of the morphological diversity of capitula across lineages of Asteraceae. This is mainly due to a lack of appropriate tools for describing such a complex and condensed structure. To address the problem, we present a protocol for characterizing the full diversity of capitula from any lineage of Asteraceae. This involves making a whole dissection of a capitulum from fresh material; it is simple and cost-effective and requires relatively easy-to-transport equipment meaning that it can be done during fieldwork.

ADDITIONAL KEYWORDS: capitulum – Compositae – inflorescence – pseudanthium – synflorescences.

INTRODUCTION

The clustering of flowers into inflorescences is a major recurrent evolutionary trend especially associated with pollinator attraction, and it has been widely recognized as playing an important role in the diversification of angiosperms (Weberling, 1992; Rudall & Bateman, 2003). Inflorescence structure controls the number and arrangement of flowers and fruits, constituting a key character influencing reproductive fitness and, sometimes, for domestication and crop production.

With the rise of the field of evo-devo, our understanding of the origin, diversification and function of reproductive traits has improved immensely. However, the study of reproductive characters is still mostly focused on the flower as a functional unit. There is now growing awareness of the need to investigate beyond 'floricentrism' and include inflorescence data to reach a thorough understanding of the overall reproductive investment (Harder *et al.*, 2004; Claßen-Bockhoff & Bull-Hereñu, 2013; Harder & Prusinkiewicz, 2013; Liao & Harder, 2014). In this sense, disentangling the relative contributions and interactions of complex floral and inflorescence traits is critical to achieving a holistic view of reproductive function (Glover, 2011).

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Among the extensive diversity of inflorescences displayed by angiosperms, the pseudanthium (a highly condensed inflorescence that mimics a single flower) constitutes an intriguing case of evolutionary convergence (Classen-Bockhoff, 1990; Prenner, Vergara-Silva & Rudall, 2009). Pseudanthia are found throughout angiosperms (in > 20 families), but are highly characteristic of the daisy family (Asteraceae), in which they are termed capitula, as in a few other plant lineages (e.g. Dipsacaceae, Proteaceae; De Craene, 2022). Asteraceae are currently considered the second most diverse family among angiosperms (after Orchidaceae), with c. 24 700 species and 1627 genera, i.e. c. 10% of the total number of flowering plants (Christenhusz & Byng, 2016; Christenhusz, Fay & Chase, 2017), but if the numerous apomictic species are included, the family may well be larger than Orchidaceae (Hind, 2018). Asteraceae represent a major asset for research due to their key role in shaping landscapes (e.g. sage bushes) and the economic relevance of several representatives (e.g. sunflower, artichoke; Palazzesi *et al.*, 2022b). Asteraceae are distributed worldwide, and they dominate many threatened ecosystems, including grasslands, deserts and high-elevation mountains (Palazzesi *et al.*, 2022a).

Despite being a stable and consistent structure in the family, the capitulum shows an impressive diversity of forms (Leppik, 1970; Harris, 1995, 1999). Among the descriptors accounting for capitulum diversity, the best studied relates to floral symmetry, depending on whether the five petals form a tube (tubular floret, actinomorphic) or are fused in a tongue-like shaped corolla (ligulate 5:0 and bilabiate 4:1 or 3:2 florets, zygomorphic). Most of the research aimed at understanding the evolutionary developmental paths underpinning capitulum formation has concentrated on model plant systems presenting both floret types, e.g. *Anacyclus* L. (e.g. Bello *et al.*, 2017), *Chrysanthemum* L. (e.g. Chen *et al.*, 2018), *Gerbera* L. (e.g. Zhao *et al.*, 2020), *Helianthus* L. (e.g. Chapman *et al.*, 2012) and *Senecio* L. (Garcês, Spencer & Kim, 2016). Nevertheless, some capitula consist of a single type of floret, either tubular, ligulate or bilabiate (Fig. 1). Certainly, capitulum diversity goes beyond symmetry of flowers alone, and it also encompasses, for example, the presence or absence of ray florets, i.e. florets arranged in such a way their corollas radiate around the capitulum and increase its diameter, and thus, its attractiveness (the other type being called disc florets). Ray florets are usually ligulate or bilabiate, and less often tubular. Capitulum diversity also includes variation in the distribution of the sex of each floret, including hermaphrodite, female, male and sterile florets, and a range of possible combinations (Fig. 2). The size, shape and colour of capitula

and each of their constituent parts (i.e. involucre bracts, florets, palea, receptacle etc.; Fig. 1) provide a further level of capitulum diversity. Although many of these characters have been described for floristic and taxonomic purposes, so far no studies have been carried out that address the extent of variation of these traits or their joint evolution across lineages of Asteraceae.

The capitulate inflorescence is seen as a key innovation, which has greatly contributed to the impressive evolutionary success of the family by enhancing reproductive performance (Burt, 1977; Panero & Funk, 2008; Panero & Crozier, 2016; Elomaa, Zhao & Zhang, 2018; Zhang *et al.*, 2021). A main argument evoked to explain the success of the capitulum refers to pollination function. The capitulum is considered to constitute a particularly efficient pollinator attraction unit, especially when presenting perianth-like organs such as ray florets or petal-like bracts (Stuessy, Spooner & Evans, 1986; Andersson, 2008; Cerca *et al.*, 2019). Whenever present, ray florets are the first to open and do not wilt until the last disc florets are at anthesis, hence maintaining capitulum attractiveness throughout the flowering period. Spiral phyllotaxis optimizes the packing of florets in the capitulum (Zhang *et al.*, 2021), resulting in a structure that is efficient as a landing platform and easily explorable by the insect, thus maximizing the number of flowers potentially pollinated per insect visit (this also depends on floral synchrony within the capitulum, which strongly varies between species). Another argument supporting the critical importance of the capitulum for the success of Asteraceae is the fact it provides greater protection of the ovaries and seeds. The involucre, present in all Asteraceae, is a protective envelope in itself, which can also have secretory or non-secretory trichomes and appendages such as spines, constituting an additional layer of protection against environmental and biotic threats, e.g. drought, UV radiation, herbivory (including predispersal seed predation) and pathogens (Villagra, Meza & Urzúa, 2014). Basal and lateral entry of seed predators is reduced by the receptacle and the involucre. When present, the pappus hairs and the palea also limit apical entry and lateral movement of seed predators to other ovaries, in addition to making the inflorescence more condensed and thereby more resistant to desiccation (Stuessy & Spooner, 1988). Functional integration is extremely pronounced: most components of the capitulum contribute to different functions (e.g. support, protection, attraction, pollen and seed production, dispersal), and this is also reflected in the integration of resources allocated to each of them (Torices & Méndez, 2014). On the basis of that, analysing the capitulum in a holistic way is fundamental to strengthening the still limited

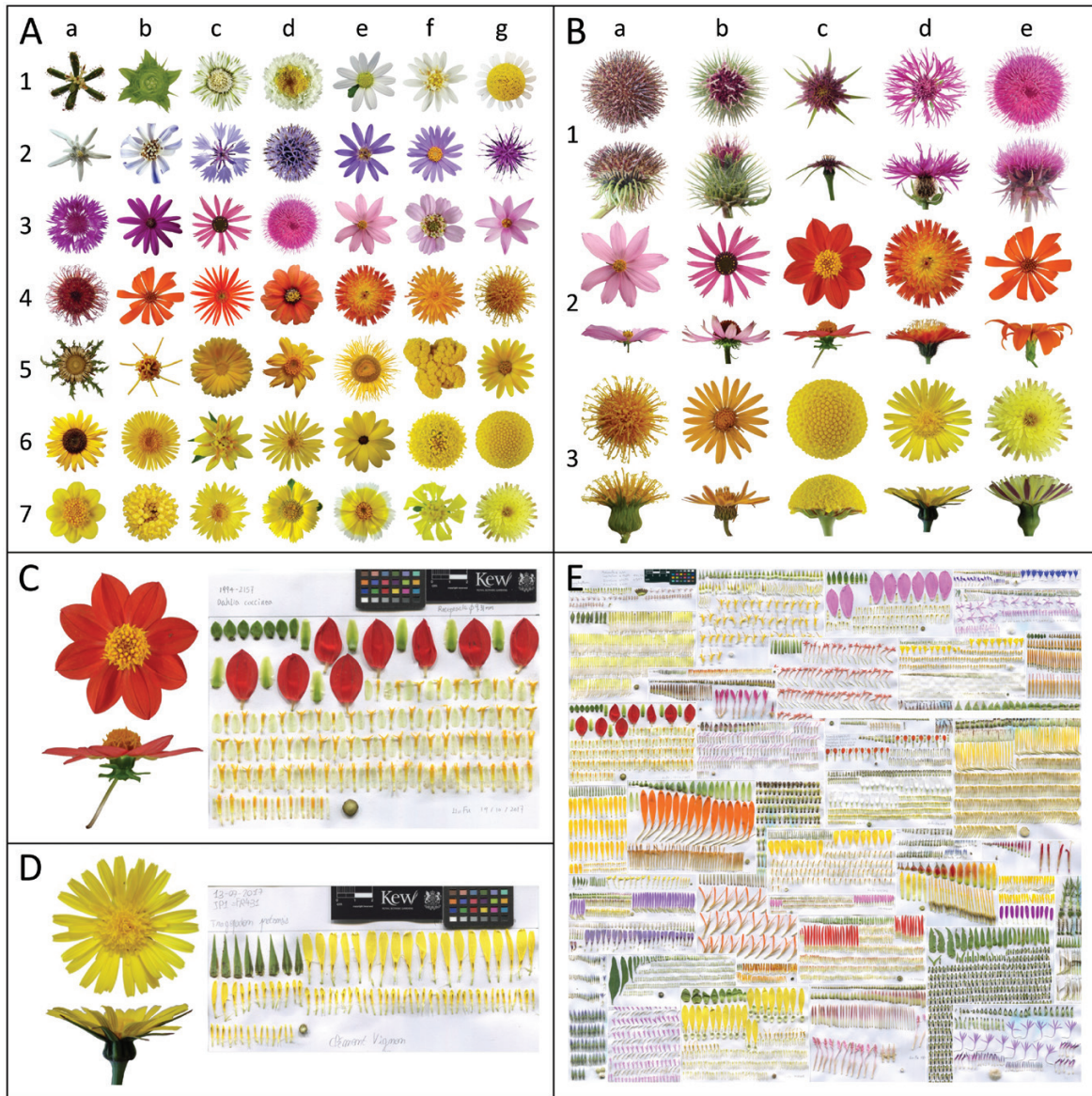


Figure 1. Diversity of capitula. A, B, Examples of capitula illustrating the diversity of forms, shapes and colours. A, Frontal views. From left to right (a–g) and from up to down (1–7): a1, *Adenocaulon chilense*; a2, *Leontopodium stracheyi*; a3, *Psephellus dealbatus*; a4, *Isostigma peucedanifolium*; a5, *Carlina acanthifolia*; a6, *Helianthus annuus*; a7, *Lasthenia* sp.; b1, *Soliva sessilis*; b2, *Perezia linearis*; b3, *Senecio macrocephalus*; b4, *Mutisia decurrens*; b5, *Chuquiraga* sp.; b6, *Pentanema oculus-christi*; b7, *Artemisia glacialis*; c1, *Chaptalia nutans*; c2, *Cyanus segetum*; c3, *Echinacea tennesseensis*; c4, *Gerbera jamesonii*; c5, *Calendula officinalis*; c6, *Trixis californica*; c7, *Grindelia chilensis*; d1, *Polycalymma stuartii*; d2, *Echinops sphaerocephalus*; d3, *Carduus nutans*; d4, *Zinnia peruviana*; d5, *Arnica montana*; d6, *Haplopappus chrysanthemifolius*; d7, *Pallenis maritima*; e1, *Leucanthemum vulgare*; e2, *Olearia phlogopappa*; e3, *Cosmos peucedanifolius*; e4, *Pilosella aurantiaca*; e5, *Telekia speciosa*; e6, *Dimorphotheca sinuata*; e7, *Layia platyglossa*; f1, *Jungia polita*; f2, *Aster alpinus*; f3, *Achillea alpina*; f4, *Crepis aurea*; f5, *Calocephalus platycephalus*; f6, *Santolina pinnata*; f7, *Gutierrezia spathulata*; g1, *Cota triumfetti*; g2, *Serratula tinctoria*; g3, *Schoenia cassiniana*; g4, *Warionia saharae*; g5, *Calendula arvensis*; g6, *Cotula sericea*; g7, *Urospermum dalechampii*. B, Frontal and lateral views. From left to right (a–e) and from up to down (1–3): a1, *Dolomiaea frolowii*; a2, *Cosmos peucedanifolius*; a3, *Warionia saharae*; b1, *Arctium lappa*; b2, *Echinacea tennesseensis*; b3, *Trichocline reptans*; c1, *Tragopogon porrifolius*; c2, *Dahlia coccinea*; c3, *Cotula sericea*; d1, *Centaurea uniflora*; d2, *Pilosella aurantiaca*; d3, *Tragopogon pratensis*; e1, *Carduus nutans*; e2, *Mutisia decurrens*; e3, *Urospermum dalechampii*. C, D, Capitula with their corresponding dissections. C, *Dahlia coccinea*. D, *Tragopogon pratensis*. E, Some examples of capitulum dissections (Images A, B, E from [Hidalgo et al., 2021](#)).

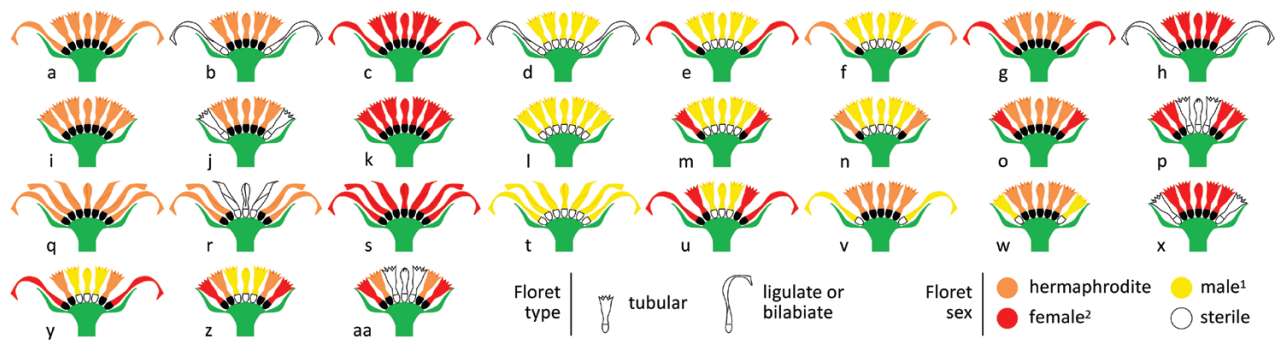


Figure 2. Schemes illustrating 27 possible distributions of floret symmetry type and sex within capitula. They provide qualitative rather than quantitative information (for example, they do not represent the number of rows of each type of flower). Examples for each configuration are given in [Supporting Information, File S1](#). ¹Male or functionally male floret. ²Female or functionally female floret.

empirical evidence supporting its role as a key innovation.

Several factors may be promoting the impressive diversity of capitula, including the following:

1. **Pollen vector.** The vast diversity of angiosperm flowers is commonly interpreted as an evolutionary response to the immobility of plants and the need to recruit vectors to transport pollen from the androecium to the female organs (Barrett, 2010). Pollen vector types strongly impact inflorescence phenotypes, giving rise to the so-called pollination syndromes. Asteraceae are usually entomophilous (pollinated by insects) and considered to have generalist insect pollinators, but the degree of pollinator specificity in the family may have been overlooked, as suggested by recent data (e.g. colour patterns of capitula were found to be linked to particular species within a pollinator functional group; Kemp *et al.*, 2019). Other pollen vectors are also found in the family (e.g. vertebrates; Vogel, 2015).
2. **Reproductive system.** Plants have evolved diverse reproductive systems and strategies that are reflected in a variety of male and female investments (pollen and ovule number, and pollen-to-ovule ratio, P/O; Cruden, 2000). Reproductive systems with low or no reliance on the pollinator [e.g. apomixis (production of seeds without sexual reproduction) or self-fertilization] are expected to have lower reproductive investment than those highly dependent on providing pollination services (Cruden, 2000).
3. **Sex distribution.** In Asteraceae, sex distribution has been shown to correlate with inflorescence size, flower density and seed size, a finding interpreted as a response to optimizing mating success and resource allocation (Torices *et al.*, 2019).
4. **Seed traits.** Asteraceae exhibit a wide variation in dispersal investment and seed dispersal strategy, tightly interwoven and constrained by floral and inflorescence architecture since it is a part of the flower that gives rise to the fruit (cypsela) in Asteraceae. The capitulum might also facilitate the evolution of diversified strategies of seed dispersal within the same inflorescence. Indeed, heterocarpy is common in Asteraceae (Imbert, 2002).
5. **Seed predation.** Predispersal seed predation was shown to relate to capitula size, with larger capitula suffering higher rates of overall seed loss by predation (Fenner *et al.*, 2002; Zhang *et al.*, 2018).
6. **Ecological conditions.** These factors (e.g. abiotic factors such as temperature, growing period, precipitation, wind and UV radiation) influence whole-plant adjustments affecting reproductive structures, but they also influence animal communities that provide pollination and seed dispersal services, thus indirectly shaping biotic interaction patterns (Tong, Wu & Huang, 2021).
7. **Genomic traits.** Polyploidy has been shown to be linked with many aspects of reproductive biology, including floral display (e.g. size and number of flowers; Vamosi *et al.*, 2007), reproductive systems (Vamosi *et al.*, 2007; Pegoraro *et al.*, 2020) and seed predation (Münzbergová, Skuhrovec & Maršík, 2015).
8. **Plant community composition and floral display density.** These have an effect on choices made by pollinators and seed predators (Tong *et al.*, 2021). Investment in attracting pollinators is thus moulded by the presence and relatedness of neighbours (Torices, Gómez & Pannell, 2018).

Disentangling the drivers of capitula evolution requires studying multiple interrelated traits and factors simultaneously. This poses both practical and analytical challenges, starting with the data collection

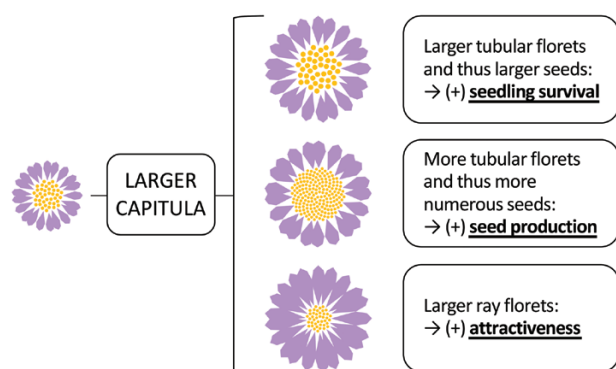


Figure 3. Consequences of larger capitula on female function. Hypothetical increase of capitulum size, leading to three capitula of same size and identical number of ligulate flowers, each reflecting, however, different trends in evolving larger capitula.

of capitulum traits. Morphological descriptors of the capitulum used in previous studies lack consistency and the level of phenotyping accuracy is often insufficient. Indeed, most studies have only described the capitulum roughly, for example by just reporting its diameter or the number of ray florets. This might miss the detection of more subtle, yet critical, variation in other characters (e.g. Fig. 3; Torices & Méndez, 2011).

For all the reasons outlined before, the main goal of this study is to present a newly developed protocol for characterizing the morphological diversity of capitula in Asteraceae. It is based on carrying out a complete dissection of a freshly collected capitulum. This protocol has been designed to preserve as much information as possible. The whole capitulum and each of its parts are photographed and scanned fresh, allowing a huge amount of data to be gathered for its characterization. It is simple, cost-effective, requires relatively easy-to-transport equipment and it can therefore be carried out during fieldwork. This protocol makes it possible to characterize capitula of all sizes and shapes belonging to any lineage of Asteraceae. The protocol works well on a wide range of synflorescences, including syncephalia (= secondary flower heads or ‘capitula of capitula’). The exception is in the most extreme cases of compact syncephalia (e.g. *Sphaeranthus angustifolius* DC.), in which the capitula are so tightly clustered together that a proper description through dissection is difficult. Capitulum dissection has the capacity to become an essential basic tool for taxonomic, evolutionary and functional studies, not only in Asteraceae, but also with some adjustments in other families with pseudanthia (e.g. Adoxaceae, Apiaceae, Calyceraceae, Campanulaceae, Caprifoliaceae, Eriocaulaceae, Myrtaceae, Proteaceae, Rubiaceae and Saururaceae).

MATERIAL AND METHODS

MATERIAL

Capitulum

The capitulum collected for dissection should either be the terminal capitulum of the primary shoot or the terminal capitulum of the distal-most lateral flowering axes (we use the branching hierarchy letter sequence of Wreath *et al.*, 2013; see section Notes, Note 1). The phenological stage of the capitulum is also crucial: at a minimum, the outermost row (i.e. section) of disc florets should be at (or past) anthesis (Note 2).

Equipment needed

1. Photographic equipment allowing for close-up photographs (recommended minimum of 8 megapixels, focal length minimum 30 mm; e.g. an Olympus Tough TG-6 camera, Olympus, Tokyo, Japan).
2. Flatbed photograph scanner (recommended minimum of 2400 dpi; e.g. Epson Perfection V370, Epson, Tokyo, Japan).
3. Computer with the scanner software (e.g. Epson Scan 2; <https://support.epson.com/>).
4. Magnifying glass or stereomicroscope (Note 3).
5. 50-mL Falcon tube, water and tissue paper (Note 4).
6. Digital calliper, ruler and measuring tape.
7. White A4 paper sheets (minimum 160 g/m²; Note 5). Prepare an A4 template as follows: leave a 2.5-cm margin at the top for noting measurements and a 2-cm margin on the left.
8. Fine-tipped tweezers and scalpel (flat tweezers optional).
9. Pencil and rubber.
10. Neutral pH and acid-free polyvinyl acetate formula glue (e.g. Lineco, Holyoke, USA), distilled water for dilution and small flat paintbrush.
11. Colour chart and small paper ruler or millimetre paper.
12. Herbarium press.

METHODS

1. Take a picture of the whole plant growing in its habitat (Fig. 4, part 1).
2. If the capitulum is not solitary, photograph the lateral (Fig. 4, part 2a) and front views (Fig. 4, part 2b) of the flowering stem and measure the width (*A*), height (*B*; the distance between the first node bearing a branch with capitula and the top of the shoot) and diameter of the stem just before the first node bearing a branch with capitula (*C*). Count the number of capitula (*N*) (Notes 6 and 7).

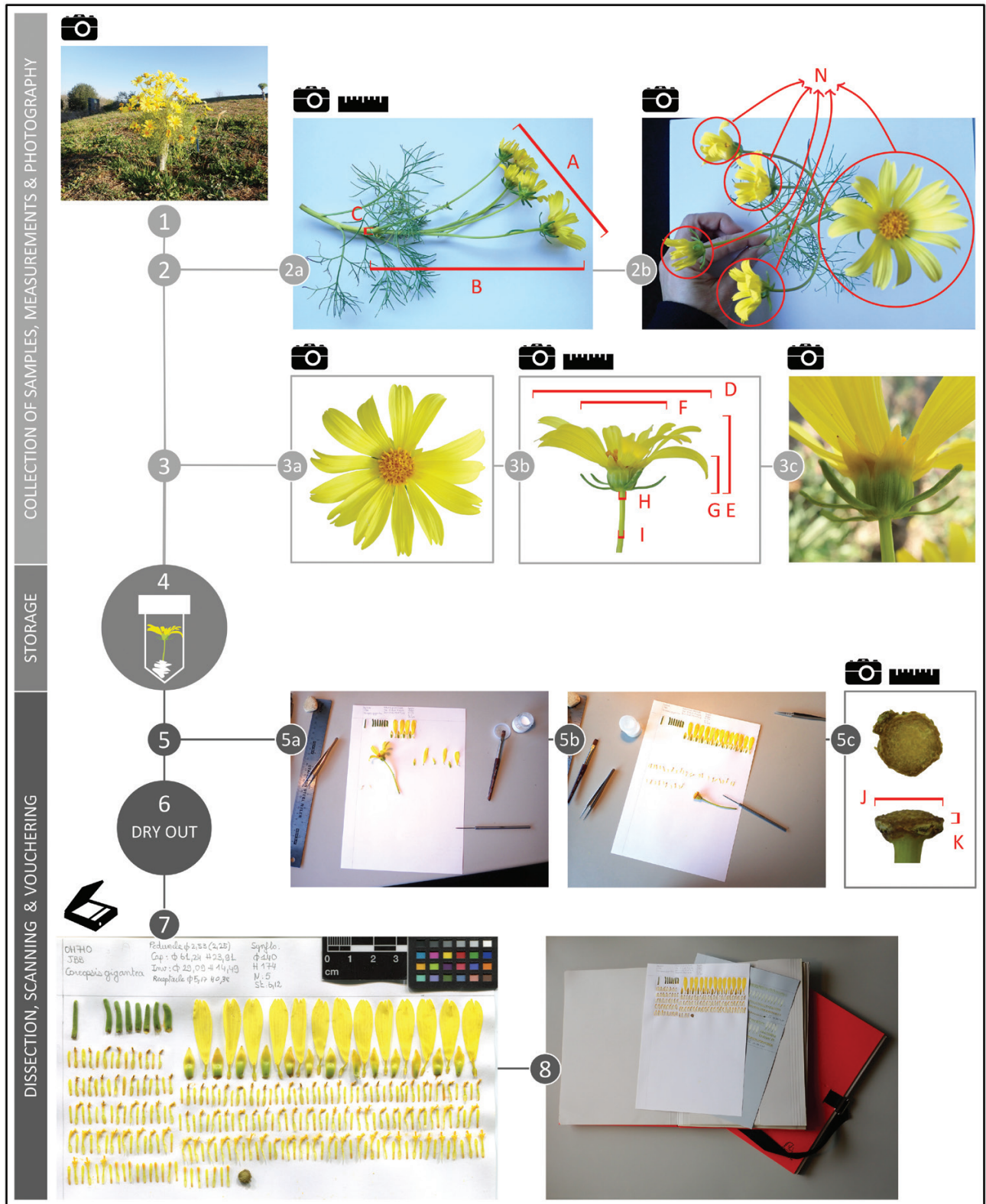


Figure 4. Illustration of the different stages of data collection and dissection. Note that the successive steps included in our protocol (from 1 to 8) are fully explained within the Methods section.

3. Take photographs of the capitulum: front view (Fig. 4, part 3a), lateral view (Fig. 4, part 3b) and a picture of the capitulum seen from below to highlight details of the involucre (Fig. 4, part 3c); take measurements with a calliper as follows: width (*D*) and height (*E*) of the capitulum, width (*F*) and height (*G*) of the involucre, diameter of the stem just below the involucre, where it is often enlarged (*H*) and minimum diameter before the last internode (*I*).
 4. Storage of the capitulum. If not dissected immediately, the capitulum can be preserved at 4 °C in a hermetically sealed box (or a Falcon tube) with the stem wrapped in damp paper tissue for a few days (although for some species capitula deteriorate quickly).
 5. Dissection of the capitulum:
 - (i) Carefully remove the structural pieces constituting the capitulum with the help of tweezers, one by one, starting from the outermost (the involucre bracts) to the innermost (the last floret at the centre of the capitulum; Notes 8 and 9; Fig. 4, part 5a).
 - (ii) Apply diluted glue to the paper sheet with a paintbrush, and glue the detached capitulum parts, arranging them sequentially in rows (Notes 10 and 11; Fig. 4, part 5b). The parts are glued on their least visible side on the capitulum: i.e. the ventral side for involucre bracts and the dorsal side for zygomorphic florets. However, if a character of interest is observed on the underside of the parts, it is possible to glue some of them on the other side.
 - (iii) Take a photograph of the receptacle and measure its width (*J*) and height (*K*). Cut the receptacle from the stem with a scalpel and glue it on the dissection sheet (Fig. 4, part 5c).
 6. Leave the glue to dry (30 min to 2 h).
 7. Scan the dissection on the same day at high resolution (e.g. 2400 dpi) with a colour chart and a ruler (Note 12).
 8. Press and store as an herbarium voucher.
- phenological stage(s) chosen depend on the objective of a given study, it is important when establishing the experimental design to take into account that capitulum traits may vary within an individual, between individuals of the same population and between populations. Also, it is recommended to collect capitula at the same phenological stage throughout a study.
3. This is only needed when the flower head or its components are small and cannot be dissected with the naked eye.
 4. Other containers can be used, but make sure the morphology of the capitulum is not compromised (squeezed/squashed). Instead of using wet tissues, a small amount of agarose gel water solution (concentration c. 2 g/L) can be placed at the bottom of each tube to keep the capitulum hydrated. This is prepared by warming up the agarose gel water solution in the tube to dissolve the agar and then leaving it to cool before using; tubes can be kept refrigerated for up to 1 week.
 5. Use of grey paper is optional for white capitula.
 6. A solid-coloured background (e.g. white or grey paper) is recommended to obtain high contrast photographs.
 7. If this is not clear from the pictures, provide a description of the flowering sequence within the synflorescence.
 8. It is recommended that only a few pieces are detached at the same time, as there is a risk of mixing them up and/or losing some parts.
 9. Dissection can be done under a magnifier or stereomicroscope if the structures are small.
 10. Bear in mind that all parts can be easily removed from the dissection sheet at any time (even months later) by re-hydrating the glue.
 11. For better adhesion, glue can be applied directly on the floral parts (e.g. for curved involucre bracts and tubular flowers). Use as many paper sheets as needed and arrange them sequentially. Dissections can be time-consuming, although this depends on the species, some occupying only a few square centimetres of one sheet and others occupying up to 16 A4 sheets (e.g. *Carlina acanthifolia* All.): make sure to allow sufficient time for dissecting!
 12. The scan is done on the same day as the dissection to avoid colour loss and size change due to desiccation.

NOTES

1. For species presenting dense synflorescences (e.g. *Achillea* L.), at least three capitula per individual should be collected and studied. These should be taken from the centre/top, middle and periphery/bottom of the synflorescence.
2. Although the number of capitula studied per individual and per population as well as the

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REFERENCES

- Andersson S. 2008.** Pollinator and nonpollinator selection on ray morphology in *Leucanthemum vulgare* (oxeye daisy, Asteraceae). *American Journal of Botany* **95**: 1072–1078.
- Barrett SCH. 2010.** Understanding plant reproductive diversity. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 99–109.
- Bello MA, Cubas P, Álvarez I, Sanjuanbenito G, Fuertes-Aguilar J. 2017.** Evolution and expression patterns of *CYC/TB1* genes in *Anacyclus*: phylogenetic insights for floral symmetry genes in Asteraceae. *Frontiers in Plant Science* **8**: 589.
- Burt BL. 1977.** Aspects of diversification in the capitulum. In: Heywood V, Harborne JB, Turner BL, eds. *The biology and chemistry of the Compositae*. Vol. 1. London: Academic Press, 41–59.
- Cerca J, Agudo AB, Castro S, Afonso A, Alvarez I, Torices R. 2019.** Fitness benefits and costs of floral advertising traits: insights from rayed and rayless phenotypes of *Anacyclus* (Asteraceae). *American Journal of Botany* **106**: 231–243.
- Chapman MA, Tang S, Draeger D, Nambeesan S, Shaffer H, Barb JG, Knapp SJ, Burke JM. 2012.** Genetic analysis of floral symmetry in Van Gogh's sunflowers reveals independent recruitment of *CYCLOIDEA* genes in the Asteraceae. *PLoS Genetics* **8**: e1002628.
- Chen J, Shen CZ, Guo YP, Rao GY. 2018.** Patterning the Asteraceae capitulum: duplications and differential expression of the flower symmetry *CYC2*-like genes. *Frontiers in Plant Science* **9**: 551.
- Christenhusz MJM, Byng JW. 2016.** The number of known plants species in the world and its annual increase. *Phytotaxa* **261**: 201–217.
- Christenhusz MJM, Fay MF, Chase MW. 2017.** *Plants of the world*. Kew, Chicago: Kew Publishing and University of Chicago Press.
- Classen-Bockhoff R. 1990.** Pattern analysis in pseudanthia. *Plant Systematics and Evolution* **171**: 57–88.
- Claßen-Bockhoff R, Bull-Hereñu K. 2013.** Towards an ontogenetic understanding of inflorescence diversity. *Annals of Botany* **112**: 1523–1542.
- Cruden RW. 2000.** Pollen grains: why so many? In: Dafni A, Hesse M, Pacini E, eds. *Pollen and pollination*. Vienna: Springer Vienna, 143–165.
- De Craene LPR. 2022.** *Floral diagrams: an aid to understanding flower morphology and evolution*. Cambridge: Cambridge University Press.
- Elomaa P, Zhao Y, Zhang T. 2018.** Flower heads in Asteraceae—recruitment of conserved developmental regulators to control the flower-like inflorescence architecture. *Horticulture Research* **5**: 36.
- Fenner M, Cresswell J, Hurley R, Baldwin T. 2002.** Relationship between capitulum size and pre-dispersal seed predation by insect larvae in common Asteraceae. *Oecologia* **130**: 72–77.
- Garcés HMP, Spencer VMR, Kim M. 2016.** Control of floret symmetry by *RAY3*, *SuDIV1B*, and *SuRAD* in the capitulum of *Senecio vulgaris*. *Plant Physiology* **171**: 2055–2068.
- Glover BJ. 2011.** Pollinator attraction: the importance of looking good and smelling nice. *Current Biology* **21**: R307–R309.
- Harder LD, Jordan CY, Gross EW, Routley MB. 2004.** Beyond floriceentrism: the pollination function of inflorescences. *Plant Species Biology* **19**: 137–148.
- Harder LD, Prusinkiewicz P. 2013.** The interplay between inflorescence development and function as the crucible of architectural diversity. *Annals of Botany* **112**: 1477–1493.
- Harris EM. 1995.** Inflorescence and floral ontogeny in Asteraceae: a synthesis of historical and current concepts. *The Botanical Review* **61**: 93–278.
- Harris EM. 1999.** Capitula in the Asteridae: a widespread and varied phenomenon. *The Botanical Review* **65**: 348–369.
- Hidalgo O, Hidalgo E, Rocabembosch M, Vallès J. 2021.** La botànica: entre art i ciència. In: Redondo M, Figueras M, eds. *HerbArt. Confluències entre art i ciència*. Barcelona: Edicions Universitat Barcelona, 226–243.
- Hind N. 2018.** Introduction to the Compositae, the largest family of flowering plants. *Curtis's Botanical Magazine* **35**: 332–338.
- Imbert E. 2002.** Ecological consequences and ontogeny of seed heteromorphism. *Perspectives in Plant Ecology, Evolution and Systematics* **5**: 13–36.
- Kadereit JW, Jeffrey C. 2007.** *The Families and Genera of Vascular Plants. VIII Flowering Plants, Eudicots, Asterales*. Berlin, Heidelberg, New York: Springer.
- Kemp JE, Bergh NG, Soares M, Ellis AG. 2019.** Dominant pollinators drive non-random community assembly and shared flower colour patterns in daisy communities. *Annals of Botany* **123**: 277–288.
- Leppik EE. 1970.** Evolutionary differentiation of the flower head of the Compositae II. *Annales Botanici Fennici* **7**: 325–352.

- Liao WJ, Harder LD. 2014.** Consequences of multiple inflorescences and clonality for pollinator behavior and plant mating. *The American Naturalist* **184**: 580–592.
- Münzbergová Z, Skuhrovec J, Maršík P. 2015.** Large differences in the composition of herbivore communities and seed damage in diploid and autotetraploid plant species. *Biological Journal of the Linnean Society* **115**: 270–287.
- Palazzesi L, Hidalgo O, Barreda VD, Forest F, Höhna S. 2022a.** The rise of grasslands is linked to atmospheric CO₂ decline in the late Palaeogene. *Nature Communications* **13**: 293.
- Palazzesi L, Pellicer J, Barreda VD, Loeuille B, Mandel JR, Pokorny L, Siniscalchi CM, Tellería MC, Leitch IJ, Hidalgo O. 2022b.** Asteraceae as a model system for evolutionary studies: from fossils to genomes. *Botanical Journal of the Linnean Society* **200**: 143–164.
- Panero JL, Crozier BS. 2016.** Macroevolutionary dynamics in the early diversification of Asteraceae. *Molecular Phylogenetics and Evolution* **99**: 116–132.
- Panero JL, Funk VA. 2008.** The value of sampling anomalous taxa in phylogenetic studies: major clades of the Asteraceae revealed. *Molecular Phylogenetics and Evolution* **47**: 757–782.
- Pegoraro L, Baker EC, Aeschimann D, Balant M, Douzet R, Garnatje T, Guignard MS, Leitch IJ, Leitch AR, Palazzesi L, Theurillat JP, Hidalgo O, Pellicer J. 2020.** The correlation of phylogenetics, elevation and ploidy on the incidence of apomixis in Asteraceae in the European Alps. *Botanical Journal of the Linnean Society* **194**: 410–422.
- Prenner G, Vergara-Silva F, Rudall PJ. 2009.** The key role of morphology in modelling inflorescence architecture. *Trends in Plant Science* **14**: 302–309.
- Rudall PJ, Bateman RM. 2003.** Evolutionary change in flowers and inflorescences: evidence from naturally occurring terata. *Trends in Plant Science* **8**: 76–82.
- Stuessy TF, Spooner DM. 1988.** The adaptive and phylogenetic significance of receptacular bracts in the Compositae. *Taxon* **37**: 114–126.
- Stuessy TF, Spooner DM, Evans KA. 1986.** Adaptive significance of ray corollas in *Helianthus grosseserratus* (Compositae). *The American Midland Naturalist* **115**: 191–197.
- Tong ZY, Wu LY, Huang SQ. 2021.** Reproductive strategies of animal-pollinated plants on high mountains: a review of studies from the ‘Third Pole’. *Journal of Systematics and Evolution* **59**: 1159–1169.
- Torices R, Afonso A, Anderberg AA, Gómez JM, Méndez M. 2019.** Architectural traits constrain the evolution of unisexual flowers and sexual segregation within inflorescences: an interspecific approach. *bioRxiv*: 356147.
- Torices R, Gómez JM, Pannell JR. 2018.** Kin discrimination allows plants to modify investment towards pollinator attraction. *Nature Communications* **9**: 2018.
- Torices R, Méndez M. 2011.** Influence of inflorescence size on sexual expression and female reproductive success in a monoecious species. *Plant Biology* **13**: 78–85.
- Torices R, Méndez M. 2014.** Resource allocation to inflorescence components is highly integrated despite differences between allocation currencies and sites. *International Journal of Plant Sciences* **175**: 713–723.
- Vamosi JC, Goring SG, Kennedy BF, Mayberry RJ. 2007.** Pollination, floral display, and the ecological correlates of polyploidy. *Functional Ecosystems and Communities* **1**: 1–9.
- Villagra CA, Meza AA, Urzúa A. 2014.** Differences in arthropods found in flowers versus trapped in plant resins on *Haplopappus platylepis* Phil. (Asteraceae): can the plant discriminate between pollinators and herbivores? *Arthropod-Plant Interactions* **8**: 411–419.
- Vogel S. 2015.** Vertebrate pollination in Compositae: floral syndromes and field observations. *Stapfia* **103**: 5–26.
- Weberling F. 1992.** *Morphology of flowers and inflorescences*. Cambridge: Cambridge University Press.
- Wreath S, Bartholmes C, Hidalgo O, Scholz A, Gleissberg S. 2013.** Silencing of *EcFLO*, a *FLORICAULA/LEAFY* gene of the California poppy (*Eschscholzia californica*), affects flower specification in a perigynous flower context. *International Journal of Plant Sciences* **174**: 139–153.
- Zhang T, Cieslak M, Owens A, Wang F, Broholm SK, Teeri TH, Elomaa P, Prusinkiewicz P. 2021.** Phyllotactic patterning of gerbera flower heads. *Proceedings of the National Academy of Sciences of the United States of America* **118**: e2016304118.
- Zhang Y, Yang Y, Xi X, Niklas KJ, Sun S. 2018.** Do species with large capitula suffer higher rates of predispersal seed loss than species with small capitula? A field survey of 34 Asteraceae species in an alpine meadow. *International Journal of Plant Sciences* **179**: 554–559.
- Zhao Y, Broholm SK, Wang F, Rijpkema AS, Lan T, Albert VA, Teeri TH, Elomaa P. 2020.** TCP and MADS-box transcription factor networks regulate heteromorphic flower type identity in *Gerbera hybrida*. *Plant Physiology* **184**: 1455–1468.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher’s website.

File S1. Examples of Asteraceae taxa presenting capitula with the different distributions of floret symmetry type and sex, following the illustrations depicted in [Figure 2](#). Unless otherwise indicated, examples are extracted from [Kadereit & Jeffrey \(2007\)](#).