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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. involucral 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 (Burtt, 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, dipersal), 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

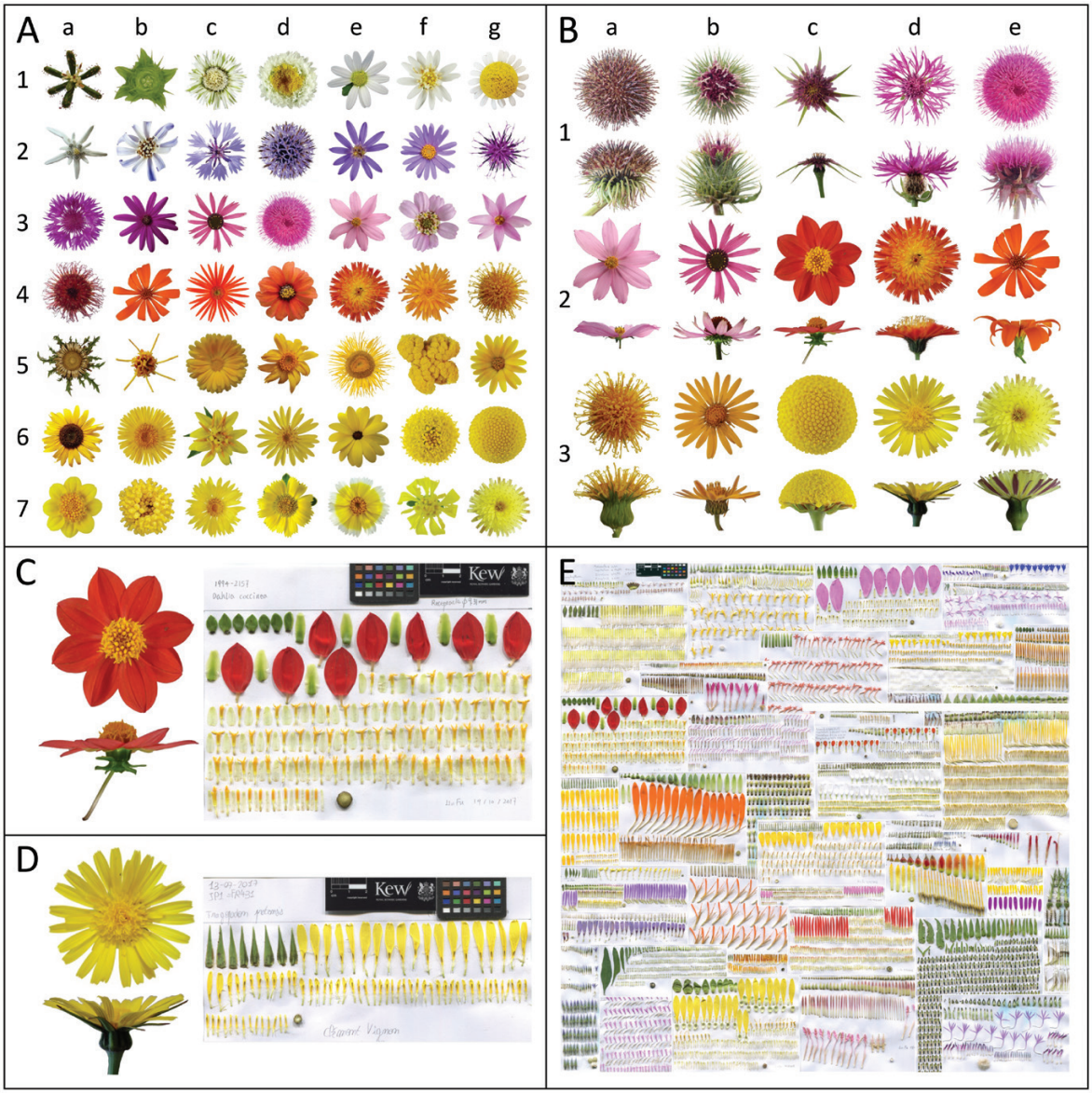

Figure 1. Diversity of capitula. A, B, Examples of capitula illustrating the diversity of forms, shapes and colours. A, Frontal views. From left to right (a–g) and from up to down (1–7): a1, *Adenocaulon chilense*; a2, *Leontopodium stracheyi*; a3, *Psephellus dealbatus*; a4, *Isostigma peucedanifolium*; 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 chiloensis*; 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).

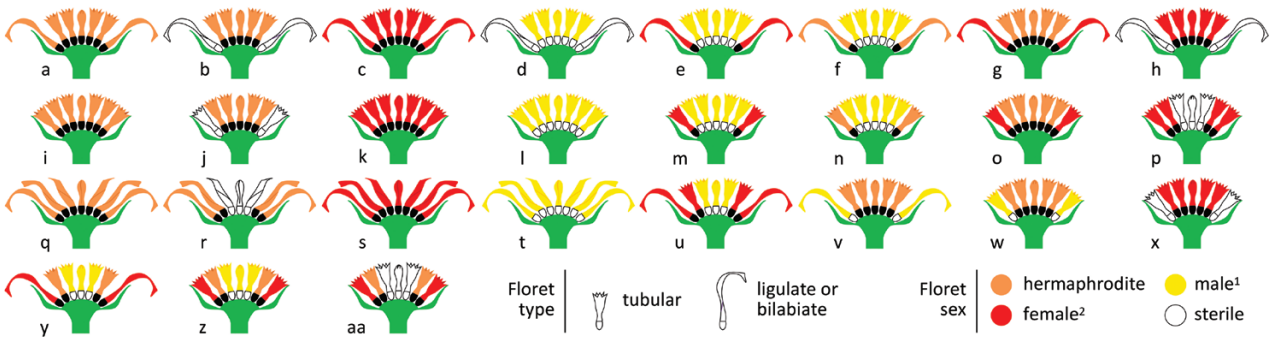

Figure 2. Schemes illustrating 27 possible distributions of floret symmetry type and sex within capitula. They provide qualitative rather than quantitative information (for example, they do not represent the number of rows of each type of flower). Examples for each configuration are given in Supporting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

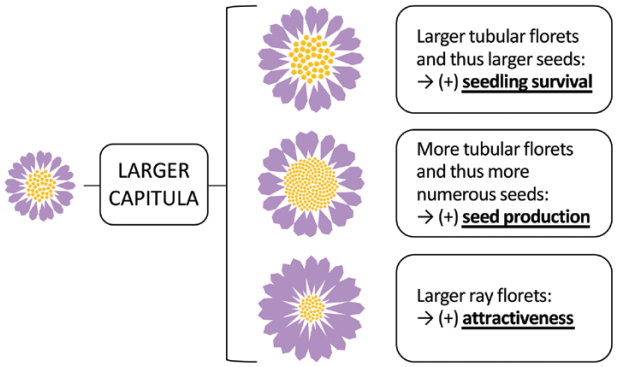

Figure 3. Consequences of larger capitula on female function. Hypothetical increase of capitulum size, leading to three capitula of same size and identical number of ligulate flowers, each reflecting, however, different trends in evolving larger capitula.

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/m^2; 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).

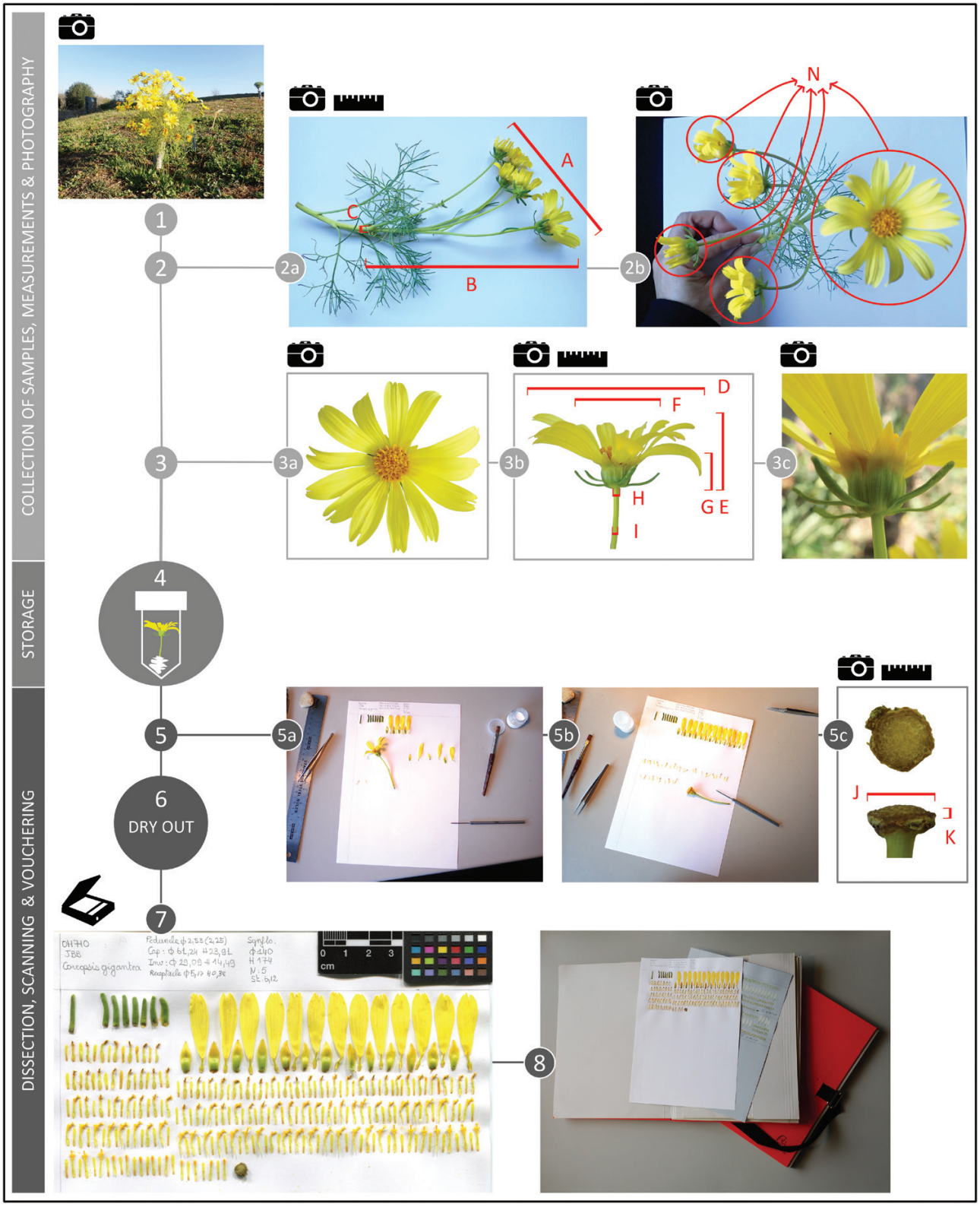

Figure 4. Illustration of the different stages of data collection and dissection. Note that the successive steps included in our protocol (from 1 to 8) are fully explained within the Methods section.

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 involucral 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 involucral 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.

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 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.

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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).