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Development and evolution of the Asteraceae capitulum

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Summary

Asteraceae represent one of the largest and most diverse families of plants. The evolutionary success of this family has largely been contributed to their unique inflorescences, capitula that mimic solitary flowers but are typically aggregates of multiple florets. Here, we summarize the recent molecular and genetic level studies that have promoted our understanding of development and evolution of capitula. We focus on new results on patterning of the enlarged meristem resulting in the iconic phyllotactic arrangement of florets in Fibonacci numbers of spirals. We also summarize the current understanding of the genetic networks regulating the characteristic reproductive traits in the family such as floral dimorphism and differentiation of highly specialized floral organs. So far, developmental studies in Asteraceae are still limited to a very narrow selection of model species. Along the recent advancements in genomics and phylogenomics, Asteraceae and its relatives provide an outstanding model clade for extended evo-devo studies to exploit the morphological diversity and the underlying molecular networks and to translate this knowledge to breeding of the key crops in the family.

Keywords
Asteraceae, capitulum, flower head, development, evolution, phyllotaxy, floret, pappus

I. Introduction

Asteraceae, also known as Compositae or sunflower plant family, with an estimated number of 25 000-35 000 species account for approximately 10% of all flowering plants (Funk et al., 2009; Mandel et al., 2019). Together with orchids (Orchidaceae) and legumes (Fabaceae), Asteraceae represents the most species rich family with 16 subfamilies and 50 tribes (Panero and Crozier, 2016; Mandel et al., 2019; Susanna et al., 2020). It extends all over the world to distinct habitats from arctic to tropics, in wide range of altitudes, and shows enormous variation in developmental traits, secondary metabolites, life histories and growth forms spanning from large trees to shrubs and herbs and even aquatic species (Palazzesi et al., 2022, and references therein). The family includes economically important crops, ornamentals, medicinal plants as well as weeds and invasive species, many of which have been targeted to genome-level studies to develop resources and strategies e.g. for crop improvement. Moreover, a handful of these species are also used as models to achieve fundamental understanding of the genetic mechanisms that drive the enormous developmental variation in the family. In this review, we aim to summarize the most recent work, in the light of key historical discoveries, to understand the development of reproductive traits in Asteraceae.

Understanding the evolutionary history and phylogenetic relationships in Asteraceae have greatly been facilitated by recent developments in genomics and transcriptomics by providing means to reconstruct a well-resolved backbone phylogeny in Asteraceae (Mandel et al., 2014, 2019; Zhang et al., 2021b). Combined with data of available fossil records, the evolutionary age of Asteraceae has been re-estimated to be much older than earlier thought and is now placed to the late Cretaceous appr. 83 MYA (Huang et al., 2016a; Mandel et al., 2019; Zhang et al., 2021b; Palazzesi et al., 2022). The origin of the family is positioned to southern South America from where the family dispersed to Asia and Africa during middle Eocene likely through North America. By the end of Eocene, further colonization associated with greatest diversification of the family occurred from Africa to all continents (except Antarctica), and most recently to North America leading to emergence of most of the present-day tribes (Huang et al., 2016a; Mandel et al., 2019).

What makes Asteraceae so successful? The proposed key innovation is the capitulum (Cronquist, 1977; Jeffrey, 2009), a highly compressed head-like inflorescence that may consist

of a single flower but is generally formed of multiple (tens, hundreds) florets that emerge on an enlarged receptacle (Fig. 1). By layman, this aggregated structure is commonly considered as a single flower and is thus called a pseudanthium or a false flower. The showy capitulum contributes to the economic value of many commercially cultivated ornamentals such as gerbera (*Gerbera hybrida*) and chrysanthemum (*Chrysanthemum morifolium*) while it also provides an efficient pollinator target with selective advantage in promoting reproductive fitness (Stuessy et al., 1986; Sun and Ganders, 1990; Andersson, 2008; Cerca et al., 2019). Additionally, specific organs such as the protective involucral bracts around the entire head as well as the pappus bristles surrounding and protecting each of the florets are considered to have contributed to the evolutionary success of the family (Panero and Crozier, 2016). Apart from developmental traits, it is worth mentioning that the richness of specific secondary metabolites is also a likely reason to the wide ecological distribution of Asteraceae (Panero and Crozier, 2016).

Genomic and genetic studies propose that many key developmental gene families have expanded in Asteraceae and acquired novel functions through neo- and sub-functionalization and/or alterations in gene expression (reviewed in Broholm et al., 2014; Elomaa et al., 2018). The recent studies based on 1087 nuclear genes from 243 Asteraceae species have placed multiple whole genome duplication (WGD) events phylogenetically and proposed altogether nine WGDs and 32 candidate WGDs in the history of the family (Zhang et al., 2021b). The results support the earlier results based on sampling of much smaller number of Asteraceae species (Barker et al., 2008, 2016; Huang et al., 2016a; Song et al., 2018; Zhang et al., 2020) but also revealed many independent WGDs in several tribes. One of the current challenges is to understand, how these duplications associate with emergence of novel traits and developmental complexity in the family and how they have shaped gene functions and gene regulatory networks. Moreover, we lack understanding whether these events may act as drives of increases in diversification rates during the evolutionary history of Asteraceae (Palazzesi et al., 2022).

II. Phenotypic diversity in Asteraceae – large playground for discoveries

Being one the largest plant families, the phenotypic diversity in Asteraceae is huge, yet poorly understood (Palazzesi et al., 2022; Fu et al., 2023). The capitulum-like organization of the inflorescences is characteristic for the whole family (Fig. 1). More generally, a capitulum

represents a type of pseudanthia that refers to flower-like inflorescences that function as single reproductive units. Capitula can also be found in a few other families outside the Asteraceae (e.g. in Dipsacaceae and Proteaceae; reviewed by Baczyński and Claßen-Bockhoff, 2023). In an Asteraceae capitulum, the individual florets emerge on the surface of a receptacle in an iconic spiral arrangement (phyllotaxis, *see below*). The variability among capitulum architectures stems from the diversity of receptacle shapes, the presence or absence of individual floret types, the variability in morphologies of individual florets as well as aggregation of capitula to form higher order structures (Fig. 1; Fig. 2; Fu et al., 2023; Zhang et al., 2021b).

A basic heterogamous capitulum consists of at least two distinct types of florets; the ray florets that occupy the outer margin of the head and the disc florets in the center (Fig. 1a–e; Fig. 2b) while a homogamous capitulum consists of a single floret type (Fig. 1f,g). In heterogamous capitula, the distinction between the floret types is clear-cut as they show differences in their sex and often also in their size and symmetry (Fig. 1b–e). Typically, the outer ray florets are showy, bilaterally symmetrical (zygomorphic), neutral or pistillate (female) while the inner disc florets are much smaller, more radially symmetrical (actinomorphic), often tubular and hermaphrodite (bisexual). The capitula are defined as radiate (Fig. 2b) if they have true ray florets or other type of marginal florets that are morphologically different from the central ones (Bremer, 1994). True ray floret is characterized by a three-lobed lamina (3:0) and is the most common marginal floret type in Asteraceae (Fig. 2b). In addition, some species develop a four-lobed lamina (4:0) (Bremer, 1994). In ray florets of sunflower all five lobes fuse together to form the showy ligule (5:0). As common in Mutisieae tribe, the ray florets in gerbera are bilabiate with three fused abaxial lobes and two tiny adaxial lobes (3:2), and consequently, the capitula are called as bilabiate or radiate-like deviating them from the true radiate capitula (Fig. 2b; Zhang et al., 2021b). In pseudobilabiate capitula the abaxial and adaxial lobes form in 4:1 configuration, respectively (Bremer, 1994). A radiant heterogamous capitula is a specific type found in *Centaurea* species. The ray florets in *Centaurea* are five lobed and their corollas are significantly longer than those in disc florets, yet they are radially symmetrical (Fig. 1d; Fig. 2b). In disciform capitula, the marginal florets are pistillate like the ‘standard’ rays but they lack the large ligule (Fig. 1e; Fig. 2b). If the capitulum is homogamous, and formed of only morphologically ray-like florets, it is called ligulate (Fig. 1f, Fig. 2b). The homogamous discoid heads instead are fully lacking the ray florets and are composed of only disc florets (Fig. 1g, Fig. 2b; Zhang et al., 2021b). This variation in flower heads is further extended by

syncephalious species that develop second order capitula, i.e. “capitula of capitula” (Fig. 1h–j; Fig. 2c). This kind of aggregation may further increase the size of the inflorescence for pollination (Harris, 1999) while its developmental basis is not fully understood.

Recently, reconstruction of ancestral states of key morphological characters in Asteraceae by Zhang et al. (2021b) indicates a transition in the capitulum architecture during evolution. Homogamous, discoid capitulum consisting of only bisexual and isomorphic disc florets is considered ancestral at the root of the Asteraceae. The transition to radiate-like and true radiate, i.e. to flower-like architecture, was found to have occurred several times independently. This transition is considered to have enhanced the attractiveness of capitula to pollinators and consequently, their reproductive success. Also, opposite transitions, from radiate to discoid or disciform capitula, were estimated to have occurred several times independently. Interestingly, the clades with radiate capitula show much larger numbers of species than their sister clades with discoid capitula giving support for the importance of the transition on their evolutionary success (Zhang et al., 2021b).

The adaptive radiations of Asteraceae have also been associated with highly specialized floral structures. The capitulum in all Asteraceae species is surrounded by involucral bracts that perform a protective function for the whole structure (Fig. 1a, Fig. 2d; Fu et al., 2023; Panero and Crozier, 2016). Thinking of the analogy of the capitulum to a single flower, they thus correspond to the sepals in solitary flowers. This analogy is also reflected in patterning of the bract primordia during early meristem development that is tightly regulated with patterning of floret primordia (*see below*, Zhang et al., 2021a). In some taxa, also the individual florets are subtended by a bract or a palea (Fig. 2d) that together with the modified calyx consisting of pappi give further protection for the developing fruit (cypsela). Pappus morphology may vary from hair/bristle- or feather-like to scaly or awn-like structures, but they are also absent in some taxa. A classic example is the parachute-like arrangement of bristly pappus hairs in dandelion (*Taraxacum officinale*) that aid fruit dispersal. In addition to the general organization of florets to form a capitulum, these important functional roles of pappi are also seen as key innovations in promoting the evolutionary success of Asteraceae (Panero and Crozier, 2016). Interestingly, pappus evolved early in the evolution of Asteraceae and have considered to have contributed to the transoceanic dispersal of Asteraceae seeds in the history of its radiation (Carlquist, 1976; Panero and Crozier, 2016). Regarding the key floral traits, the ancestral state reconstruction suggests that the ancestor of Asteraceae most likely lacked the floral subtending bracts (palea)

and developed hair- or feather-like (capillary or plumose) pappi (Zhang et al., 2021b). Furthermore, Zhang et al. (2021b) proposes that the change from ancestral woody to herbaceous habit has played a central role in diversification of Asteraceae.

Due to the enormous morphological variation across the family, Asteraceae provides a promising model clade for evo-devo studies (Fu et al., 2023; Elomaa et al., 2018). So far molecular level understanding of capitulum development is limited by the number of species with existing mutant collections as well as routine protocols for gene functional studies through genetic transformation. Nevertheless, the existing models such as sunflower (*Helianthus annuus*), gerbera, *Chrysanthemum* sp., *Senecio* sp. and lettuce (*Lactuca sativa*) represent distinct types of capitula and show diversification in various key floral traits. Here, we summarize selected, recent work focusing on genetic basis of meristem patterning, flower type differentiation and organ diversity.

III. Patterning and maturation of florets – Fibonacci spirals and pseudowhorls

1. Meristem expansion growth drives the phyllotactic patterning

Capitulum development in Asteraceae is fundamentally different from branched inflorescences, involving key differences already during early ontogeny and patterning of the inflorescence meristem (IM). The major differences relate to meristem size and configuration (Fig. 3). After transition from vegetative to reproductive phase, the IM is rapidly expanding. In sunflower, this expansion has been shown to coincide with activation of the central zone of the meristem resulting in changes in its histological organization (Steeves et al., 1969; Marc and Palmer, 1982). Subsequently, the meristem transforms into a mantle-core configuration consisting of a meristematic surface forming a mantle with five to seven layers of mitotically active cells, and a less active interior core composed of highly vacuolated cells (Harris, 1995; Kwiatkowska, 2008; Claßen-Bockhoff and Bull-Hereñu, 2013; Zhang and Elomaa, 2021). Although this organization resembles a single flower meristem, the size of the final undifferentiated IM e.g., in gerbera and sunflower is extremely large, more than one millimeter in diameter which is approximately ten times larger than the Arabidopsis IM (Fig. 3a–c). Some species in Asteraceae (e.g. *Chrysanthemum morifolium*) show a distinguishable transition apex that is larger than the vegetative shoot apical meristem but fails to initiate bract and floret primordia until exposed to additional cues for flowering (Harris, 1995).

The individual bracts and florets emerge on the expanding IM (Fig. 3d). Their phyllotactic arrangement in spirals, called parastichies, is characteristic for the Asteraceae family. The geometric regularity of this pattern is intriguing; the numbers of intersecting, clock- and counterclockwise spirals are typically consecutive numbers in the Fibonacci sequence (1, 1, 2, 3, 5, 8, 13, 21, 34, 55 etc.). In contrast to Arabidopsis inflorescences, where flowers are arranged in 3 and 5 spirals in each direction, many Asteraceae species exhibit high spiral numbers, e.g., gerbera with 34 and 55 spirals, sunflower with 55 and 89 spirals (Elomaa et al., 2018; Fig. 3a-c). Theoretical studies have suggested that the transition from low to high spiral numbers is linked to changes in the meristematic area and primordium size (van Iterson, 1907; Douady and Couder, 1996). Experimentally, alterations in photoperiodic conditions or gibberellic acid treatments have been shown to affect meristem size, leading to transitions in phyllotaxis from (2,3) to (3,5) spirals in *Xanthium* (Heliantheae, Asteraceae) (Maksymowych and Erickson, 1977; Erickson and Meicenheimer, 1977). So far, little is known how such dynamic changes in meristem size and configuration are genetically regulated.

Meristem expansion growth has been shown to drive phyllotactic patterning in the model plant gerbera (Zhang et al., 2021a; Fig. 3d,e). Versatile microscopic studies indicated that the patterning process can be divided into three major phases (Zhang et al., 2021a). During meristem expansion stage, patterning starts with an increasing number of bract primordia piling along the rim of the meristem (Fig. 3d,e). As the expansion growth ceases, the patterning or generative front (a morphogenetically active zone where the new primordia emerge) moves towards the meristem center with newly formed bract primordia initiating a template for lattice of florets. During the final phase, the central meristematic region gradually decreases in size, the spiral numbers are reduced in reverse Fibonacci numbers, and eventually the IM becomes consumed by the floret primordia (Zhang et al., 2021a; Fig. 3d). The position of the active ring was shown to associate with gerbera *CLAVATA3* (*GhCLV3*) expression domain that is highly dynamic and defines the undifferentiated meristematic area (Zhang et al., 2021a). Considering the resemblance of IM to single flower meristems, the components of the WUSCHEL/CLAVATA signalling network are strong candidates that putatively have evolved to regulate IM expansion growth and active ring dynamics.

2. How do the Fibonacci spirals emerge?

For more detailed analysis of pattern initiation and progression, Zhang et al. (2021a) generated transgenic gerbera plants expressing the *DR5rev:3xVENUS-N7* auxin reporter (Heisler et al., 2005) that marks the incipient bract and floret primordia (initia). During the bract initiation phase, the number of auxin maxima along the rim of the expanding IM increased in preference to Fibonacci numbers (Fig. 3e). The emergence of Fibonacci numbers was found to result from an asymmetry in the space between the neighbouring initia; these gaps are not uniform in size but follow a bimodal distribution being either large (L) or small (S) (Fig. 3e). As the new initia were found to always be inserted in the larger gaps, their total numbers increased according to Fibonacci numbers. The only exception is the second initium whose position is random. Further live-imaging indicated that the asymmetry between the adjacent initia emerged through movement of auxin maxima (inset at Fig. 3e). While an auxin maximum first emerged in the middle between its closest two neighbours, it then moved both radially outwards and laterally towards its older neighbour. Such lateral displacement results in subdivision of gaps into long and short segments (Zhang et al., 2021a; Fig. 3e). By integrating positional information extracted from the micro-CT scanning data, a 3D computational model was further generated to recapitulate the patterning process observed in a real gerbera capitulum (Zhang et al., 2021a; *see* comparison between Fig. 3d and f).

Conventionally, a key measure for robustness of spiral phyllotaxis is the sequential initiation of individual initia in a fixed divergence angle of 137,5°, the golden angle (Mirabet et al., 2012). In Arabidopsis, such robustness is disturbed by the increased size of meristem or loss of inhibitory field caused by cytokinin signalling (Landrein et al., 2015; Besnard et al., 2014). The findings from gerbera capitulum emphasizes that the robustness of spiral phyllotaxis is controlled by precise positioning of the new initia in relation to their neighbouring ones, resulting in Fibonacci numbers of primordia and spirals along an expanding meristem (Reinhardt and Gola, 2022, Godin et al., 2020). Interestingly, regular Fibonacci spirals are often found in non-circular, elliptic or fasciated capitula, where the divergence angle cannot be measured (reviewed in Prusinkiewicz et al., 2022). The computational model developed for circular IM of gerbera (Zhang et al., 2021a) was further extended to these cases emphasizing the role of local interactions in patterning (Prusinkiewicz et al., 2022). What if the local interactions are interfered? Both mechanical wounding as well as laser ablation of the IM results in *de novo* patterning of auxin in the wound margin, but the initiation of new bracts and florets does not occur in Fibonacci spirals (Palmer and Marc, 1982; Hernández and Palmer, 1988; Zhang et al., 2021c). These results indicate that spiral phyllotaxis requires continuous

and undisrupted propagation of positional information from earlier formed primordia. Although phyllotactic patterns in gerbera emerge *de novo* in IMs located in the axillary positions in the shoot rosette (Zhang et al., 2021a), in sunflower Fibonacci numbers of spirals result from continuous progression of the pattern from cotyledons to leaves and further to bracts and florets in the capitulum (Douady and Couder, 1996; Couder, 1998). Considering the diversity of plant architectures in Asteraceae, understanding of early capitulum ontogeny may help to clarify how spiral phyllotaxis is established at mechanistic level in terms of continuity from earlier formed organs.

Similarly, physical treatments to constrain meristem expansion in one direction (resulting in oval meristems) in sunflower disrupted the spiral organization of florets (Hernández and Green, 1993). Moreover, the subdivision of the florets failed, and only large bracts were formed suggesting that mechanical forces also affect organ identities. According to the 'buckling theory' proposed by Hernández and Green (1993) floret patterning emerges from "nothing" and progresses continuously through repeated folding (buckling) of the epidermis, initially on the boundary condition but also over the large meristematic surface. By microsurgical manipulations (cuts and fractures) as well as computer simulations, Dumais and Steele (2000) proposed differences in stress distribution between the meristematic regions. They indicate that the meristem is under radial tension while a zone of circumferential compressive stress is localizing to the generative front to control initiation (buckling) of new primordia. So far, we lack understanding of the factors that define the highly dynamic generative front – could they be physical in nature (as proposed by the buckling theory), and how they potentially affect hormone responses and gene expression or *vice versa*? What is the potential role of internal tissues, and changes in meristem geometry along the development on patterning processes occurring on the surface?

3. Floret maturation follows pseudowhorls

In Asteraceae, efficient reproduction relies on secondary pollen presentation that is a characteristic and ancestral feature of the whole family (Jeffrey, 2009), and strictly coordinated by the daily rhythm to prevent selfing (Baroncelli et al, 1990; Marshall et al., 2023). Pollen presentation occurs through a plunger-style mechanism that separates pollen release and stigma presentation temporally and spatially. During anthesis, and under natural photoperiodic conditions, ovaries first elongate during the night and lift the corolla tubes above the surface

of the capitulum. Next, the anther filaments extend, and pollen is released. After the dawn, the rapidly elongating style pushes the pollen from the anther tube, and at last, stigmas become receptive to pollen on the following morning. In sunflower, anther filament elongation is strongly affected by the photoperiod, and controlled by the phytochrome photoequilibrium (Baroncelli et al., 1990). Continuous white light was shown to suppress filament elongation. *In vitro* treatments by auxin reversed this inhibition while high gibberellic acid concentrations reproduced the continuous white light response (Lobello et al., 2000).

Interestingly, while the initiation of florets in a capitulum occurs in Fibonacci spirals, the final stages of their maturation i.e., timing of anthesis occurs in discrete, ring-like pseudowhorls (Marshall et al., 2023). Recent study by Marshall et al. (2023) in sunflower show how timing of floret opening is controlled by the circadian clock with each whorl of florets undergoing anthesis on successive days. When the circadian oscillator was disrupted under constant light conditions or distinct temperature cycles, the coordination of floret maturation in pseudowhorls was lost and in fact, the florets aged continuously along the spirals (Marshall et al. 2023). Fast and synchronous maturation in pseudowhorls, rather than spirals, was shown to increase pollinator visits showing the importance of the phenomenon for efficient reproduction (Marshall et al. 2023). Interestingly, expansion of individual organs (ovaries, anther filaments, styles) have been shown to respond differently to diverse light and temperature treatments suggesting involvement of distinct regulatory mechanisms (Creux et al. 2021; Marshall et al. 2023). Marshall et al. (2023) also proposed a presence of unknown, local signals between adjacent pseudowhorls that together with developmental and environmental cues as well as the circadian clock are needed to synchronize the onset of anthesis. How are these signaling cascades integrated? What are the molecular components that trigger floret maturation in whorls and not in spirals? It is also not known, how widely a clock-regulated floret development is observed within Asteraceae.

IV. Rays are special

1. Early ontogeny of ray florets

Loss and gain of the marginal ray florets have occurred multiple times independently within Asteraceae (Panero and Funk, 2008; Chen et al., 2018; Spencer and Kim, 2018). The initiation of ray florets and consequently, transitions between radiate and discoid capitula, has been

suggested to be controlled by one or two major genes and an unknown number of modifier genes (Gillies et al., 2002). Although few of them have been identified, the genetic networks are still poorly understood.

The early ontogeny of ray florets deviates them from the disc florets. While in almost all homogamous capitula the florets emerge in an acropetal manner, from the margins towards the center, a general observation in numerous species with heterogamous capitula is that the development of ray florets is visibly delayed compared to the adjacent disc florets (Harris, 1995; Harris, 1999; Bello et al., 2013; Broholm et al., 2014; Ren and Guo, 2015). Harris (1995) interpreted that the ray primordia do initiate but they become suppressed or dormant so that the subsequently formed disc florets surpass them in development. The ontogenetic studies in gerbera indicate that ray primordia initiate at the axils of the innermost involucral bracts and are spatially and temporally separated from the adjacent disc primordia that bulge out earlier (Zhao et al., 2016; Fig. 4a). Similar initiation is apparent in multiple scanning electron microscopy (SEM) figures of distinct Asteraceae species published by Harris (1995). Live-imaging of transgenic gerbera expressing the DR5 auxin reporter show a presence of a common auxin maxima that then separates into two marking the positions of future bracts and rays (Fig. 4b). Functional studies in gerbera showed that the early ontogeny of ray florets is regulated by the meristem identity gene *GhLEAFY* (*GhLFY*) whose expression is localizing to the axils of the bracts (Zhao et al., 2016; *see below*). Interestingly, in specific cases in Asteraceae the 'border zone' between the distinct floret types is not located in the capitulum margin, but in the midway of the highly convex IM (Harris et al., 1991; Harris, 1995). For example, in *Erigeron philadelphicus*, the disc floret primordia are the first to emerge, while the first, and much smaller, ray primordia are only recognized after one to three disc primordia in each parastichy. The IM is consumed in a bidirectional manner - ray primordia emerging basipetally towards the IM margin and disc primordia acropetally towards the center. As in gerbera or sunflower, the ray and disc primordia in *Erigeron* form continuous parastichies (Harris et al., 1991). These findings emerge from relatively late stages of inflorescence development, observed with SEM. However, it is not known, how auxin patterning occurs in an early IM of *Erigeron* – are the florets patterned in continuous parastichies from the margin or is their patterning temporally separated? Moreover, it is not known if the expression of *LFY* homolog of *Erigeron* is associated with ray primordia.

The *missing flowers* (*mf*) mutant in sunflower completely lacks ray florets but also shows reduced numbers of disc florets and lack of shoot branching because of defects in axillary meristem development (Fambrini et al., 2003). The phenotype is caused by a single recessive mutation in a bHLH transcription factor encoding gene, *REGULATOR OF AXILLARY MERISTEM FORMATION-LIKE* (*Ha-ROXL*) (Fambrini et al., 2017). In the IM, *Ha-ROXL* is transiently expressed in an arch-like region that marks the initiating disc primordia. Later, this primordium is separated into two parts with the adaxial part adopting the fate of a floret and abaxial a bract (palea) (Fambrini et al., 2017). In *mf* mutant, only the large floret subtending bracts develop, leaving an empty space in the place of the floret primordia. The phenotype suggests that *Ha-ROXL* defines the competence of these meristematic cells to initiate florets (Basile et al., 2019). Interestingly, the expression *Ha-PIN1*, an auxin efflux carrier, was highly reduced in *Ha-ROXL* silenced plants (Basile et al., 2019). Further studies are required to define the role of *Ha-ROXL* in ray initiation, potentially involving LFY and/or other boundary specifying genes as part of the early regulatory cascade, downstream of auxin.

In addition to *ROXL*, additional candidate genes for early ray initiation have been proposed. Transcriptome profiling in chrysanthemum identified *NAM*, *CUC2/3* and *LOB3* genes as potential hub genes involved in differentiation of ray and disc florets (Wen et al., 2022). Interestingly, *NAM* and *LOB3* gene expression was detected in species with radiate capitula (several *Chrysanthemum* sp., *Erigeron brevisca*, *Helianthus annuus*) while they were not expressed in discoid (*Hippolytia alashanensis*, *Helenium aromaticum*) and ligulate (*Lactuca sativa*, *Taraxacum kok-saghyz*) species. Predicted protein interactions revealed LFY as a potential interactor of NAM/CUC and LOB3 proteins to regulate ray primordia development (Wen et al., 2022). Detailed *in situ* hybridization analyses to localize the expression domains of these genes as well as functional studies to verify their roles are still needed.

2. Regulation of ray floret identity – the role of *CYCLOIDEA*-like genes

The lack of ray-like, marginal florets in discoid capitula has been associated with *CYCLOIDEA* (*CYC*)-like TCP domain transcription factor gene functions. CYC2-clade proteins are well-known, conserved regulators of flower symmetry and extensively studied across angiosperms (for recent reviews *see* Fambrini and Pugliesi, 2017; Spencer and Kim, 2018; Jiang and Moubayidin, 2022; Chai et al., 2023; Viola and Gonzalez, 2023). In Asteraceae, it has been challenging to separate the potential early functions of CYC2-clade genes in defining ray floret

initiation from their apparent late functions in petal and stamen development in defining floret identity.

The polymorphism in capitula of *Senecio vulgaris* (groundsel), a native species in British Isles with both discoid and radiate variants, is controlled by a single locus (Trow, 1912; Ingram and Taylor, 1982). The radiate trait in groundsel has resulted from introgression of the RAY locus from *Senecio squalidus* (Oxford ragwort), an introduced garden escape on the Isles (Harris, 2002; Marshall and Abbot, 1980). Kim et al. (2008) showed that the RAY locus comprises of two, tightly linked CYC2-clade genes, *RAY1* and *RAY2*, both of which are specifically expressed in the marginal ray primordia. Interestingly, although *RAY1* and *RAY2* segregated with the capitulum phenotypes, both were also expressed in the periphery of the discoid capitula, but at higher level (Kim et al., 2008). This suggested that *RAY1* and *RAY2* might negatively regulate ray primordia initiation. However, the functional studies in transgenic *Senecio* did not reveal clear correlation between the observed phenotypes and gene expression levels (Kim et al., 2008). The *Senecio RAY3* was shown to promote *RAY1* and *RAY2* expression in ventral petals indicating their late functions in ligule elongation and establishment of bilateral symmetry of ray florets (Garcês et al., 2016). In *Chrysanthemum lavandulifolium*, overexpression of *ClCYC2d*, an ortholog of *RAY1*, was shown to suppress the development ligules and stamens in marginal florets (Chen et al., 2018). However, it is not clear whether the effect of *ClCYC2d* was restricted to organ growth and whether the ray primordia still initiated in these lines.

In sunflower, *HaCYC2c* has been identified as the major gene to regulate ray floret identity (Fambrini et al., 2011; Chapman et al., 2012). Mutations suppressing *HaCYC2c* expression resulted in replacement of ray florets by radialized, tubular florets (Chapman et al., 2012; Fambrini et al., 2011). In multiple cultivars, an insertion of a truncated CACTA transposable element (TE) in the promoter, instead, resulted in ectopic expression of *HaCYC2c* across the capitula converting the central florets into ray-like, with non-functional carpels and anthers (Chapman et al., 2012). However, Fambrini et al. (2014) discovered that the insertion of the TE in *HaCYC2c* promoter does not always lead to ectopic expression and shift towards zygomorphic florets suggesting that the regulation of flower type identity is much more complex and genotype specific. In sunflower, discoid capitula are found in *Helianthus radula*, a species widespread in southeast of USA (Mason et al., 2015; Fambrini et al., 2020). Although *H. radula* occasionally forms ray florets, they are few and tiny, and not comparable to any other

Helianthus species (Heiser et al. 1969; Fambrini et al., 2020). Fambrini et al. (2020) showed that a functional allele of *HrCYC2c* gene is necessary, but not sufficient, for ray initiation. The homozygous plants with mutated *HrCYC2c-m* failed to initiate ray florets and formed discoid heads. In homozygous *HrCYC2c/HrCYC2c* and heterozygous *HrCYC2c/HrCYC2c-m* plants ray florets were initiated but in low frequency and often with developmental abnormalities indicating that additional genes are needed to form a complete radiate capitula (Fambrini et al., 2020).

CYC2-clade gene family has expanded in Asteraceae with distinct paralogs recruited to define ray identity in different species (Chapman et al., 2008; Kim et al., 2008; Tähtiharju et al., 2012; Garcês et al., 2016; Huang et al., 2016b; Bello et al., 2017; Chen et al., 2018). As in sunflower, the expression of many (but not all) CYC2-clade homologs in gerbera (Broholm et al., 2008; Tähtiharju et al., 2012; Juntheikki-Palovaara et al., 2014), chrysanthemum (Huang et al., 2016b; Chen et al., 2018; Shen et al. 2021) and *Anacyclus* (Bello et al., 2017) are localized into marginal floret primordia. Transgenic or mutant lines show variable phenotypes mostly affecting, either positively or negatively, and in a species-specific manner, the elongation growth and fusion of ligules as well as differentiation of stamens (reviewed in Fambrini and Pugliesi, 2017; Elomaa et al., 2018; Spencer and Kim, 2018; Zhang and Elomaa, 2021). Apparently, silencing of single CYC2-clade genes is not sufficient to abolish ray floret initiation suggesting potential redundancy among the gene family members or involvement of additional factors. Moreover, the complex regulatory interactions among and between the CYC/TB1-like proteins may have hampered the functional studies (Tähtiharju et al., 2012; Garcês et al., 2016). So far, the functional studies have not led to clear mechanistic understanding, if and how CYC2-clade gene functions would define the early initiation of ray primordia apart from their role in establishing bilateral symmetry of rays by affecting late growth of floral organs.

Very little is known of upstream regulators of CYC2-clade genes. Zhao et al. (2020) applied yeast one-hybrid screens to identify putative regulators of *GhCYC3*, a key gene that specifies ray identity in gerbera. Among the candidate transcription factors, two CINCINNATA-like TCP proteins (GhCIN1, GhCIN2) were shown to activate the *GhCYC3* promoter-reporter construct. Similarly to *GhCYC3*, *GhCIN1* expression was localizing to the initiating ray primordia in the axils of involucral bracts. Suppression of *GhCIN1/2* expression resulted in down-regulation of *GhCYC3* expression and altered the early ontogeny of ray primordia. The

emerging ray primordia did not show the typical delay in early organogenesis but in fact, they developed faster than the adjacent disc primordia (Zhao et al., 2020). *GhCYC3* was also shown to have a late function during ligule elongation downstream of a SEPALLATA-like MADS-box protein GRCD5.

Recently, Castricum et al. (2023) identified mutant lines in *Chrysanthemum morifolium* with increased disc:ray floret ratio. As the total number of florets in the mutants were not changed, the phenotypes suggest a change in floret identity resulting in reduced number of ray florets. Silencing of two candidate genes identified in comparative transcriptome analyses mimicked the mutant phenotypes. Downregulation of the *CmDWF1* (*DWARF1*), a brassinosteroid (BR) biosynthetic gene, or a HD-ZIP class IV homeodomain transcription factor gene *CmPDF2* (*PROTODERMAL FACTOR* 2), resulted in increased disc:ray ratio (Castricum et al., 2023). The role of BR was supported by BR inhibitor (brassinazole) treatments that significantly increased the percentage of disc florets. Castricum et al. (2023) proposes a gradient of BR across the capitulum to regulate the identity of the florets. Interestingly, an asymmetrically expressed CYC2 clade gene *TCP1* in Arabidopsis (Cubas et al., 2001) has been shown to activate BR biosynthesis by directly binding to the promoter of *DWARF4* that encodes the rate limiting enzyme of the pathway (Guo et al., 2010; Gao et al., 2015). Moreover, *TCP1* expression itself was shown be activated by BR (Guo et al., 2010). A similar feedback loop between the ray specific *CYC2* clade genes and BRs in Asteraceae could potentially contribute to regulation of ray floret identity. Also the plant hormone auxin has been shown to form a temporal gradient across the capitulum in *Senecio vulgaris* (Zoulias et al., 2019). In *Matricaria inodora*, exogenous auxin treatment converted the central disc florets into bracts or ray florets in a concentration-dependent manner. In *Matricaria*, auxin was shown to regulate the expression of *LFY* and a CYC2 clade gene *MiRAY2* known to define ray identity (Zoulias et al., 2019).

3. Further elaborations on ray floret ligules

The bilateral symmetry and large size of ray florets contribute to the showy appearance of the capitula. Moreover, ray florets have evolved specialized color patterns that promote the reproductive fitness of the plants. In nature, color and UV patterns in petals have been shown to be crucial for pollinator preferences (Reverté et al., 2016). For example, *Chrysanthemum* (*sl.*) species exhibit white ray floret ligules that are different from the yellow disc florets. This

trait is controlled by ray-specific expression of a gene encoding carotenoid cleavage dioxygenase (*C. morifolium* CmCCD4a) that catalyzes degradation of yellow carotenoids (Ohmiya et al., 2006). Recent studies indicate that CYC2g, a major regulator of ray floret identity, binds the promoter region of *CcCCD4a* of *C. chanetii* and confers its ray-specific expression. The data indicates evolutionary co-option of two distinct pathways regulating ray floret development and pigmentation (Zhang et al., 2022).

Not limited to visible light, the ligules of sunflower ray florets display variable patterns under UV reflection forming classical bullseyes phenotypes visible to pollinators (Wojtaszek and Maier, 2014). Through genome wide association analysis, Todesco et al. (2022) found out that variation in UV reflection can be attributed to a conserved gene *HaMYB111* that regulates the biosynthesis of UV-absorbing flavonol glycosides. Consistently with well-known functions of UV patterns as visual cues, they were shown to affect pollinator attraction in sunflower. However, the authors further found that variation in UV patterns was associated with environmental factors such as drought. Interestingly, the large UV patterns prevented water loss from ligules and helped the plant to prevent drought stress. The work nicely demonstrates how floral diversity in Asteraceae is shaped by both biotic and abiotic factors (Todesco et al., 2022).

The ray floret ligules may also show more complex color patterns. In *Gorteria diffusa*, the ligules develop special, black-colored spots, typically arranged 137,5° apart from each other, to functionally mimicry the female *Megapalpus* flies (Ellis and Johnson, 2009; Thomas et al., 2009). Recently, Kellenberger et al. (2023) found out that the evolution of petal spots in *Gorteria diffusa* originates from a sequential co-option of genes from three distinct regulatory modules; the ion homeostasis genes for colors, a root hair gene for epidermal cell elaboration, and miR156-GdSPL1 for spatial coordination of petal positions. Taken together, all these examples, having evolved independently in distinct tribes of Asteraceae, illustrate how complex traits pyramid through co-option and interplay of distinct regulatory genes, adding further selective advantage to the showy ray florets.

V. Pappus bristles – a specialized floral organ type to aid seed dispersal

In many Asteraceae species, the outermost organ whorl of individual florets is occupied by specialized organs, the pappus bristles (Fig. 5). Their presence across early diverging tribes

indicates their ancient role associated with Asteraceae evolution (Bremer, 1994). Pappus bristles form a bundle of bristly filaments that are generally considered as modified calyx (Fig. 5a,b; Small, 1919). Developmentally, up to hundreds of pappus primordia emerge from a ring meristem in the perianth of a floret primordium (Fig. 5c,d; c.f. Harris, 1995). Functional studies in gerbera revealed that overexpression of B-class MADS box genes led to homeotic transformation of pappi into petals (Yu et al., 1999), whereas loss of function of E-class *SEPALLATA*-like genes converted them into bract or leaf-like structures (Zhang et al., 2017). These results support a sepaloid origin of pappus with E function genes playing a key role in regulating their highly modified morphology.

Pappus bristles offer unique advantage for long-distance seed dispersal and have even been proposed to have contributed to the transoceanic dispersal of seeds during radiation of Asteraceae (Panero and Crozier, 2016). The plumed seeds in dandelion (*Taraxacum* sp.) may fly over a few kilometers before landing. Cummins et al. (2018) employed a vertical wind tunnel and revealed a novel flying mechanism in dandelion seeds mediated by a separated vortex ring (SVR) forming underneath the circular disk-like structures formed by pappus bristles (Fig. 5e). The size and shape of SVR, which directly determines the stability and velocity of flight, is not only affected by the porosity and thickness of pappus (Cummins et al., 2018; Ledda et al., 2019), but also by the opening angles of them (Seale et al., 2022a). Interestingly, the opening angles are regulated by coordinated swelling of a group of actuator cells where pappus bristles are attached (Seale et al., 2022b). The dandelion seeds can thus adjust their pappus bristles into open, flat (in dry) or closed, cone-shaped (in wet) planes to fine-tune their flying velocity and their ability to detach from the receptacle to accommodate surrounding environmental conditions (Seale et al., 2022a).

VI. Evolution of Asteraceae capitula

Within Asterales the so called MGCA-clade consists of families of Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae, of which Calyceraceae, the small South American family with only 47 species, is sister to Asteraceae (Hansen, 1992; Lundberg, 2009; Denham et al., 2016). During evolution, the inflorescence architectures in the MGCA-clade were modified through stepwise condensations leading to emergence of the compressed capitulum architecture in Asteraceae (Fig. 6a; Jeffrey, 1977; Harris, 1999; Pozner et al., 2012). The inflorescences in the basal families Menyanthaceae and Goodeniaceae are elongated,

branched structures that combine a racemose main axis with lateral cymose branches (Fig. 6a). The inflorescences in Calyceraceae instead form condensed head-like structures, called cephalioids, that are surrounded by involucral bracts (Pozner et al., 2012; Denham et al., 2016; Fig. 6a,b). In cephalioids, internode elongation is highly suppressed in the main axis, in lateral branches as well as in pedicels. Different from the Asteraceae capitula, cephalioids develop a distal terminal flower that is surrounded by individual florets, each subtended by a bract (Fig. 6b,c). Moreover, cephalioids in the basal Calyceraceae species develop so called peripheral cymose units formed of 2–7 florets. These units correspond to the extended cymose branches observed in Menyanthaceae and Goodeniaceae (Pozner et al., 2012; Fig. 6a). Pozner et al. (2012) thus proposed that, in addition to suppressed internode elongation, Asteraceae capitula were derived from cephalioids through two additional morphological changes: loss of the terminal flower and reduction of the cymose units into single (ray) florets (Fig. 6a).

The presence or absence of a terminal flower is considered as a key criterion to differentiate determinate and indeterminate inflorescences (Weberling, 1989). Due to lack of a terminal flower, Asteraceae capitula were previously classified as indeterminate (Harris, 1999). However, the IM of the capitulum follows a determinate growth pattern resulting in production of relatively fixed number of florets (Teeri et al., 2006). Considering the ontogeny, Claßen-Bockhoff and Bull-Hereñu (2013) introduced a concept of a flower unit meristem (FUM) that are distinct from indeterminate IMs and are proposed to have evolved from single FMs. FUMs resemble single FMs in lacking apical growth but also by their histological organization in forming a distinct mantel-core structure (Kwiatkowska, 2008; Marc and Palmer, 1982; Zhang and Elomaa, 2021). Analogous to single FMs that produce floral organs, FUM grows by expansion and produces florets by subdivision (fractionation) of the meristem. Molecular studies in gerbera show that the conserved floral regulators *GhLFY* (Zhao et al., 2016) and *SEPALLATA*-like *GRCD2/7* (Zhang et al., 2017) have been recruited to function at the level of FUM/IM (reviewed in Elomaa et al., 2018; Zhang and Elomaa, 2021). *LFY* and *GRCD* genes are uniformly expressed on the expanding, dome-shaped IM before bulging of the individual floret primordia (Zhao et al., 2016; Zhang et al., 2017; Li et al., 2019; Castricum et al., 2023). The transgenic gerbera lines with downregulated *GhLFY* or *GRCD2/7*, develop IMs that are indeterminate and produce infinite number of florets (Uimari et al., 2004; Zhao et al., 2016; Zhang et al., 2017; Fig. 6d-f). The gerbera homolog of the FM identity gene *UNUSUAL FLORAL ORGAN* (*UFO*) instead is associated with FM identity. Overexpression of *GhUFO* converts the capitulum into a single flower that produces floral organs in concentric whorls

(Zhao et al., 2016). Interestingly, *GhUFO* overexpression lines with mild phenotypes first produce a few floret primordia and then a giant terminal flower as in cephalioids in Calyceraceae (Zhao et al., 2016; Fig. 6g). The absence of *GhUFO* expression during late IM development in gerbera (Zhao et al., 2016) suggests that it may cause the lack of terminal flower development in a FUM. Alternatively, potential candidate regulators are those that maintain indeterminacy during late IM development such as orthologs of TERMINAL FLOWER 1.

As discussed in the previous chapter, ray florets in Asteraceae initiate from the axils of involucral bracts. It has been proposed that the delayed development of ray florets in Asteraceae can be interpreted as remnants of the cymose peripheral units that are still observed in some species of Calyceraceae (Pozner et al., 2012). Functional studies in gerbera revealed a key role for *GhLFY* in early ontogeny of ray florets (Zhao et al., 2016). Suppression of *GhLFY* expression in transgenic gerbera converted the ray primordia into large, oval-shaped structures that further branched into two or three primordia. These structures develop without any delay (Zhao et al., 2016), and their ontogeny resembles the peripheral cymose units in Calyceraceae (Pozner et al., 2012; Harris, 1999). The data suggests that *GhLFY* has evolved a major role in defining the floral fate of ray primordia in Asteraceae through suppression of cymose branching. Interestingly, in *Lagascea* species of Asteraceae, meristems with similar cymose branching were observed in their syncephalia (Harris et al., 1994).

So far, the interpretations of the evolutionary origin of Asteraceae capitula by both Pozner et al. (2012) and Claßen-Bockhoff and Bull-Hereñu (2013) have been supported by molecular studies. Future investigations on spatio-temporal changes in the expression of meristem identity genes and their functions in Calyceraceae, and in Asteraceae species with syncephalia are required to unravel the details of evolution of capitulum architecture.

VII. Conclusions and perspectives

The phenotypic diversity in Asteraceae is huge. Apparently, many morphological novelties, and most importantly the showy ray florets with their main role in defining the type of the capitulum (Fig. 1), have evolved multiple times independently in the family in association with complex radiation and diversification events. We do not currently understand whether same genes and/or gene networks are recruited for all these transitions across Asteraceae and how

they relate to distinct whole genome duplication events in the family. Only a few candidate genes affecting ray floret initiation and their differentiation have been identified, and those in a limited number of model species. The recent results in developmental patterning (Fig. 4; Zhao et al., 2016) indicate that most analyses comparing distinct floret types have focused on relatively late developmental stages when organ differentiation has already been initiated and thus, are not likely to reveal the early regulators of floret primordia initiation. Alternative strategies such as spatial or single cell transcriptomics or laser capture microdissection may provide more detailed understanding e.g., of the highly localized initiation of ray florets.

The resemblance of Asteraceae IM with single flower meristems is intriguing. Many floral regulators have been recruited to function at IM level through gene duplications and subsequent sub- and neofunctionalization (Elomaa et al., 2018). Thereby, it is tempting to consider whether IMs can be used as models to understand patterning of flower meristems. The large size of the IM provides several benefits. For example, the gerbera IMs can be grown in tissue culture for live-imaging (Zhang et al., 2021a) and they can be targeted to laser ablation treatments (Zhang et al., 2021c). Spiral phyllotactic patterning is driven by the expansion growth the IM but the regulators are still not known neither are the mechanism for lateral movement of auxin maxima. Are they universal in all spirally organized systems including individual flowers?

Recent molecular data gives support for the two key hypotheses of the evolutionary origin of capitula. How do these hypotheses – evolution from branched inflorescences or single flower meristems – fit together? What are the key genetic changes behind the compression of heads and their expansion? Are they shared with Calyceraceae? Future evo-devo studies should discover the potential for much broader scale functional studies. Especially appealing are the close relatives in Asteraceae e.g., in Calyceraceae that still lack methods for gene functional studies using transgenic plants.

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Author contributions

P.E. and T.Z. designed and wrote the manuscript. T.Z. generated the figures.

Competing interests

None declared.

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Figure legends:

Fig. 1 The basic structure and examples of the phenotypic diversity in Asteraceae capitula. (a) Overall structure of a capitulum of *Gerbera hybrida* shown by a longitudinal section. (b-e) Examples of heterogamous capitula with at least two types of florets. Based on the morphology of the marginal florets, the capitula can be classified as (b) radiate (*Bellis perennis*), (c) bilabiate (*Gerbera hybrida*), (d) radiant (*Centaurea cyanus*, image source: iNaturalist, Douglas Goldman), and (e) disciform (*Ajania pacifica*, image courtesy: Prof. Guangyuan Rao). (f,g) Homogamous capitula composed of only one floret type: (f) ligulate capitulum of *Lactuca sativa* and (g) discoid capitulum of the rayless *Helianthus radula* (image source: iNaturalist, Nash Turley). (h–j) Higher order arrangements of capitula. Branches supporting individual capitula may vary from highly elongated ones in *Achillea millefolium* (h), to more reduced ones in *Flaveria bidentis* (i). A secondary capitulum, syncephalium, in *Echinops ritro* develops on a globular receptacle (j).

Fig. 2 Schematic summary of the phenotypic diversity in Asteraceae capitula. (a) Diverse receptacle shapes of capitula. (b) Classification of Asteraceae capitula based on floret types. Heterogamous capitula consist of two distinct types of florets that differ in their sex. Ray florets and bilabiate marginal florets are both bilaterally symmetrical and form a fused, enlarged ligule. In radiant and disciform capitula, the marginal florets are radially symmetrical but deviate from each other by the elongation of individual petals. Homogamous capitula are formed of single, bisexual floret types. Ligulate capitula form only bilaterally symmetrical florets while in discoid capitula, all florets are radially symmetrical and of disc identity. (c) In syncephalium, secondary capitula develop in place of individual florets. (d) Classification of capitula based on absence (ebracteate) or presence (bracteate) of floral subtending bracts (arrow).

Fig. 3 Expansion growth and phyllotactic patterning of Asteraceae inflorescence meristem (IM). (a-c) Scanning electron micrographs indicating the size difference of Arabidopsis (a), gerbera (b), and sunflower (c) IMs (yellow circles, scale bars: 50 μm in (a), 1 mm in (b,c)). Flowers in all species follow regular spiral phyllotaxis with left (red) and right (blue) winding spirals in consecutive Fibonacci numbers. (d) Gerbera capitulum development reconstructed from 3D micro-CT scans. The size of the central undifferentiated domain (shaded in yellow) shows highly dynamic changes during distinct stages of patterning (scale bar: 1 mm). (e) Pattern progression of the first bract initia marked by the auxin reporter *DR5rev:3xVENUS-N7*.

The red circles mark the expansion growth of the meristem. The initia are not equally spaced but separated by large (L) and small (S) gaps. During patterning, a new initium (white arrows) is always inserted into the large gap and moves laterally towards its older neighboring initium (P, inset). Consequently, the number of primordia increases following consecutive Fibonacci numbers. (f) An integrative model showing changes in receptacle shape and phyllotactic patterning on a developing gerbera capitulum (modified from Zhang et al., 2021a).

Fig. 4 Initiation of ray florets in gerbera. (a) SEM figure indicating the position of an emerging ray floret (yellow dashed line) in the axil of an involucral bract (green dashed line). Note the delayed development of the ray initia compared to the nearby trans florets. (b) Live imaging of a DR5 auxin reporter line of gerbera indicates a common auxin maximum at the timepoint T0 that then separates into two maxima (timepoints T1 and T2) marking the emerging bract and ray primordia (marked with green and yellow lines, respectively). Scale bars: 50 μm.

Fig. 5 Specialized pappus bristles occupy the whorl 1 in the florets of Asteraceae. (a) Hairy pappus bristles in the perianth of a gerbera ray floret. (b) A SEM image of filamentous pappus bristles as in (a). (c,d) Confocal microscopic images show initiation and elongation of pappus bristles in transgenic gerbera expressing the DR5 auxin reporter. Pappus bristles arise from a ring-shaped meristem surrounding the developing petals (c). (e) A vertical wind tunnel image showing air fluid dynamics surrounding a flying dandelion seed. Image courtesy: Dr. Naomi Nakayama, under CC-BY-4.0 license. Scale bars: 100 μm.

Fig. 6 Development and evolution of inflorescence structures in Asteraceae and its close relatives Goodeniaceae and Calyceraceae. (a) Based on Pozner et al. (2012), key differences and proposed morphological changes during evolution of Asteraceae heads. The terminal flower (TF) and peripheral cymose unit (PU) are highlighted in red and orange, respectively. (b) An example of inflorescence in Calyceraceae (*Acicarpha tribuloides*). Different from Asteraceae, the inflorescence axis ends with a terminal flower (TF). *Acicarpha* does not develop peripheral cymose units shown in panel (a). (c) An example of Asteraceae capitulum (*Lactuca sativa*) shows that the inflorescence meristem (IM) gets consumed by floret primordia (FP) and does not develop any terminal flower. (d-f) Developing capitula of wild-type (d) and

transgenic gerbera lines with down-regulated *GhLFY* (e) and *GRCD2/7* (f). At a similar developmental stage, the IMs in (e,f) remain undifferentiated while in (d) the IM has been consumed with floret primordia. (g) The developing capitulum of *GhUFO* overexpression gerbera line shows conversion of the central IM into a giant flower meristem (shaded in red) producing floral organs in whorls. Scale bars: 2 mm.

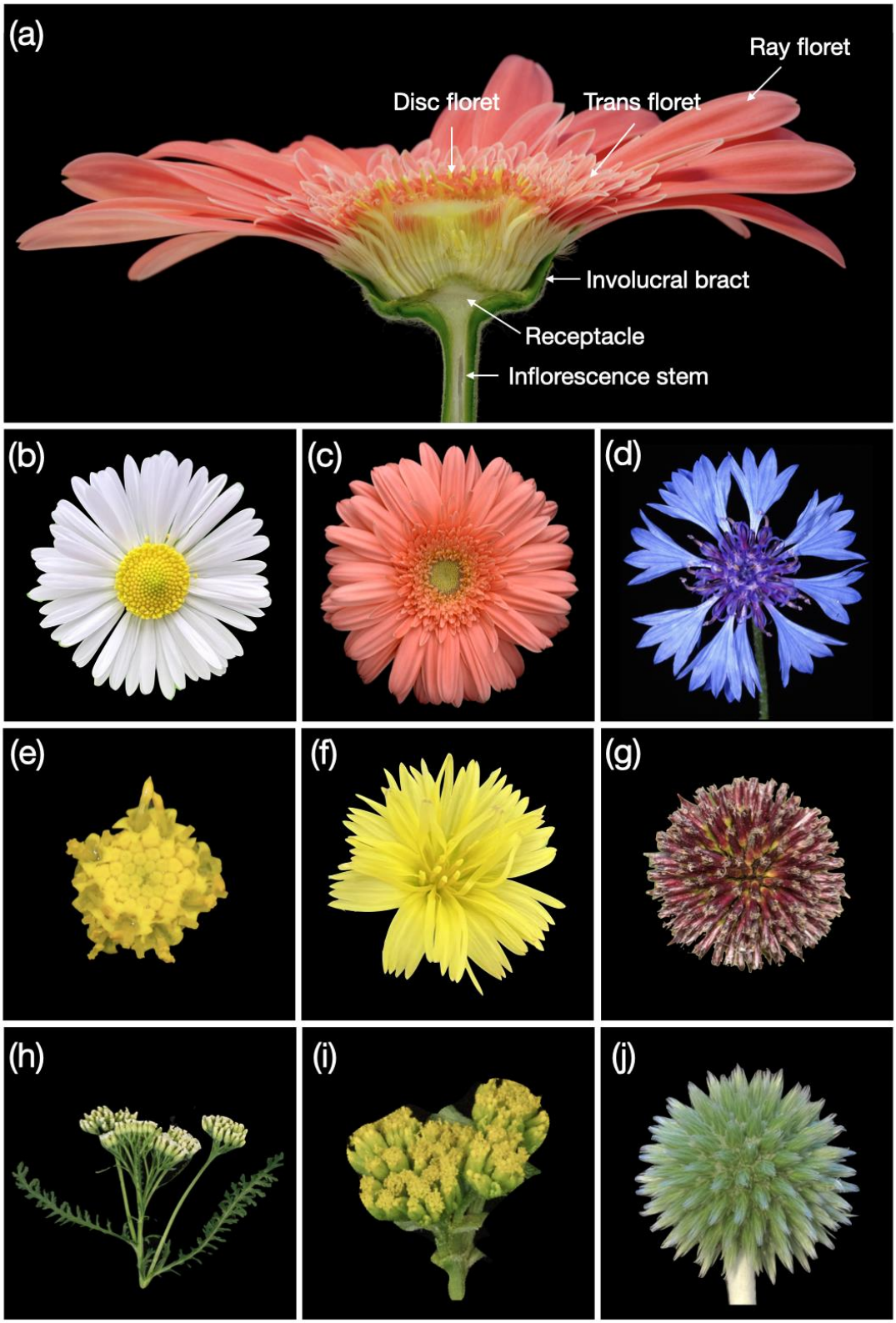
(a)
Ray floret
Disc floret
Trans floret
Involucral bract
Receptacle
Inflorescence stem
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)

Fig. 1

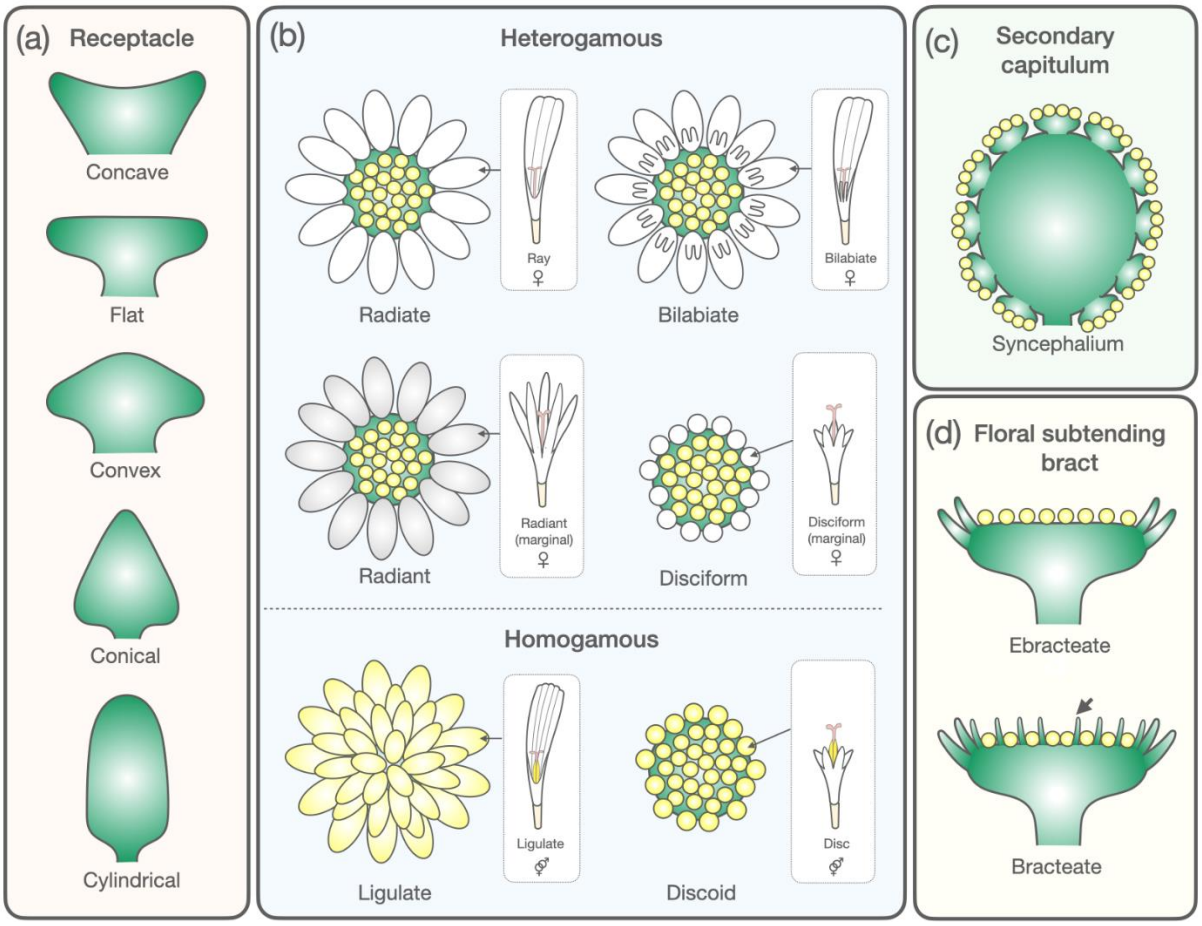
(a) Receptacle
Concave
Flat
Convex
Conical
Cylindrical
(b)
Heterogamous
Ray
Radiate
Bilabiate
Bilabiate
Radiant (marginal)
Radiant
Disciform
Disciform (marginal)
Homogamous
Ligulate
Ligulate
Discoid
Disc
(c) Secondary capitulum
Syncephalium
(d) Floral subtending bract
Ebracteate
Bracteate

Fig. 2

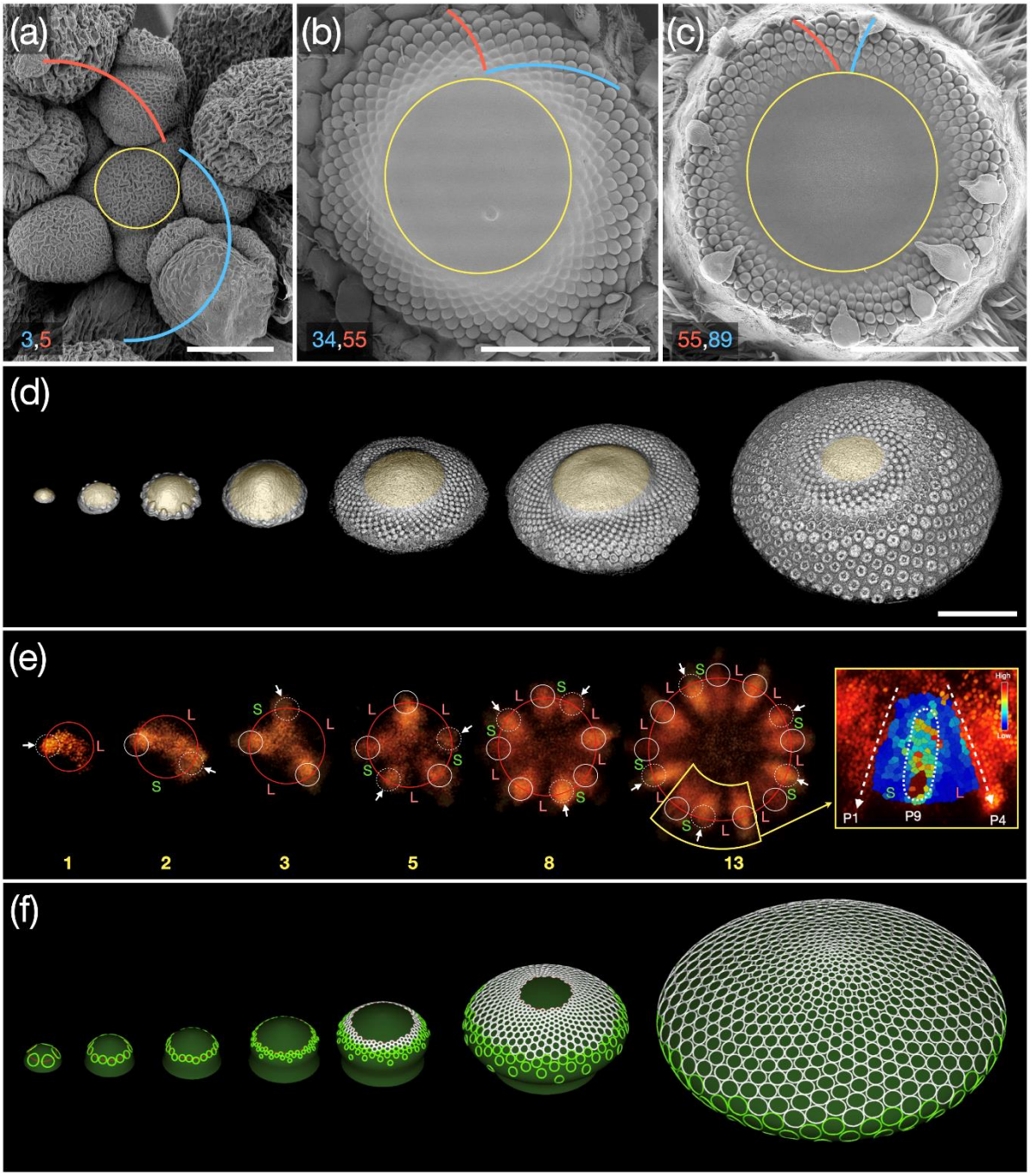

Fig. 3

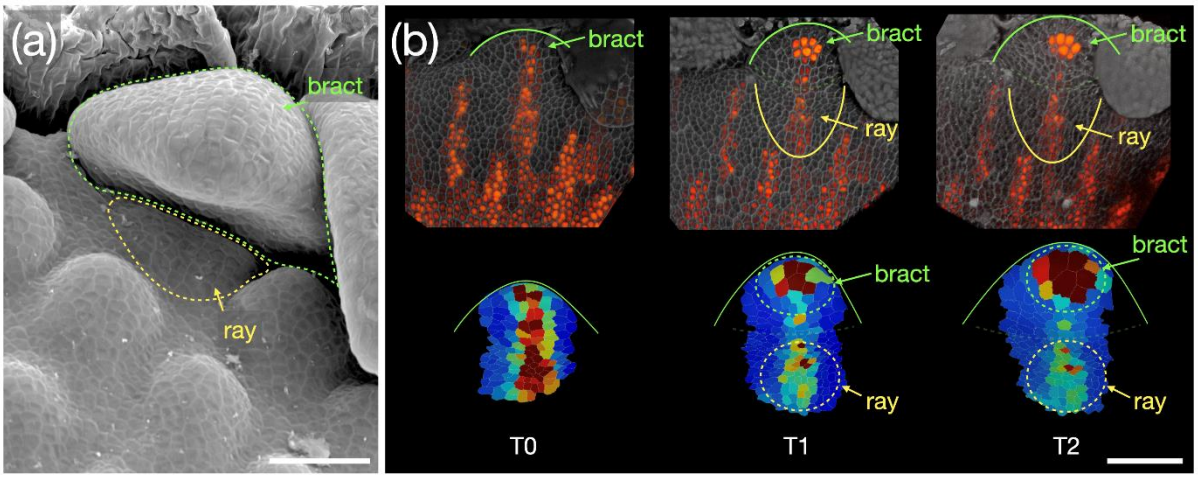
(a)
bract
ray
(b)
bract
bract
bract
ray
ray
bract
bract
ray
ray
T0
T1
T2

Fig. 4

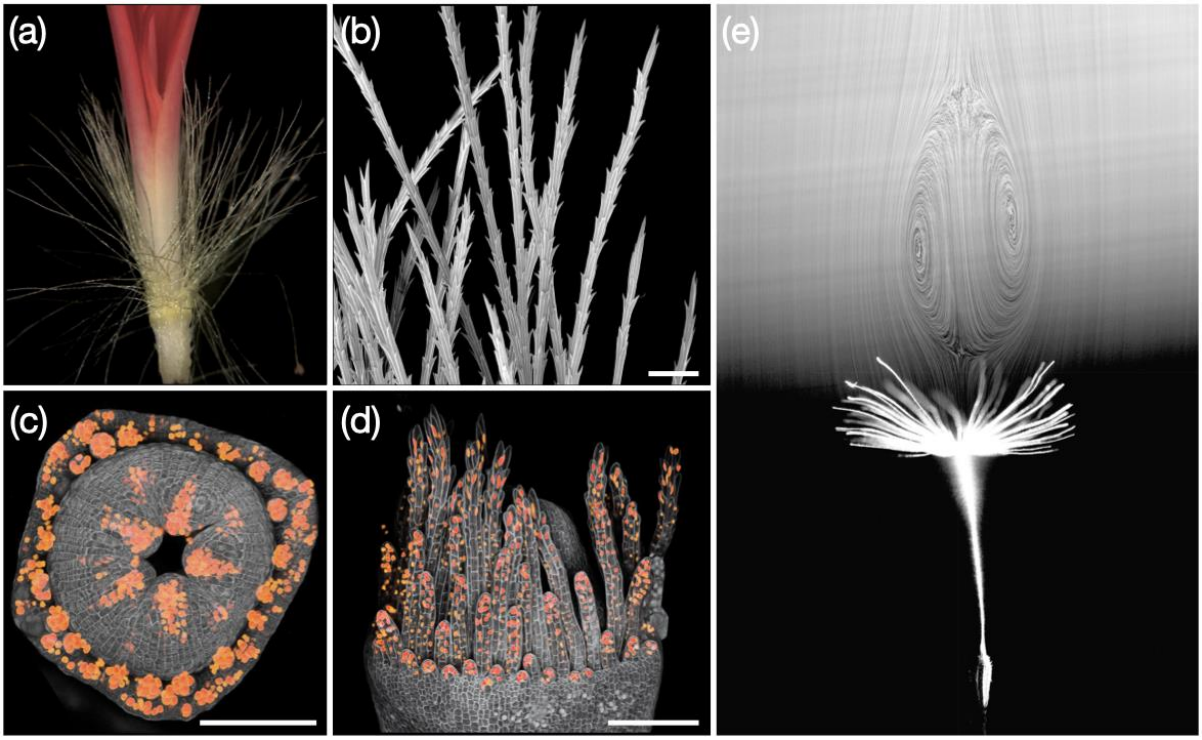

Fig. 5