

## Pseudanthia in angiosperms: a review

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- **Background** Pseudanthia or ‘false flowers’ are multiflowered units that resemble solitary flowers in form and function. Over the last century the term ‘pseudanthium’ has been applied to a wide array of morphologically divergent blossoms, ranging from those with easily noticeable florets to derived, reduced units in which individual flowers become almost indistinguishable. Although initially admired mostly by botanists, the diversity and widespread distribution of pseudanthia across angiosperms has already made them a fascinating topic for evolutionary and developmental comparative studies.
- **Scope** This review synthesizes historical and current concepts on the biology of pseudanthia. Our first aim is to establish a clear, operational definition of pseudanthium and disentangle common terminological misconceptions surrounding that term. Our second aim is to summarize knowledge of the morphological and developmental diversity of pseudanthia and embed it within a modern phylogenetic framework. Lastly, we want to provide a comprehensive overview on the evolution and ecological importance of pseudanthia and outline perspectives for future studies.
- **Conclusions** The understanding of pseudanthia has changed multiple times and reflects three different interpretations of their ‘flower-like’ qualities: developmental (similarity in structure), figural (similarity in form and function) and phylogenetic (homology between angiosperm flowers and monoecious reproductive shoots in gymnosperms). Here, we propose to narrow the term *pseudanthium* to multiflowered blossoms resembling zoophilous flowers in form, i.e. in being structurally subdivided in a showy periphery and a reproductive centre. According to this definition, pseudanthia *sensu stricto* evolved independently in at least 41 angiosperm families. The recurrent acquisition of pseudanthia *sensu stricto* in all major lineages of flowering plants indicates repeated interactions between developmental constraints (smallness of flowers, meristematic conditions) and selective pressures, such as demands of pollinators and/or environmental conditions.

**Key words:** Aggregation, development, division of labour, evolution, floral unit, flowering plants, genetic regulation, inflorescence, meristem conditions, pollination biology, ray flower, showy bract.

### INTRODUCTION

#### *A historical perspective on pseudanthia*

The fact that *multiflowered blossoms* can mimic the appearance of a single flower was already well recognized by the dawn of modern botany. In *Methodus Plantarum Nova*, John Ray (1682) for the first time referred to the capitulum of Asteraceae as a *flos compositus* (compound flower), according to a pharmaceutical convention making no distinction between true flowers and flower-heads (i.e. *Matricariae flos* = head of chamomile, see Drobnik, 2022). The same term for capitula was later adopted by Linné (1792), while Ehrhart (1787), on the other hand, considered it misleading; for him, proceeding from a synthetical rather than analytical perspective, calling a multiflowered structure a ‘compound flower’ seemed like ‘calling a group of people a compound human’. Instead, he re-adopted the term *anthodium* for blossoms of which *form* resembles a solitary flower (originally used by Linnaeus in 1770 to describe the involucre of Asteraceae). The use of *anthodium* in that sense was later corroborated in

the works of Stokes (1812), Link (1837), Hanstein (1882) and Johow (1884).

The proper term *pseudanzio* was first introduced by the Italian botanist Federico Delpino (1889), one of the co-founders of pollination biology. Delpino was particularly interested in flowers in which the arrangement of floral organs broke the rules of phyllotaxy (i.e. with obdiplostemony or stamen fascicles). He postulated that these were in fact contracted inflorescences and, thus, ‘false flowers’ (*pseudanzia*), compared to ‘true flowers’ or *euanzia*. This difference in *structure* served as the basis for his new classification of angiosperms (Delpino, 1890, 1892): *Pseudante* included spurge (*Euphorbia* L., Euphorbiaceae), the cyathia of which constitute a single reproductive unit consisting of highly reduced flowers, but also Rosaceae or Malvaceae with stamen fascicles, while *Euante* united plants with ‘conventional’ flowers.

Almost 20 years later, Richard von Wettstein (1907) applied the term pseudanthium to multi-axial reproductive units found in gnetalean gymnosperms and proposed that angiosperm flowers evolved from such structures, based on the

assumption of the close relationship between those two groups. This hypothesis, frequently referred to as ‘pseudanthial theory of flower origin’, remained highly influential throughout the 20<sup>th</sup> century (Melville, 1960; Meeuse, 1972; Crane, 1985; Doyle, 1994; Krassilov, 1997; Sun *et al.*, 2002) and served as alternative to the euanthial theory (Arber and Parkin, 1907; Doyle and Donoghue, 1986), under which flowers were interpreted as simple uniaxial systems similar to those of cycads and extinct Bennettitales. The ideas of von Wettstein added *phylogenetic* context to a belief that at least some angiosperm flowers might be derived from ‘inflorescence-like’ structures. Although the pseudanthial theory became untenable with the demise of the anthophyte hypothesis (assuming a sister relationship between angiosperms and Gnetales, see Donoghue and Doyle, 2000), it is sometimes evoked in the light of relatively recent studies suggesting that strobili in cordaites, conifers and Gnetales may be derived from ancestral multiaxial structures (Mundry and Stützel, 2004; Rudall and Bateman, 2010).

Apart from von Wettstein, the current understanding of pseudanthia was strongly influenced by Wilhelm Troll (1928, 1964), a famous plant morphologist who was heavily rooted in German *Naturphilosophie* (Nickel, 1996; Weberling, 1999; Claßen-Bockhoff, 2001; Rieppel, 2011). His belief in idealistic morphology understood as an immanent urge to a certain form (*Gestalt*, understood as the manifestation of a given type) found its support in the study of asteracean capitula. Pseudanthia *sensu* Troll were correspondingly flower-like *forms* realized on the material level of an inflorescence. As multiflowered blossoms with clearly distinguishable individual florets, they include the same examples as *anthodia sensu* Ehrhart (Claßen-Bockhoff, 1991a).

Troll also postulated that the transition from an inflorescence to a pseudanthium may have occurred in three steps: (1) aggregation and miniaturization of flowers, (2) formation of *pseudocorollas* through differentiation of peripheral flowers and (3) co-option of extrafloral organs. This sequence served as inspiration for various theories on the morphological evolution of pseudanthia (Froebe and Ulrich, 1979; Claßen-Bockhoff, 1990; Harris, 1999); however, it is important to note that Troll’s view was purely typological and disconnected from a phylogenetic and evolutionary perspective (Claßen-Bockhoff, 2001).

Ronald Good (1956) came across pseudanthia *sensu* Troll during his systematic studies. For him, pseudanthia ‘function as and simulate a single true flower’ (p. 276); they evolved due to a general *aggregation tendency* in nature leading to *evolutionary repetitions*. However, the increasing association of flowers is based only on aggregation until it reaches a certain threshold defined by spatial conditions. Beyond this ‘last extreme state, there is, over and beyond any mere aggregation of the flowers, such a measure of arrangement, organization and division of labour [ ... ] that the inflorescence as a whole attains a design and function greater than any that may result simply from the proximity or contiguity of units all like one another’ (Good 1956: 276). By considering developmental constraints triggering pseudanthia formation he paved the way for an *evo-devo* understanding of pseudanthia.

Elmar Emil Leppik presented yet another interesting perspective on pseudanthia. While primarily focusing on *form* (similarly to Ehrhart, Troll and Good), his approach encompassed

ecological and evolutionary aspects. Based on studies on the pollination biology of Asteraceae, Leppik (1959, 1970) formulated the hypothesis of *pseudanthic recapitulation*, which implies that densely aggregated flower-heads not only increase general attraction, but also repeat well-established evolutionary patterns in response to pollinator-mediated selection. Next to an ‘*unexplained genetic mechanism*’ (Leppik 1959) reducing flower size to a minimum, he saw co-evolution between floral patterns and pollinator sensory perceptions as the two main evolutionary forces triggering pseudanthia formation. Like Good (1956), Leppik had the view that the entire pseudanthium can serve as an equivalent of a single pollination unit.

Regine Claßen-Bockhoff (1990, 1991a, 1992) provided a comprehensive summary of pseudanthia (*sensu* Troll) in angiosperms. She distinguished four types: floral vs. hyperfloral pseudanthia based on the purely floral constitution of the blossom vs. integration of extrafloral elements, and undifferentiated vs. differentiated blossoms dependent on the absence vs. presence of a pseudocorolla surrounding the reproductive centre. She reconstructed the morphological changes from inflorescences to pseudanthia within selected lineages and demonstrated that pseudanthia only differed gradually from inflorescences making a clear definition almost impossible. She concluded that aggregation, miniaturization and colouring might be the result of inhibition processes ranging from internode inhibition and developmental simplification to inhibition of chlorophyll synthesis. Ontogenetic abbreviations (neoteny) thus appear to play a major role also expressed by the persistence of juvenile stages and, most importantly, pattern repetition on the multi-flowered level. Beyond heterochrony, spatial constraints (ray flower formation) and shifts in function (from protective to showy organs) may promote flower similarity. Summarizing, the parallel evolution of flower-like patterns was assumed to be driven by a combination of lineage-specific phylogenetic traits, combined with developmental options and selective pressures.

At the beginning of the 21<sup>st</sup> century, Paula Rudall introduced the term *fuzzy pseudanthia* to describe peculiar reproductive units in which florets become so highly reduced that the boundaries between flower and inflorescence become indistinct or blurred. Initially, she identified this pattern in cyathia (Prenner and Rudall, 2007) and in reproductive units of Hydatellaceae (Rudall *et al.*, 2009), which, based on ontogenetic data, were interpreted as ‘hybrid structures’. Later, fuzzy pseudanthia were also applied to reproductive structures of mycoheterotrophic Triuridaceae, including bizarre inside-out flowers (with centrally located stamens that are surrounded by carpels) of *Lacandonia schismatica* E. Martínez & Ramos (Triuridaceae, Rudall *et al.*, 2016) and staminal fascicles of *Ricinus communis* L. (Euphorbiaceae, Prenner *et al.*, 2008), re-interpreted as multiflowered floral units by Claßen-Bockhoff and Frankenhäuser (2020). The idea of an imprecise inflorescence–flower boundary is also clearly visible in her earlier studies on Pandanales (Rudall and Bateman, 2006). Having *structure* as a background, fuzzy pseudanthia approach closely to pseudanthia *sensu* Delpino. The situation in which an uncommon flower reveals itself as a multifloral unit upon closer inspection is also applicable to *synanthia*, which, according to

Mattfeld (1938), gave rise to monoecious units of some sedges (Cyperaceae).

#### Definition of *pseudanthia*

To analyse the diversity of *pseudanthia* one must adopt a precise definition of what is and – more importantly – what is not the real subject of the study. Following historical meanings of the term, the most logical choice would be to focus on structure and development, but such data are rarely available for most *pseudanthia*. The ecological definition of *pseudanthia* (*inflorescence-blossoms sensu* Claßen-Bockhoff, 1991a) is also problematic, as it requires making the distinction between *pollination unit* and *attraction unit* (Faegri and Pijl, 1979). Without a sharp ecological definition of *pseudanthia*, we are left with *anthodia* (*pseudanthia sensu* Troll) or blossoms the form of which resembles that of a single flower. But what does exactly floral form mean? Being aware that a sharp separation of *pseudanthia* from modified inflorescences is almost impossible, we take the heteromorphic heads of composites for the most unambiguous examples of the expression of a floral *Gestalt* in multifloral units. We thus focus on structurally subdivided *pseudanthia* (*sensu* Claßen-Bockhoff, 1990) and define them as *clearly multiflowered blossoms divided into a central part that serves reproductive functions and peripheral, usually radiating advertising/protective structures consisting of (1) distinctly enlarged, often sterile peripheral flowers and/or (2) showy, coloured extrafloral organs (e.g. bracts, prophylls, stem leaves)*.

This definition does not encompass modified inflorescences which share only a few flower-like characters (Fig. 1). Such inflorescences may have showy bracts below (Fig. 1A, B) or above the flowers (tuft blossoms, Fig. 1C, D), or enlarged single florets (Fig. 1E, F), but lack aggregation and smallness of flowers. Inflorescences with a transitory flower-like appearance due to flowering sequence (Fig. 1G) or delayed internode elongation (Fig. 1H) do not match our *pseudanthium* definition, too. Contrary to Claßen-Bockhoff (1990), we do not consider *pseudanthia* that are not structurally subdivided into centre and periphery (Fig. 2). They are characterized by flowers which lost their individuality by becoming part of a pincushion blossom (Fig. 2B, C), polymeric disc-blossom (Fig. 2D) or globular blossom (Fig. 2E, F). These types of blossoms may resemble a single flower (Fig. 2A), but lack the subdivision into reproductive field and surrounding showy structures. It is important to note that while homomorphic heads of some Asteraceae (Fig. 2D) do not fall under our definition of *pseudanthia sensu stricto*, others, such as those of *Tragopogon pratensis* L. (with distinctly enlarged peripheral ray flowers) or *Cichorium intybus* L. (with sexual centre formed by stamens and carpels of ray flowers and showy margin consisting of their ligules), may do so. Finally, reproductive units for which similarity to flowers is only reflected in development are also excluded, i.e. those that fulfil the definition of *pseudanthia sensu* Delpino or fuzzy *pseudanthia*.

#### DIVERSITY OF PSEUDANTHIA

*Pseudanthia sensu stricto*, i.e. the structurally subdivided forms of *pseudanthia* (referred to simply as *pseudanthia* in the

following paragraphs), show an immense diversity that results from the evolutionary history of various angiosperm lineages and specific morphological and ecological constraints.

#### Phylogenetic distribution of *pseudanthia*

*Pseudanthia* can be found in at least 41 plant families (Claßen, 1984; Claßen-Bockhoff, 1990; Table 1). However, they have never been referred to the current phylogenetic framework, hindering us from drawing firm conclusions about macroevolutionary trends. Herein, we provide a simple juxtaposition of *pseudanthial* diversity onto the most recent angiosperm phylogenetic tree (Chase *et al.*, 2016), which reveals some interesting patterns (Fig. 3).

*Pseudanthia* occur in all major clades of flowering plants (Table 1). They were described at the base of the angiosperm phylogeny (Fig. 3A) in Hydatellaceae (Rudall *et al.* 2009), mycoheterotrophic representatives of which produce inconspicuous, predominantly self-pollinated blossoms (Taylor *et al.*, 2010). Among magnoliids, flower-like inflorescences are characteristic of Saururaceae (Hutchinson, 1926), notably the genera *Houttuynia* Thunb. (Tucker, 1981; Fig. 3B) and *Anemopsis* Hook. & Arn. (Tucker, 1985). In monocots, inflorescence-blossoms originated multiple times (Fig. 3C–F) but are relatively infrequent. Apart from Araceae (Fig. 3C), none of the species-rich families described within this clade can be considered entirely or predominantly *pseudanthial* while in most of them such architecture is restricted to only a few representatives. The greatest architectural variety of *pseudanthia* is unequivocally associated with eudicots. In some lineages, only single and isolated species are *pseudanthial*, such as in Rutaceae (*Eucheaetis longibracteata* Schltr.; Fig. 3J) or Hamamelidaceae (*Parrotiopsis jacquemontiana* Decne., *Rhodoleia championi* Hook.; Fig. 3H1, H2), whereas in others *pseudanthia* are ubiquitous, as in Euphorbiaceae (with *Euphorbia* including ~2000 species, Fig. 3L), Rubiaceae (Fig. 3V) and Apiaceae (Fig. 3S). Occasionally, *pseudanthia* may even constitute a major synapomorphy, an example being the largest angiosperm family Asteraceae with ~20 000 species (Fig. 3R).

#### Morphological diversity of showy elements

Perianth-like structures, which serve as the basis for the definition of the *pseudanthium sensu stricto*, can develop from almost every type of organ (Fig. 4; Table 1 and citations therein). Co-option of bracts is probably the most widespread architectural solution. Bracts are defined as phyllomes that appear below or within the flowering zone and differ from the green (frondose) leaves in being smaller and inconspicuous or larger and showy. They are usually simple in shape and inserted with a broad base, emphasizing their frequent function as protective elements. Some are sterile [as in *Etlingera elatior* (Jack) R.M.Sm (Fig. 5K)], others subtend a flower (Fig. 4: red, Fig. 5D), a partial inflorescence (Fig. 5F) or hold a prophyll position (Fig. 4: violet, Fig. 5J). Prophylls are filiform in the blossoms of some *Tacca* J.R.Forst. & G.Forst. (Taccaceae) and *Dorstenia* Plum. ex L. (Moraceae) species (Fig. 5G). Stipules contribute to the hexamerous pattern in *Parrotiopsis jacquemontiana* (Decne.) Rehder (Fig. 4: blue, Fig. 5N; Claßen-Bockhoff, 1992), fused

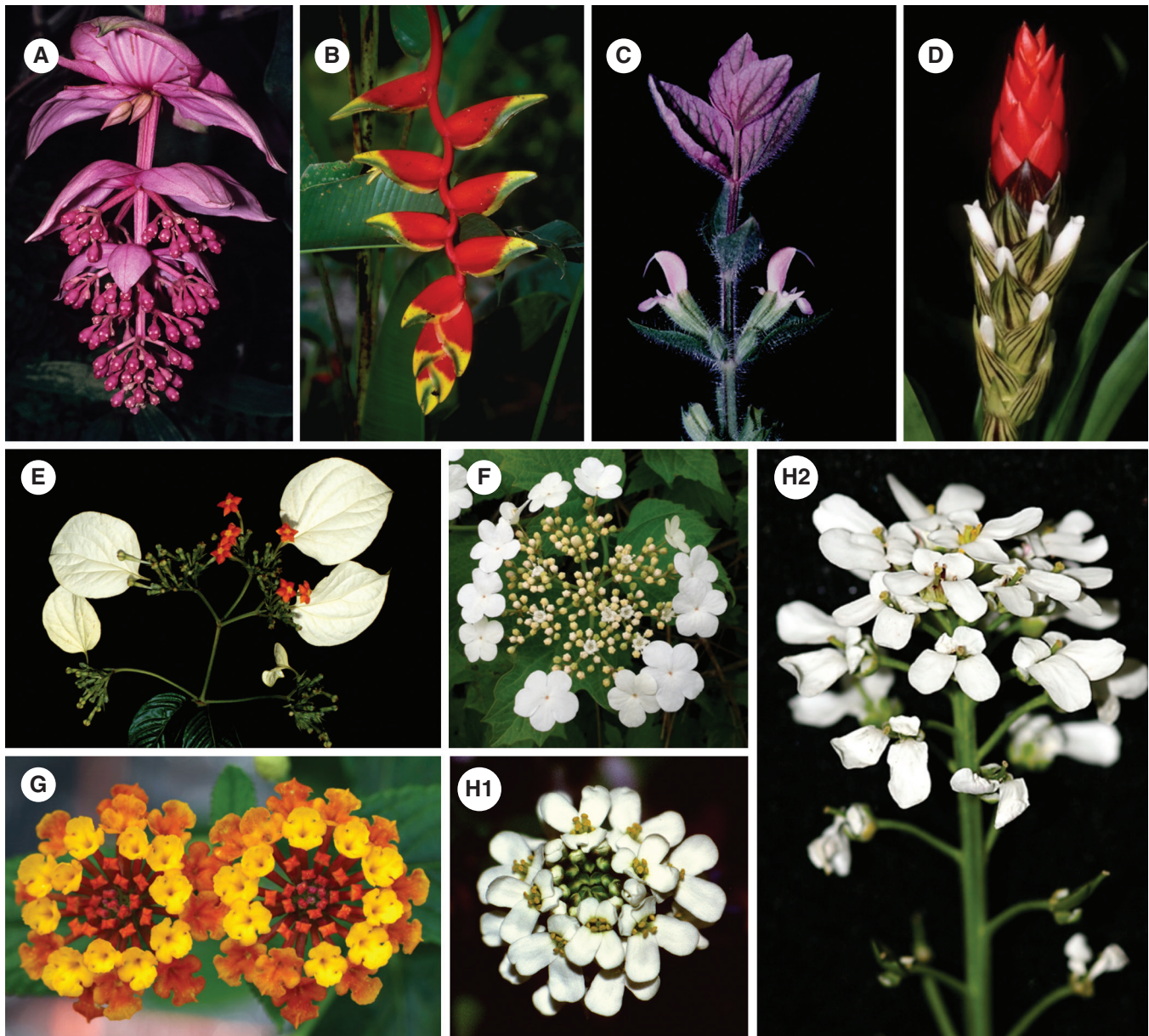


FIG. 1. Modified inflorescences. (A, B) Inflorescences with showy bracts lacking aggregation: (A) *Medinilla magnifica* Lindl. (Melastomataceae); (B) *Heliconia rostrata* Ruiz & Pavon (Heliconiaceae). (C, D) Tuft blossoms: (C) *Salvia viridis* L. (Lamiaceae); (D) *Guzmania monostachia* (L.) Rusby ex Mez, (Bromeliaceae). (E, F) Inflorescences with ray flowers lacking aggregation: € *Mussaenda frondosa* L. (Rubiaceae); (F) *Viburnum opulus* L. (Adoxaceae). (G, H) Temporary flower-like inflorescences: (G) *Lantana camara* L. (Verbenaceae); (H) *Iberis amara* L. (Brassicaceae): young (H1) and older, elongated raceme (H2). Photos: B–E from Claßen-Bockhoff (2023).

prophylls to the trimery of *Congea velutina* Wight (Lamiaceae; Fig. 5D; Claßen, 1985), and asymmetrical involucellar bracts to an umbel-centred arrangement of white elements in *Xanthosia rotundifolia* DC. (Apiaceae; Fig. 5V; Froebe, 1979). Stipular excrescences form actinomorphic and zygomorphic blossoms in the genus *Euphorbia* (Fig. 4: orange, Fig. 5W, X; Michaelis, 1924) and short shoots with several white bracts and prophylls surround the flower-head in the pseudanthium of *Actinodium cunninghamii* Schauer ex Lindl. (Myrtaceae; Fig. 4: turquoise, Fig. 5S; Claßen-Bockhoff et al., 2013). Pseudanthia with showy bracts are either polymorous (Fig. 5T) or have a fixed organ

number (Fig. 5H). Both patterns usually reflect the phyllotaxis of the vegetative shoot system. Showy bracts can be white (e.g. Fig. 5A, M, V), sometimes due to a dense pubescence (Fig. 5D, F, O), or coloured, with red and reddish as dominant tones (e.g. Fig. 5B, I, K). Few species show a gradual colouring of their bracts with white or red spots at the base of otherwise green leaves (i.e. *Euphorbia heterophylla* L., Fig. 4: pink).

Pseudanthia with flower dimorphism are rare at the family level (Table 1) and generally restricted to only a few groups of campanulid eudicots (Asteraceae, Caprifoliaceae, Apiaceae; Fig. 3R, S, U). Interestingly, whereas some loosely aggregated

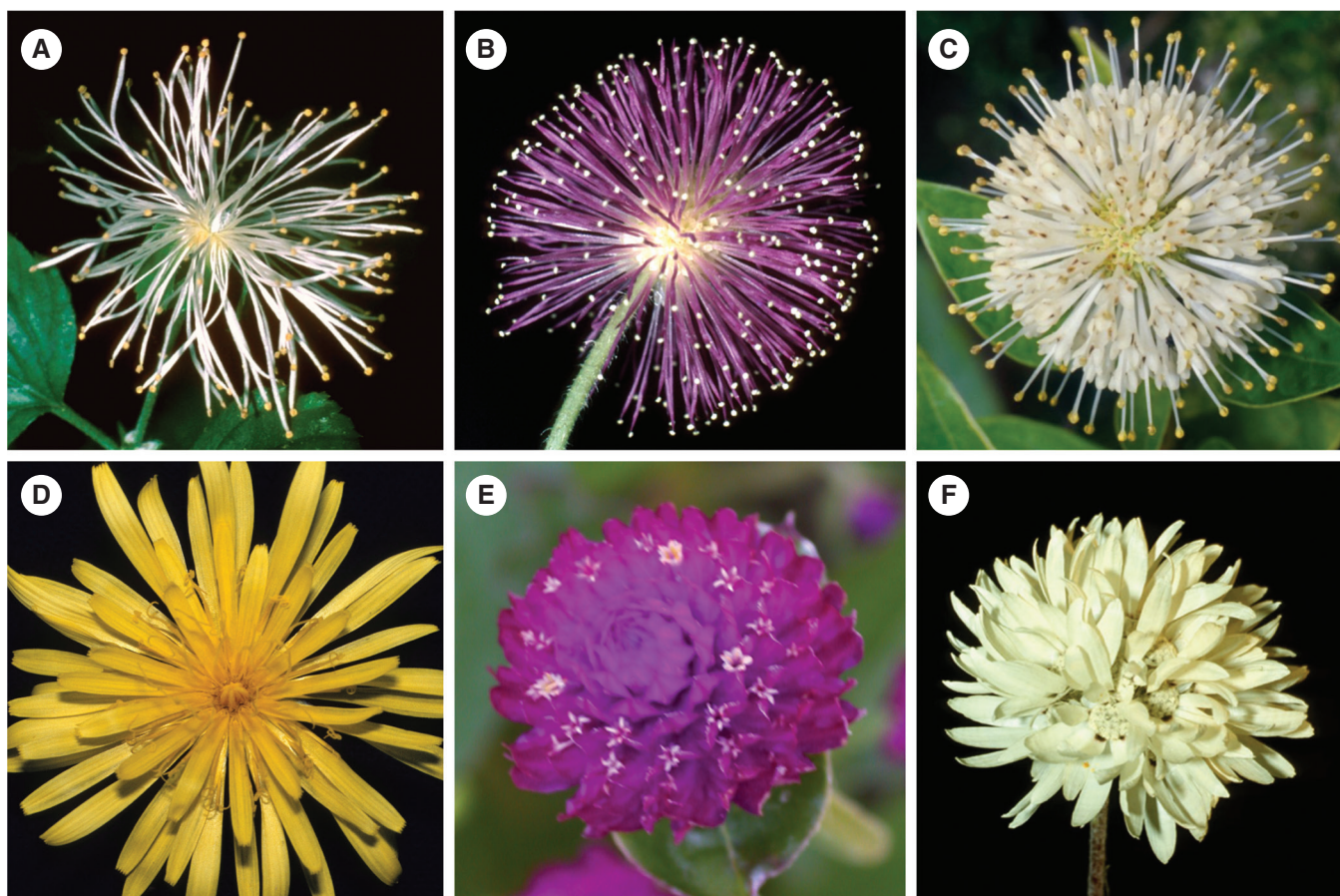


FIG. 2. Pseudanthia *sensu lato*, lacking structural subdivision. (A–C) Pincushion-blossoms: (A) *Neviusia alabamensis* (Rosaceae) – flower with many stamens, included for comparative reasons; (B) *Mimosa pudica* (Fabaceae) – about 100 flowers, each with four stamens and one style; (C) *Cephalanthus occidentalis* (Rubiaceae) – thyrs-like floral unit (head with cymes) with many flowers, each secondarily presenting pollen on its style. (D) Homomorphic heads: *Taraxacum officinale* (Asteraceae). All flowers zygomorphic. (E, F) Pseudanthia *s.l.* with showy extrafloral elements: (E) *Gomphrena globosa* (Amaranthaceae) – minute flowers, each with two violet prophylls; (F) *Cephalipterum drummondii* (Asteraceae) – head-like raceme with many capitula, each with a showy white involucre. Photos: A–C from Claßen-Bockhoff (2023).

inflorescences with actinomorphic flowers (Fig. 1E, F) develop advertising structures consisting of enlarged sepals, calyx or corolla lobes in peripheral position, floral pseudanthia always have monosymmetrical (zygomorphic) ray flowers with one or several petals (Fig. 6F–H) or sympetalous corolla lobes (Fig. 6A–E) as showy elements. Ray flowers usually surround a simple head (Fig. 6A–C, E, F) or umbellet (Fig. 6H), but can also develop at the margin of complex pseudanthia composed of multiple such units (Fig. 6D, G). An example of floral pseudanthia outside campanulids is the mimosoid genus *Neptunia* Lour. In some of its representatives, an inflorescence is a head (probably derived from a highly congested spike) with three types of flowers: perfect flowers occupying the distal two-thirds of the entire blossom, a narrow zone of male flowers situated just below them and a basal zone of sterile florets with showy petaloid staminodes (Tucker, 1988). Apart from *Neptunia*, *Calliandra surinamesis* Benth. has pseudanthia *sensu stricto*, whereas in other mimosoid genera with heteromorphic flowers [*Xylia* Benth., *Parkia* R.Br., *Dichrostachys*

(DC.) Wight & Arn] compactness or structural subdivision is lacking.

Beyond dimorphic floral pseudanthia, there are few examples in which flower similarity is based alone on a specific arrangement of zygomorphic flowers. *Rhodoleia championi*, representing a monotypic subfamily in the Hamamelidaceae, has bell-shaped pseudanthia (Fig. 6F) 4–7 extremely zygomorphic flowers, arranged radially in a single row (Claßen-Bockhoff, 1990). The three enlarged petals of each flower are directed towards the periphery of the blossom and their stamens and styles form a homogenous centre. Pseudanthia of *Heteranthera gardneri* (Hook.f.) M.Pell. (Pontederiaceae) and *Thalia geniculata* L. (Marantaceae; Fig. 6I) are formed by two mirror image flowers (Rutishauser, 1983; Claßen-Bockhoff, 1991b). They are monosymmetrical in the former and asymmetrical in the latter resulting in an actinomorphic disc blossom and zygomorphic lip blossom, respectively. Additionally, actinomorphic pseudanthia comprising three zygomorphic flowers (Fig. 6J) can be found in *Allionia* L. (Nyctaginaceae).

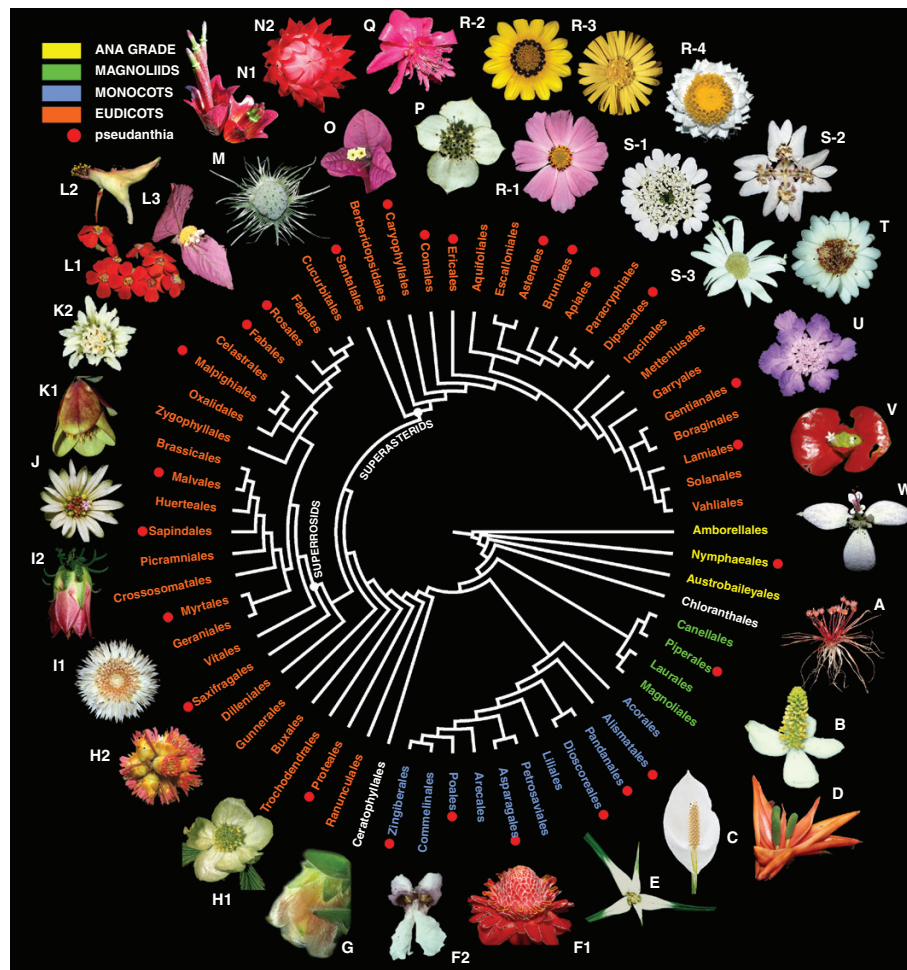


FIG. 3. Phylogenetic diversity of pseudanthia *sensu stricto*. ANA grade. (A) Nymphaeales: *Trithuria submersa* (Hydatellaceae). Magnoliids. (B) Piperales: *Houttuynia cordata* (Saururaceae). Monocots. (C) Alismatales: *Spathiphyllum cochlearispathum* (Araceae). (D) Pandanales: *Freycinetia* sp. (Pandanaaceae). (E) Poales: *Dichromena ciliata* (Cyperaceae). (F) Zingiberales: (1) *Etilingera elatior* (Zingiberaceae), (2) *Thalia geniculata* (Marantaceae). Basal eudicots. (G) Proteales: *Orothamnus zeyheri* (Proteaceae). Superrosids. (H) Saxifragales: (1) *Parrotiopsis jaquemontiana* (Hamamelidaceae), (2) *Rhodoleia championi* (Hamamelidaceae). (I) Myrtales: (1) *Darwinia lejostyla* (Myrtaceae), (2) *Actinodium cunninghamii* (Myrtaceae). (J) Sapindales: *Euchaetis longibractea* (Rutaceae). (K) Malvales: (1) *Pimelea physodes* (Thymeleaceae), (2) *Lasiopetalum discolor* (Malvaceae). (L) Malpighiales: (1) *Euphorbia fulgens* (Euphorbiaceae), (2) *Euphorbia* (sect. *Pedilanthus macrocarpa* (Euphorbiaceae), (3) *Dalechampia spathulata* (Euphorbiaceae). (M) Rosales: *Dorstenia yambuyaensis* (Moraceae). Superasterids. (N) Santalales: (1) *Tolypanthus lagenifer* (Loranthaceae), (2) *Thonningia sanguinea* (Balanophoraceae). (O) Caryophyllales: *Bougainvillea glabra* (Nyctaginaceae). (P) Cornales: *Cornus canadensis* (Cornaceae). (Q) Ericales: *Cavendishia adenophora* (Ericaceae). (R) Asterales: (1) *Cosmos bipinnatus* (Asteraceae), (2) *Gazania rigens* (Asteraceae), (3) *Eroeda capensis* (Asteraceae), (4) *Ammobium alatum* (Asteraceae). (S) Apiales: (1) *Arteria squamata* (Apiaceae), (2) *Xanthosia rotundifolia* (Apiaceae), (3) *Actinotus leucocephalus* (Apiaceae). (T) Bruniales: *Staavia dodii* (Bruniaceae). (U) Dipsacales: *Scabiosa* sp. (Caprifoliaceae). (V) Gentianales: *Palicourea* sp. (Rubiaceae). (W) Lamiales: *Congea velutina* (Lamiaceae). Cladogram based on Li *et al.* (2019). Photos: A, Kevin Thiele, Wikimedia Commons. C, J.J. Harrison, Wikimedia Commons. N1, Vinyaraj, Wikimedia Commons. N2, KAKPO Sunday Berlioz, Wikimedia Commons. Q, Marcelo Aguilar, Wikimedia Commons.

### Underlying organization

Pseudanthia cannot be unequivocally linked to a particular type of reproductive shoot architecture (Table 1). Proceeding from the view that all pseudanthia are modified inflorescences, Claßen-Bockhoff (1990) formally classified different types of pseudanthial architectures with respect to the absence or presence of a terminal flower, the branching pattern of the inflorescence, and the presence or absence of extrafloral bracts or ray flowers. Based on her analysis, pseudanthia are common in head-shaped blossoms which lack (Fig. 5U) or have common receptacles (as in Asteraceae; Fig. 6A, B, D, E). More rarely, spikes (Fig. 5A), a cluster of spadices (Fig. 5B) or spikelets (Fig. 5C), cymes (Fig. 5D), thyrses (and thyrses-like floral units,

see Fig. 5H–J), or cyathia (Fig. 5W, X) are found. In some families, pseudanthia are formed by pattern repetition on a more complex organizational level. Examples occur in Asteraceae (Figs 5M, 6E), Apiaceae (Figs 5V and 6F) and Bruniaceae (*Brunia fragarioides* Willd., Claßen-Bockhoff, 2000), but also in the monocot lineage Eriocaulaceae (Stützel & Trovó 2013).

In recent years, ontogenetic studies have revealed that numerous pseudanthia do not develop from inflorescence meristems. They, instead, fulfil the definition of floral units *sensu* Claßen-Bockhoff & Bull-Hereñu (2013) originating from expanding, determinate meristems (floral unit meristems, FUMs) with flower-like qualities (Fig. 7). As of now, floral units have been thoroughly investigated in Asteraceae (Harris, 1995;



FIG. 4. Diversity of showy organs in pseudanthia *sensu stricto*. The scheme shows a three-flowered inflorescence with the main petaloid elements. Colours: blue – stipules, green – stem leaf (pink indicating petaloid area), orange – stipular excrescences, red – flower-subtending bract, turquoise – modified lateral shoot, violet – prophyll, yellow – ray flower.

Zhang & Elomaa, 2021), Apiaceae (Baczyński *et al.*, 2022a), Nyssaceae (Claßen-Bockhoff and Arndt, 2018; Gong *et al.*, 2018) and Euphorbiaceae (Prenner and Rudall, 2007; Prenner *et al.*, 2011; Claßen-Bockhoff and Frankenhäuser, 2020), but they can be also identified in other lineages with pseudanthial representatives, including Saururaceae (Tucker, 1981, 1985; Fig. 5A), Araceae (Barabé and Lacroix 2008a, b), Eriocaulaceae (Stützel & Trovó, 2013), Hamamelidaceae (Claßen-Bockhoff and Bull-Hereñu, 2013), Rutaceae (Claßen-Bockhoff *et al.*, 1991), Moraceae (Leite *et al.*, 2021), Cornaceae (Liu *et al.*, 2013; Fig. 5H), Dioscoreaceae (Caddick *et al.*, 2000) and Caprifoliaceae–Dipsacoideae (Naghiloo and Claßen-Bockhoff, 2017; Fig. 6D).

An interesting (still unpublished) pattern of pseudanthium formation has been found in the South African genera *Staavia* Dahl (Bruniaceae) and *Euchaetis* Bartl. & H.L.Wendl. (Rutaceae). *Staavia dodii* Bolus (Fig. 5T) and *Euchaetis longibracteata* (Fig. 5U) share head-like blossoms of similar shape, size and symmetry. In both species, the terminal flower

is the first to bloom, followed by bilateral flowers arising basipetally (for *Staavia* see Claßen-Bockhoff, 2000). In contrast to the basipetal flowering sequence, such a completely basipetal initiation of flowers is rare among pseudanthia.

The examples of *Actinodium cunninghamii* (Myrtaceae, inflorescence with modified short shoots; Fig. 5S), *Myriocephalus helichrysoides* A. Gray (Asteraceae, secondary floral unit with showy bracts; Fig. 5M) and *Staavia dodii* (Bruniaceae, basipetally initiated cluster of flowers with showy bracts; Fig. 5T) clearly demonstrate that similar flower-like patterns evolved repeatedly based on different meristem conditions. Thus, structural diversity is much higher than the figural similarity may suggest.

#### ECOLOGICAL PATTERNS IN PSEUDANTHIA

Pseudanthia can be described by a character syndrome with density, smallness and division of labour being the most important traits. These characters evolve independently from

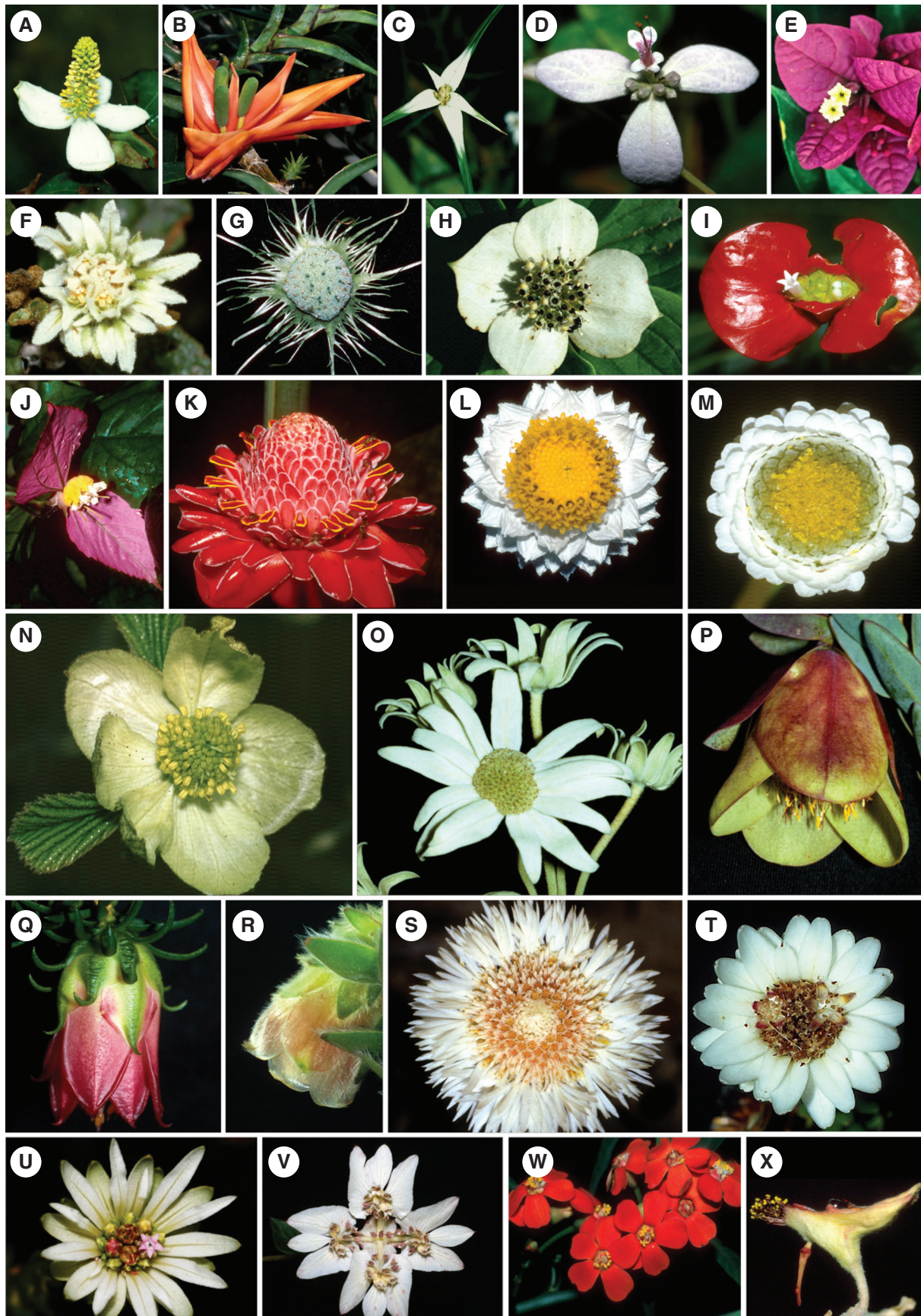


FIG. 5. *Pseudanthia sensu stricto* with showy extrafloral elements. (A) Spike with showy bracts: *Houttuynia cordata* (Saururaceae). (B) Three spadices with showy bracts: *Freycinetia* sp. (Pandanaeae). (C) Cluster of spikelets with showy bracts: *Dichromena ciliata* (Cyperaceae). (D) Cyme with showy bracts: *Congea velutina* (Lamiaceae). (E) Three-flowered unit: *Bougainvillea glabra* (Nyctaginaceae). (F) Cymoid with showy bracts: *Lasiopetalum discolor* (Malvaceae). (G) Cymoid-like head with showy bracts: *Dorstenia yambuyaensis* (Moraceae). (H, I) Thyrses with showy bracts: (H) *Cornus canadensis* (Cornaceae); (I)



each other as documented by the multiple examples of modified inflorescences (Fig. 1). Taking the Asteracean capitulum as the prototype of a pseudanthium, it is clear that the combination of all three characters results in unambiguous flower-like similarity. If the ray flowers or showy bracts dominate the blossom, large (*Congea* Roxb, Fig. 5D; *Bougainvillea* Comm. ex Juss., Fig. 5E, Nyctaginaceae) or loosely arranged florets (*Xanthosia*, Fig. 5V) do not hinder its overall flower-like appearance. However, the gradual transition between modified inflorescences and pseudanthia makes the grouping subjective. This is the reason why we focus on clear examples here and do not insist on a sharp definition.

#### Degree of flower similarity

Leppik (1969) reconstructed the evolution of angiosperm flower forms in different lineages and found actinomorphic, cup-shaped flowers with unstable numerical patterns to be ancestral, followed by those with a fixed number of organs, stereomorphic and finally monosymmetrical flowers. According to him, this evolutionary trajectory, coupled with increased synorganization and specialization, created the present diversity of angiosperm flowers. Interestingly, within core eudicots, the formation of asteracean heads somehow ‘reversed’ the trend of floral specialization. While individual florets of composites are highly derived, the entire blossom recapitulates conditions of ancestral flowers in being actinomorphic and generalistic in terms of pollination. Indeed, floral miniaturization and aggregation may present a chance for despecialization, creating new adaptive options (Claßen-Bockhoff, 1992) including shifts from anemophily to generalized zoophily as described for some Cyperaceae (Villa-Machío *et al.*, 2020; da Costa *et al.*, 2021).

Leppik (1969) proceeded from the view that pollinator-mediated selection is crucial for pseudanthia formation. Once adapted to a certain flower form, pollinators would eagerly visit similar-shaped blossoms, irrespective of them being a single flower or flower aggregate. The most obvious example of this morphological convergence is the functional division of pseudanthia into a central part that performs reproductive function and a peripheral, sterile part that serves pollinator attraction. The importance of visual cues from showy bracts/ray flowers has been attested to in numerous studies, including both observations (Andersson, 1996; Armbruster *et al.*, 2005; Song *et al.*, 2012; Pérez-Barrales *et al.*, 2013) and manipulation experiments (Celedón-Neghme *et al.*, 2007; Song *et al.*, 2012) and at least in some species their effect seems dependent on the overall size of the floral display and abundance of pollinators (Andersson 1999, 2008).

Numerous pseudanthia seem well suited for generalist pollinators. They are frequently whitish/yellowish, actinomorphic, flat or cup-shaped, and similar in size to medium to large flowers

(2–4 cm). However, the form of the pseudanthium and its flowers may diverge considerably; that is, generalistic-looking heads may include long-tubed flowers adapted to butterflies or long-tongued flies. *Bougainvillea* species (Fig. 5E), with a funnel-formed pseudanthium and narrow-tubed sphingophilic flowers, demonstrate that adaptation to specialized pollinators is due to flower rather than blossom form.

Some pseudanthia underwent a profound morphological and ecological specialization linked to a high degree of synorganization, creating unique forms such as bat-pollinated bell-blossoms (Amorim *et al.*, 2021) or deceptive traps known from Araceae (Gottsberger and Amaral, 1984; Bernhardt, 2000). The adaptation to certain groups of pollinators has ultimately led to several independent shifts from actinomorphy to monosymmetry in pseudanthia – a common and well-recognized evolutionary transition found in single flowers (Reyes *et al.*, 2016). The zygomorphic blossoms of *Dalechampia* Plum. ex L. (Euphorbiaceae) present resin as reward for euglossine bees (Armbruster and Webster, 1979) and some of them [i.e. *D. spathulata* (Scheidw.) Baill., Fig. 5J] develop perfume blossoms with a morphologically derived oil-secreting centre (Froebel *et al.*, 1983). The floral pseudanthium of *Thalia geniculata* (Fig. 6I) forms a zygomorphic blossom adapted to pollination by *Xylocopa* (Latreille, 1802) bees (Claßen-Bockhoff, 1991b), while some hummingbird-pollinated *Euphorbia* species (e.g. *E. tithymaloides* L., *E. macrocarpa* Boiss. & Buhse.; Fig. 5X) develop tube-like blossoms with separate nectar chambers using involucre excrecences (Michaelis, 1924; Dressler, 1957).

A relatively large number of pseudanthia are bird-pollinated (Porsch, 1923), showing traits such as reddish or bright red coloration, production of a large amount of low-concentration nectar and stability necessary for their passerine and honey-eater pollinators (Keighery, 1975; Gu *et al.*, 2010). Based on blossom construction, two different forms of ornithophilous pseudanthia can be distinguished. Bell-shaped blossoms tend to have a homogeneous centre which accumulates nectar from all flowers, creating a huge supply for visiting birds. Claßen-Bockhoff (1992) postulated that the evolution of such architecture in *Darwinia* (Myrtaceae) Raf. species and *Pimelea physodes* Hook. (Thymeleaceae, Fig. 5P, Q; Keighery, 1975) might have been a side effect of bract enlargement necessary for bud protection in mountainous habitats. Heads, in contrast, may provide pollinators with a landing place on top of the flowers. In *Etilingera elatior* (Fig. 5K), the inflorescence axis elongates with the acropetal flowering sequence, maintaining a constant distance between the sitting bird and nectar reward (Classen, 1987). Additionally, each open flower presents a strong visual cue in the form of a contrasting yellow margin which resembles the open bill of a young bird.

Many pseudanthia are bicoloured as the showy bracts differ in colour from the centre (e.g. Fig. 5J, L, M). In some Apiaceae,

*Palicourea* sp. (Rubiaceae). (J) Thyse-like head with showy prophylls: *Dalechampia spathulata* (Euphorbiaceae). (K, L) Heads with showy bracts: (K) *Etilingera elatior* (Zingiberaceae); (L) *Ammobium alatum* (Asteraceae). (M) Heads of headlets with showy bracts: *Myriocephalus helichrysoides* (Asteraceae). (N) Head with showy bistipulate bracts: *Parrotiopsis jacquemontiana* (Hamamelidaceae). (O) Head-like floral units with showy bracts: *Actinotus helianthi* (Apiaceae). (P–R) Bell-shaped heads with showy bracts: (P) *Pimelea physodes* (Thymeleaceae); (Q) *Darwinia leiostyla* (Myrtaceae); (R) *Orothamnus zeyheri* (Proteaceae). (S) Head with modified short-shoots: *Actinodium cunninghamii*. (T, U) Clusters of single flowers with showy bracts: (T) *Staavia doddii* (Bruniaceae); (U) *Euchaetis longibracteata* (Rutaceae). (V) Umbel of umbellets with showy involucre bracts: *Xanthosia rotundifolia* (Apiaceae). (W, X) Cyathia with showy stipular excrecences (Euphorbiaceae): (W) *Euphorbia fulgens*; (X) *Euphorbia macrocarpa*. A–P, R, T–W from -Claßen-Bockhoff (2023).

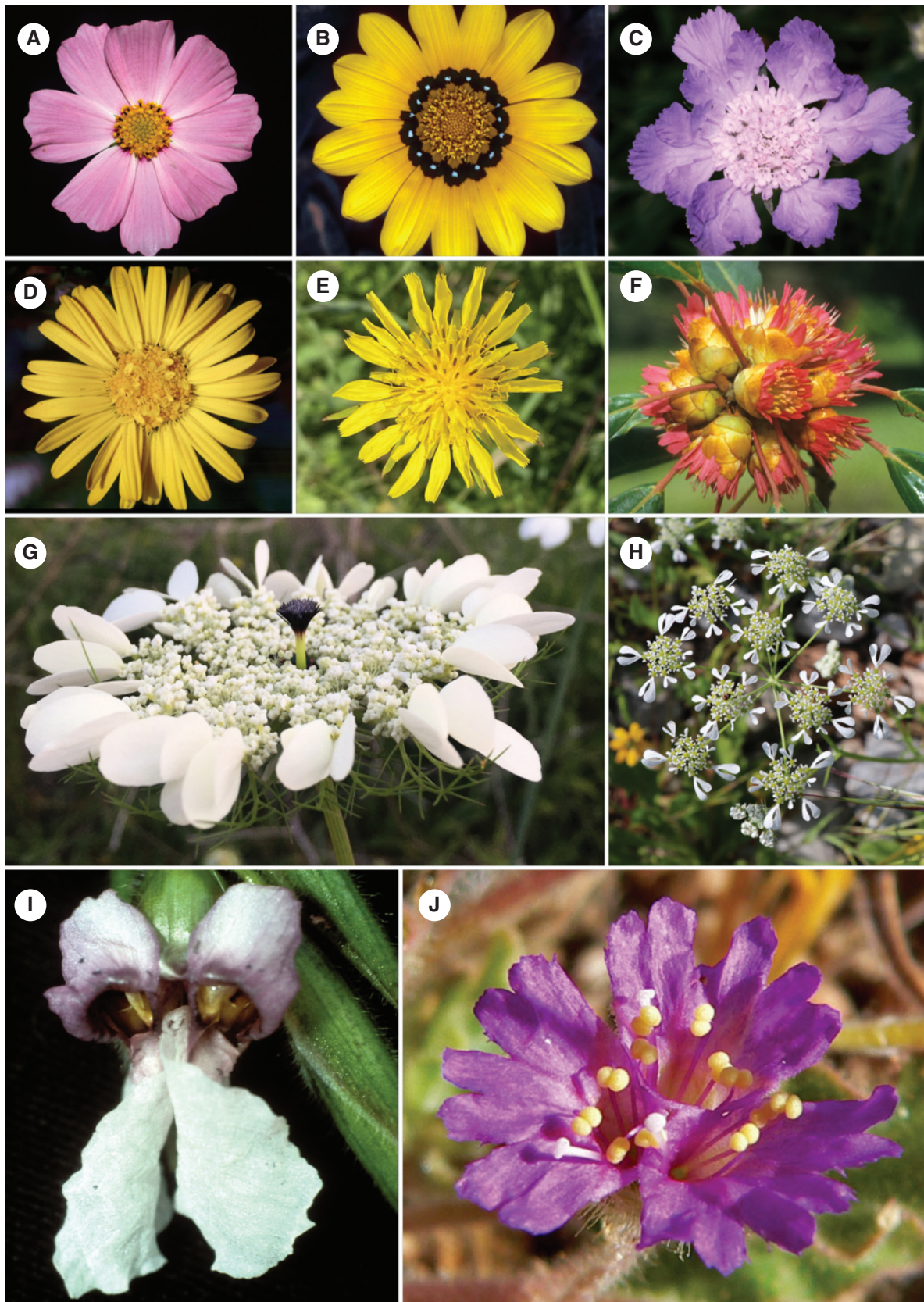


FIG. 6. Floral pseudanthia *sensu stricto*. (A–C) Heads with actinomorphic central florets and monosymmetric ray florets: (A) *Cosmos bipinnatus* (Asteraceae); (B) *Gazania rigens* (Asteraceae); (C) *Scabiosa* sp. (Caprifoliaceae). (D) Head of headlets with monosymmetric ray flowers at the periphery of the entire blossom: *Oedera capensis* (Asteraceae). (E–F) Head with monosymmetric flowers only: (E) *Tragopogon pratensis* (Asteraceae); (F) *Rhodoleia championii* (Hamamelidaceae). (G) Umbel of umbellets with ray flowers at the margin of entire blossom: *Artedia squamata* (Apiaceae). (H) Umbel of umbellets with ray flowers at the margin of individual umbellets: *Tordylium apulum* (Apiaceae). (I) Zygomorphic blossom made of mirror-imaged pair of asymmetric flowers with showy staminodes: *Thalia geniculata* (Marantaceae). (J) Triad of monosymmetric florets forming an actinomorphic blossom: *Allionia incarnata* (Nyctaginaceae). Photos: B, E, I from Claßen-Bockhoff (2023), H, Stan Shebbs, Wikimedia Commons.

TABLE I. List of families with *pseudanthia* sensu stricto

| Systematics   | Morphology  | Ov.  | References   |
|---|---|------|--|
| <b>ANA Grade</b>  |   |      |  |
| <b>Hydatellaceae</b>  |   |      |  |
| <i>Trithuria</i> Hook.f.  | Minute head (FU) with bracts, monoclinal flowers reduced to a single stamen or carpel; carpellate florets usually surround the staminate ones | 1    | Hamann 1998<br>Rudall <i>et al.</i> 2009   |
| <b>Magnoliids</b>   |   |      |  |
| <b>Saururaceae</b>  |   |      |  |
| <i>Houttuynia cordata</i> Thunb.<br><i>Anemopsis californica</i> (Nutt.) Hook. & Arn.   | Dense spike with white bracts, flowers monoclinal, staminate at the tip of the inflorescence  | 6–16 | Tucker 1981<br>Tucker 1985<br>Cheng-Yih and Kubitzki 1993  |
| <b>Monocotyledons</b>   |   |      |  |
| <b>Bromeliaceae</b>   |   |      |  |
| <i>Canistrum</i> É.Morren<br><i>Edundoa</i> Leme<br><i>Wittrockia superba</i> Lindm.<br><i>Wittrockia cyathiformis</i> (Vell.) Leme                               | Simple or compound racemes with white or coloured bracts  | num  | Smith and Till 1998<br>Santos-Silva <i>et al.</i> 2017<br>Nogueira <i>et al.</i> 2021                  |
| <b>Cyperaceae</b>   |   |      |  |
| <i>Rhynchospora</i> (L.) Vahl., sev. spec.  | Cluster of spikelets with few white bracts  | 1    | Leppik 1955<br>Goetghebeur 1998<br>da Costa <i>et al.</i> 2021   |
| <i>Ficinia radiata</i> (L.f.) Kunth   | Cluster of spikelets with many yellow bracts  |      | Claßen-Bockhoff 1990<br>Goetghebeur 1998   |
| <b>Eriocaulaceae, e.g.</b>  |   |      |  |
| <i>Eriocaulon xeranthemum</i> Mart.<br><i>Syngonanthus</i> Ruhland<br><i>Comanthera</i> L.B.Sm. <i>Mesanthemum</i> Körn.<br><i>Paepalanthus</i> Mart., sev. spec. | Head (FU) with many white or yellow bracts, flowers monoclinal, staminate florets in the median part of the head                              | 2–3  | Hensold, 1988<br>Stützel, 1998<br>Stützel and Trovó 2013   |
| <b>Poaceae</b>  |   |      |  |
| <i>Sokinochloa australis</i> S. Dransf.   | Cluster of spikelets with brownish bracts   | 1    | Kellogg 2015<br>Dransfield 2016  |
| <b>Pontederiaceae</b>   |   |      |  |
| <i>Heteranthera</i> (syn. <i>Hydrothrix</i> )<br><i>Gardneri</i> (Hook.f.) M.Pell.  | Pair of zygomorphic flowers forming an actinomorphic, hexamerous blossom  | num  | Rutishauser 1983<br>Cook 1998  |
| <b>Marantaceae</b>  |   |      |  |
| <i>Thalia</i> L.  | Pair of asymmetric flowers forming a bilabiate blossom with showy staminodes  | 1    | Claßen-Bockhoff 1991b<br>Andersson 1998<br>Dworaczek and Claßen-Bockhoff 2016                          |
| <b>Zingiberaceae</b>  |   |      |  |
| <i>Etilingera</i> (syn. <i>Nicolaia</i> ) <i>elatior</i> (Jack) R.M.Sm.   | Head with many red bracts   | num  | Claßen 1987<br>Larsen <i>et al.</i> 1998   |
| <b>Amaryllidaceae</b>   |   |      |  |
| <i>Haemanthus</i> L. sev. spec.<br><i>Scadoxus</i> Raf. sev. spec.  | Umbel-like cymoid with coloured spathe bracts   | 3–6  | Müller-Doblies and Müller-Doblies 1975<br>Meerow and Snijman 1998<br>Martínez-Gómez <i>et al.</i> 2022 |
| <b>Orchidaceae</b>  |   |      |  |
| <i>Rhizanthella gardneri</i> R.S.Rogers   | Head with white bracts that serve protective function (all species are mycoheterotrophic and bloom underground)                               | num  | Balogh 1982<br>Dixon <i>et al.</i> 1990  |
| <b>Colchicaceae</b>   |   |      |  |
| <i>Colchicum</i> L. sev. spec. (syn. <i>Androcymbium</i> Willd.)  | Few-flowered head with two white or reddish bracts  | num  | Vogel 1963<br>Nordenstam 1998<br>Manning <i>et al.</i> 2007  |
| <b>Dioscoreaceae</b>  |   |      |  |
| <i>Tacca</i> J.R.Forst. & G.Forst. sev. spec.   | cymoid with ≥2 brown large bracts and many dark filamentous prophylls   | num  | Huber 1998<br>Zhang <i>et al.</i> 2011<br>Chua <i>et al.</i> 2020<br>Martínez-Gómez <i>et al.</i> 2022 |
| <b>Pandanaceae</b>  |   |      |  |
| <i>Freycinetia</i> Gaudich, sev. spec.  | Compound spadix with coloured, fleshy bracts, flowers monoclinal, blossoms dioecious  | num  | Cox 1990<br>Stone <i>et al.</i> 1998   |

TABLE 1. *Continued*

| Systematics  | Morphology  | Ov.      | References   |
|--|---|----------|--|
| <b>Triuridaceae (?)</b><br><i>Lacandonia schismatica</i> . E.Martínez & Ramos  | Minute head with radiating bracts, highly reduced female flowers surround male ones; alternatively interpreted as a flower with inside-out morphology   | 1        | <b>Rudall 2003</b><br><b>Ambrose et al. 2006</b>   |
| <i>Sciaphila</i> Blume<br><i>Triuris</i> Miers<br><i>Triuridopsis</i> H.Maas & Maas  | Dioecious heads with radiating bracts; alternatively interpreted as monoclinal flowers  | 1        | <b>Rudall 2003</b> ;<br><b>Ambrose et al. 2006</b>   |
| <b>Araceae several genera</b> , e.g.<br><i>Philodendron</i> Schott.  | spadix (FU) with spathe, flowers monoclinal or perfect  | 1 to num | <b>Vogel 1963</b><br><b>Gottsberger and Amaral 1984</b><br>Mayo et al. 1998<br><b>Barabé and Lacroix 2008b</b>                       |
| <b>Aponogetonaceae</b><br><i>Aponogeton distachyos</i>   | Spike; white flower-subtending bracts floating on the water surface   | num      | <b>Bruggen 1998</b>  |
| <b>Eudicotyledons</b>  |   |          |  |
| <b>Proteaceae</b> , e.g.<br><i>Orothamnus</i> Pappe ex Hook.<br><i>Serruria</i> Burm. ex Salisb.   | Head with coloured bracts, cup- or bell-shaped  | 1 to num | <b>Weston 2007</b>   |
| <b>Hamamelidaceae</b><br><i>Parrotiopsis jacquemontiana</i> (Decne.) Rehder  | Head (FU) with two bistipulate bracts forming a hexamerous blossom  | 2        | <b>Claßen-Bockhoff 1990</b><br>Endress 1993<br><b>Claßen-Bockhoff and Bull-Hereñu 2013</b>   |
| <i>Rhodoleia</i> Champ. ex Hook.   | Head with red, zygomorphic flowers, the peripheral petals of them enlarged  | num      | <b>Claßen-Bockhoff 1990</b><br>Endress 1993<br><b>Gu et al. 2010</b>   |
| <b>Rhamnaceae</b><br><i>Phyllica plumosa</i> L.<br><i>Stenanthemum pimeleoides</i> (Hook.f.) Benth.<br><i>Siegfriedia darwinioides</i> C.A.Gardner<br><i>Spyridium</i> Fenzl sev. spec.  | Head-like cymes or thyrses with white showy bracts  | 2–8      | <b>Claßen-Bockhoff 1990</b><br>Medan and Schirarend 2004   |
| <b>Moraceae</b><br><i>Dorstenia</i> L. sev. spec.  | Head-like FU* ('cymoid') with a collar of filamentous bracts, monoclinal flowers united in a monoecious pseudanthium  | 1        | <b>Bernbeck 1932</b><br>Rohwer and Berg 1993<br>Leite 2016   |
| <i>Antiaropsis</i> K.Schum.  | Head-like unit with red bracts  |          |  |
| <b>Peraceae</b><br><i>Pera</i> Mutis   | FU ('composed cyme') with bracts; plant dioecious with distinct staminate and carpellate pseudanthia  | 3        | <b>Webster 2014</b><br><b>Gagliardi et al. 2018</b>  |
| <b>Phyllanthaceae</b><br><i>Uapaca</i> Baill   | Head subtended by large creamy-yellowish bracts, plant dioecious  | 6        | <b>McPherson 2011</b><br><b>Webster 2014</b>   |
| <b>Euphorbiaceae</b> , e.g.<br><i>Euphorbia milii</i> L.<br><i>Euphorbia heterophylla</i> L.<br><i>Euphorbia fulgens</i> Karw. ex Klotzsch<br><i>Euphorbia macrocarpa</i> Boiss & Buhse. | Cyathium (FU) with two red prophylls<br>Cyathium (FU) with (partially) red leaves<br>Cyathium (FU) with five red, stipular excrescences, actinomorphic blossom<br>Cyathium (FU) with five red, stipular excrescences, zygomorphic | 3–6      | <b>Claßen-Bockhoff 1990</b><br><b>Webster 2014</b><br><b>Michaelis 1924</b><br><b>Prenner and Rudall 2007</b><br><b>Webster 2014</b> |
| <i>Neoguillauminia cleopatra</i> (Baill.) Croizat  | FU ('flower/inflorescence hybrid') with white stipular excrescences   |          | <b>Prenner and Rudall 2007</b><br><b>Webster 2014</b>  |
| <i>Dalechampia spathulata</i> (Scheidw.) Baill.  | FU (? 'complex sciadoid') with two coloured prophylls; staminate cyme surrounded by carpellate cymes  |          | <b>Froebe et al. 1983</b><br><b>Webster 2014</b>   |
| <b>Fabaceae</b><br><i>Neptunia</i> Lour.   | Head with peripheral perfect flowers and a centre consisting of by staminate and carpellate flowers   | 6        | <b>Tucker 1988</b>   |

TABLE 1. *Continued*

| Systematics  | Morphology   | Ov.  | References  |
|--|--|------|---|
| <i>Calliandra surinamesis</i> Benth.   | Pincushion-blossom with few nectar flowers in the centre having elongated androecial tubes                               |      | <b>Claßen 1984</b>  |
| <b>Myrtaceae</b>   |  |      |   |
| <i>Darwinia</i> Rudge sev. gen.  | Bell-shaped head (FU?) with reddish bracts   | 2–10 | <b>Claßen-Bockhoff 1992</b><br>Wilson 2011  |
| <i>Actinodium cunninghamii</i> Schauer   | Proliferating head (inflorescence) with showy short shoots (white bracts and prophylls)                                  | 1    | Wilson 2011<br><b>Claßen-Bockhoff et al. 2013</b>                                   |
| <b>Malvaceae</b>   |  |      |   |
| <i>Lasiopetalum</i> Sm. sev. spec.   | Cymoid with whitish hairy bracts   | 6–8  | <b>Claßen 1988</b><br>Bayer and Kubitzki 2003                                       |
| <b>Rutaceae</b>  |  |      |   |
| <i>Diplolaena</i> R.Br. sev. spec.   | FU ('reduced panicle') with reddish bracts   | sev. | <b>Claßen-Bockhoff et al. 1991</b><br>Kubitzki et al. 2011                          |
| <i>Euchaetis longibracteata</i> Schltr.  | Flowering shoot system with single flowers in basipetal order* and white bracts  |      | Kubitzki et al. 2011  |
| <b>Thymelaeaceae</b>   |  |      |   |
| <i>Pimelea physodes</i> Hook   | Bell-shaped head with reddish bracts   | 1    | <b>Claßen-Bockhoff 1992</b><br>Beaumont et al. 2001                                 |
| <i>Pimelea sulphurea</i> Meisn.<br><i>Gnidia somalensis</i> (Franch.) Gilg                               | Head with bright yellow bracts   |      | Herber 2003   |
| <b>Balanophoraceae</b>   |  |      |   |
| <i>Langsdorffia</i> Mart.<br><i>Thonningia</i> Vahl,   | Head with coloured bracts; flowers monoclinal, plant dioecious (rarely monoecious)                                       | nn   | Hansen 1980   |
| <b>Loranthaceae</b>  |  |      |   |
| <i>Tolypanthus</i> (Blume) Rchb.   | Few-flowered head with fused, coloured bracts  | nn   | Dixit 1961<br><b>Kuijt 1981</b><br>Kuijt and Hansen 2015                            |
| <b>Nyctaginaceae</b>   |  |      |   |
| <i>Bougainvillea</i> Comm. ex Juss.  | Triad ('partial cymose inflorescence') with three coloured bracts  | 1    | Bittrich and Kühn 1993<br><b>Xu et al. 2009</b>                                     |
| <i>Allionia</i> L.   | Triad ('partial cymose inflorescence') of zygomorphic flowers  |      | Bittrich and Kühn 1993 Richman and Venable 2018                                     |
| <b>Nyssaceae</b>   |  |      |   |
| <i>Davidia involucrata</i> Baill.  | Head (FU) with two white, flag-like bracts; andromonoecious with a single perfect flower or completely staminate         | 6–10 | Kubitzki 2004<br><b>Claßen-Bockhoff and Arndt 2018</b>                              |
| <b>Cornaceae</b>   |  |      |   |
| <i>Cornus</i> L. sev. spec.  | FU* ('paniculate cyme', 'minidichasium', 'thyrsus-panicle') with four white or pinkish bracts; flowers rarely monoclinal | 1–2  | Kubitzki 2004<br><b>Feng et al. 2011</b>  |
| <b>Asteraceae</b> , e.g.   |  |      |   |
| <i>Ammobium alatum</i> R. Br.  | Head (FU) with white involucre bracts  | 1    | Anderberg et al. 2007<br><b>Claßen-Bockhoff 1996a</b>                               |
| <i>Polycalymma stuartii</i> F.Muell. & Sond. ex F.Muell. & Sond.   | Pleiochasial cymoid with heads (FUs) surrounded by white bracts  |      |   |
| <i>Myriocephalus guerinae</i> F. Muell.  | Head (FU) of headlets (FUs) with secondary receptacle and white bracts   |      |   |
| <i>Cosmos bipinnatus</i> Cav.  | Head (FU) with zygomorphic, carpellate ray flowers; plant gynomonocious  |      | <b>Troll 1928</b><br>Anderberg et al. 2007  |
| <i>Centaurea jacea</i> L.  | Head (FU) with radial, perfect ray flowers   |      |   |
| <i>Tragopogon pratensis</i> L.   | Homomorphic head (FU) with peripheral ray flowers being distinctly larger than the central ones                          |      |   |
| <i>Dyssodia decipiens</i> (Bartl.) M.C.Johnst. ex M.C.Johnst. & L.Turner<br><i>Oedera capensis</i> Druce | Botryoid composed of heads (FU) with ray flowers only on the outer heads; plants gynomonocious                           |      | <b>Strother 1977</b><br><b>Claßen-Bockhoff 1992, 1996a</b><br>Anderberg et al. 2007 |

TABLE 1. *Continued*

| Systematics   | Morphology   | Ov. | References   |
|---|--|-----|--|
| <b>Bruniaceae</b>   |  |     |  |
| <i>Staavia dodii</i> Bolus<br><i>Staavia glutinosa</i> (P.J.Bergius) Dahl                         | Flowering shoot system with single flowers in basipetal order and white bracts         | 1   | <b>Claßen-Bockhoff 2000</b><br>Claßen-Bockhoff 2016<br>Anderberg <i>et al.</i> 2007      |
| <i>Brunia paleacea</i> P.J.Bergius  | Head (FU?) with wwhite bracts  | 1–2 |  |
| <b>Caprifoliaceae</b>   |  |     |  |
| <i>Scabiosa</i> L.<br><i>Knautia</i> L.   | Head (FU*) with zygomorphic ray flowers  | 1   | Carlson <i>et al.</i> 2011<br>Hofmann and Bittrich 2016                                  |
| <b>Ericaceae</b>  |  |     |  |
| <i>Cavendishia Adenophora</i> Mansf.<br><i>Cavendishia nitens</i> Sleumer                         | Axillary, head-like racemose inflorescence with pinkish bracts                         | num | Luteyn 1983<br>Stevens <i>et al.</i> 2004  |
| <b>Apiaceae, e.g.:</b>  |  |     |  |
| <i>Xanthosia</i> Rudge  | Umbel (FU) of umbellets (FUs) with ≥4 white involucellar bracts, plant andromonoecious | 2   | <b>Froebe, 1979</b><br>Plunkett <i>et al.</i> 2018                                       |
| <i>Actinotus</i> Labill.<br><i>Alepidea</i> F. Delaroché<br><i>Astrantia</i> L.                   | Capitate FU with several whitish involucre bracts, plants andromonoecious              |     | <b>Froebe 1964, 1979</b><br>Plunkett <i>et al.</i> 2018                                  |
| <i>Echinophora trichophylla</i> Sm.<br><i>Artedia squamata</i> L.<br><i>Coriandrum sativum</i> L. | Umbel (FU) of umbellets (FUs), zygomorphic ray flowers, plants andromonoecious         |     | <b>Froebe 1980</b><br>Plunkett <i>et al.</i> 2018<br><b>Baczyński <i>et al.</i> 2022</b> |
| <b>Rubiaceae</b>  |  |     |  |
| <i>Psychotria</i> (incl. <i>Cephaelis</i> ) L., <i>Palicourea</i> Aubl. sev. spec.                | Thyrse (FU?) with ≥4 coloured bracts, flowers perfect, rarely monoclinal               | 2   | <b>Claßen-Bockhoff 1996b</b>   |
| <i>Stipularia africana</i> P. Beauv.  | Cymoid enclosed by stipulate bracts  | num |  |
| <b>Lamiaceae</b>  |  |     |  |
| <i>Congea</i> Roxb.<br><i>Symphorema</i> Roxb.<br><i>Sphenodesme</i> Jack                         | Cyme with flower-subtending bracts, tetramerous or trimerous (after bract fusion)      | 4   | <b>Claßen 1985</b><br>Harley <i>et al.</i> 2004  |

Systematics: after APG IV 2017. Morphology: cymoid is defined as a simple, cymosely branched unit. FU, floral units; question marks indicate probable FUs that require further investigation. \*Unpubl. data. sev. spec., several species. Ov, ovules per flower; nn, not known (due to extreme flower reduction); num, numerous. Quotation marks indicate original morphological terms used in references. References: selection of references referring to the morphology and/or patterning of the pseudanthia (bold type) and to systematic aspects, respectively.

white umbels present a black centre (Fig. 6G) which has been postulated to create a ‘fly catcher’ effect (Eisikowitch, 1980) or other form of insect mimicry (Goulson *et al.*, 2009). Unlike flowers, nectar guides (in the human visual spectrum) are largely lacking in pseudanthia. Exceptions are found in some heteromorphic heads of Asteraceae with ring-like patterns overarched all ray flowers, or a colour contrast between disc and ray flowers. These visual cues probably play a role similar to the UV-patterns found in some species (Burr *et al.*, 1995). An exciting example of flower-like specialization in pseudanthia evolved in *Gorteria diffusa* Thunb. (Asteraceae). Its ray flowers produce a distinct bullseye pattern (Ellis *et al.*, 2014) in the form of dark spots which act as a sexual deception for its main pollinator *Megapalpus capensis* (Wiedeman, 1828). Thomas *et al.* (2009) also found that those apparently randomized spots reflected the divergence angle during flower meristem initiation.

When compared against the background of ‘true flowers’, pseudanthia constitute a remarkable example of convergent evolution in many angiosperm lineages. Their repeated acquisition in the highly derived Asteridae alone (when analysed on the level of species/genera) can be seen as support for Leppik’s view of *pseudanthic recapitulation*. However, note that the term *recapitulation* is slightly misleading as it suggests that pseudanthia arose repeatedly only by convergence and excludes the view that developmental constraints such as meristem

changes may have paved the way towards pseudanthia formation as a predisposition.

#### *Selective advantages of small-flowered aggregates*

Good (1956) held the view that pseudanthia formation was the result of an *aggregation tendency* closely linked to flower miniaturization and ultimately ending in the emergence of flower-like units. However, he only briefly discussed the selective advantages and developmental conditions triggering aggregation in angiosperms.

Densely packed aggregates of small flowers are a common phenomenon across angiosperms. Both features affect the pollination and breeding systems of the plant. Species with flat blossoms, including simple flowers, tend to be ecological generalists (i.e. many Apiaceae or Asteraceae) providing food or other rewards to diverse flower visitors. They rarely suffer from pollinator limitation, allowing them to colonize new habitats. In other plant lineages, floral aggregation probably arose with a switch to wind (Linder and Rudall, 2005) or rodent pollination (Rourke, 1998; Johnson *et al.*, 2001; Kleizen *et al.*, 2008).

Small flowers are cheap in investment and usually have a small number of ovules. Being aggregated, they can compensate for a short flowering time by the large number of flowers.

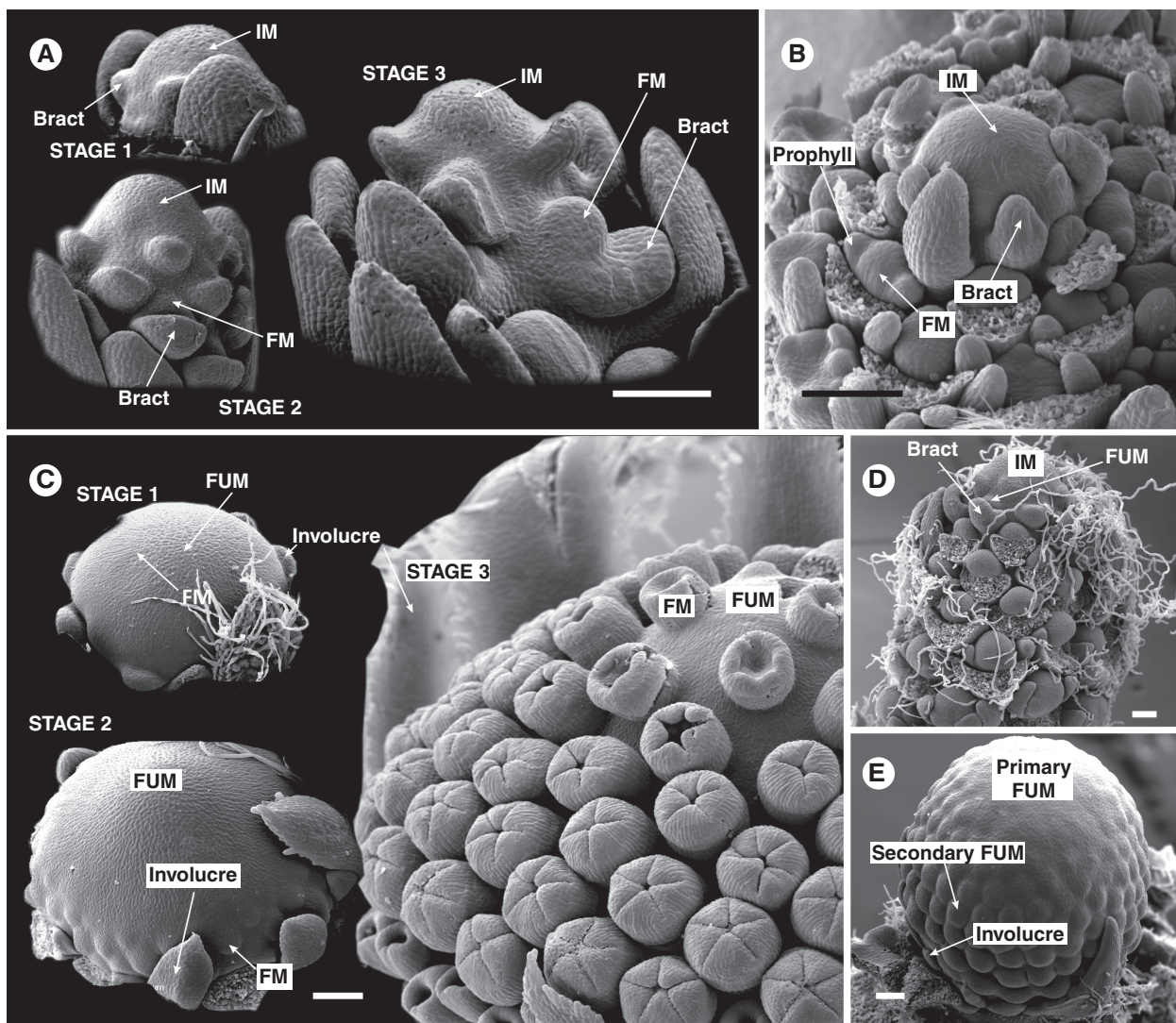


FIG. 7. Inflorescences and floral units. (A, B) Inflorescence meristems with flowers: (A) *Veronica albicans* (Plantaginaceae): three developmental stages of the raceme meristem showing the acropetal segregation of bract-subtended flower meristems; (B) *Actinodium cunninghamii* (Myrtaceae, see Fig. 5S for mature blossom): head meristem with floral meristems. (C) Floral unit meristem with flowers: *Calendula officinalis* (Asteraceae): three developmental stages of the capitulum meristem with flower meristems (stages 1 and 2) and young bract-less florets (stage 3). (D) Inflorescence meristem with floral units: *Ligularia stenocephala* (Maxim.) Matsum. & Koidz. (Asteraceae): bract-subtended capitulum meristems (FUM) in a raceme (IM) occupying flower position. (E) Floral unit meristem with floral units: *Echinops bannaticus* Rochel ex. Schrad.: headlet meristems fractionating from a head meristem. Abbreviations: FUM – floral unit meristem, IM – inflorescence meristem, FM – floral meristem. Photo: B, from Claßen-Bockhoff *et al.* (2013).

If the aggregate is surrounded by ray flowers or showy bracts, ephemeral flowers benefit from the enduring attraction of these structures. The prolonged presentation of many few-ovuled flowers is beneficial for pollination as it may lead to higher rates of outcrossing compared to single flowers with many ovules (Burt, 1961). Indeed, according to our investigation, the majority of pseudanthial plants with highly aggregated blossoms (especially among eudicots) produce flowers with a single or relatively sparse (<10) number of ovules (Table 1).

Aggregation is entwined with evolution of diverse reproductive systems found in flowering plants. Pollinator movements on condensed, flat-surfaced inflorescences are less consistent than on loosely aggregated and three-dimensional ones, which increases pollen discounting (loss of pollen available for outcrossing) and the chances of geitonogamy

(Hardegger and Sturm, 1998; Jordan, 2000; Ishii *et al.*, 2008). When miniaturization makes it hard to avoid self-pollination by physically separating male and female function within florets, a plant is forced to regulate it on the level of an entire inflorescence through either temporal (protandry, protogyny) or spatial (andromonoecy, androdioecy, gynomonoecey, gynodioecy) flower-phase segregation (Plitmann, 1995).

The expression of breeding systems is precisely controlled via resource partitioning (Charlesworth and Charlesworth, 1978; Saur Jacobs and Wade, 2003; Goldberg *et al.*, 2017) that can additionally fuel the process of pseudanthic recapitulation. In andromonoecious Apiaceae, the number of staminate flowers generally declines with increasing order (and decreasing size) of the produced umbels which implies that in these plants, the reproductive outcome is predominantly controlled by a

variable investment in male function (Spalik, 1991; Schlessman and Graceffa, 2002; Schlessman *et al.*, 2004; Reuther and Claßen-Bockhoff, 2010). Due to the centripetal developmental sequence, resources are first allocated to peripheral floral meristems that develop into hermaphrodite flowers. Such increased nourishment of marginal florets can potentially promote their evolution into ray flowers. Bawa and Beach (1981) hypothesized that the prevalence of gynomonocy in Asteraceae can result from evolution of showy rays, as resources that could be otherwise allocated to stamens in marginal florets are spent on enlargement of petals. Although tentative, this explanation is not easily applicable to all composites, as both homogamous and heterogamous heads consisting entirely of monoclinal flowers occur in this family (Kilian and Gemeinholzer, 2009; Torices and Anderberg, 2009).

The distribution of the reproductive organs in individual flowers is remarkably constant. Carpels are almost inevitably surrounded by stamens. While numerous pseudanthia recapitulate this pattern, the arrangement of staminate and carpellate flowers in blossoms is not as highly constrained. Consequently, pseudanthia combine the selective advantages of flower-like patterns for pollinator attraction with developmental plasticity of inflorescences for shaping breeding systems. For example, in Euphorbiaceae, spurge mimic the organization of a typical flower (cyathia composed of carpellate flower surrounded by staminate ones), whereas in *Dalechampia* staminate flowers are those that occupy the central position within the blossom (Prenner and Rudall, 2007; Gagliardi *et al.*, 2018). Pseudanthia of Eriocaulaceae are frequently arranged so that the few staminate flowers develop in the median part of the head (Stützel, 1998). In many Asteracean heads, the outermost flowers are carpellate. They open first, increasing the chance of outcrossing and making capitula an equivalent of protogynous flowers (despite individual disc florets being strongly protandrous). Even blossoms of *Lacandonia schismatica* and *Trithuria*, usually considered to be the only examples of inside-out flowers, have been interpreted as pseudanthia by some authors (Rudall, 2003; Rudall *et al.*, 2016).

Apart from pollination biology, blossoms may aggregate in response to abiotic conditions. For example, secondary heads in Asteraceae–Nassuavinae could have evolved in response to colonization of arid habitats, as enlarged flower-subtending receptacles may function as an additional water storage organ (Katinas *et al.*, 2008). Moreover, inflorescence condensation creates an opportunity to transfer protective function from sepals of individual flowers to bracts that can later evolve into advertising structures. The aggregation of (partial) inflorescences in some Bromeliaceae allows for flower enclosure by enlarged bracts. These serve as canisters for rainwater, which is necessary for heat transfer and proper floral development (Nogueira *et al.*, 2019, 2021), but also create showy display for pollinators. Similar elongated bracts evolved in some Himalayan genera of Asteraceae, such as *Cremanthodium* Benth. (Chen *et al.*, 2013) and *Saussurea* DC. (Tsukaya *et al.*, 2002; Yang and Sun, 2009), to preserve heat and protect pollen from UV radiation. The dual protective and attractive function of enlarged bracts was also confirmed for *Davidia involuocrata* L. (Sun *et al.*, 2008) and *Rheum nobile* (Song *et al.* 2012).

## EVOLUTIONARY PATHWAYS: AGGREGATION VS. CHANGE IN MERISTEM QUALITIES

Recently, it has become clear that a purely typological classification of reproductive shoots hinders our understanding of their diversity and evolution. Although detailed molecular studies of selected plants (Castel *et al.*, 2010; Bartlett and Thompson, 2014; Périlleux *et al.*, 2014) were helpful in recognizing the basic principles of branching and meristem determinacy, an incorrect application of confounded morphological terminology and a model-oriented approach makes it hard to properly interpret structures that deviate from these patterns. Therefore, dense flower clusters are usually interpreted as condensed inflorescences. However, they can also result without aggregation from profoundly altered meristems, for example when the reproductive meristem merges into a floral unit meristem with flower-like qualities. The finding that pseudanthia can originate from different types of reproductive meristems (Fig. 7) results in two hypothetical explanations for their evolution, the aggregation and meristem change theories.

### Aggregation theory

Inflorescence meristems (Figs 7A, B and 8B, C, F) are characterized by acropetal segregation of inflorescence elements. Internodes are elongated late in development and shape the architecture of the inflorescence. The first theory for formation a pseudanthium from an inflorescence meristem is thus internode inhibition, called aggregation. Maresquelle (1970) and Sell (1976) illustrated series of increasing aggregation in selected angiosperm lineages. Pozner *et al.* (2012), likewise, interpreted the capitulum of the Asteraceae as an aggregated inflorescence having originated from an ancestral thyrse. However, as recently proven, the capitulum does not develop from an inflorescence but from a floral unit meristem (Figs 7C, E and 8D, E, G; Zhang and Elomaa 2021).

According to the transient model (Prusinkiewicz *et al.*, 2007), inflorescence development is controlled by the level of a *vegetativeness* (*veg*) factor which declines as indeterminate shoot apical meristems (SAMs) segregate lateral meristems (branches). When the level of *veg* becomes sufficiently low, lateral meristems transform into determinate floral meristems. This simple model can be superimposed onto the flowering-time gene regulatory network (FTGRN, see Davila-Velderrain *et al.*, 2016; C. Liu *et al.*, 2009; Ratcliffe *et al.*, 1999; Valentim *et al.*, 2015). In *Arabidopsis thaliana* (Fig. 8F), a high level of *veg* corresponds to the expression of the shoot identity gene *TERMINAL FLOWER 1* (*TFL1*), a low level to the expression of the flower identity gene *LEAFY* (*LFY*), and the transient stage (branching) to the expression of conserved flowering-time regulators such as *SUPPRESSOR FOR OVEREXPRESSION OF CONSTANS* (*SOC1*), *SHORT VEGETATIVE PHASE* (*SVP*), *AGAMOUS-LIKE 24* (*AGL24*) and *XANTHAAL2* (*XAL2*). Although the rapid decline of *veg* (and alterations to FTGRN in general) can explain the origin of some highly aggregated inflorescences (Azpeitia *et al.*, 2021), the transient model cannot be easily applied to floral units due to different meristem conditions.



*Meristem change theory*

FUMs (Figs 7C, E and 8D, E, G) are characterized by determinacy, understood as the lack of stem-cell activity (not to be confused with ‘openness’ or the lack of terminal flowers, which may or may not develop into floral units depending on available space; see Bull-Hereñu & Claßen-Bockhoff, 2010). Consequently, flower primordia are not continuously segregated from the meristem apex, but instead arise by the process of fractionation that subdivides the available meristem until the entire surface of the FUM is used (Claßen-Bockhoff & Bull-Hereñu, 2013; Claßen-Bockhoff, 2016). Apart from the difference in size, FUMs share most qualities with flower meristems (FMs), which might explain their numerous flower-like genetic and developmental patterns (Broholm *et al.*, 2008; Carlson *et al.*, 2011; Zhao *et al.*, 2016; Baczyński *et al.*, 2022a).

Our knowledge about the genetic patterning of FUMs comes predominantly from studies conducted on their most notable example: flower-heads of Asteraceae (Fig. 8G; Elomaa *et al.*, 1993). The greatest difference between typical Asteracean FMs and FUMs is their initial bulk. Flower-head meristems can reach a few millimetres in diameter (as in sunflower), while FMs rarely exceed a tenth of this size. Additionally, both meristems are patterned by the same process of subapical expansion and fractionation controlled by gradients of auxins established by transmembrane localized exporters belonging to the PIN-FORMED (PIN) protein family (Zhou and Luo, 2018). Disruption of these natural auxin flows can lead to severe changes in the morphology of both flowers (Cheng and Zhao, 2007) and floral units. Exogenous application of IAA (indole-3-acetic acid) onto developing flower-heads of *Matricaria inodora* L. (Zoulias *et al.*, 2019) leads to bracts or ray flowers developing in the centre of the unit. A similar morphogenetic alteration can be achieved by mechanical force, as proven by historical experiments on sunflower meristems (Palmer and Marc, 1982; Hernandez and Palmer, 1988). Recent analyses conducted on *Gerbera* L. indicate that wounding can disrupt the expression of its *CLV3* orthologue (*GhCLV3*), causing auxin-mediated re-patterning of the capitulum. These results constitute a substantial background for future studies, which will probably aim to disentangle the relationships between PIN-mediated transport, local biosynthesis of auxins and development of FUMs.

Although capitula lack a terminal flower, the uniform expression of the *LFY* orthologue (*GhLFY*) in the early flower-head meristem of *Gerbera* defines it as a determinate (lacking stem cell activity) structure, similar to an FM. The suppression of *GhLFY* results in an altered FUM, the centre of which is never fully consumed by flowers or, in the case of strong transgenic lines, a complete loss of flower identity and their substitution with bract-like organs (Zhao *et al.*, 2016). Interestingly, MADS-box *SEPALLATA*-like genes (*SEP*), which similarly to *LFY* account for identity of FMs in *Arabidopsis* (Pelaz *et al.* 2000), underwent duplication and neofunctionalization to control the determinacy of both flowers and entire head of Asteraceae (Zhang *et al.*, 2017). *Gerbera*'s orthologue of *UNUSUAL FLORAL ORGANS* (*UFO*), *GhUFO*, is yet another gene involved in patterning of the capitulum, but its function is conserved and related to FM identity. Silencing of *GhUFO* converts the asteracean floral unit into a structure reminiscent of a single flower with multiple organs initiated in a whorl-like pattern (Zhao *et al.*, 2016). These results indicate that while *LFY*

and *SEP* are implicated in the early patterning of FUM, their co-expression with *UFO* is required to specify future florets. When expression of *UFO* is lacking, flower-heads assume the developmental trajectory of a single flower, what can be seen as support for a peramorphic origin of FUMs (Claßen-Bockhoff & Frankenhäuser, 2020; Baczyński *et al.*, 2022).

The association between FUs and pseudanthia is very clear. However, without further research it is impossible to confirm if acquisition of the former constitutes an important prerequisite for evolution of the latter. Various forms of showy bracts are common in flowering plants, including not only highly condensed (Table 1) but also relatively loosely aggregated inflorescences in which individual flowers constitute a basic pollination unit (Fig. 1). Such petaloid phyllomes are more likely to form in aggregated blossoms, but are not necessarily linked to floral

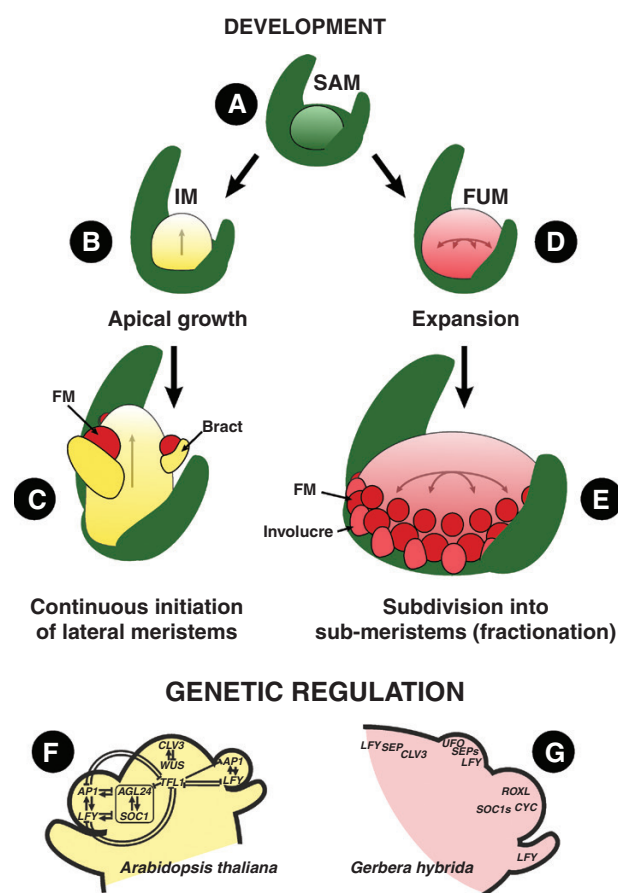


FIG. 8. Development of IMs and FUMs. (A) Indeterminate SAM. (B) SAM transforms into an IM showing continuous (but limited) apical growth. (C) IM sequentially initiates (segregates) lateral meristems. (D) SAM transforms into a determinate FUM that grows with expansion. (E) FUM rapidly subdivides (fractionates) into new sub-meristems. (F) Regulation of raceme development in *Arabidopsis thaliana* (based on Davila-Velderrain *et al.*, 2016; C. Liu *et al.*, 2009; Ratcliffe *et al.*, 1999; Valentim *et al.*, 2015). The upregulation of *TFL1* and maintenance of the regulatory loop between *WUS* and *CLV3* allows for continuous growth of the inflorescence apex through stem-cell activity. (G) Regulation of head development in *Gerbera hybrida* (based on Zhao *et al.*, 2016; Zhang and Elomaa, 2021; T Zhang *et al.*, 2021). Determinate FUMs show an expanded domain of *CLV3* expression, as well as uniform expression of *SEP* and *LFY* orthologues in the mantle zone at the incipient developmental stages. Abbreviations: FUM – floral unit meristem, IM – inflorescence meristem, FM – floral meristem.

units. On the other hand, flower dimorphism including ray flower formation is generally restricted to campanulids and evolved independently numerous times in three of their major clades – Asteraceae (C Zhang *et al.*, 2021), Apiaceae (Baczyński *et al.*, 2022), Caprifoliaceae–Dipsacoideae (Carlson *et al.*, 2011; Panero *et al.*, 2014). In each of these groups, floral units pre-date ray flowers, suggesting that unique qualities of floral unit meristems may drive the evolution of enlarged marginal florets.

#### GENETIC PATTERNING OF RAY FLOWERS AND SHOWY BRACTS

Pseudanthia arose independently in dozens of angiosperm lineages, but the genetic mechanisms underlying the evolution of ray flowers and showy bracts may be remarkably homogeneous. The patterning of ray flowers has been thoroughly studied in Asteraceae (Fig. 8G). Their identity is established primarily by TCP genes: a family of plant-specific transcription factors, which play a crucial role in environment-mediated growth responses (Danisman, 2016). The sequence of the TCP domain encodes a DNA-binding bHLH motif, which was initially identified in maize (*TEOSINTE BRANCHED1*, *TB1*), snapdragon (*CYCLOIDEA*, *CYC*) and rice (*PROLIFERATING CELL FACTOR1* and *PROLIFERATING CELL FACTOR2*, *PCF1* and *PCF2*) (Cubas *et al.*, 1999). Eudicot TCP genes are subdivided in two classes. The TCP I class encompasses orthologues of *PCF* genes, whereas the TCP II class includes orthologues of *TB1* and *CYC* genes (Martín-Trillo and Cubas, 2010). The canonical function of *CYC* is related to establishment of monosymmetry in individual flowers (Luo *et al.*, 1996); however, in Asteraceae, *CYC*-like genes underwent several duplications, creating multiple paralogues that subsequently neo-functionalized creating differential expression patterns in central and peripheral florets. Overexpression of the *GhCYC2* gene in *Gerbera* (the transcript of which is normally found in the ligule of ray flowers) transforms central radially symmetrical disc flowers into bilaterally symmetrical units similar to those found on the periphery of the capitulum (Broholm *et al.*, 2008; Tähtiharju *et al.*, 2012; Juntheikki-Palovaara *et al.*, 2014). Gene expression patterns recovered in *Senecio vulgaris* L. indicate that its three *CYC2* clade genes regulate ray flower development in a similar manner, promoting growth of the ventral ligule (Garcês *et al.*, 2016). Interestingly, *CYC2* genes had independently expanded in Apiaceae (Baczyński *et al.*, 2022) and Caprifoliaceae–Dipsacoideae (Carlson *et al.*, 2011; Berger *et al.*, 2016) and their paralogues also show differential expression in central and ray florets.

The development of showy bracts has been linked to heterotopic expression of MADS-box genes, including orthologues of class B genes *APETALA3* (*AP3*) and *PISTILLATA* (*PI*) from *A. thaliana*, which canonically take part in the establishment of identity of petals and stamens (Theißen *et al.*, 2000; Becker and Theißen, 2003). In pseudanthial dogwoods (*Cornus* L., Fig 5H), petaloid bracts evolved independently in the so-called DW (dwarf) and BB (big-bracted) groups with important differences visible not only in the bract position but also in the expression of B-class orthologues during their morphogenesis (Zhang *et al.*, 2008; Feng *et al.*, 2012).

The handkerchief-like semaphylls of *Davidia involucreta* are also patterned with the aid of B-class and C-class MADS-box genes and might have evolved to compensate for apetalacy in Nyssaceae (Manchester *et al.*, 1999; Vekemans *et al.*, 2012). Outside Cornales, the MADS-box-related organ petaloidy has been inferred for nectariferous bracts of *Marcgravia* L. (Marcgraviaceae; Geuten *et al.* 2006) that show heterotopic expression of E-class *SEPALLATA*-like genes during development (Pelaz *et al.*, 2000).

#### CONCLUSIONS AND FUTURE PROSPECTS

This review summarizes the historical and current concepts on the structure, form and function of pseudanthia and provides their clear operative definition, by narrowing the term to structurally subdivided flower-like blossoms (or pseudanthia *sensu stricto*). Its overarching goal, however, is to give an overview of the phylogenetic and phenotypic diversity of pseudanthia and evoke a broader interest in these fascinating structures, as until now they have rarely been recognized as a distinct evolutionary phenomenon. This matches the prevalent ‘floricentrism’ (Harder *et al.*, 2004) and general disinterest in inflorescences. What adds insult to injury is that some of the largest pseudanthial families (i.e. Asteraceae or Apiaceae) are renowned for their highly generalized, ‘boring’ floral morphology and promiscuous pollinator interactions which are notoriously difficult to study due to seasonal and geographical variability (Dellinger, 2020). However, considering that pseudanthia recapitulate some well-established morphological patterns recognized in single flowers, they may provide unique insights into the evolution of not only generalized but also specialized pollination syndromes. Manipulative experiments, i.e. addition/removal of showy bracts or alteration of merism/symmetry, can potentially provide links between the resource partitioning, architecture and pollination biology of pseudanthia. In addition to ecology, pseudanthia constitute a fascinating subject for macroevolutionary studies, as factors contributing to their evolvability are virtually unknown. Moreover, the fact that pseudanthia and other forms of modified inflorescences seem associated with spectacular instances of adaptive radiation (i.e. Asteraceae, *Euphorbia*) indicates that aggregated, flower-like blossoms, at least in some instances, can be considered as potential key evolutionary innovations.

Reproductive shoots are usually regarded only as mature structures (and the source of auxillary traits in taxonomic studies) but to fully understand the evolution of pseudanthia, we need to focus on their basic patterning mechanisms. The development of inflorescences has as yet been sufficiently described only in selected model species, such as *Arabidopsis* or *Petunia*. With formal recognition of floral units (Claßen-Bockhoff and Bull-Hereñu, 2013) and other potentially new types of lineage-specific reproductive modules (Zhong and Kong, 2022), it has become clear that additional morphological and ontogenetic data from distantly related angiosperm groups are crucial for our understanding of this diversity. Campanulid eudicots constitute a good candidate system for evo-devo studies on pseudanthia, as several lineages in this speciose clade independently acquired FUMs, as well as pseudanthia with showy

ray flowers or extrafloral elements. Moreover, transformation protocols (Elomaa *et al.*, 1993; Knittel *et al.*, 1994; Hardegger and Sturm, 1998; Baranski, 2008; Klimek-Chodacka *et al.*, 2018; Yildirim *et al.*, 2022) and genomic resources (Iorizzo *et al.*, 2016; Badouin *et al.*, 2017) that could facilitate gene discovery and functional studies, are already available for selected taxa.

## LITERATURE CITED

- Ambrose BA, Espinosa-Matías S, Vázquez-Santana S, *et al.* 2006. Comparative developmental series of the Mexican triurids support a euanthial interpretation for the unusual reproductive axes of *Lacandonia schismatica* (Triuridaceae). *American Journal of Botany* **93**: 15–35.
- Amorim MD, Costa D da S, Krahl DRP, Fischer E, Rech AR. 2021. *Gongylolepis martiana*, an Asteraceae pollinated by bats in the Amazon. *Plant Biology* **23**: 728–734.
- Anderberg AA, Baldwin BG, Bayer RG, *et al.* 2007. Compositae In: Kadereit JW, Jeffrey Charles, eds. *The families and genera of vascular plants: flowering plants, eudicots: Asterales*. Berlin: Springer, 61–588.
- Andersson S. 1996. Floral display and pollination success in *Senecio jacobaea* (Asteraceae): Interactive effects of head and corymb size. *American Journal of Botany* **83**: 71–75. doi:10.1002/j.1537-2197.1996.tb13876.x.
- Andersson L. 1998. Marantaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 278–293.
- Andersson S. 1999. The cost of floral attractants in *Achillea ptarmica* (Asteraceae): evidence from a ray removal experiment. *Plant Biology* **1**: 569–572. doi:10.1111/j.1438-8677.1999.tb00785.x.
- Andersson S. 2008. Pollinator and nonpollinator selection on ray morphology in *Leucanthemum vulgare* (oxeye daisy, Asteraceae). *American Journal of Botany* **95**: 1072–1078. doi:10.3732/ajb.0800087.
- Arber EN, Parkin J. 1907. On the origin of angiosperms. *Botanical Journal of the Linnean Society* **38**: 29–80.
- Armbruster WS, Antonsen L, Pélabon C. 2005. Phenotypic selection on *Dalechampia* blossoms: honest signaling affects pollination success. *Ecology* **86**: 3323–3333. doi:10.1890/04-1873.
- Armbruster WS, Webster GL. 1979. Pollination of two species of *Dalechampia* (Euphorbiaceae) in Mexico by euglossine bees. *Biotropica* **11**: 278–283. doi:10.2307/2387919.
- Azpeitia E, Tichtinsky G, Le Masson M, *et al.* 2021. Cauliflower fractal forms arise from perturbations of floral gene networks. *Science* **373**: 192–197.
- Baczyński J, Ferhat C, Spalik K, Claßen-Bockhoff R. 2022a. Flower-like meristem conditions and spatial constraints shape architecture of floral pseudanthia in Apioideae. *EvoDevo* **13**: 19.
- Baczyński J, Sauquet H, Spalik K. 2022b. Exceptional evolutionary lability of flower-like inflorescences (pseudanthia) in Apiaceae subfamily Apioideae. *American Journal of Botany* **109**: 437–455. doi:10.1002/ajb2.1819.
- Badouin H, Gouzy J, Grassa CJ, *et al.* 2017. The sunflower genome provides insights into oil metabolism, flowering and Asterid evolution. *Nature* **546**: 148–152. doi:10.1038/nature22380.
- Balogh P. 1982. *Rhizanthella* RS Rogers, a misunderstood genus (Orchidaceae). *Selbyana* **7**: 27–33.
- Barabé D, Lacroix C. 2008a. Developmental morphology of the flower of *Anthurium jenmanii*: a new element in our understanding of basal Araceae. *Botany* **86**: 45–52. doi:10.1139/b07-113.
- Barabé D, Lacroix C. 2008b. Hierarchical developmental morphology: the case of the inflorescence of *Philodendron ornatum* (Araceae). *International Journal of Plant Sciences* **169**: 1013–1022. doi:10.1086/590444.
- Baranski R. 2008. Genetic transformation of carrot (*Daucus carota*) and other Apiaceae species. *Transgenic Plant Journal* **2**: 18–38.
- Bartlett ME, Thompson B. 2014. Meristem identity and phyllotaxis in inflorescence development. *Frontiers in Plant Science* **5**: 508. doi:10.3389/fpls.2014.00508.
- Bawa KS, Beach JH. 1981. Evolution of sexual systems in flowering plants. *Annals of the Missouri Botanical Garden* **68**: 254–274. doi:10.2307/2398798.
- Bayer C, Kubitzki K. 2003. Malvaceae In: Kubitzki K, Bayer C, eds. *The families and genera of vascular plants: flowering plants, dicotyledons: Malvales, Capparales and non-betain Caryophyllales*. Berlin: Springer, 225–311.
- Beaumont AJ, Edwards TJ, Smith FR. 2001. Patterns of diversity among involucre bracts, inflorescences and flowers in *Gnidia* (Thymelaeaceae). *Systematics and Geography of Plants* **71**: 419–431. doi:10.2307/3668689.
- Becker A, Theißen G. 2003. The major clades of MADS-box genes and their role in the development and evolution of flowering plants. *Molecular Phylogenetics and Evolution* **29**: 464–489.
- Berger BA, Thompson V, Lim A, Ricigliano V, Howarth DG. 2016. Elaboration of bilateral symmetry across *Knautia macedonica* capitula related to changes in ventral petal expression of *CYCLOIDEA*-like genes. *EvoDevo* **7**: 8. doi:10.1186/s13227-016-0045-7.
- Bernbeck F. 1932. Vergleichende Morphologie der Urticaceen und Moraceen-Infloreszenzen. *Botanische Abhandlungen und Beobachtungen* **19**: 1–100.
- Bernhardt P. 2000. Convergent evolution and adaptive radiation of beetle-pollinated angiosperms In: Dafni A, Hesse M, Pacini E, eds. *Pollen and pollination*. Vienna: Springer, 293–320.
- Bittrich V, Kühn U. 1993. Nyctaginaceae In: Kubitzki K, Rohwer JG, Bittrich, eds. *The families and genera of vascular plants: flowering plants, dicotyledons: magnoliid, hamamelid and caryophyllid families*. Berlin: Springer, 473–486.
- Broholm SK, Tähtiharju S, Laitinen RA, Albert VA, Teeri TH, Elomaa P. 2008. A TCP domain transcription factor controls flower type specification along the radial axis of the *Gerbera* (Asteraceae) inflorescence. *Proceedings of the National Academy of Sciences* **105**: 9117–9122. doi:10.1073/pnas.0801359105.
- Bruggen HWE van. 1998. Aponogetonaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 21–25.
- Bull-Hereñu K, Claßen-Bockhoff R. 2010. Developmental conditions for terminal flower production in apoid umbellules. *Plant Diversity and Evolution* **128**: 221–232. doi:10.1127/1869-6155/2010/0128-0010.
- Burr B, Rosen D, Barthlott W. 1995. Untersuchungen zur Ultravioletreflexion von Angiospermenblüten. III. Dilleniidae und Asteridae. *Tropische und Subtropische Pflanzenwelt* **93**: 186.
- Burt BL. 1961. Compositae and the study of functional evolution. *Transactions of the Botanical Society of Edinburgh* **39**: 216–232. doi:10.1080/13594866109441703.
- Caddick LR, Rudall PJ, Wilkin P. 2000. Floral morphology and development in Dioscoreales. *Feddes Repertorium* **111**: 189–230. doi:10.1002/fedr.4911110313.
- Carlson SE, Howarth DG, Donoghue MJ. 2011. Diversification of *CYCLOIDEA*-like genes in Dipsacaceae (Dipsacales): implications for the evolution of capitulum inflorescences. *BMC Evolutionary Biology* **11**: 325. doi:10.1186/1471-2148-11-325.
- Castel R, Kusters E, Koes R. 2010. Inflorescence development in petunia: through the maze of botanical terminology. *Journal of Experimental Botany* **61**: 2235–2246. doi:10.1093/jxb/erq061.
- Celedón-Neghme C, Gonzáles WL, Gianoli E. 2007. Cost and benefits of attractive floral traits in the annual species *Madia sativa* (Asteraceae). *Evolutionary Ecology* **21**: 247–257. doi:10.1007/s10682-006-9002-6.
- Charlesworth B, Charlesworth D. 1978. A model for the evolution of dioecy and gynodioecy. *American Naturalist* **112**: 975–997. doi:10.1086/283342.
- Chase MW, Christenhusz MJM, Fay MF, *et al.* 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* **181**: 1–20.
- Chen J, Yang Y, Zhang Z, Niu Y, Sun H. 2013. A nodding capitulum enhances the reproductive success of *Cremanthodium campanulatum* (Asteraceae) at high elevations in the Sino-Himalayan Mountains. *Plant Ecology & Diversity* **6**: 487–494.
- Cheng Y, Zhao Y. 2007. A role for auxin in flower development. *Journal of Integrative Plant Biology* **49**: 99–104. doi:10.1111/j.1744-7909.2006.00412.x.
- Cheng-Yih W, Kubitzki K. 1993. Saururaceae In: Kubitzki K, Rohwer JG, Bittrich, eds. *The families and genera of vascular plants: flowering plants, dicotyledons: magnoliid, hamamelid and caryophyllid families*. Berlin: Springer, 586–588.
- Chua KS, Borkent A, Wong SY. 2020. Floral biology and pollination strategy of seven *Tacca* species (Taccaceae). *Nordic Journal of Botany* **38**: e02594.

- Claßen R. 1984.** *Untersuchungen zur sStruktur und Phylogenie von Pseudanthien unter besonderer Berücksichtigung ihrer Analogie zu zoophilen Einzelblüten.* PhD dissertation, Rheinisch-Westfälische Technische Hochschule Aachen, Germany.
- Claßen R. 1985.** Organisation und Funktion der blumenbildenden Hochblatthüllen bei Symphoremnoideae (Verbenac.). *Beiträge zur Biologie der Pflanzen* **60**: 383–402.
- Claßen R. 1987.** Morphological adaptations for bird pollination in *Nicolaia elatior* (Jack) Horan (Zingiberaceae). *Gardens' Bulletin (Singapore)* **40**: 37–43.
- Claßen R. 1988.** Beiträge zur Kenntnis der Gattung *Lasiopetalum* (Sterculiaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **109**: 501–527.
- Claßen-Bockhoff R. 1990.** Pattern analysis in pseudanthia. *Plant Systematics and Evolution* **171**: 57–88.
- Claßen-Bockhoff R. 1991a.** Anthodien, Pseudanthien und Infloreszenzblumen. *Beiträge zur Biologie der Pflanzen* **66**: 221–240.
- Claßen-Bockhoff R. 1991b.** Untersuchungen zur Konstruktion des Bestäubungsapparates von *Thalia geniculata* (Marantaceae) [Investigations on the construction of the pollination apparatus of *Thalia geniculata* (Marantaceae)]. *Botanica Acta* **104**: 183–193.
- Claßen-Bockhoff R. 1992.** (Prä-)Disposition, Variation und Bewährung am Beispiel der Infloreszenzblumenbildung. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **89**: 37–72.
- Claßen-Bockhoff R. 1996a.** Functional units beyond the level of the capitulum and cypselae in Compositae In: *Proceedings of the International Compositae Conference, Kew, 1994. Compositae: biology and utilization.* Kew, UK: Royal Botanic Gardens, 129–160.
- Claßen-Bockhoff R. 1996b.** A survey of flower-like inflorescences in the Rubiaceae. *Opera Botanica Belgica* **7**: 329–367.
- Claßen-Bockhoff R. 2000.** Inflorescences in Bruniaceae: with general comments on inflorescences in woody plants. *Opera Botanica Belgica* **12**: 5–310.
- Claßen-Bockhoff R. 2001.** Plant morphology: the historic concepts of Wilhelm Troll, Walter Zimmermann and Agnes Arber. *Annals of Botany* **88**: 1153–1172. doi:10.1006/ambo.2001.1544.
- Claßen-Bockhoff R. 2016.** Bruniaceae In: Kadereit JW, Bittrich V, eds. *The Families and genera of vascular plants: flowering plants, eudicots: Aquifoliales, Boraginales, Bruniales, Dipsacales, Escalloniales, Garryales, Paracryphiales, Solanales (except Convolvulaceae), Icacinaeae, Metteniusaceae, Vahliaeeae.* Cham: Springer, 103–115.
- Claßen-Bockhoff R. 2023.** *Die Pflanze. Morphologie, Entwicklung und Evolution von Vielfalt.* Heidelberg: Springer Spektrum.
- Claßen-Bockhoff R, Armstrong JA, Ohligschläger M. 1991.** The inflorescences of the Australian genera *Diplolaena* R. Br. and *Chorilaena* Endl. (Rutaceae). *Australian Journal of Botany* **39**: 31–42.
- Claßen-Bockhoff R, Arndt M. 2018.** Flower-like heads from flower-like meristems: pseudanthium development in *Davidia involucreta* (Nyssaceae). *Journal of Plant Research* **131**: 443–458. doi:10.1007/s10265-018-1029-6.
- Claßen-Bockhoff R, Bull-Hereñu K. 2013.** Towards an ontogenetic understanding of inflorescence diversity. *Annals of Botany* **112**: 1523–1542. doi:10.1093/aob/mct009.
- Claßen-Bockhoff R, Frankenhäuser H. 2020.** The ‘male flower’ of *Ricinus communis* (Euphorbiaceae) interpreted as a multi-flowered unit. *Frontiers in Cell and Developmental Biology* **8**: 313. doi:10.3389/fcell.2020.00313.
- Claßen-Bockhoff R, Ruonala R, Bull-Hereñu K, Marchant N, Albert VA. 2013.** The unique pseudanthium of *Actinodium* (Myrtaceae)-morphological reinvestigation and possible regulation by CYCLOIDEA-like genes. *EvoDevo* **4**: 8. doi:10.1186/2041-9139-4-8.
- Cook CDK. 1998.** Pontederiaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae).* Berlin: Springer, 395–403.
- da Costa ACG, Thomas WW, Maia ACD, Navarro DM do AF, Milet-Pinheiro P, Machado IC. 2021.** A continuum of conspicuousness, floral signals, and pollination systems in *Rhynchospora* (Cyperaceae): Evidence of ambophily and entomophily in a mostly anemophilous family. *Annals of the Missouri Botanical Garden* **106**: 372–391.
- Cox PA. 1990.** Pollination and the evolution of breeding systems in Pandanaceae. *Annals of the Missouri Botanical Garden* **77**: 816–840. doi:10.2307/2399673.
- Crane PR. 1985.** Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Garden* **72**: 716–793. doi:10.2307/2399221.
- Cubas P, Lauter N, Doebley J, Coen E. 1999.** The TCP domain: a motif found in proteins regulating plant growth and development. *The Plant Journal* **18**: 215–222. doi:10.1046/j.1365-313x.1999.00444.x.
- Danisman S. 2016.** TCP transcription factors at the interface between environmental challenges and the plant's growth responses. *Frontiers in Plant Science* **7**: 1930. doi:10.3389/fpls.2016.01930.
- Davila-Velderrain J, Martinez-Garcia JC, Alvarez-Buylla ER. 2016.** Dynamic network modelling to understand flowering transition and floral patterning. *Journal of Experimental Botany* **67**: 2565–2572. doi:10.1093/jxb/erw123.
- Dellinger AS. 2020.** Pollination syndromes in the 21st century: where do we stand and where may we go? *New Phytologist* **228**: 1193–1213. doi:10.1111/nph.16793.
- Delpino F. 1889.** Teoria della pseudanzia. Preparazione ed inizi nelle Euforbiaceae. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna, Classe di Scienze Fisiche* **10**: 572–580.
- Delpino F. 1890.** Contribuzione alla teoria della pseudanzia. *Malpighia* **4**: 302–312.
- Delpino F. 1892.** Esposizione della teoria della pseudanzia In: *Atti del Congresso Botanico Internazionale di Genova.* Genova: Tipografia del R. Istituto Sordo-Muti, 205–213.
- Dixit SN. 1961.** Morphological and embryological studies in the family Loranthaceae VIII. *Tolypanthus* Bl. *Phytomorphology* **11**: 335–345.
- Dixon KW, Pate JS, Kuo J. 1990.** The Western Australian fully subterranean orchid *Rhizanthella gardneri*. *Orchid Biology* **5**: 37–62.
- Donoghue MJ, Doyle JA. 2000.** Seed plant phylogeny: Demise of the anthophyte hypothesis? *Current Biology* **10**: R106–R109. doi:10.1016/s0960-9822(00)00304-3.
- Doyle JA. 1994.** Origin of the angiosperm flower: a phylogenetic perspective In: Endress PK, Friis EM, eds. *Plant systematics and evolution supplement 8. Early evolution of flowers.* Vienna: Springer, 7–29.
- Doyle JA, Donoghue MJ. 1986.** Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *The Botanical Review* **52**: 321–431. doi:10.1007/bf02861082.
- Dransfield S. 2016.** *Sokinochloa*, a new bamboo genus (Poaceae-Bambusoideae) from Madagascar. *Kew Bulletin* **71**: 1–16.
- Dressler RL. 1957.** The genus *Pedilanthus* (Euphorbiaceae). *Contributions from the Gray Herbarium of Harvard University* no. 179-184 **1956-58**: 1–186. doi:10.5962/p.336384.
- Drobnik J. 2022.** The botanical lexicon of latin vegetable materia medica. A dictionary of nomenclature, taxonomy, and morphology of historical medicinal herbal materials Part I, A. *Pharmaceutical Historian* **52**: 63–64.
- Dworaczek E, Claßen-Bockhoff R. 2016.** ‘False resupination’ in the flower-pairs of *Thalia* (Marantaceae). *Flora* **221**: 65–74. doi:10.1016/j.flora.2015.08.007.
- Ehrhart F. 1787.** *Beiträge zur Naturkunde, und den damit verwandten Wissenschaften.* Hannover: Schmidtischen Buchhandlung.
- Eisikowitch D. 1980.** The role of dark flowers in the pollination of certain umbelliferae. *Journal of Natural History* **14**: 737–742. doi:10.1080/00222938000770611.
- Ellis AG, Brockington SF, de Jager ML, Mellers G, Walker RH, Glover BJ. 2014.** Floral trait variation and integration as a function of sexual deception in *Gorteria diffusa*. *Philosophical Transactions of the Royal Society B: Biological Sciences* **369**: 20130563. doi:10.1098/rstb.2013.0563.
- Elomaa P, Honkanen J, Puska R, et al. 1993.** Agrobacterium-mediated transfer of antisense chalcone synthase cDNA to *Gerbera hybrida* inhibits flower pigmentation. *Biotechnology* **11**: 508–511. doi:10.1038/nbt0493-508.
- Endress PK. 1993.** Hamamelidaceae In: Kubitzki K, Rohwer JG, Bittrich V, eds *The families and genera of vascular plants: flowering plants, dicotyledons: magnoliid, hamamelid and caryophyllid families.* Berlin: Springer, 322–331.
- Faegri K, Pijl LVD. 1979.** *Principles of pollination ecology.* Oxford, UK: Pergamon Press.
- Feng C-M, Liu X, Yu Y, Xie D, Franks RG, Xiang Q-Y (Jenny). 2012.** Evolution of bract development and B-class MADS box gene expression in petaloid bracts of *Cornus* s. l. (Cornaceae). *New Phytologist* **196**: 631–643. doi:10.1111/j.1469-8137.2012.04255.x.

- Feng C-M, Xiang Q-Y, Franks RG. 2011. Phylogeny-based developmental analyses illuminate evolution of inflorescence architectures in dogwoods (*Cornus* s.l., Cornaceae). *New Phytologist* **191**: 850–869.
- Froebe HA. 1964. Die Blütenstände der Saniculoideen (Umbelliferae): eine vergleichend-morphologische und entwicklungsgeschichtliche Untersuchung. *Beiträge zur Biologie der Pflanzen* **40**: 325–388.
- Froebe HA. 1979. Die Infloreszenzen der Hydrocotyloideen (Apiaceae). *Tropische und Subtropische Pflanzenwelt* **40**: 325–388.
- Froebe HA. 1980. Randmusterbildung und Synorganisation bei strahlenden Apiaceendolden. *Plant Systematics and Evolution* **133**: 223–237. doi:10.1007/bf00984381.
- Froebe HA, Magin N, Jöhlinger H, Netz M. 1983. Re-evaluation of the inflorescence of *Dalechampia spathulata* (Scheidw.) Baillon (Euphorbiaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **104**: 249–260.
- Froebe HA, Ulrich G. 1979. Pseudanthien bei Umbelliferen. *Beiträge zur Biologie der Pflanzen* **52**: 175–206.
- Gagliardi KB, Cordeiro I, Demarco D. 2018. Structure and development of flowers and inflorescences in Peraceae and Euphorbiaceae and the evolution of pseudanthia in Malpighiales. *PLoS One* **13**: e0203954. doi:10.1371/journal.pone.0203954.
- Garcés HMP, Spencer VM, Kim M. 2016. Control of floret symmetry by *RAY3*, *SvDIV1B*, and *SvRAD* in the capitulum of *Senecio vulgaris*. *Plant Physiology* **171**: 2055–2068. doi:10.1104/pp.16.00395.
- Geuten K, Becker A, Kaufmann K, et al. 2006. Petaloidy and petal identity MADS-box genes in the balsaminoid genera *Impatiens* and *Marcgravia*. *The Plant Journal* **47**: 501–518. doi:10.1111/j.1365-313X.2006.02800.x.
- Goetghebeur P. 1998. Cyperaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 141–190.
- Goldberg EE, Otto SP, Vamosi JC, et al. 2017. Macroevolutionary synthesis of flowering plant sexual systems. *Evolution* **71**: 898–912. doi:10.1111/evo.13181.
- Gong JZ, Li QJ, Wang X, et al. 2018. Floral morphology and morphogenesis in *Camptotheca* (Nyssaceae), and its systematic significance. *Annals of Botany* **121**: 1411–1425. doi:10.1093/aob/mcy041.
- Good R. 1956. *Features of evolution in the flowering plants*. London: Longmans, Green & Co.
- Gottsberger G, Amaral A. 1984. Pollination strategies in Brazilian *Philodendron* species. *Berichte der Deutschen Botanischen Gesellschaft* **97**: 391–410.
- Goulson D, McGuire K, Munro EE, et al. 2009. Functional significance of the dark central floret of *Daucus carota* (Apiaceae) L.; is it an insect mimic? *Plant Species Biology* **24**: 77–82. doi:10.1111/j.1442-1984.2009.00240.x.
- Gu L, Luo Z, Zhang D, Renner SS. 2010. Passerine pollination of *Rhodoleia championii* (Hamamelidaceae) in subtropical China. *Biotropica* **42**: 336–341. doi:10.1111/j.1744-7429.2009.00585.x.
- Hamann U. 1998. Hydatellaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 231–234.
- Hansen B. 1980. Balanophoraceae. *Flora Neotropica* **23**: 1–80.
- Hanstein JLER von. 1882. *Beiträge zur allgemeinen Morphologie der Pflanzen*. Bonn: Adolph Marcus.
- Hardegger M, Sturm A. 1998. Transformation and regeneration of carrot (*Daucus carota* L.). *Molecular Breeding* **4**: 119–127.
- Harder LD, Jordan CY, Gross WE, Routley MB. 2004. Beyond floricentrism: the pollination function of inflorescences. *Plant Species Biology* **19**: 137–148. doi:10.1111/j.1442-1984.2004.00110.x.
- Harley RM, Atkins S, Budantsev AL, et al. 2004. Labiatae In: Kadereit JW, ed. *The families and genera of vascular plants: flowering plants, dicotyledons: Lamiales (except Acanthaceae including Avicenniaceae)*. Berlin: Springer, 167–275.
- Harris EM. 1995. Inflorescence and floral ontogeny in Asteraceae: a synthesis of historical and current concepts. *Botanical Review* **61**: 93–278. doi:10.1007/bf02887192.
- Harris EM. 1999. Capitula in the Asteridae: A widespread and varied phenomenon. *The Botanical Review* **65**: 348–369. doi:10.1007/bf02857754.
- Hensold N. 1988. Morphology and systematics of *Paepalanthus* subgenus *Xeractis* (Eriocaulaceae). *Systematic Botany Monographs* **23**: 1–150. doi:10.2307/25027709.
- Herber BE. 2003. Thymelaeaceae In: Kubitzki K, Bayer C, eds. *The families and genera of vascular plants: flowering plants, dicotyledons: Malvales, Capparales and non-betain Caryophyllales*. Berlin: Springer, 373–396.
- Hernandez LF, Palmer JH. 1988. Regeneration of the sunflower capitulum after cylindrical wounding of the receptacle. *American Journal of Botany* **75**: 1253–1261. doi:10.1002/j.1537-2197.1988.tb14185.x.
- Hofmann U, Bittrich V. 2016. Caprifoliaceae (with *Zabelia* incert. sed.) In: Kadereit JW, Bittrich Volker, eds. *The families and genera of vascular plants: flowering plants, eudicots: Aquifoliales, Boraginales, Bruniales, Dipsacales, Escalloniales, Garryales, Paracryphiales, Solanales (except Convolvulaceae), Icacinaceae, Metteniusaceae, Vahliaceae*. Cham: Springer, 117–129.
- Huber H. 1998. Dioscoreaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Lilianae (except Orchidaceae)*. Berlin: Springer, 216–235.
- Hutchinson J. 1926. *The families of flowering plants, I: dicotyledons, arranged according to a new system based on their probable phylogeny*. London: Macmillan & Co.
- Iorizzo M, Ellison S, Senalik D, et al. 2016. A high-quality carrot genome assembly provides new insights into carotenoid accumulation and asterid genome evolution. *Nature Genetics* **48**: 657–666. doi:10.1038/ng.3565.
- Ishii HS, Hirabayashi Y, Kudo G. 2008. Combined effects of inflorescence architecture, display size, plant density and empty flowers on bumble bee behaviour: experimental study with artificial inflorescences. *Oecologia* **156**: 341–350. doi:10.1007/s00442-008-0991-4.
- Johnson SD, Pauw A, Midgley J. 2001. Rodent pollination in the African lily *Massonia depressa* (Hyacinthaceae). *American Journal of Botany* **88**: 1768–1773.
- Johow F. 1884. Zur Biologie der floralen und extrafloralen Schau-Apparate. *Jahrbuch des Königlichen Botanischen Garten Berlin* **3**: 47–68.
- Jordan CY. 2000. *The consequences of inflorescence architecture for bumble bee behaviour and plant mating*. PhD dissertation, University of Calgary.
- Juntheikki-Palovaara I, Tähtiharju S, Lan T, et al. 2014. Functional diversification of duplicated CYC2 clade genes in regulation of inflorescence development in *Gerbera hybrida* (Asteraceae). *The Plant Journal* **79**: 783–796. doi:10.1111/tplj.12583.
- Katinas L, Crisci JV, Jabaily RS, et al. 2008. Evolution of secondary heads in Nassauviinae (Asteraceae, Mutisieae). *American Journal of Botany* **95**: 229–240. doi:10.3732/ajb.95.2.229.
- Keighery GJ. 1975. Parallel evolution of floral structures in *Darwinia* (Myrtaceae) and *Pimelea* (Thymelaeaceae). *The Western Australian Naturalist* **13**: 46–50.
- Kellogg EA. 2015. The families and genera of vascular plants: flowering plants. In: Kubitzki K, ed. *Monocots: Poaceae*. Cham: Springer.
- Kilian N, Gemeinholzer B. 2009. Cichorieae. In: Patterson B, ed. *Systematics, evolution, and biogeography of Compositae*. Vienna: International Association for Plant Taxonomy, 343–383.
- Kleizen C, Midgley J, Johnson SD. 2008. Pollination systems of *Colchicum* (Colchicaceae) in Southern Africa: evidence for rodent pollination. *Annals of Botany* **102**: 747–755. doi:10.1093/aob/mcn157.
- Klimek-Chodacka M, Oleszkiewicz T, Lowder LG, Qi Y, Baranski R. 2018. Efficient CRISPR/Cas9-based genome editing in carrot cells. *Plant Cell Reports* **37**: 575–586. doi:10.1007/s00299-018-2252-2.
- Knittel N, Gruber V, Hahne G, Lénée P. 1994. Transformation of sunflower (*Helianthus annuus* L.): a reliable protocol. *Plant Cell Reports* **14**: 81–86. doi:10.1007/BF00233766.
- Krassilov VA. 1997. *Angiosperm origins: morphological and ecological aspects*. Sofia: Pensoft Publishers.
- Kubitzki K. 2004. Cornaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales*. Berlin: Springer, 82–90.
- Kubitzki K, Kallunki JA, Duretto M, Wilson PG. 2011. Rutaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*. Berlin: Springer, 276–356.
- Kuijt J. 1981. Inflorescence morphology of Lorantheae. *Blumea* **27**: 1–73.
- Kuijt J, Hansen B. 2015. Lorantheae In: Kuijt J, Hansen (deceased) B, eds. *The families and genera of vascular plants: flowering plants, eudicots: Santalales, Balanophorales*. Cham: Springer, 73–119.
- Larsen K, Lock JM, Maas H, Maas PJM. 1998. Zingiberaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 474–495.
- Leite VG. 2016. *Desenvolvimento da flor e da inflorescência em espécies de Moraceae*. PhD dissertation, Universidade de São Paulo, Brazil.

- Leite VG, Kjellberg F, Pereira RAS, Teixeira SP. 2021. What makes a fig: insights from a comparative analysis of inflorescence morphogenesis in Moraceae. *Annals of Botany* **127**: 621–631. doi:10.1093/aob/mca202.
- Leppik EE. 1955. *Dichromena ciliata*, a noteworthy entomophilous plant among Cyperaceae. *American Journal of Botany* **42**: 455–458. doi:10.1002/j.1537-2197.1955.tb11147.x.
- Leppik EE. 1959. Evolutionary differentiation of the flower head of the Compositae. *Annales Botanici Societatis Zoologicae-Botanicae Fennicae Vanamo* **14**: 466–481.
- Leppik EE. 1969. Homologous and analogous series in the evolution of flower types. *Genetika* **5**: 12–23.
- Leppik EE. 1970. Evolutionary differentiation of the flower head of the Compositae II. *Annales Botanici Fennici* **7**: 325–352.
- Li H-T, Yi T-S, Gao L-M, et al. 2019. Origin of angiosperms and the puzzle of the Jurassic gap. *Nature Plants* **5**: 461–470. doi:10.1038/s41477-019-0421-0.
- Linder HP, Rudall PJ. 2005. Evolutionary history of Poales. *Annual Review of Ecology, Evolution, and Systematics* **36**: 107–124. doi:10.1146/annurev.ecolsys.36.102403.135635.
- Link JHF. 1837. *Elementa philosophiae botanicae*. Berlin: Haude und Spensersche Buchhandlung.
- Linné C von. 1792. *Termini botanici explicati*. Erlangen: Apud I. I. Palm.
- Liu J, Franks RG, Feng C-M, Liu X, Fu C-X, Xiang Q-Y. 2013. Characterization of the sequence and expression pattern of *LFY* homologues from dogwood species (*Cornus*) with divergent inflorescence architectures. *Annals of Botany* **112**: 1629–1641.
- Liu C, Xi W, Shen L, Tan C, Yu H. 2009. Regulation of floral patterning by flowering time genes. *Developmental Cell* **16**: 711–722. doi:10.1016/j.devcel.2009.03.011.
- Luo D, Carpenter R, Vincent C, Copsey L, Coen E. 1996. Origin of floral asymmetry in *Antirrhinum*. *Nature* **383**: 794–799. doi:10.1038/383794a0.
- Luteyn JL. 1983. Ericaceae: part I. *Cavendishia*. *Flora Neotropica* **35**: 1–289.
- Manchester SR, Crane PR, Golovneva LB. 1999. An extinct genus with affinities to extant *Davidia* and *Camptotheca* (Cornales) from the paleocene of North America and Eastern Asia. *International Journal of Plant Sciences* **160**: 188–207. doi:10.1086/314114.
- Manning J, Forest F, Vinnersten A. 2007. The genus *Colchicum* L. redefined to include *Androcymbium* Willd. based on molecular evidence. *Taxon* **56**: 872–882. doi:10.2307/25065868.
- Maresquelle H-J. 1970. Le thème évolutif des complexes d'inflorescences. Son aptitude à susciter des problèmes nouveaux. *Bulletin de la Société botanique de France* **117**: 1–4. doi:10.1080/00378941.1970.10838739.
- Martín-Trillo M, Cubas P. 2010. TCP genes: a family snapshot ten years later. *Trends in Plant Science* **15**: 31–39. doi:10.1016/j.tplants.2009.11.003.
- Martínez-Gómez J, Atluri TA, Rose IJ, Holliday AJ, Strock CF, Lynch JP, Miller WB, Stevenson DW, Specht CD. 2022. Developmental morphology and anatomy shed light on both parallel and convergent evolution of the umbellate inflorescence in monocots, underlain by a new variant of metatopy. *Frontiers in Plant Science*, **1138**. doi:10.3389/fpls.2022.873505.
- Martínez-Gómez J, Atluri TA, Rose IJ, Holliday AJ, Strock CF, Lynch JP, Miller WB, Stevenson DW, Specht CD. 2022. Developmental morphology and anatomy shed light on both parallel and convergent evolution of the umbellate inflorescence in monocots, underlain by a new variant of metatopy. *Frontiers in Plant Science*, **1138**. doi:10.3389/fpls.2022.873505.
- Matfeld J. 1938. Das morphologische Wesen und die phylogenetische Bedeutung der Blumenblätter. *Berichte der Deutschen Botanischen Gesellschaft* **56**: 86–116.
- Mayo SJ, Bogner J, Boyce PC. 1998. Araceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 26–74.
- McPherson G. 2011. A review of Madagascan *Uapaca* (Euphorbiaceae s.l.). *Adansonia* **33**: 221–231. doi:10.5252/a2011n2a7.
- Medan D, Schirarend C. 2004. Rhamnaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales*. Berlin: Springer, 320–338.
- Meerow AW, Snijman DA. 1998. Amaryllidaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Liliaceae (except Orchidaceae)*. Berlin: Springer, 83–110.
- Strother JL. 1977. Tagetae - systematic review. In: Heywood VH, Harborne JB, Turner BL, eds. *The biology and chemistry of Compositae*. II. London: Academic Press, 769–783.
- Meuse ADJ. 1972. Sixty-five years of theories of the multiaxial flower. *Acta Biotheoretica* **21**: 167–202. doi:10.1007/bf01557178.
- Melville R. 1960. A new theory of the angiosperm flower. *Nature* **188**: 14–18. doi:10.1038/188014a0.
- Michaelis P. 1924. Blütenmorphologische Untersuchungen an den Euphorbiaceen, unter besonderer Berücksichtigung der Phylogenie der Angiospermenblüte. *Botanische Abhandlungen* **3**: 1–150.
- Müller-Doblies U, Müller-Doblies D. 1975. De Liliifloris notulae. 1. Zum Merkmalsbestand von *Haemanthus* (Amaryllidaceae). *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **96**: 324–327.
- Mundry M, Stützel T. 2004. Morphogenesis of the reproductive shoots of *Welwitschia mirabilis* and *Ephedra distachya* (Gnetales), and its evolutionary implications. *Organisms Diversity & Evolution* **4**: 91–108.
- Naghiloo S, Claßen-Bockhoff R. 2017. Understanding the unique flowering sequence in *Dipsacus fullonum*: Evidence from geometrical changes during head development. *PLoS One* **12**: e0174091. doi:10.1371/journal.pone.0174091.
- Nickel G. 1996. Wilhelm Troll (1897–1978): eine Biographie. *Acta Historica Leopoldina* **25**: 9–240.
- Nogueira FM, Palombini FL, Kuhn SA, Oliveira BF, Mariath JE. 2019. Heat transfer in the tank-inflorescence of *Nidularium innocenti* (Bromeliaceae): Experimental and finite element analysis based on X-ray microtomography. *Micron* **124**: 102714. doi:10.1016/j.micron.2019.102714.
- Nogueira FM, Palombini FL, Kuhn SA, Rua GH, Mariath JEA. 2021. The inflorescence architecture in Nidularioid genera: Understanding the structure of congested inflorescences in Bromeliaceae. *Flora* **284**: 151934.
- Nordenstam B. 1998. Colchicaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Liliaceae (except Orchidaceae)*. Berlin: Springer, 175–185.
- Palmer JH, Marc J. 1982. Wound-induced initiation of involucre bracts and florets in the developing sunflower inflorescence. *Plant and Cell Physiology* **23**: 1401–1409.
- Panero JL, Freire SE, Ariza Espinar L, Crozier BS, Barboza GE, Cantero JJ. 2014. Resolution of deep nodes yields an improved backbone phylogeny and a new basal lineage to study early evolution of Asteraceae. *Molecular Phylogenetics and Evolution* **80**: 43–53. doi:10.1016/j.ympev.2014.07.012.
- Pelaz S, Ditta GS, Baumann E, Wisman E, Yanofsky MF. 2000. B and C floral organ identity functions require *SEPALLATA* MADS-box genes. *Nature* **405**: 200–203. doi:10.1038/35012103.
- Pérez-Barrales R, Bolstad GH, Pélabon C, Hansen TF, Armbruster WS. 2013. Pollinators and seed predators generate conflicting selection on *Dalechampia* blossoms. *Oikos* **122**: 1411–1428.
- Périlleux C, Lobet G, Tocquin P. 2014. Inflorescence development in tomato: gene functions within a zigzag model. *Frontiers in Plant Science* **5**: 121. doi:10.3389/fpls.2014.00121.
- Plitmann U. 1995. Distribution of dimorphic flowers as related to other elements of the reproductive strategy. *Plant Species Biology* **10**: 53–60. doi:10.1111/j.1442-1984.1995.tb00120.x.
- Plunkett GM, Pimenov MG, Reduron J-P, et al. 2018. Apiaceae. In: Kadereit JW, Bittrich V, eds. *The families and genera of vascular plants: flowering plants, eudicots: Apiales, Gentianales (except Rubiaceae)*. Cham: Springer, 9–206.
- Porsch O. 1923. Blütenstände als Vogelblumen. *Österreichische Botanische Zeitschrift* **72**: 125–149. doi:10.1007/bf01660046.
- Pozner R, Zanotti C, Johnson LA. 2012. Evolutionary origin of the Asteraceae capitulum: insights from Calyceraceae. *American Journal of Botany* **99**: 1–13. doi:10.3732/ajb.1100256.
- Prenner G, Box MS, Cunniff J, Rudall PJ. 2008. The branching stamens of *Ricinus* and the homologies of the angiosperm stamen fascicle. *International Journal of Plant Sciences* **169**: 735–744. doi:10.1086/588071.
- Prenner G, Cacho NI, Baum D, Rudall PJ. 2011. Is *LEAFY* a useful marker gene for the flower–inflorescence boundary in the *Euphorbia* cyathium? *Journal of Experimental Botany* **62**: 345–350. doi:10.1093/jxb/erq275.
- Prenner G, Rudall PJ. 2007. Comparative ontogeny of the cyathium in *Euphorbia* (Euphorbiaceae) and its allies: exploring the organ–flower–inflorescence boundary. *American Journal of Botany* **94**: 1612–1629. doi:10.3732/ajb.94.10.1612.
- Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E. 2007. Evolution and development of inflorescence architectures. *Science* **316**: 1452–1456. doi:10.1126/science.1140429.

- Ratcliffe OJ, Bradley DJ, Coen ES. 1999. Separation of shoot and floral identity in Arabidopsis. *Development* **126**: 1109–1120. doi:10.1242/dev.126.6.1109.
- Ray J. 1682. *Methodus Plantarum nova*. London: Impensis Henrici Fäitborne.
- Reuther K, Claßen-Bockhoff R. 2010. Diversity behind uniformity—inflorescence architecture and flowering sequence in Apiaceae-Apioideae. *Plant Diversity and Evolution* **128**: 181–220. doi:10.1127/1869-6155/2010/0128-0009.
- Reyes E, Sauquet H, Nadot S. 2016. Perianth symmetry changed at least 199 times in angiosperm evolution. *Taxon* **65**: 945–964. doi:10.12705/655.1.
- Richman SK, Venable DL. 2018. Aggregate enantiostyly: floral visitor interactions with a previously unreported form of floral display. *Journal of Pollination Ecology* **22**: 49–54. doi:10.26786/1920-7603(2018)seven.
- Rieppel O. 2011. Wilhelm Troll (1897–1978): idealistic morphology, physics, and phylogenetics. *History and Philosophy of the Life Sciences* **33**: 321–342.
- Rohrer JG, Berg CC. 1993. Moraceae In: Kubitzki K, Rohrer JG., Bittrich V, eds. *The families and genera of vascular plants: flowering plants, dicotyledons: magnoliid, hamamelid and caryophyllid families*. Berlin: Springer, 438–453.
- Rourke JP. 1998. A review of the systematics and phylogeny of the African Proteaceae. *Australian Systematic Botany* **11**: 267–285. doi:10.1071/sb97027.
- Rudall PJ. 2003. Monocot pseudanthia revisited: floral structure of the mycoheterotrophic family Triuridaceae. *International Journal of Plant Sciences* **164**: S307–S320. doi:10.1086/376879.
- Rudall PJ, Alves M, das Graças Sajo M. 2016. Inside-out flowers of *Lacandonia brasiliiana* (Triuridaceae) provide new insights into fundamental aspects of floral patterning. *PeerJ* **4**: e1653.
- Rudall PJ, Bateman RM. 2006. Morphological phylogenetic analysis of Pandanales: Testing contrasting hypotheses of floral evolution. *Systematic Botany* **31**: 223–238. doi:10.1600/036364406777585766.
- Rudall PJ, Bateman RM. 2010. Defining the limits of flowers: the challenge of distinguishing between the evolutionary products of simple versus compound strobili. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 397–409. doi:10.1098/rstb.2009.0234.
- Rudall PJ, Remizowa MV, Prenner G, Prychid CJ, Tuckett RE, Sokoloff DD. 2009. Nonflowers near the base of angiosperms? Spatiotemporal arrangement of organs in reproductive units of Hydatellaceae and its bearing on the origin of the flower. *American Journal of Botany* **96**: 67–82. doi:10.3732/ajb.0800027.
- Rutishauser R. 1983. *Hydrothrix gardneri*: Bau und Entwicklung einer eigenartigen Pontederiacee. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **104**: 115–141.
- Santos-Silva F, Venda A, Hallbritter H, Mantovani A, Forzza R. 2017. Nested in chaos: Insights on the relations of the ‘Nidularioid Complex’ and the evolutionary history of *Neoregelia* (Bromelioideae-Bromeliaceae). *Brittonia* **69**: 133–147.
- Saur Jacobs M, Wade MJ. 2003. A synthetic review of the theory of gynodioecy. *The American Naturalist* **161**: 837–851. doi:10.1086/375174.
- Schlessman MA, Graceffa LM. 2002. Protogyny, pollination, and sex expression of andromonoecious *Pseudocymopterus montanus* (Apiaceae, Apioideae). *International Journal of Plant Sciences* **163**: 409–417. doi:10.1086/339513.
- Schlessman MA, Underwood N, Watkins T, Graceffa LM, Cordray D. 2004. Functions of staminate flowers in andromonoecious *Pseudocymopterus montanus* (Apiaceae, Apioideae). *Plant Species Biology* **19**: 1–12.
- Sell Y. 1976. Tendances évolutives parmi les complexes inflorescentiels. *Revue Générale de Botanique* **83**: 247–267.
- Smith LB, Till W. 1998. Bromeliaceae In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 74–99.
- Song B, Zhang Z-Q, Stöcklin J, et al. 2012. Multifunctional bracts enhance plant fitness during flowering and seed development in *Rheum nobile* (Polygonaceae), a giant herb endemic to the high Himalayas. *Oecologia* **172**: 359–370. doi:10.1007/s00442-012-2518-2.
- Spalik K. 1991. On evolution of andromonoecy and ‘overproduction’ of flowers: a resource allocation model. *Biological Journal of the Linnean Society* **42**: 325–336. doi:10.1111/j.1095-8312.1991.tb00566.x.
- Stevens PF, Luteyn J, Oliver EGH, et al. 2004. Ericaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, dicotyledons: Celastrales, Oxalidales, Rosales, Cornales, Ericales*. Berlin: Springer, 145–194.
- Stokes J. 1812. *A botanical materia medica*. London: J. Johnson and Co.
- Stone BC, Huynh K-L, Poppendieck H-H. 1998. Pandanaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Liliaceae (except Orchidaceae)*. Berlin: Springer, 397–404.
- Stützel T. 1998. Eriocaulaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, monocotyledons: Alismatanae and Commelinanae (except Gramineae)*. Berlin: Springer, 197–207.
- Stützel T, Trovó M. 2013. Inflorescences in Eriocaulaceae: taxonomic relevance and practical implications. *Annals of Botany* **112**: 1505–1522. doi:10.1093/aob/mct234.
- Sun J-F, Gong Y-B, Renner SS, Huang S-Q. 2008. Multifunctional bracts in the dove tree *Davidia involucrata* (Nyssaceae: Cornales): rain protection and pollinator attraction. *The American Naturalist* **171**: 119–124. doi:10.1086/523953.
- Sun G, Ji Q, Dilcher DL, Zheng S, Nixon KC, Wang X. 2002. Archaefractaceae, a new basal angiosperm family. *Science* **296**: 899–904. doi:10.1126/science.1069439.
- Taylor ML, Macfarlane TD, Williams JH. 2010. Reproductive ecology of the basal angiosperm *Trithuria submersa* (Hydatellaceae). *Annals of Botany* **106**: 909–920. doi:10.1093/aob/mcq198.
- Tähtiharju S, Rijpkema AS, Vetterli A, Albert VA, Teeri TH, Elomaa P. 2012. Evolution and diversification of the CYC/TB1 gene family in Asteraceae—a comparative study in *Gerbera* (Mutisieae) and sunflower (Heliantheae). *Molecular Biology and Evolution* **29**: 1155–1166. doi:10.1093/molbev/msr283.
- Theißen G, Becker A, Di Rosa A, et al. 2000. A short history of MADS-box genes in plants. *Plant Molecular Biology* **42**: 115–149.
- Thomas MM, Rudall PJ, Ellis AG, Savolainen V, Glover BJ. 2009. Development of a complex floral trait: the pollinator-attracting petal spots of the beetle daisy, *Gorteria diffusa* (Asteraceae). *American Journal of Botany* **96**: 2184–2196. doi:10.3732/ajb.0900079.
- Torices R, Anderberg AA. 2009. Phylogenetic analysis of sexual systems in Inuleae (Asteraceae). *American Journal of Botany* **96**: 1011–1019. doi:10.3732/ajb.0800231.
- Troll W. 1928. *Organisation und Gestalt im Bereich der Blüte*. Berlin: Springer.
- Troll W. 1964. *Die Infloreszenzen: typologie und stellung im aufbau des vegetationskörpers, Vol 1*. Stuttgart: Gustav Fischer Verlag.
- Tsukaya H, Fujikawa K, Wu S-G. 2002. Thermal insulation and accumulation of heat in the downy inflorescences of *Saussurea medusa* (Asteraceae) at high elevation in Yunnan, China. *Journal of Plant Research* **115**: 263–268. doi:10.1007/s10265-002-0030-1.
- Tucker SC. 1981. Inflorescence and floral development in *Houttuynia cordata* (Saururaceae). *American Journal of Botany* **68**: 1017–1032. doi:10.1002/j.1537-2197.1981.tb06385.x.
- Tucker SC. 1985. Initiation and development of inflorescence and flower in *Anemopsis californica* (Saururaceae). *American Journal of Botany* **72**: 20–31. doi:10.1002/j.1537-2197.1985.tb05341.x.
- Tucker SC. 1988. Flower development in *Neptunia pubescens*, a mimosoid legume. *American Journal of Botany* **75**: 205–224. doi:10.1002/j.1537-2197.1988.tb13432.x.
- Valentim FL, Mourik S van, Posé D, et al. 2015. A quantitative and dynamic model of the *Arabidopsis* flowering time gene regulatory network. *PLoS One* **10**: e0116973.
- Vekemans D, Viane T, Caris P, Geuten K. 2012. Transference of function shapes organ identity in the dove tree inflorescence. *New Phytologist* **193**: 216–228. doi:10.1111/j.1469-8137.2011.03915.x.
- Villa-Machío I, Zamora JC, Sandoval-Sierra JV, Blanco-Pastor JL, Fernández-Mazuecos M, Jiménez-Mejías P. 2020. Insect pollination in temperate sedges? A case study in *Rhynchospora alba* (Cyperaceae). *Plant Biosystems* **156**: 196–202. doi:10.1080/11263504.2020.1845846.
- Vogel S. 1963. Duftdrüsen im Dienste der Bestäubung. Über Bau und Funktion der Osmophoren. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse der Akademie der Wissenschaften Mainz* **10**: 600–763.
- Weberling F. 1999. Wilhelm Troll, his work and influence. *Systematics and Geography of Plants* **68**: 9–24. doi:10.2307/3668585.
- Webster GL. 2014. Euphorbiaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, eudicots: Malpighiales*. Berlin: Springer, 51–216.
- Weston PH. 2007. Proteaceae. In: Kubitzki K, ed. *The families and genera of vascular plants: flowering plants, eudicots: Berberidopsidales, Buxales, Crossosomatales, Fabales p.p., Geraniales, Gunnerales, Myrtales p.p., Proteales, Saxifragales, Vitales, Zygophyllales, Clusiaceae Alliance*.

- Passifloraceae* Alliance, *Dilleniaceae*, *Huaceae*, *Picramniaceae*, *Sabiaceae*. Berlin: Springer, 364–404.
- Wettstein R.** 1907. Die Entwicklung der Blüte der angiospermen Pflanzen aus derjenigen der gymnospermen. *Wissen für alle* **45**: 705–708.
- Wilson PG.** 2011. Myrtaceae. In: **Kubitzki K**, ed. *The families and genera of vascular plants: flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*. Berlin: Springer, 212–271.
- Xu S, Huang Q, Shu Q, Chen C, Vick BA.** 2009. Reproductive organography of *Bougainvillea spectabilis* Willd. *Scientia Horticulturae* **120**: 399–405. doi:10.1016/j.scienta.2008.11.023.
- Yang Y, Sun H.** 2009. The bracts of *Saussurea velutina* (Asteraceae) protect inflorescences from fluctuating weather at high elevations of the Hengduan Mountains, Southwestern China. *Arctic Antarctic and Alpine Research* **41**: 515–521. doi:10.1657/1938-4246-41.4.515.
- Yildirim K, Sevgen İ, Kondić-Špika A, Cvejić S, Jocić S, Miladinović D.** 2022. The first report on efficient CRISPR-based protocol for sunflower In: Proceedings, 20th International Sunflower Conference, 20–23 June 2022, Novi Sad, Serbia. Paris: International Sunflower Association.
- Zhang T, Cieslak M, Owens A, et al.** 2021a. Phyllotactic patterning of gerbera flower heads. *The Proceedings of the National Academy of Sciences* **118**: e2016304118. doi:10.1073/pnas.2016304118.
- Zhang T, Elomaa P.** 2021. Don't be fooled: false flowers in Asteraceae. *Current Opinion in Plant Biology* **59**: 101972. doi:10.1016/j.pbi.2020.09.006.
- Zhang C, Huang C-H, Liu M, et al.** 2021b. Phylotranscriptomic insights into Asteraceae diversity, polyploidy, and morphological innovation. *Journal of Integrative Plant Biology* **63**: 1273–1293. doi:10.1111/jipb.13078.
- Zhang L, Li H-T, Gao L-M, et al.** 2011. Phylogeny and evolution of bracts and bracteoles in *Tacca* (Dioscoreaceae). *Journal of Integrative Plant Biology* **53**: 901–911. doi:10.1111/j.1744-7909.2011.01076.x.
- Zhang W, Xiang Q-Y (Jenny), Thomas DT, Wiegmann BM, Frohlich MW, Soltis DE.** 2008. Molecular evolution of *PISTILLATA*-like genes in the dogwood genus *Cornus* (Cornaceae). *Molecular Phylogenetics and Evolution* **47**: 175–195.
- Zhang T, Zhao Y, Juntheikki I, et al.** 2017. Dissecting functions of *SEPALLATA*-like MADS box genes in patterning of the pseudanthial inflorescence of *Gerbera hybrida*. *New Phytologist* **216**: 939–954. doi:10.1111/nph.14707.
- Zhao Y, Zhang T, Broholm SK, et al.** 2016. Evolutionary co-option of floral meristem identity genes for patterning of the flower-like Asteraceae inflorescence. *Plant Physiology* **172**: 284–296. doi:10.1104/pp.16.00779.
- Zhong J, Kong F.** 2022. The control of compound inflorescences: insights from grasses and legumes. *Trends in Plant Science* **27**: 564–576. doi:10.1016/j.tplants.2021.12.002.
- Zhou J-J, Luo J.** 2018. The PIN-FORMED auxin efflux carriers in plants. *International Journal of Molecular Sciences* **19**: 2759–2759. doi:10.3390/ijms19092759.
- Zoulias N, Duttke SHC, Garcês H, Spencer V, Kim M.** 2019. The role of auxin in the pattern formation of the Asteraceae flower head (capitulum). *Plant Physiology* **179**: 391–401. doi:10.1104/pp.18.01119.