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Review

Duckweeds as a model for minimal floral development

Christian Siadjeu[1,#], Abhisek Chakraborty[1,#], and Shuqing Xu (徐树青)[1,*]

While most frameworks of floral evolution are based on complex, multi-whorled flowers, duckweeds represent the opposite extreme, with highly reduced angiosperm reproductive structures comprising a single gynoecium and one or two stamens embedded within the frond. We review current work on the genetic regulation and evolution of duckweed flowers. Morphological evidence indicates duckweed flowers arose by progressive miniaturisation from a typical aroid spadix–spathe inflorescence. We outline how single-cell and multiomic atlases, integrated with comparative and population genomics, can reconstruct developmental trajectories across lineages. Treating duckweeds as a 'minimal flower' model could shed new insights into the minimal cellular and genetic programme required for flower development, and open opportunities to rationally engineer reproductive traits in crops and other plant systems.

Highlights

Duckweeds harbour among the simplest known angiosperm flowers, representing an extreme reduction of the aroid spadix–spathe inflorescence.

Fossil, morphological, and phylogenomic evidence suggest that duckweed flowers evolved through progressive miniaturisation and condensation.

Genomic evolution in duckweeds involves selective pruning of flowering and reproductive gene networks, but it retains key regulators of sexual reproduction.

Single-cell and single-nucleus omics, combined with evolutionary genomics, can reveal the minimal cellular and genetic programme required to develop a flower.

Understanding the genetic and developmental basis of the minimal flower will inform comparative evo-devo, crop improvement, and plant synthetic biology.

A minimal floral programme

Flowers are typically defined as determinate shoots composed of modified leaves organised into successive whorls—sepals, petals, stamens, and carpels surrounding a floral meristem [1]. While this basic architecture is conserved across angiosperms, floral organs can be elaborated, fused, or reduced in lineage-specific ways, generating enormous morphological diversity [2]. Most theories about the origin and evolution of flowers derive from complex examples and seek to reconstruct the ancestral angiosperm flower.

Duckweed flowers offer an alternative perspective. These tiny, free-floating aquatic plants often have fronds less than 1 cm in size and are widely recognised as the smallest and simplest angiosperms [3]. As in many Araceae, duckweed flowers lack a conspicuous perianth. Their distinctive reduction instead lies in the extreme condensation of the spadix–spathe system into a minute reproductive unit embedded within the frond, typically comprising a single unicarpellate gynoecium and one or two stamens. Although duckweeds predominantly propagate clonally, they retain the ability to flower and set seed, indicating that sexual reproduction remains part of their life history.

What is the minimal genetic and developmental programme required to develop a flower, and how far can floral simplification proceed while retaining functionality? We argue that duckweed flowers provide a uniquely tractable system to address these questions. We first summarise the morphological and evolutionary context of duckweed flowers within Araceae. We then synthesise current knowledge about their development and environmental control, the genomic changes associated with floral simplification, and how single-cell and evolutionary genomics can be combined to define a minimal floral programme. Finally, we outline how this knowledge can advance plant biology more broadly, from evo-devo to synthetic biology.

[1]Institute of Organismic and Molecular Evolution (IomE), Johannes Gutenberg University Mainz, Mainz 55128, Germany
[#]These authors contributed equally

*Correspondence:
shuqing.xu@uni-mainz.de (S. Xu).

Morphological evolution of the minimal flower

Duckweeds are often treated as a separate family (Lemnaceae) because of their highly derived vegetative and reproductive morphology [4]. Recent phylogenetic analyses place them as part of Araceae [5,6], even though some authors continue to argue for family-level separation [7]. Regardless of whether duckweeds are treated as Lemnaceae or nested within Araceae, their position as a relatively distant clade of Araceae implies that their reproductive structures are best interpreted as extreme reductions of the typical aroid inflorescence rather than as independent inventions.

Araceae flowers are either bisexual or unisexual. In bisexual-flowered taxa, flowers are typically distributed uniformly along the spadix, whereas in unisexual-flowered taxa, female flowers occupy the basal part of the spadix, and male flowers are located above them, often with additional sterile zones or an appendix [5,8]. The canonical Araceae inflorescence consists of a fleshy spadix, subtended or partially enclosed by a spathe [8] (Figure 1). In duckweeds, these

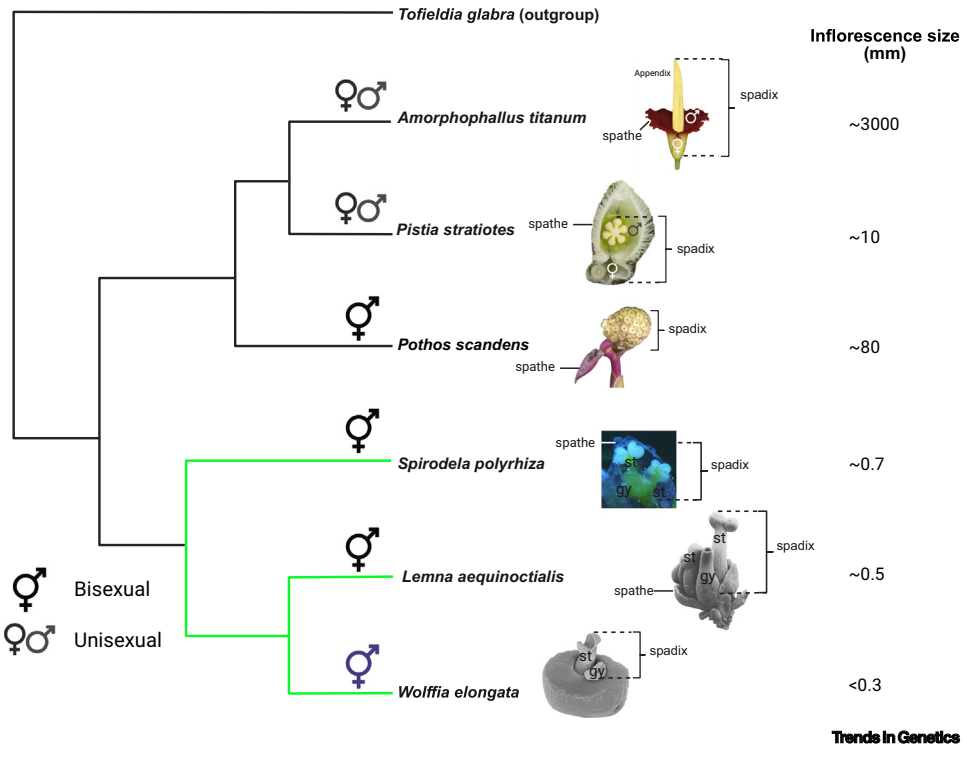

Figure 1. Phylogenetic placement of duckweeds within Araceae and comparative reproductive-unit morphology. Schematic phylogeny of Araceae created in BioRender (after Haigh *et al.* [6] and the TimeTree database: https://timetree.org), rooted with *Tofieldia glabra* (Tofieldiaceae) as an outgroup from Alismatales. The spathe and spadix provide the basis for comparing homology between duckweed reproductive units and those of other aroids. In many derived Aroideae, the spadix is differentiated into a sterile appendix and male and female flower zones. Bisexual flowers are ancestral in Araceae, whereas unisexual zonation is derived in Aroideae. *Pistia stratiotes* is included to illustrate that floating habit evolved independently and is convergent with duckweeds. Duckweeds represent an extreme condensation of the spadix–spathe system into a highly miniaturised reproductive unit partially embedded within the frond; homologous components are indicated as stamen (st), and a unicarpellate gynoecium (gy). Branches of duckweeds are shown in green. Images were assembled and adapted in BioRender from Bogner [10], Fourounjian *et al*. [11], Claudel and Lev-Yadun [12], Landolt [13], and Claudel (C. Claudel, PhD thesis, University of Hamburg, 2025) under CC BY 4.0. The *Pistia stratiotes* image is reproduced with permission from Himesh Dilruwan Jayasinghe. BioRender content used under a publication license.

reproductive structures are extremely reduced and are often interpreted as having bisexual reproductive units [10,13].

Within Araceae, inflorescence size and complexity span several orders of magnitude. At one extreme, *Amorphophallus titanum* produces spadices exceeding 3 m in height, with large thermogenic spathes releasing volatile blends to attract carrion pollinators [14]. Intermediate forms, such as *Anthurium* and *Arum,* bear hundreds of flowers on smaller spadices with multiday, sex-phased anthesis [8]. Much smaller relatives, including *Pothos scandens*, have spadices only a few centimetres long and reduced spathes (Figure 1) [9]. Duckweeds sit at the far end of this gradient, pushing size and organ number towards their minima.

Morphological and fossil analyses converge on the view that duckweed reproductive units are hyper-reduced spadices enclosed in spathelike structures [10]. In *Lemna* and *Spirodela*, the membranous envelope surrounding the reproductive organs (Figure 1) is best interpreted as a spathe, whereas the inflorescence axis corresponds to a highly reduced spadix bearing a single bisexual flower (with a single stamen plus gynoecium) and one male flower [10,13]. In *Wolffia*, the floral axis develops subepidermally and briefly emerges through a dorsal pore, yet the enclosing frond still fulfils spathelike functions [15,16]. In homology with other aroids, duckweeds compress the spadix–spathe system into an extremely compact configuration.

This interpretation is supported by the fossil record. *Limnobiophyllum scutatum*, a free-floating plant from the Cretaceous–Eocene, bore stolons and roots reminiscent of *Pistia* and duckweeds. Some fossils contain pollen assignable to *Pandaniidites*, a pollen type linked to aroid inflorescences [10,17]. Duckweeds retain similar reproductive features: their pollen is spherical, ulcerate, and spinulose, resembling that of *Limnobiophyllum* [10,18]. Additionally, duckweed species such as *Lemna gibba* and *Lemna minor* produce stigmatic fluid before pollen release [11]. These characteristics indicate that, despite their extreme miniaturisation and reduced floral display, duckweeds maintain a functional pollen–stigma interface that supports effective pollination. Such fossils bridge larger floating aroids and modern duckweeds, implying a long history of progressive reduction along an aquatic trajectory within Araceae.

Duckweed floral simplification is better interpreted as an extreme **condensation of the aroid spadix–spathe system** rather than as neoteny [10]. The shortening of the reproductive axis and restriction of organ initiation produce a highly compact reproductive unit with a unicarpellate gynoecium and one or two stamens. Since perianth reduction is common in Araceae, the key innovation in duckweeds is not simply the absence of sepals and petals, but the pronounced miniaturisation and internalisation of the reproductive unit within the frond.

A recent study integrating three extant duckweed species with ancestral fossil evidence likewise revealed a stepwise reduction across multiple traits [19]. At the genus level, molecular phylogenies broadly parallel a gradient of morphological reduction. Target-capture and plastid phylogenies resolve duckweeds as a monophyletic clade: *Spirodela* splits first, then *Landoltia, Lemna*, followed by *Wolffia* and *Wolffiella* [5,6]. This order correlates with both vegetative and floral simplifications (floral organs and the inflorescence architecture). *Spirodela* has multiple roots (7–21), relatively large fronds, and bears two stamens plus a unicarpellate gynoecium. *Landoltia* is morphologically intermediate, for example, in terms of the number of roots (2–7). *Lemna* carries a single root; most *Lemna* species show protogynous flowers with two stamens and a single gynoecium [20]. *Wolffia* is rootless, submillimetre in size, and shows protogynous flowers with a single stamen and a unicarpellate gynoecium [3,21,22]. Recently, Ware *et al*. also showed progressive reduction in root anatomy across duckweed genera, and duckweed roots have lost their salient ancestral

function in nutrient acquisition, accompanied by a redistribution of nutrient transporter expression away from stereotypical 'root-biased' patterns [23]. It remains unclear whether seed number shows a similar reduction trend across duckweed genera, as seeded fruits are rare and specific to certain species or genotypes. The phylogeny, therefore, is consistent with the scenario of a sequence of progressive miniaturisation and organ loss, including floral organs, among duckweeds.

Taken together, morphological, fossil, and phylogenetic evidence support a scenario in which the reproductive unit of duckweed evolved through a process of sequential condensation within the Araceae family. This evolution involved several key changes: a significant reduction in the length of the spadix and the number of flowers per reproductive unit, a decrease in the number of stamens, the maintenance of a unicarpellate gynoecium, and ultimately, extreme miniaturisation and partial internalisation of the reproductive axis within the frond.

Developmental processes and environmental control of duckweed flowering

In typical aroids, numerous flowers are exposed on a spadix, and anthesis unfolds over days, often accompanied by thermogenesis and scent production to attract pollinators [24,25]. Duckweeds internalise nearly all aspects of this process into their fronds, with major consequences for floral meristems, organ initiation, and timing.

In *Lemna aequinoctialis*, floral primordia arise in lateral pouches that also generate daughter fronds, so that the same meristem alternates between clonal and sexual fates [26]. In *Wolffia australiana*, primordia form beneath the dorsal epidermis, and the stamen and gynoecium briefly emerge through a shared pore [15,16]. In both cases, a short axis and an enclosing structure are retained, consistent with the reduced spadix–spathe interpretation [10].

Across Araceae, anthesis is commonly partitioned into female and male phases and is frequently protogynous; floral structure is also developmentally specialized and reduced in multiple lineages [27,28]. In bisexual-flowered groups, anthesis may last several days, whereas in many monoecious Aroideae, it typically ends within 1–2 days [29]. Compared with other aroids, duckweeds show an especially reduced and partly concealed flowering display. Although most duckweeds are protogynous, in *L. aequinoctialis*, stamens elongate before full gynoecium maturation [26], potentially creating partial overlap between male and female function and thereby facilitating self-pollination. In *Wolffia*, anthesis is protogynous (pistil protrudes first, followed by stamen elongation and anther dehiscence) but remains minute and largely hidden within a dorsal cavity [30]. These abbreviated, partially hidden flowering events might reflect adaptation to ephemeral and disturbance-prone aquatic habitats [11].

Flower induction in duckweeds is strongly tied to environmental and hormonal signals, often linked to stress responses. A short-day photoperiod induces flowering in *L. aequinoctialis*, but this response might be modulated by a circadian system that has locally adapted across latitudes [11,26,31]. Salicylic acid (SA) induces flowering in several duckweed species, and iron chelators such as ethylenediamine-di-o-hydroxyphenylacetic acid (EDDHA) are broadly effective floral inducers, suggesting that biotic and abiotic stress signals have been co-opted as triggers of sexual reproduction [11,32,33].

In the highly reduced *Wolffia microscopica*, nutrient limitation, the stress hormone abscisic acid, and high temperature also promote flowering [21]. However, this stress-coupled network appears to be attenuated or rewired in many lineages: *W. australiana* remains largely unresponsive to flowering induction under a broad range of laboratory treatments [15], hinting that its near-obligate clonal lifestyle may be associated with the silencing or strict gating of ancestral induction pathways.

At the molecular level, duckweed studies implicate familiar angiosperm flowering regulators. Integrative transcriptome and proteome analyses in *L. gibba* have proposed regulatory models in which canonical flowering genes such as *AP1, SVP*, *TEM1*, and *FT* act as key nodes to mediate SA-induced flowering [32,33]. In *L. aequinoctialis, FT* homologs, *LaFTL1* and *LaFTh1,* might integrate photoperiodic and circadian signals and control the transition of axillary meristems to floral meristems [26,31]. In *W. australiana, FT* and *FPF1* are among the most strongly induced genes in flowering fronds, alongside additional candidate floral regulators emerging from network analyses [15]. In *Arabidopsis* and other angiosperms, these same nodes sit within a multilayered regulatory architecture, where diverse environmental and endogenous pathways converge on *FT*, and FT protein acts at the shoot apex with FD to activate floral meristem identity programmes, involving *AP1, LFY*, and other genes [34,35]. Therefore, these studies support the idea that duckweeds retain a core flowering network shared with other angiosperms, but that its input and output wiring likely has been simplified in a highly reduced developmental context.

A key outstanding question is how this network differs between species/genotypes that readily flower under laboratory conditions (e.g., *L. aequinoctialis, L. gibba*) and those that flower infrequently. For example, Yoshida *et al*. showed that flowering *in L. aequinoctialis* can be induced under short-day conditions [26]. Similarly, Fu *et al*. showed SA-induced flowering in *L. gibba*, co-regulated by photoperiod and stress factors [32]. Despite having optimised laboratory conditions for flowering induction in several duckweed species, flowering occurs at low frequency and is not synchronised under inductive laboratory conditions in species like *W. australiana* [15]. Comparative analyses across species and hybrids [11,20] could reveal genetic changes that decoupled floral induction from environmental cues in the most simplified taxa.

So far, most insights into the genetics of duckweed floral development derive from genome content, bulk transcriptomes, and regulatory inferences. Bulk transcriptomes and proteomes can identify candidate regulators, but they can neither unambiguously assign them to floral versus somatic lineages nor resolve the developmental decision point at which meristems alternate between clonal budding and sexual differentiation. The main reason is that the duckweed reproductive structures are minute and embedded within the frond, and most molecular measurements inevitably mix reproductive and vegetative tissues. Therefore, cell-type-centric approaches (single-cell/single-nucleus transcriptomics and chromatin accessibility) are essential to computationally segregate reproductive cell lineages from the dominant somatic tissues and to reconstruct developmental trajectories and cell-type-specific regulatory modules.

Genomic changes associated with floral simplification

At the genomic level, duckweeds combine small genome sizes with strong gene content reduction [22,36–38]. All sequenced species, nonetheless, retain a representative core plant gene set [39], indicating that the reduction is selective rather than indiscriminate.

Comparisons with *Arabidopsis* and rice reveal that *Spirodela polyrhiza* has a reduced complement of key floral regulatory gene families, including SBP, PEBP, and MADS-box genes, alongside an expansion of floral repressors [40,41]. Gramzow and Theißen [41] showed that duckweeds have the lowest number of MIKC-type MADS-box clades—central regulators of floral organ identity—among surveyed angiosperms, with losses of clades such as *FLC, AGL9*, and *MADS32*. Members of the Argonaute family that are highly expressed in seeds and pollen in *Arabidopsis*, including *AGO2, AGO3*, *AGO6*, and *AGO9,* are also reduced in Lemnaceae [39]. Chromosome-scale assemblies across duckweed species have revealed repeated losses of flowering-related genes, including the absence of a complete *SOC1* in several genomes [39]. Notably, a complete *SOC1*, containing both the MADS and keratin-like domains, is present in *L. aequinoctialis*, a duckweed species

reported to complete a seed-to-seed sexual cycle under laboratory conditions [26]. Interestingly, in *S. polyrhiza*, insertions and deletions in a *SOC1* homolog lacking the keratin-like domain appear to be associated with variation in sexual reproduction frequency among populations [42]. These observations suggest lineage-specific retention, truncation, or divergence of *SOC1*-like loci in duckweeds. Given the central role of *SOC1* as an integrator of flowering signals in other angiosperms, reduction or loss of *SOC1* function in duckweeds might contribute to weak, genotype-dependent, or incomplete floral induction, potentially through altered activation of downstream floral meristem identity regulators such as *LFY* and *AP1* [34,35]. Together with overall low levels of genome-wide DNA methylation, particularly in *S. polyrhiza* [42], these changes suggest that sexual reproduction and reproductive small-RNA pathways have been relaxed, but not eliminated, during the evolution of predominantly clonal life histories.

Despite extensive gene pruning, duckweeds have not completely abandoned sexuality. Population-genomic analyses of *S. polyrhiza* revealed substantial recent genomic recombination, indicating that sexual reproduction still occurs in nature and contributes to long-term genetic variation, despite predominantly clonal propagation. This is also consistent with evidence of strong positive selection on genes involved in floral development, flowering time, seed maturation, and pollen development, including several MADS-box genes [42]. These results imply that sexual reproduction, although infrequent, is under ongoing selection and contributes to long-term evolutionary success by mitigating the costs of clonal reproduction.

Genomic and bulk transcriptomic approaches are powerful for identifying gene families lost or reduced during miniaturisation [39–41] and for building coarse models of floral induction [11,15,26,31–33]. However, they are limited in three important ways. First, gene loss does not necessarily equate to morphological simplification. For example, most genes required for root development in *Arabidopsis* can still be identified in the rootless *W. australiana* genome [15]. Second, bulk expression analyses cannot resolve pleiotropy: genes expressed in flowers may also function in vegetative tissues. Third, current evidence provides little insight into which genes and cell types are strictly required for minimal flower formation versus those that are dispensable or redundant. This underscores that morphological miniaturisation can precede, accompany, or follow genomic pruning, and that gene content alone is insufficient to infer the minimal programme required for floral organ formation. These limitations motivate a shift from gene-centric descriptions to cell-type-resolved models of duckweed flower development.

Concluding remarks and future perspectives

The minimal organ set, comprising a single unicarpellate gynoecium and one or two stamens [15,26], suggests that duckweeds can reveal the smallest set of cell types and gene modules needed to construct a functional flower.

High-quality genomes [22,38,39] and recent advances in single-cell and single-nucleus RNA-seq and Assay for Transposase-Accessible Chromatin using sequencing (ATAC-seq) now make such analyses feasible [15,43–47]. While single-cell approaches have successfully deciphered developmental trajectories in model plants like *Arabidopsis* and rice [48,49], applications to duckweed, for example, *Lemna minuta* and *W. australiana*, have so far been limited to vegetative tissues and stress responses [15,44,45].

To define the 'minimal flower', a central goal is to generate high-coverage single-cell atlases of induced flowering fronds. These atlases will enable: (i) the unbiased definition of minimal floral cell types, allowing researchers to test for vestigial signatures of lost organs (e.g., perianth);

Outstanding questions

How many distinct floral cell types exist in duckweed flowers, and are any unique to Lemnaceae?

What aspects of floral organ number, arrangement, and cell-type diversity are strictly required for successful sexual reproduction, and which are evolvable extras?

Which genes and regulatory modules constitute the minimal core network necessary and sufficient to develop a flower?

How do floral and stress-response networks become intertwined in lineages that shift from primarily sexual to predominantly clonal reproduction, and can they be decoupled again?

Can minimal floral circuits identified in duckweeds be transplanted into other species to control flowering time or reproductive investment in a predictable way?

Can insights from duckweed floral circuits be used to rationally engineer flowering behaviour or reproductive allocation in crops and other plants?

(ii) the reconstruction of developmental trajectories that resolve the critical decision point where the meristem bifurcates between clonal budding and sexual differentiation [50]; and (iii) the construction of cell-type-specific gene regulatory networks to identify the core master regulators retained during miniaturisation [49]. Furthermore, multiomic integration of transcriptomes and chromatin accessibility can dissect the underlying regulatory logic, mapping transcription factor (TF) binding motifs to the specific *cis*-regulatory elements that drive this streamlined development [46]. A comparative framework across duckweeds and other aroids will help identify regulators that contributed to the gradual reduction of floral cell types during development.

To understand the evolutionary forces shaping the minimal floral cell types, one critical aspect will be to identify the floral cell types that were under selection to evolve most rapidly. To this end, we propose using a Transcriptome Divergence Index (TDI) score in future studies by integrating evolutionary genomics with the single-cell atlas to provide novel insights into the evolutionary responses to natural selection at cellular resolution (Box 1). By computing the TDI for each cell type, which summarises the evolutionary history or selective constraint of its expressed genes [51], one could identify which cell types evolve most rapidly.

These analyses can be complemented by gene family evolution, genomic synteny, and comparative phylogenomics focused on floral marker genes and regulatory modules. Copy number variations and contraction of gene families are already evident in duckweed genomes [39,41]. Extending these analyses to marker genes from specific floral cell types could identify which families are conserved, expanded, or lost relative to more complex flowers in Araceae (e.g., *Amorphophallus*,

Box 1. A TDI for duckweed floral cell types

The TDI, inspired by phylotranscriptomic approaches [51], provides a quantitative measure of the evolutionary divergence of genes expressed in a given cell type.

Concept

Each gene is assigned an evolutionary divergence parameter, such as a divergence or selection metric (e.g., $\frac{dN}{dS}$, or an evolutionary constraint score at the population level).

For each cell type, the TDI is computed as the expression-weighted mean of this parameter across all expressed genes:

$$\text{TDI (cell type)} = \frac{\sum(\omega_i E_i)}{\sum E_i}$$

where ω_i is the evolutionary parameter (e.g., $\frac{dN}{dS}$) for gene i and E_i is its expression level in that cell type.

Interpretation

Low TDI: transcriptome dominated by evolutionarily highly constrained genes.

High TDI: transcriptome enriched in rapidly evolving genes.

Application to duckweed flowers

By calculating TDI for duckweed floral and vegetative cell types and comparing them to TDI of homologous cell types in other aroids or model species, one can ask:

Which cell types are the hotspots for evolutionary innovations in duckweeds?

Which floral cell types in duckweeds are evolutionarily innovative versus conserved compared to other aroids?

Such analyses will help pinpoint the cell types, in the lineage from complex aroid inflorescences to minimal duckweed flowers, where evolutionary innovation has been concentrated.

Anthurium, and *Pistia*) and in other angiosperms. Synteny analyses could further identify developmental and stress-related genes in fractionated blocks that were preferentially lost or rearranged during duckweed miniaturisation [22]. Branch-site models could test for positive selection on floral regulators in particular duckweed lineages [52]. If quantitative floral traits become available across species, phylogenetic comparative analyses could then be used to test whether shifts in specific cell types, gene families, or regulatory modules are associated with repeated reductions in floral complexity [53].

Therefore, integrating single-cell profiling with comparative and evolutionary genomics offers a direct route to resolve the genetic architecture of the minimal duckweed flowers at cell-type and organ-scale resolution, and to link that architecture to the evolutionary forces that shaped it. For instance, genes that are (i) highly expressed and specific to a given floral cell type, (ii) embedded within a cell-type-specific regulatory module, and (iii) show signatures of selection across species or genotypes can be considered candidate master regulators of the corresponding floral structure. Once candidate master regulators and minimal regulatory modules for duckweed floral cell types are identified, synthetic biology offers tools to test their sufficiency and necessity.

Stable transformation and CRISPR/Cas-based genome editing are increasingly being established in duckweeds, particularly *S. polyrhiza* [54]. These tools can be used to knock out, knock down, or ectopically express candidate floral regulators and assess their effects on organ identity, number, and morphology. Synthetic promoters designed from enriched TF motifs can drive precise perturbations in specific floral cell types [55].

Because duckweeds grow rapidly and clonally, experimental cycles are short, and mutant lines can be maintained indefinitely without seeds. This makes them attractive platforms for (i) dissecting how many regulators are needed to specify a minimal flower; (ii) exploring the robustness of floral circuits to gene loss; and (iii) engineering novel floral traits (e.g., synchronised flowering, modified reproductive allocation) that may be desirable for crop relatives or biotechnological applications.

In summary, duckweeds demonstrate that a functioning angiosperm flower can be built from a remarkably small number of organs and likely a streamlined genetic programme. Understanding this minimal system will address several broader and fundamental questions in plant biology (see Outstanding questions). By combining comparative morphology, genomics, and cutting-edge single-cell methods, duckweeds can serve as a model for the lower limit of floral complexity that still supports successful sexual reproduction. Lessons learned from this extreme will be valuable not only for understanding flower evolution but also for designing synthetic reproductive systems in plants.

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Declaration of interests

The authors declare no conflicts of interest.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT and Gemini to identify language errors and search for literature. After using the tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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