1   Rethinking convergence in plant parasitism integrating molecular and population genetic
2   processes
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12 **Running Heads**
13 Origins of convergent evolution in parasitic plants
14

15 **ABSTRACT**
16 The need for photosynthesis has largely shaped the body plan, physiology, as well as gene
17 repertoire of seed plants. However, shifts to a heterotrophic lifestyle have independently evolved
18 twelve times in more than four thousand parasitic plants. Among these parasites, otherwise rare
19 features have evolved repetitively at both the molecular and phenotypical levels, including reduced
20 vegetative body, carrion mimicking, and abundant alien genetic materials. Here, I propose an
21 integrated conceptual model to describe the general evolutionary trajectory of parasitic plants and
22 provide a mechanistic explanation for their convergent evolution. This model connects our
23 empirical understanding of the plants' regulatory network with classic theories in molecular and
24 population genetics. It emphasizes the cascading effects driven by the loss of photosynthesis as one
25 major force shaping the genomic landscape of parasitic plants. In this paper, I review recent studies
26 in the anatomy, physiology, and genetics of parasitic plants to support the photosynthesis-centered
27 hypothesis of their convergent evolution. Focusing on non-photosynthetic holoparasites, I elucidate
28 how they inevitably reach an evolutionary terminal status and highlight the utility of an explicitly
29 described, falsifiable model for future studies in parasitic plants.
30

34
35 The ca. 4,750 parasitic plants live intimately with their hosts, stealing water, nutrients, metabolites,
36 and genetic materials through a specialized organ called haustoria (Nickrent, 2020). These plants
37 display a variety of lifeforms from canopy-forming sandalwoods to thread-like dodder vines. This
38 morphological diversity spans a wide spectrum of photosynthetic capacity and host dependence.
39 Based on these two axes, parasitic plants are classified as hemi- or holo-parasites (photosynthetic
40 vs. non-photosynthetic), and as facultative or obligate parasites (can vs. cannot complete lifecycle
41 without hosts). Botanists' formal recognition of parasitic plants traces back to the 18th century. In
42 particular, Micheli (1729), among others, first realized that Cynomoriaceae, Balanophoraceae, and
43 Hydnoraceae were root parasites instead of fungi (Thunberg, 1775; Blume, 1858). This interesting
44 historical twist epitomizes the extensive morphological modification in parasitic plants, often
45 manifested in a convergent manner. Famous examples of convergence include the resemblance
46 between dodders (*Cuscuta*, Convolvulaceae) and woe vines (*Cassytha*, Lauraceae), both are thread-
47 like leaf-lacking parasitic vines separated by more than 100 million years of evolution (Ramirez-
48 Barahona et al., 2020). Early morphological-based classification similarly grouped Rafflesiaceae,

49 Apodanthaceae, and Cytinaceae under the same order, which was later demonstrated to be
50 paraphyletic based on molecular phylogenetic studies (Barkman et al., 2007).
51
52 The advent of the modern genetic and phylogenetic era has greatly advanced our understanding of
53 the mechanism and evolution of plant parasitism. Unlocking genomic resources from various
54 parasitic lineages in recent years has led to revolutionary discoveries in systematics (Nickrent,
55 2020), anatomy and development (Teixeira-Costa, 2021; Teixeira-Costa et al., 2021), host
56 interactions (Mutuku et al., 2021; Nelson, 2021), and genomics (Lyko and Wicke, 2021; Yoshida and
57 Kee, 2021). Across all disciplines, convergence is a repeated theme. This is manifested not only at
58 the phenotypical level such as the shared haustoria anatomy and embryological development, but
59 also at the molecular level including consistent patterns of gene loss and horizontal gene transfer
60 (Yang et al., 2019; Cai et al., 2021; Teixeira-Costa et al., 2021). On the other hand, the evolution of
61 plant parasitism is also envisioned to progress through an irreversible manner. The best example
62 comes from Orobanchaceae, the only clade that retains all transitional stages from free-living taxa
63 to facultative hemiparasites and obligate holoparasites. In this family and all other parasitic
64 lineages, the unidirectional evolution of parasitism is reflected by decreasing photosynthetic
65 capacity, increasing host reliance, as well as other hallmarks of regressive evolution such as low
66 diversification rate. These predictable convergences highlight the fundamental question in the
67 study of parasitic plants: What constrains the evolutionary landscape and drives parallelism among
68 parasitic plants?
69
70 To address this question, a general framework describing the evolutionary trends in parasitic
71 plants is needed. One such framework is the "Three Phase Hypothesis", where parasitic plants are
72 expected to go through innovation–relaxation–optimization as time lapses (Searcy and MacInnis,
73 1970; dePamphilis, 1995). This model has been successfully combined with molecular data to
74 explain the genome evolution of the hemiparasites *Striga* (Orobanchaceae; Yoshida et al., 2019).
75 However, it has several limitations. First, the concept of 'phase' in the original model is misleading
76 because it suggested sequential order of these evolutionary processes, while they are demonstrated
77 to simultaneously shape the genetic landscape of parasitic plants (Lyko and Wicke, 2021).
78 Moreover, the three-phase model provides important insights into the transition from hemi- to
79 holoparasitism, but offers very limited explanatory and predicative power beyond that point. For
80 example, it struggles to explain the convergence in highly modified endoparasites, which live inside
81 the hosts. To improve on this model and provide a formal, falsifiable framework, I propose an
82 integrated conceptual model for the evolution of parasitic plants. This model bridges our empirical
83 understanding of the genetic architecture and metabolic network in angiosperms with theories of
84 molecular genetics and population genetics. It is suited to explain the irreversible nature of plant
85 parasitism and highlights the dynamics of the evolutionary forces shaping parallelism at different
86 stages of plant parasitism. In this paper, I highlight novel and emerging trends of convergence
87 predicted by the model and discuss critical evolutionary forces driving these changes.

88 **A funnel model for the evolution of parasitic plants**

89 Plant parasitism can be induced by multiple independent trajectories that diverge arbitrarily during
90 the early phase of evolution. Yet the loss of photosynthesis in holoparasites significantly imperils
91 their gene space and functional integrity. While these plants evolve to optimize their parasitic
92 lifestyle with limited option for raw genetic material, a series of predictable cascading effects
93 trigger the widely recognized parallelism among parasites. Therefore, I propose that the evolution
94 of parasitism arises from a funnel-shaped architecture, bottlenecked by the loss of photosynthesis,

95   constrained by molecular and population genetic processes, and leading to convergent outputs (Fig.
96   1A).
97
98   This model concerns photosynthetic capacity as the main axis along which various stages of
99   parasitism can be mapped. The constraining molecular and population processes are crucial
100   components of the model (Fig. 1B), the identification of which provides an explicit framework for a
101   mechanistic understanding of the evolution of plant parasitism. I propose that the molecular drive
102   shaping convergence consists of three aspects: 1) an ancestrally inherited ubiquitous metabolic and
103   genetic roadmap, the center of which is photosynthesis; 2) shared selective pressure to optimize
104   parasitism; and 3) unidirectionality of regressive evolution featured by gene loss and relaxed
105   selection. Here, the common genetic/metabolic roadmap determines the parallelism in which
106   functional modules co-evolve or co-degenerate. Specifically, photosynthesis related functions are
107   overrepresented in highly conserved pathways, and are tightly linked with various metabolic
108   modules such as circadian rhythm, pigment production, and redox homeostasis. The disfunction of
109   this module can spread to the adjacent modules in a cascading manner. These clues lead to the
110   predictions that functional modules directly associated with photosynthesis are more likely to be
111   impacted in the same way among all parasites.

112   Superimposed on this molecular genetic force is the population process, which has a stronger
113   influence during the later phase of parasitism in holoparasites. Molecular changes initiated in the
114   photosynthesis module can impact modules that impact population processes. For example, the
115   reliance on host-derived photosynthetic products may lead to higher host specificity, which can
116   cause smaller and more isolated populations (Fig. 1B). Such reduction in the effective population
117   size (N_e) will cause decreased selection efficiency, increased drift, parthenogenic accumulation of
118   deleterious mutations, and decreased fixation of adaptive changes. These oscillations will then
119   feedback on the molecular evolution process in a largely negative way. Collectively, the mutational
120   burden and population size limitation suggest that the fitness landscape of any parasitic organisms
121   deteriorates overtime.

122   Verification and refinement of this model requires a thorough understanding of the genomic
123   architecture and functional regulation network across multiple independently evolved parasitic
124   plant lineages, which is being actively constructed (Kösters et al., 2021). Using available resources, I
125   show that this model is compatible with all existing data. It also provides additional power to
126   elucidate the molecular mechanisms of enigmatic convergent trends among parasites.

127   **From photosynthesis to ABA metabolism**

128   Under this funnel model, early phases of plant parasitism are largely shaped by selection to
129   optimize parasitism and to dispense with useless traits. At the morphological level, Kuijt (1969)
130   pointed out the systematic reduction in leaf size, complexity, and stomata density in parasites. At
131   the molecular level, the minuscule plastid genomes are one of the most well studied genetic
132   features among parasitic plants, and continue to be a captivating area of research (e.g., Wolfe et al.,
133   1992; Wicke et al., 2013). Recent genomic studies enabled comprehensive surveys of the gene
134   repertoire in *Cuscuta*, Orobanchaceae, and Rafflesiaceae. They consistently reported significant
135   gene losses in photosynthesis related functions including plastid organization and pigment
136   metabolism, which aligns well with the prediction of the funnel model (Vogel et al., 2018; Cai et al.,
137   2021; Xu et al., 2022; Chen et al., 2022). Meanwhile, unexpected gene losses were found in the
138   biosynthesis of abscisic acid (ABA) in *Sapria* (Rafflesiaceae; Cai et al., 2021). While the classic three-

139 phase model struggles to explain the loss of this conserved plant hormone, the funnel model
140 provides an explanation for this potentially widespread trend among holoparasites.

141 Biosynthesis of ABA is reliant on the precursor carotenoids, which also serve as photosynthetic
142 pigments and photoprotector in plants. In *Sapria,* the biosynthesis of carotenoids is completely
143 absent due to the loss of photosynthesis. Thus the molecular basis for the absence of ABA
144 biosynthesis can be easily explained by the cascading effect after the loss of photosynthesis (Fig. 2).
145 Moreover, the reduced need for drought response in parasites provides a further selective drive for
146 such loss. One important function of ABA is to combat water loss by triggering stomatal closure
147 (Wasilewska et al., 2008). However, holoparasites acquire the bulk of their water from the host and
148 have very few to absent stomata (Kuijt and Dong, 1990; Mursidawati et al., 2020). The need to
149 regulate these abiotic stresses is thus diminished. Both the molecular and selective constraints
150 accommodating the loss of ABA are not restricted to Rafflesiaceae. In fact, insensitivity to ABA was
151 also reported in *Cuscuta australis* (Li et al., 2015)*.* Future studies focusing on other holoparasitic
152 lineages are likely to find similar patterns.

153 On the other hand, the apparent dilemma between the absence of stomata and water transportation
154 opens a new avenue for hydraulic evolution in parasitic plants: how do holoparasites effectively
155 stream fluid and nutrient iron from the host when transpiration is limited? The answer to this
156 question is particularly relevant for Rafflesiaceae, which produces the largest flowers in the world,
157 through thread-like vegetative tissue, without any stomata (Nikolov and Davis, 2017; Mursidawati
158 et al., 2020). Along these lines, Heide-Jørgensen (2008) commented on the possibility of an energy-
159 consuming water pumping system in *Lathraea* (Orobanchaceae) to explain its water excreting
160 hydathode glands under the moist subterranean habitat. The presence and significance of these
161 active water transporters remain to be characterized in Orobanchaceae and other stomata-lacking
162 parasites.

163 **Bold reproductive strategies**

164 While extensive effort has been dedicated to the comparative studies of vegetative organs, the
165 evolutionary trends in reproduction have not been well studied in parasitic plants. These plants
166 often exhibit specialized strategies that facilitate rapid regional colonization but may limit their
167 evolutionary opportunities in the long run (e.g., specialized pollination syndrome). As predicted by
168 the funnel model, many of these convergent features arise from the cascading effect of gene loss
169 and are retained for their adaptive value.

170 The first example comes from the synchronized phenology between the host and the parasites. This
171 phenomenon has been reported in *Cuscuta,* Loranthaceae, and Orobanchaceae (Holdsworth and
172 Nutman, 1947; Fratianne, 1965; Candia et al., 2014; Teixeira-Costa et al., 2017) and is hypothesized
173 to be achieved by the translocation of bio-active molecules (Smith et al., 2013). In *Cuscuta*, such a
174 molecule has been pinpointed to a flowering signaling protein FT (Shen et al., 2020). Here, hijacking
175 host-derived signal is a necessity because the native FT pathway in *Cuscuta* is disrupted due to the
176 loss of key genes in its upstream circadian clock and vernalization pathways (e.g., *CO*, *FLC*, and *SVP*;
177 Sun et al., 2018). These losses can be traced back to relaxed selection on light sensing and abiotic
178 stress response when the species transitions to a holoparasitic lifestyle (Fig. 2). On the other hand,
179 such synchronization may confer an increased reproductive success on short-lived hosts, thus
180 favored by selection. In addition to *Cuscuta*, a very similar pattern of flowering synchronization is
181 observed in the lesser broomrape *Orobanche minor* (Holdsworth and Nutman, 1947). As more
182 genomic resources become available in Orobanchaceae (Xu et al., 2022), comparative genomic tools

183   can be used to identify the pathways modulating life-cycle events in *Orobanche* and test whether
184   their evolution follows a similar coordinated manner as in *Cuscuta*.

185   Another more widespread, yet poorly characterized trend is the presence of the intense red
186   colorants in holoparasites (Fig. 2), whose composition, biosynthesis, and eco-evolutionary function
187   remain largely unknown. A reasonable hypothesis for such convergence is that holoparasites do not
188   produce (or at very low level) photosynthetic pigments including chlorophylls and carotenoids,
189   leaving flavonoids, especially anthocyanin, as the sole option for pigmentation. Indeed, a number of
190   ethnobotanical studies have reported the abundance of anthocyanins in *Sapria* (Iwashina et al.,
191   2020)*, Cynomorium* (Cynomoriaceae; FM et al., 1996; Zheng et al., 2021), *Hydnora* (Hydnoriaceae;
192   Wintola and Afolayan, 2015), and *Ombrophytum* (Balanophoraceae; Nina et al., 2020), which often
193   demonstrate in vitro antioxidant and antimicrobial properties. Compared with mycoheterotrophic
194   plants, which are also non-photosynthetic and ground dwelling but much lighter in coloration, the
195   pigments present in holoparasites must provide additional adaptive value specific to this lifestyle.
196   But how? Reasonable hypotheses include the demonstrated antimicrobial and antioxidant
197   properties, but may also come from their role in photoprotection, pollinator attraction, or carbon
198   sink (Steyn et al., 2002; Hughes et al., 2005; Cisowska et al., 2011; Bustos et al., 2012; Narbona et al.,
199   2021). Future studies focusing on this question will need to investigate systems exhibiting intra- or
200   inter-species variation in pigment composition and then look for molecular and environmental
201   factors that covary with this phenotype.

202   Finally, parasites are inevitably faced with a series of reproductive challenges. In holoparasites, the
203   altered floral coloration and structure, the ephemeral inflorescence, and the ground dwelling habit
204   do not fit with the search image for a rewarding flower in the eye of a canonical pollinator. As a
205   result, these plants come up with creative alternative solutions. These include the carrion
206   mimicking in *Rafflesia, Cynomorium, and* possibly *Pilostyles* (Apodanthaceae), the catch-and-release
207   of hide beetles in *Hydora*, and the recruitment of ants and roaches in *Mitrastemon*
208   (Mitrastemonaceae) and *Balanophora* (Balanophoraceae; Fig. 2) (Bolin et al., 2009a; Bellot and
209   Renner, 2013; Sipes et al., 2014; Wee et al., 2018; Suetsugu, 2019; Suetsugu and Hisamatsu, 2020;
210   Wang et al., 2021). In all systems, distinct scent profiles are catered to the taste of their pollinators.
211   Among them, carrion scents including indole and dimethyl disulphide are frequently produced.
212   Whether their biosynthesis also follows convergent pathways remains to be explored. Besides
213   pollination, seed dispersal and germination are another major challenge. Many parasitic plants have
214   a strong bearing on the exudate from the host for germination. These species have become r-
215   strategists that produce numerous tiny seeds to hedge their investments in each individual
216   offspring. To take an example from Orobanchaceae, the facultative hemiparasite *Melampyrum*
217   produces large single seeded capsules that can germinate and complete their lifecycle without a
218   host; the obligate hemiparasite *Striga* produces smaller seeds packed with hundreds in a single
219   fruit; the capsule of the holoparasite *Orobanche* contains thousands of dust-like seeds (Fig. 3). The
220   most extreme cases come from *Rafflesia* and *Hydnora,* whose big fleshy fruits contain tens of
221   thousands of minute seeds. Given the odds of successful reproduction in these genera — distantly
222   located dioecious flowers, highly skewed sex ratio, animal vectored pollination and seed dispersal,
223   and host stimulated germination — fecundity is a necessity (Bolin et al., 2009b; Pelser et al., 2013).

224   Macroevolutionary implications

225   So, is parasitism a cursed strategy? From the macroevolutionary perspective, my answer is yes. A
226   comprehensive evaluation of parasitic plant diversification across all clades, time, and space is
227   currently lacking. But even without rigorous evaluations, it is obvious that parasitism is negatively

228 associated with diversification rates — older lineages have been left with much fewer extant
229 species compared with younger clades such as *Cuscuta* and Orobanchaceae (Table 1). This reverse
230 time–diversity relationship suggests a high extinction rate especially in holoparasites.

231 Hemiparasites likely have comparable rates of diversification to free-living plants. Rapid radiation
232 is well-documented in *Pedicularis* (Orobanchaceae) and Loranthaceae, primarily fueled by
233 ecological speciation (Ree, 2005; Liu et al., 2018). However, hemiparasitism is evolutionarily
234 unstable. This is evidenced by the lack of transition series in all parasitic lineages except
235 Orobanchaceae and arguably Santalales. Here, the reliance on host-derived water and nutrient
236 relaxes the selection pressure maintaining autotrophic functions. The accumulation of deleterious
237 mutations will eventually shut down photosynthesis. This process takes around thirty million years
238 in *Cuscuta* and Orobanchaceae, but can also take more than sixty million years in Krameriaceae and
239 Santalales, which are still photosynthetic (Table 1).

240 The transition to holoparasitism is a hallmark of a steeper evolutionary landscape, leading to a
241 series of extensive and widespread changes that reshape the morphology, physiology, and
242 reproduction. At the molecular level, deleterious mutations such as gene loss, selfish element
243 proliferation, and non-coding region expansion are constantly accumulated in the genome. At the
244 population level, high levels of host specificity and specialized pollination and seed dispersal
245 mechanisms make them vulnerable to environment upheavals and local extinctions. Founder effect
246 may therefore repetitively bottleneck the genetic diversity, which contributes to the parthenogenic
247 accumulation of more deleterious mutations. In fact, the overrepresentation of animal pollination
248 and functional dioecy in holoparasites (Bellot and Renner, 2013) could be driven by the need for
249 outcrossing to maintain genetic diversity. Nonetheless, this vicious circle will eventually reach a
250 terminal point (extinction) where it is no longer sustainable.

251 **Routes to genetic innovations**

252 Despite overpowering gene losses and isolated populations, parasites like Rafflesiaceae are still
253 able to persist over dozens of millions of years and invade novel habitats (Pelser et al., 2019). This
254 raises the question of how genetic variation as the raw material for adaptation is generated to offset
255 deleterious mutations and open new ecological opportunities.

256 In eukaryotes, horizontal gene transfer (HGT) and tandem/genome duplication are two common
257 ways for genetic innovation. HGT is especially well known in parasitic plants where alien genetic
258 materials from the host(s) are fixed in the genome of parasites (Davis and Xi, 2015). The
259 introduction of HGT across species boundaries can bring game-changing innovations. In ferns, an
260 insecticidal protein acquired from bacteria contributes to their well-documented resistance against
261 phytophagous insects (Li et al., 2018a). In parasitic plants, despite the ubiquitous presence of HGT,
262 few studies have attempted to address their functionality beyond gene ontology (GO) inferences
263 (but see a preprint from (Ono et al., 2021) on the biosynthesis of sesamin in *Cuscuta*). The best
264 evidence towards the adaptive role of HGT perhaps comes from the convergent HGTs in *Cuscuta*
265 and Orobanchaceae, where the same genes are repetitively acquired from the host and highly
266 expressed in the haustoria (Yang et al., 2019). Such parallelism may be shaped by selection or
267 genome architecture, which I term as the 'functional necessity' and 'mechanistic convenience'
268 hypotheses, respectively (Fig. 4). Here, the 'functional necessity' scenario posits selection as a
269 mechanism for convergence — HGTs rescue the loss of housekeeping functions that are susceptible
270 to disruption in all parasites. Therefore, convergent HGT is more common in essential pathways
271 closely linked with photosynthesis or other autotrophy related pathways. On the other hand, the

272 'mechanistic convenience' scenario proposes that some genes are more likely to be transferred
273 because they are structurally more mobile (e.g., hitchhiked to transposable elements (TEs)). The
274 parallelism is thus determined by conservation in genome architecture across species.

275 In addition to HGT, gene duplications can bring novelty through sub- and neofunctionalization
276 (Ohno, 1970). In parasitic plants, the most well-known example comes from the strigolactone
277 receptor gene *KAI2d* in Orobanchaceae, which proliferated in the genome via tandem and genome
278 duplication and contributed to host range expansion (Conn et al., 2015; Yoshida et al., 2019). A
279 recent comprehensive survey across six Orobanchaceae genomes reported that 11% of the highly
280 expressed genes in the haustoria originated from a shared genome duplication event in the
281 common ancestor of Orobanchaceae and *Mimulus* (Xu et al., 2022). In *Sapria,* however, GO analysis
282 on expanded gene families only identified broad categories including chromosome organization,
283 DNA metabolism, and cell cycle (Cai et al., 2021), suggesting that the creation and retention of
284 duplicated genes are likely to be a lineage specific process. Meanwhile, the proliferation of TEs is a
285 non-neglectable force shaping the anatomy and function of the parasitic plant genome. In *Cuscuta,*
286 LTR and satellite DNA drove a 102-fold variation in genome sizes within 23 Myr (Neumann et al.,
287 2021). In both *Sapria* and *Phelipanche* (Orobanchaceae), TEs account for ~90% of the total genome
288 sizes (Cai et al., 2021; Neumann et al., 2021; Xu et al., 2022). Besides being a constant threat to
289 genome integrity, TEs also generate adaptive phenotypes in the face of stressful conditions (Capy et
290 al., 2000; Kazazian Jr, 2004). No studies have attempted to comprehensively evaluate the adaptive
291 value of TEs in parasites. As more comparative genomic datasets become available, it will be
292 possible to look for signatures of adaptation such as selective sweep of TEs (Li et al., 2018b),
293 flanking genes promoting phenotypical innovation (Studer et al., 2011), and signs of differential
294 evolutionary rates and N_e in TE islands (Schrader et al., 2014).

Concluding remarks

296 The funnel model offers an explicit framework to describe and understand the evolutionary
297 trajectory of parasitic plants. It underscores the enormous value of these plants as an emerging
298 system to study the battle between chances and necessities in evolution. If we replay the tape of life,
299 will it culminate at the same scene? Numerous questions in comparative genomics, population
300 genetics, and macroevolution emerge from this general framework. These questions are well suited
301 to be tested as more genomic resources become available. Here, the application of medium-
302 coverage genome sequencing can quickly and economically survey the gene spaces of multiple
303 parasitic lineages. This can serve as the proof-of-concept for the funnel model and guide future
304 investigations. Perhaps a more important value of the framework is to connect the community of
305 parasitic plant biologists with various branches of ecology-evolutionary disciplines. The study of
306 parasitic plants has been hindered by their scarce occurrence in the wild and the failure to cultivate
307 them under laboratory conditions. Consequently, the bulk of our knowledge towards parasitic
308 plants is limited to *Cuscuta* and Orobanchaceae, which are established systems for *in vitro*
309 manipulation. While these plants will continue to be promising systems for functional investigation,
310 the application of single cell and spatial expression techniques in particular will provide
311 unprecedented details on the fine-scale interaction between host and parasite. It is also crucial to
312 incorporate insights from other families, especially those representing more derived stages. The
313 application of techniques from population genetics, comparative methods, and herbarium-based
314 sciences will be essential to understand the evolution of these most unusual branches on the Tree
315 of Life.

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325

326 **Author contributions**
327 L.C. designed the study and wrote and edited all drafts.
328

329 **Data Availability Statement**
330 No new data have been generated.
331

332 **Supporting Information**
333 **Appendix S1** Seed dimension database in parasitic plants. The length and width of each seed is
334 measured in mm and is directly cited from two published databases. Please see the 'Reference'
335 column for data source. The number of seeds per fruit is obtained from literature or by counting
336 herbarium specimens in TEX-LL. These counts should be interpreted as estimations.
337

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Figure Captions
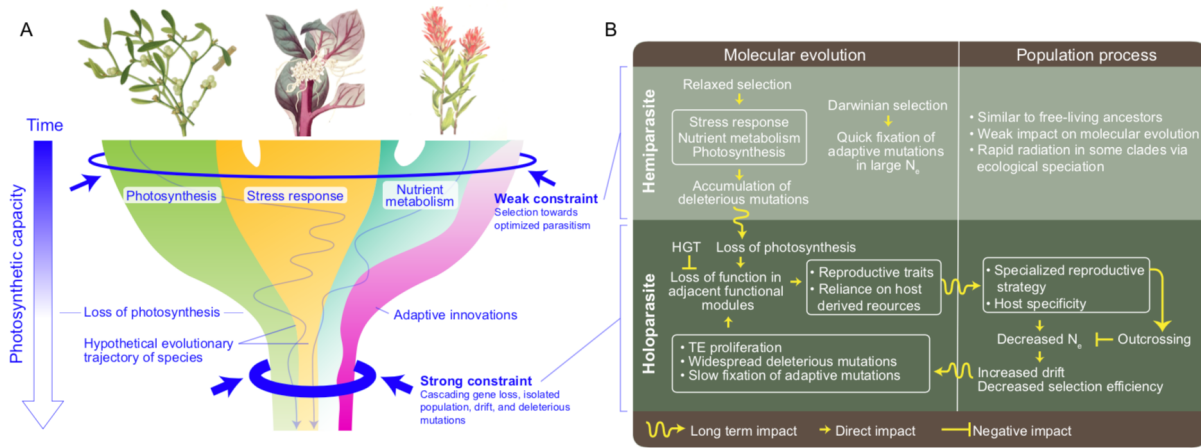
535
536 **Figure 1** The funnel model of parasitic plant evolution. (A) The overall architecture of the funnel
537 model. The onset of parasitism can be induced by multiple independent pathways, as hinted by the
538 diverse life history strategies in *Viscum* (stem parasites), *Cuscuta* (stem and leaf parasites), and
539 *Castilleja* (root parasites). At this stage, weak evolutionary constraints largely come from the
540 selective pressure to optimize parasitism, leading to moderate levels of gene loss in photosynthesis,
541 stress response, and nutrient metabolism. Genetic innovations are also accumulated to promote
542 adaptation. However, the loss of photosynthesis in holoparasites significantly increases the
543 evolutionary constraints by triggering widespread gene loss. The smaller and more isolated
544 population also leads to the parthenogenic accumulation of deleterious mutations and prevents the
545 fixation of adaptive mutations. (B) Dynamics of molecular and population constraints governing the
546 funnel model. Compared to hemiparasites, more intense interactions between mutation, drift, and
547 selection are present in holoparasitic plants, reducing their overall fitness. These negative impacts
548 may necessitate the introduction of horizontal gene transfer (HGT) to rescue interrupted functions
549 or the evolution of outcrossing to enrich the effective population size (N_e). Illustrations of plants are
550 obtained from the Biodiversity Heritage Library (https://www.biodiversitylibrary.org/).

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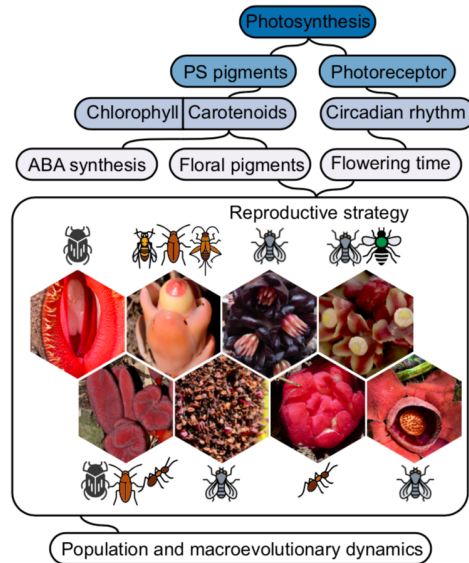
Figure 2 Phenotypical convergence in parasitic plants originates from concerted degradation of functionally linked modules. The loss of photosynthesis (PS) in holoparasitic plants triggers the disfunction of PS pigment biosynthesis and circadian rhythm, causing the parallel evolution of otherwise rare traits. Particularly, traits affecting reproductive strategies, such as the convergent recruitment of anthocyanins for floral pigmentation, can further impact population and macroevolutionary processes. Photo panels highlight the red colorants commonly found in holoparasites. Their corresponding pollinators is shown on the top or bottom of each photo. Species from top left to bottom right: *Hydnora africana* (Hydnoroideae, Aristolochiaceae), *Mitrastemon kawasasakii* (Mitrastemonaceae), *Bdallophytum americanum* (Cytinaceae), *Pilostyles thurberi* (Apodanthaceae), *Balanophora laxiflora* (Balanophoraceae), *Cynomorium coccineum* (Cynomoriaceae), *Cytinus ruber* (Cytinaceae), and *Rafflesia kerrii* (Rafflesiaceae). Images are obtained under the Creative Commons license from iNatualist and Flickr. Please see Acknowledgement for specific contributors.

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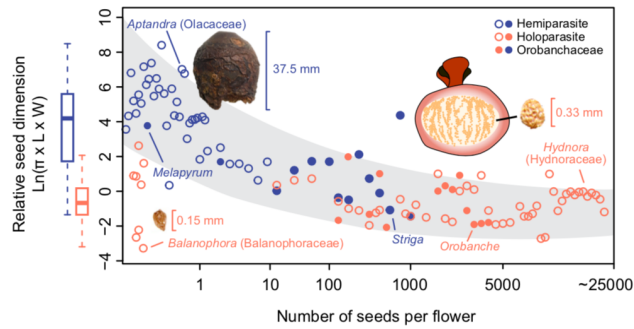
Figure 3 Evolutionary trend of seed size and number in parasitic plants. Holoparasites (orange) produce smaller seeds that are greater in number compared to hemiparasites (blue). This trend is consistent within Orobanchaceae (solid circles). Representative species with extreme seed size and number are highlighted. The box plot on the left shows the seed size from holoparasites (orange) and hemiparasites (blue). This dataset contains 113 representative species from 17 parasitic plant families, summarized primarily from two seed morphology databases (Ganhão and Dias, 2019; Baskin and Baskin, 2022). The relative seed dimension is calculated by a log-transformed area: Relative dimension = log(π x length x width). The x-axis (number of seeds per flower) should be interpreted as categorical rather than precise values, especially for species with more than 100 seeds per fruit. Please refer to Appendix S1 for data and reference (see Supplemental Data with this article).

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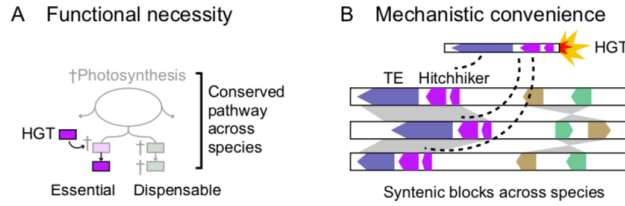
580
581 **Figure 4** The 'functional necessity' and 'mechanistic convenience' hypotheses for convergent
582 horizontal gene transfer (HGT) in parasitic plants. (A) Under the functional necessity scenario, HGT
583 can rescue the loss of essential functions that are susceptible to disruption in parasites. For
584 example, HGTs are recruited to compensate the convergent loss of an essential gene triggered by
585 the loss of photosynthesis in multiple species. (B) Under the mechanistic convenience scenario,
586 convergent HGT is endowed by consistent structural mobility. For example, genes hitchhiked to
587 transposable elements (TEs) can form long genetic blocks that translocate as HGT. When this
588 genetic block nests within a conserved syntenic region across multiple species, convergent HGT can
589 take place.
590
591 **Table**
592
593 **Table 1** Age and diversity of twelve independently evolved parasitic lineages. The stem group age
594 is cited from Nickrent (2020) and the species number is cited from the Angiosperm Phylogeny
595 Website (Stevens, 2016).
596

Clade	Classification	Stem group age (Ma)	Species number
Cassytha (Lauraceae)	Hemiparasite	77	19
Hydnoroideae (Aristolochiaceae)	Holoparasite	133	15
Santalales	Hemi + Holoparasite	108-110	2428
Cynomoriaceae	Holoparasite	100	2
Krameriaceae	Hemiparasite	60.9	18
Rafflesiaceae	Holoparasite	101	26
Cytinaceae	Holoparasite	72	11
Apodanthaceae	Holoparasite	75	10
Mitrastemonaceae	Holoparasite	78.3	2
Lennooideae (Boraginaceae)	Holoparasite	88	4
Cuscuta (Convolvulaceae)	Hemi + Holoparasite	34.6	195
Orobanchaceae	Hemi + Holoparasite	35.68	2025

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