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► **To cite this version:**

Jeanne Tonnabel, Patrice David, Tim Janicke, Arnaud Lehner, Jean-Claude Mollet, et al.. The Scope for Postmating Sexual Selection in Plants. *Trends in Ecology & Evolution*, Elsevier, 2021, 36 (6), pp.556-567. 10.1016/j.tree.2021.02.013 . hal-03190294

HAL Id: hal-03190294

<https://hal-normandie-univ.archives-ouvertes.fr/hal-03190294>

Submitted on 27 Nov 2021

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1 The scope for post-mating sexual selection in plants

2

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11 Short title : Sexual selection during pollen-pistil interactions

12 **Abstract**

13

14 Sexual selection is known to shape plant traits that affect access to mates during the pollination
15 phase, but it is less well understood to what extent it affects traits relevant to interactions between
16 pollen and pistils after pollination. This is surprising, because both of the two key modes of sexual
17 selection, male-male competition and female choice, could plausibly operate during pollen-pistil
18 interactions where physical male-female contact occurs. Here, we consider how the key processes
19 of sexual selection might affect traits involved in pollen-pistil interactions, including ‘Fisherian
20 runaway’ and ‘good-genes’ models. We review aspects of the molecular and cellular biology of
21 pollen-pistil interactions on which sexual selection could act and point to research that is needed to
22 investigate them.

23 **Key-words :** sexual selection, pollen-pistil interactions, mate choice, genetic correlation, Fisherian
24 runaway, good-genes model

25 **Scope for sexual selection in plants**

26

27 The concept of **sexual selection** (see Glossary) emerged with Darwin's [1] conjecture that selection
28 for accessing sexual partners could explain extravagant animal phenotypes. Two selective forces are
29 traditionally recognized in sexual selection theory: competition for access to the mate's gametes
30 (typically by males), and choice of sexual partners (typically by females). Remarkably, Darwin [1]
31 explicitly considered plants to fall beyond the reach of his theory. The main perceived obstacles to
32 applying sexual selection to plants was their frequent hermaphroditic nature, their lack of sensory
33 organs, and the modest levels of sexual dimorphism found in dioecious species [2]. Yet none of
34 these attributes precludes the action of sexual selection, as shown by recent empirical investigations
35 in animals [3-6]. Following much initial debate, plant evolutionary biologists have thus come to
36 reject Darwin's reticence to consider sexual selection for plants [2,7-13]. It is now accepted that
37 sexual selection may operate in all anisogamous organisms in which females produce larger but
38 fewer gametes than males, thus including both plants and hermaphrodites [14,15]. Revealingly,
39 Bateman [16] explicitly included flowering plants when setting out our modern perspective of how
40 to measure sexual selection, now known as the three **Bateman principles**. In accordance with
41 Bateman's third principle, male reproductive success showed a steeper relationship with the number
42 of genetic partners than female reproductive success in both a moss [17] and a flowering plant
43 species [18].

44

45 Plant populations display all necessary elements for the operation of sexual selection. For instance,
46 sexual dimorphism in gamete size and number, classically measured via pollen:ovule ratios, is
47 pervasive in flowering plants [19]. Examination of seed paternity within fruits in natural
48 populations has repeatedly found evidence for polyandry, with several pollen donors effectively
49 competing to sire ovules on a given plant [20]. Finally, variance in the reproductive success of

50 pollen donors [21] can be related to various traits including those that influence pollen production
51 [22], the dispersal of pollen to pistils of potential sexual partners (during the pre-pollination phase)
52 [18], and the outcome of pollen competition in the pistil (during the post-pollination phase).

53

54 Most research on sexual selection in plants has involved investigating the transfer of pollen to
55 recipient stigmas. Selection during this pre-pollination phase most typically involves indirect
56 competition with other pollen donors, and acts on traits that affect the attraction of pollinators and
57 pollen export to mates (Fig. 1a) [23]. In general, these traits include both aspects of morphology and
58 phenology, e.g., selection of males that flower concomitantly to females (Fig. 1b) [24]. A case of
59 physical male-male competition was reported in the pre-pollination phase in the form of ‘horns’
60 placed on structures that disperse pollen (pollinaria), preventing the attachment of pollen from rival
61 males to pollinators’ bodies (Fig. 1c) [25]. Pollen morphology more generally has been shown to
62 affect the efficacy of attachment of pollen to pollinator bodies (Fig. 1d) [26]. Yet, despite these
63 revealing examples, we still have a surprisingly poor understanding of whether enhanced pollinator
64 attraction and/or pollen removal actually corresponds to an increased number of mates, the most
65 relevant parameter in theories of sexual selection. The first direct estimations of mate numbers in
66 plants identified increased clonal growth [17] and more slender plant architecture (Fig. 1e) [18,21]
67 as targets of sexual selection, because these traits promoted pollen dispersal over greater distances
68 to more numerous mates.

69

70 In contrast to our growing understanding of how sexual selection acts during the pre-pollination
71 phase, we know little about its operation after pollen has landed on the pistil (Fig. 1f). This
72 asymmetry is puzzling, for two reasons. First, the post-pollination phase represents the only
73 instance of direct contact between male and female mating partners where female choice might be
74 able to act, a mode of sexual selection that has received much attention from zoologists. Second, the

75 post-pollination phase of mating represents an additional opportunity for the action of intra-sexual
76 competition between male gametophytes (the pollen grains and tubes). In contrast to the
77 accumulating evidence for intra-sexual competition operating during the pre-pollination phase, we
78 lack any sort of synthesis about the possibility that female choice might shape pollen traits, with
79 obvious parallels with post-copulatory selection in animals [27].

80

81 Several observations suggest that a search for evidence of sexual selection during the post-
82 pollination phase might be fruitful. Typically, many more pollen grains are deposited on stigmas
83 than the number of ovules [in the corresponding ovaries](#) [28 but see 29]. High pollen loads combined
84 with strong polyandry set the stage for intense sexual selection during pollen-pistil interactions.
85 Moreover, individual plants vary in several pollen competitive traits identified as key determinants
86 of variance in fertilization success (Table S1; [30]). These findings raise the question of the relative
87 importance of **intra-sexual competition** among pollen donors for accessing ovules, and **inter-**
88 **sexual mate choice** exerted by pistil tissues for explaining the observed variance in fertilization
89 success.

90

91 In this synthesis, we aim at reviewing knowledge about pollen-pistil interactions in the light of their
92 support for the occurrence of sexual selection in flowering plants. Strikingly, pistil tissues not only
93 facilitate the growth of pollen tubes by providing nutritive resources, but they also influence the
94 ability of pollen tubes to perceive the pistil cues that guide pollen towards the ovules [31-34].
95 Molecular knowledge about pollen-pistil interactions offers several candidates for the action of
96 sexual selection which we present in the light of their potential congruence with classical models of
97 sexual selection [35-39].

98

99 **Pollen-pistil interactions in a nutshell: the active role of pistil tissues**

100

101 Pollen-pistil interactions have been the focus of fruitful research on plant mating in terms of self-
102 fertilization avoidance and the promotion of outcrossing, in fields ranging from theoretical and
103 empirical population genetics [40-42], to molecular genetics and cellular biology [43,44]. In this
104 sense, pollen-pistil interactions represent an area of biological enquiry that, unusually, links both
105 evolutionary and population-based thinking with functional considerations of mechanisms at the
106 molecular level. Other studies of pollen-pistil interactions are relevant to our understanding of
107 asymmetries of mating between hybridising species [45,46]. Though rich in data and concept, most
108 of this work nonetheless has focused on questions not directly relevant to sexual selection. Yet
109 molecular biologists have recently uncovered a rather complex molecular dialogue [between pollen](#)
110 [and pistil](#), with potential implications for sexual selection.

111

112 After their successful arrival on a pistil, pollen grains need to adhere to the stigma and to uptake
113 water to re-hydrate, germinate and produce a pollen tube (Fig. 2). The initial growth of pollen tubes
114 in the stigma is autotrophic, [but](#) becomes heterotrophic when reaching the style. Secretion of
115 nutritive molecules by pistils nourishes pollen tubes, which deplete nutritive molecules from the
116 stilar extracellular matrix (listed in Table S2). Although the mechanisms of the fuel transfer from
117 pistil to pollen tubes are not yet fully understood, it is clear that pistil cells modify their metabolism
118 in response to pollen tube growth [47], and that pollen tubes have evolved ways of harvesting pistil
119 nutritive resources [48]. Pistil tissues also secrete molecules facilitating pollen germination and
120 [promoting pollen tube penetration](#) (Table S2).

121

122 Stilar tissues also provide guidance cues that ensure the successful orientation of pollen tubes
123 towards the unfertilized ovules (Fig. 2; [49,50]). This process involves the very modification of
124 pollen tubes by the pistil to confer upon them a ‘competence’ to localize ovules [34,51]; remarkably,

125 pollen tubes grown *in vitro* can locate dissected ovules only if they have previously navigated
126 through excised pistil tissues [33]. Accordingly, multiple changes in gene expression occur in pollen
127 tubes after their growth through pistil tissues, and *vice versa* [47,52].

128

129 The final guidance of pollen tubes within the ovary is undoubtedly the best understood phase of
130 pistilar control, which is largely dependent on signals produced by the haploid female gametophyte
131 [34,53,54]. Ablation studies have shown that both the embryo sac and integuments of the ovule are
132 involved in pollen tube guidance within the ovary [55]. Synergid cells play a central role by
133 producing small peptides that re-orient the tip-focused pollen tube growth towards the embryo sac.
134 A complex dialogue between the synergids and the pollen tube further leads to the double
135 fertilization [32]. The expression of attractive peptides are then blocked, repellent ethylene is
136 produced to prevent more than one pollen tube from entering the ovule [56], and degeneration of
137 the remaining synergid is induced [57].

138

139 **Candidate pollen traits for intra-sexual competition**

140

141 Sexual selection theory predicts that increased competition for accessing mates selects for higher
142 investment in competitive traits [37]. This prediction may translate to pollen-pistil interactions
143 through selection for greater allocation to pollen competitive traits with increased number of
144 competing pollen donors. At the macroscopic scale, several studies indicate that certain pollen
145 phenotypes confer greater fertilization success than others, pointing to the action of intra-sexual
146 competition (Table S1). Yet we have little knowledge about the extent to which such within-
147 generation variance in fertilization ability has translated into pollen trait evolution. A handful of
148 studies have estimated heritabilities from 9% to 49% for male gametophyte traits [10,58-60].
149 Studying the evolutionary consequences of variation in the number of pollen donors applied via

150 hand-pollination in chinese innocence (*Collinsia heterophylla*), Lankinen *et al.* [61] observed
151 enhanced pollen performance in a line that evolved four generations under two pollen donor crosses
152 compared to a single pollen donor line.

153

154 Several molecular features of the ability of pollen to draw upon pistil resources and guidance cues
155 are obvious candidates for the action of male-male competition (Table S3 lists candidate molecules
156 for evolutionary testing). Pollen tube performance involves the expression of molecule transporters
157 [62], the constant reorganization of actin filaments [63], vesicle trafficking at the pollen tube apex
158 to build cell walls [64], active cell wall remodeling [65] and, sometimes, a plastic decrease in pollen
159 tube diameter to allow better movement between pistil cells [66]. Suppressing the growth of a
160 competitor's pollen tubes could constitute an efficient strategy to bias paternity in polyandrous
161 systems, except perhaps when competing pollen grains come from the same pollen donor (Fig. 2).
162 Yet, negative effects of the number of pollen donors on pollen performance have rarely been
163 reported [67,68], and the molecular basis of any putative antagonistic pollen-pollen interactions is
164 not yet established. In fact, positive effects of greater numbers of pollen grains on pollen
165 performance have often been reported, pointing to the possible role of diffusible molecules in
166 fostering pollen performance and softening pistil tissues (mentoring effect [69,70]).

167

168 A major prediction of sexual selection theory is that male-male competition should select for
169 individuals in better 'condition', i.e., those efficient at mating because of their higher genetic
170 qualities [71]. Such 'condition-dependent' sexual selection is expected to be able to purge
171 deleterious mutations at low demographic cost [39,40]. Could selection on pollen traits conform to
172 this prediction by reflecting the genetic quality of pollen donors? Investigations of the effect of
173 natural selection acting on pollen suggest that 'condition-dependent' sexual selection may indeed
174 apply to pollen-pistil interactions. Interestingly, enhanced pollen competition and more competitive

175 pollen traits can lead to improved progeny growth [72,73], and the very success of angiosperms
176 over gymnosperms has even been attributed, in part, to such interactions [74]. While these ideas
177 have been explored specifically in the context of competition among pollen originating from a
178 single plant, they are also relevant to competition among different pollen donors, and empirical
179 results tantalizingly suggest that ‘condition-dependent’ male-male competition may indeed apply.

180

181 **Scope for female choice during pollen-pistil interactions?**

182

183 There is growing evidence that plants have developed mate-filtering mechanisms in a number of
184 contexts. Genetic incompatibility and other mechanisms of inbreeding or outbreeding avoidance are
185 known to affect pollen donor siring success in the context of different recipients (Table S3). It is
186 clear that plants can reject pollen tubes from closely or distantly related plant genotypes [75,76], or
187 from individuals displaying certain incompatibility alleles [77,78]. These processes may explain
188 why multiple mating generally enhances plant progeny vigor [20]. Such mechanisms of plant mate
189 choice fall into what was recently defined as ‘grey zones’ of sexual selection, where variation in
190 components of male reproductive success depends on mate identity [79]. But to what extent does
191 mate choice occur among compatible mating based on traits reflecting the performance of
192 prospective mates? Could plants exert **inter-sexual female choice** in a way that conforms to cryptic
193 female choice, where pollen with certain traits is filtered within the maternal tissues [80]?

194

195 **Female choice** may occur through what we might label ‘**post-pollination mate choice**’, whereby a
196 bias in paternity with respect to particular pollen traits is brought about by virtue of the morphology
197 or physiology of the maternal plant. Such a manifestation of sexual selection should ultimately be
198 distinguishable from incompatibility and inbreeding or outbreeding avoidance, because the former

199 should elicit directional selection for particular pollen traits, while the latter should favour different
200 pollen donors on different recipients.

201

202 It remains questionable whether the envisioned post-pollination mate choice in plants conforms to
203 predictions made by animal-oriented classical models of mate choice (Fig. 3). Both the ‘Fisherian
204 runaway’ and the ‘good-genes’ models of sexual selection have focused on how female choice for
205 male attributes may evolve in spite of costs associated with both female preference and male
206 preferred traits [81]. Fisher’s [82] ‘runaway’ theory postulates that females’ preferences for male
207 traits should evolve because choosy females ultimately produce progeny with both the sexual
208 preference and the preferred trait. Such models predict evolutionarily stable female preferences
209 driven by a genetic correlation between the preference and the preferred trait when sufficient
210 genetic variance in preferred traits is maintained by deleterious mutations [35] or by spatial
211 variation in selection on the preferred trait [83].

212

213 It is important to note that ‘good-genes’ models build on the Fisher’s ‘runaway’ model by assuming
214 that preferred traits are also informative about their bearer’s overall genetic quality (Fig. 3; [36,71]),
215 i.e., these models should be seen as two facets of a single theory of female choice [81]. ‘Good-
216 genes’ models predict evolutionarily stable female preferences stemming from genetic associations
217 between the male trait and fitness components [36,81]. Initially, ‘good-genes’ models were
218 criticized because of the absence of erosion of genetic variance in male performance in natural
219 populations subject to female choice [71]. However, it is now accepted that genetic variance in
220 condition-dependent traits may be maintained because the ‘condition’ is determined by a large
221 number of genes scattered throughout the genome, thus allowing for genetic variation despite low
222 mutation rates [71]. ‘Condition-dependent’ sexual selection provides the basis for the general
223 prediction that sexual selection should clear mutation loads, a prediction that has received

224 substantial empirical support in the animal kingdom [84-86]. But could it apply to plants in the
225 context of pollen-pistil interactions?

226

227 There are good reasons to think that models of female choice should apply to plants during the post-
228 pollination phase. For instance, a pistil trait (e.g., style length) might bias paternity towards certain
229 pollen traits (e.g., fast pollen tube growth), which may become genetically coupled. Pollen traits
230 offer good candidates for a ‘good-genes’ process, because the pollen performance correlates with
231 various fitness components [10,72,73,87]. In contrast to the male gametes of animals, haploid
232 pollen tubes maintain high gene expression [88], with **significant** overlap with gene expression at
233 the sporophytic stage [89], **potentially** rendering pollen traits honest signals of pollen donor’s
234 genetic quality. **Consistent with the possibility of** post-pollination mate choice, a genetic correlation
235 between pollen size and style length was reported in the field mustard (*Brassica rapa*) [90]. Yet any
236 process of sexual selection operating during pollen-pistil interactions may also bring about **sexual**
237 **conflict** [91]. Such conflicts might involve the evolution of female resistance traits in response to
238 fitness costs inflicted by pollen competitive traits, with some peculiarities in hermaphroditic plants
239 (Box 1).

240

241 The growing awareness of the importance of the post-copulatory component of sexual selection in
242 animals [27] led to an extension of female choice theory to explain the evolution of polyandry
243 [92,93]. ‘Sexy-sperm’ and ‘good-sperm’ models predict that genetic correlations between male
244 fertilization success (equivalent to male preferred trait), female polyandry (equivalent to female
245 preference trait), and fitness components can drive the evolution of polyandry [92,93]. Verbal
246 analogies have been made between these models and cases of post-copulatory female traits biasing
247 paternity for certain sperm traits [3] and may therefore have implications for post-pollination mate

248 choice, too. Yet it seems to us that such situations might apply better to classical models of female
249 choice than to the evolution of polyandry.

250

251 Given the above descriptions, we **conjecture** that both ‘Fisherian runaway’ and ‘good-genes’
252 processes may apply to pollen-pistil interactions. These models consider, on the one hand, generic
253 processes of the evolution of a costly maternal trait that biases paternity towards a costly paternal
254 trait (Fig. 3), and, on the other hand, genetic correlations that may establish among these traits, as
255 well as between them and other fitness components. Similar to the mechanisms envisioned here,
256 simple genetic correlations between the size of the female copulatory organ and that of sperm has
257 been shown to conform to these models [3]. Sexual selection theory may therefore contribute to
258 understanding the extraordinarily rapid growth of pollen tubes, **which ranks** among the fastest **cell**
259 **growth** known for **eukaryotes** [94].

260

261 **Candidate pistil traits for post-pollination mate choice**

262

263 Biasing the paternity towards pollen donors with specific pollen traits may be achieved by simple
264 pistil traits (Fig. 2; Table S2). The accumulation of more numerous pollen donors could be
265 facilitated by a longer flower opening and larger stigmas while competition among pollen donors
266 could be enhanced by longer styles, decreased expression of molecules that provide nutrition and
267 guidance and, a reduction of space provided to pollen tubes [95]. There have been several reports of
268 reduced style diameter and gradients of nutritive resources [96], which have also been shown to
269 limit the number of pollen tubes that reach the pistil base, leading to ‘pollen tube attrition’ [97].
270 Controlling the quantity and quality of the nutritive and guiding molecular matrix can be effected
271 by diminishing molecular excretion through exocytosis and transporter expression, and by

272 inactivating or deteriorating assisting molecules. Future studies should also establish whether
273 variation in pollen tube signals can manipulate resource provision by pistil tissues.

274

275 Sexual selection may also target [the capacity of](#) pistils to constrain pollen tube growth, thus
276 bringing into competition pollen donors whose pollen landed on stigmas at different times. Stigma
277 receptivity, controlled by stigmatic inhibitors of pollen germination, constitutes the first opportunity
278 for pistils to delay the germination of pollen grains [98]. Further down the path to fertilization,
279 styles can constrain pollen tube kinetics by providing discontinuous nutritive resources, or by
280 delaying the maturation of their basal sections – which typically occurs after flower opening. One
281 extreme version of pistil control in angiosperms is exemplified by obturators, a placental
282 protuberance that regulates access of pollen tubes to the ovary [99]. The switch to a secretory phase
283 of the obturator ensures that only one pollen tube enters the ovary. Pollen recipients that delay
284 access of pollen to the ovary may permit the accumulation of pollen tubes from different pollen
285 donors, allowing selection among pollen genotypes that are particularly efficient at perceiving the
286 molecular switch. The most convincing description of female choice in plants [so far](#) concerns **post-**
287 **zygotic mate choice** when embryos compete for accessing maternal resources (Box 2).

288

289 **Concluding remarks**

290

291 The scope for sexual selection during pollen-pistil interactions has largely been studied by means of
292 within-generation characterizations of siring patterns. Such approaches, while useful and revealing,
293 fail to disentangle male-male competition from mate choice, not least because the former needs to
294 occur for the latter to be possible [100]. To provide further insights on post-mating sexual selection
295 (see Outstanding Questions), it would be useful to identify pistil traits affecting the siring success
296 hierarchy among pollen donors displaying different pollen traits. Attributing a paternity bias

297 unambiguously to a female trait can be achieved by comparing paternity on recipient plants
298 displaying variable pistil traits. Testing female choice models further requires quantifying the
299 genetic correlations between the identified pollen and pistil traits. Examining the intra-specific
300 variation of pollen-pistil traits between populations informs on mate choice divergence, while inter-
301 specific patterns of joint evolution of pollen-pistil traits would allow identifying a non-neutral effect
302 of pistil tissues. [Comparing pollen-pistil interactions among closely related species that differ in](#)
303 [relevant traits \(e.g., outcrossing rates\) might help reveal the underlying mechanisms.](#)

304

305 Applying **experimental evolution** to vary the opportunity for sexual selection could prove efficient
306 at evaluating the scope for sexual selection, as has been done in numerous studies with animals
307 [84]. Comparing pistil and pollen phenotypes of experimental populations that evolved with
308 monogamy *versus* polygamy during the post-pollination phase may help to both test predictions of
309 the theory of sexual selection, and to identify new molecules involved in pollen-pistil interactions
310 (Fig. 3). Provided that maternal and paternal traits are involved in paternity bias (determined
311 through paternity analyses), quantitative genetics constitutes a key methodology for testing
312 predictions of female choice models. By favouring the reproduction of high-quality pollen donors
313 through male-male competition or female choice, ‘condition-dependent’ sexual selection could clear
314 mutation loads [71], with implications for plant conservation and crop management. Future studies
315 should establish whether sexual selection may have positive effects on plant fitness.

316 **Box 1: Sexual conflict in hermaphroditic plants**

317

318 Sexual conflicts arise when sexes cannot reach their sex-specific phenotypic optima, owing to
319 antagonistic interactions or genetic correlations with the other sex. Studying sexual selection in
320 hermaphrodites opens yet unresolved questions about sexual conflicts [101]. The particularity of
321 hermaphroditic species is that resource allocation trade-offs may give rise to intersex interactions
322 directly within individuals [102]. Intra-locus sexual conflict (e.g., when the optimum for a
323 phenotypic trait differs between male and female functions) may arise in plants because male and
324 female reproduction rely on the acquisition of different resource types, and on different deployment
325 of such resources. Strategies maximizing donor success can sometimes be detrimental to the gamete
326 recipient, causing inter-locus sexual conflict (e.g., when gamete performance harms the recipient's
327 reproductive success; [103]). For instance, despite scant investigations on sexual conflict in plants,
328 the evolution of greater pollen competitive abilities in chinese innocence (*Collinsia heterophylla*)
329 induced female fitness costs to the pollen recipient [61]. A range of sexual conflicts may arise in the
330 context of pollen-pistil interactions. For instance, female fitness may be compromised by the
331 evolution of more competitive pollen tubes that harvest nutritive resources from the pistil or
332 damaging pistil tissues [31]. Alternatively, increased competitive abilities of pollen traits may have
333 evolved as counter-adaptations to female control over mates. The evolution of manipulative traits
334 by male gametophytes could also trigger inter-locus sexual conflicts, e.g., by coercing the diversion
335 of maternal resources for the growth of the ovules they have fertilized at the expense of other
336 maternal fitness components. A male-female genetic conflict may emerge because embryos
337 expressing higher hormonal levels are likely to attract additional maternal resources [103]. In
338 maize, embryos from different paternal genotypes have been shown to compete for maternal
339 resources, with associated costs to female fitness [104]. Accordingly, such inter-locus sexual
340 conflict may favour the evolution of resistance traits (e.g., decreased perception in the embryonic

341 hormonal signal). Importantly, **however**, the benefits of purging mutations through sexual selection
342 in animals **may** be **compromised** by the disadvantage of sexual conflicts, such as **the** harassment of
343 females by males [105].

344 **Box 2: Some evidence for post-zygotic mate choice in plants**

345

346 Despite the scant attention so far given to female choice in plants, early studies of plant sexual
347 selection did in fact document some evidence for it. In wild radish, a decrease in plant water
348 provisioning was shown to induce differential seed abortion, favouring the siring success of
349 individuals with pollen tubes able to travel further down the mate's ovary [106]. When water is
350 limiting, plants may abort embryos higher up in the ovary, thus biasing paternity towards pollen
351 donors able to fertilize ovules further down [106]. Such selective seed abortion may lead to non-
352 random use of pollen in a way consistent with a hypothesis of post-pollination mate choice – though
353 it remains to be shown whether such choice is due to selection under the 'good-genes' or the
354 'runaway' model. Selective seed abortion may also increase offspring quality [107], but such a
355 result may well be attributable to inbreeding or outbreeding avoidance rather than to directional
356 sexual selection. Paternity analyses performed across the reproductive season in the trumpet wine
357 (*Campsis radicans*) revealed a consistent decrease in the number of pollen donors throughout the
358 season while controlling for the intensity of pollen competition [108], perhaps suggesting increased
359 selectivity by females over their mates as maternal resources become more and more limiting [108].
360 Similar results were found for some animals in which there is a higher opportunity for post-
361 copulatory selection with decreasing resources [109]. Studies aimed at distinguishing between the
362 effects of maternal control and competition among embryos on patterns of seed abortion also
363 potentially provide valuable information on the extent to which seed abortion is under the control of
364 pistil tissues. Indeed, cellular and molecular investigations in several plants indicate that embryo
365 abortion may be controlled by degradation of maternal tissues, followed secondarily by degradation
366 of the embryo (e.g., deposition of lignin and cellulose in the integuments; [110]). Viable embryos
367 are commonly aborted by plants, as highlighted by their successful *in vitro* culture [111]. Together,

368 these results suggest that maternal plants may indeed exert some control over embryo development,
369 and future research should evaluate its relevance for sexual selection.

370 **Glossary box**

371

372 **Bateman principles:** [the principles that](#) formalized Darwin's hypothesis [1] that male reproductive
373 success should depend on access to mating partners more than female reproductive success, a
374 disparity ultimately rooted in anisogamy [16]. Bateman principles decompose into three predictions:
375 variance in (1) reproductive and (2) mating success should be larger in the sex that produces greater
376 numbers of smaller gametes (generally males), and (3) this sex should show a steeper relationship
377 between reproductive success (i.e., number of offspring) and mating success (i.e., the number of
378 sexual partners) than the sex producing large and less numerous gametes [16].

379 **Cryptic female choice:** inter-sexual selection driven by female mechanisms resulting in biased
380 sperm use and altering the male paternity share [80].

381 **Experimental evolution:** study of evolutionary responses to experimental conditions of
382 independent experimental populations.

383 **Intra-sexual competition for mates and/or their gametes:** competition within one sex (typically
384 males) for access to sexual partners (i.e., reach a pistil mate) and/or their gametes (ovules).

385 **Inter-sexual female choice:** female choice involves a female trait inducing a bias in paternity for
386 males displaying particular traits (e.g., displays, pollen traits, incompatibility alleles); in this review,
387 we particularly focus on female choice eliciting directional selection for a particular male [pollen](#)
388 trait.

389 **Post-pollination mate choice:** paternity bias favouring pollen donors that display specific pollen or
390 pollen tube trait(s) elicited by a pistil morphological or molecular trait.

391 **Post-zygotic mate choice:** maternally controlled variance in resource allocation to embryos [causing](#)
392 paternity bias and favouring pollen donors that display particular trait(s); such embryo abortion may
393 be the consequence of varying resource allocation to different fruits or different embryos within
394 fruits.

395 **Sexual conflict:** sexual conflict arises when a trait beneficial for the fitness of one sex is detrimental
396 to that of the other. Sexual conflict may involve a single locus when its optimum expression differ
397 between sexes, or several loci when the mating performance of one sex compromises the fitness of
398 the other sex.

399 **Sexual selection:** ‘differences in reproduction that arise from variation among individuals in traits
400 that affect success in competition over mates and fertilizations’ (as defined by [112], but see [79] for
401 a review of various alternative definitions).

402 **Figure legends:**

403 **Figure 1: Examples of potentially sexually selected plant traits.** Field mustard plants (*Brassica*
404 *rapa*) (a.) pollinated during nine generations by bumblebees were taller, produced more scent and
405 changed their ultraviolet reflection compared to plants pollinated by hoverflies [pointing to a rapid](#)
406 evolution of traits involved in pollen export ([23] courtesy of Florian Schiestl). In the dioecious
407 white campion (*Silene latifolia*) (b.), differences in male flower sizes induced through artificial
408 selection led to an earlier flower phenology in the ‘small-flower’ line which better matched female
409 phenology, thus offering greater mating opportunities to males from the ‘small-flower’ compared to
410 the ‘large-flower’ lines ([24] courtesy of Lynda Delph). Dispersal structures containing pollen
411 grains, called pollinaria (c.), evolved ‘horns’ in various milkweed species which decrease the
412 pollination success of rival pollen donors by preventing the attachment of a subsequent pollinarium
413 ([25] courtesy of Andrea Cocucci). Pollen morphology (d.), including their size and spine density,
414 affects the probability of attachment on pollinator’s bodies [26] ([pollen of *Catananche caerulea*](#),
415 courtesy of Agnès Mignot, [ISEM reference palynological database](#)). Male plant architecture of the
416 wind-pollinated annual mercury (*Mercurialis annua*) (e.), including longer branch size and longer
417 peduncles of male-flower bearing inflorescences, was shown to enhance pollen dispersal to a
418 greater number of [mates](#) [18,21]. Pollen-pistil interactions during compatible matings offers several
419 candidate mechanisms for the operation of both intra-sexual competition for fertilization, and inter-
420 sexual mate choice that may conform to the theory of sexual selection ([image of pollen germinating](#)
421 on a *Solanum lycopersicum* pistil by J-C. Mollet).

422

423 **Figure 2: Pollen success after arrival on the stigma depends on successive male-female**
424 **interactions providing as many opportunities for sexual selection.** Intra-sexual competition
425 among pollen donors may increase variance in paternity via the expression of pollen traits: pollen
426 from different donors may express different abilities to adhere to a dry pistil stigmatic surface (1);

427 to re-hydrate pollen (2); to produce a pollen tube and grow down the stigmatic tissue and the style
428 (3); to monopolize pistilar nutritive resources and perceive cues guiding pollen towards the ovule
429 through the style (4); to penetrate an unfertilized ovule following pistilar guidance, mostly exerted
430 by **haploid** female gametophyte within the ovary (5); to achieve double fertilization (6); and to
431 ensure resource provisioning to developing seeds (7). Male-male competition may ultimately bring
432 about negative pollen-pollen interactions provided that such interactions can occur. Inter-sexual
433 post-pollination mate choice may also bias paternity as a result of the evolution of simple pistil
434 traits at all steps in the course of pollen-pistil interactions: larger stigmatic surfaces and flowers
435 opened for longer periods may enhanced the number of pollen competitors; longer styles or
436 decreased expression of pollen-tube assisting molecules may select for the most efficient pollen
437 tubes; pistil control over pollen tube growth may select for the pollen tubes most capable of
438 perceiving the ovary guidance signal; and pistil tissues may direct resource to certain developing
439 embryos (Box 2). Pollen-pistil interactions may conform to classical models of the theory of sexual
440 selection, modeling intra-sexual competition and inter-sexual mate choice.

441

442 **Figure 3: Research agenda for testing models of female choice during pollen-pistil interactions**
443 **in angiosperms.** The ‘runaway’ model predicts an evolutionarily stable female preference because
444 females expressing a preference for a preferred male trait produce more attractive progeny with
445 correspondingly greater access to mates. This preference for attractive males results in a genetic
446 correlation between the preference and preferred trait. ‘Good-genes’ models add to the runaway
447 model a fitness component shared by both sexes, **and** predict evolutionarily stable female choice
448 because females expressing a preference produce progeny with greater fitness, besides their greater
449 access to sexual partners; i.e., because the preferred trait is a good indicator of male quality. The
450 negative genetic correlation found between sperm length and spermatheca size in the taurus scarab,
451 a trait known to bias paternity for males of smaller sizes provided an example of a post-copulatory

452 female choice [3]. We propose a research agenda for testing whether putative post-pollination mate
453 choice may conform to these predictions: experimental evolution may allow identifying whether
454 several generations of evolution of enforced monogamy (where no competition or mate choice can
455 occur) *versus* polygamy during the post-pollination phase (through hand-pollination) can elicit the
456 evolution of pollen and pistil traits; paternity analyses further allows determining whether evolved
457 pollen and pistil traits can be considered as preferred and preference traits because evolved pistil
458 traits cause paternity bias for evolved pollen traits; finally, quantitative genetics allows tests for
459 established genetic correlations between pollen, pistil and fitness traits, conforming to ‘runaway’
460 and ‘good-genes’ models.

461 **Acknowledgments**

462 J.T. was funded by a Marie Skłodowska-Curie grant (#844321). AL and JCM were funded by the
463 University of Rouen Normandy and the French Ministry of Research and Higher Education. T.J.
464 was funded by the Centre national de la recherche scientifique (CNRS) and the German Research
465 Foundation (DFG grant number: JA 2653/2-1).

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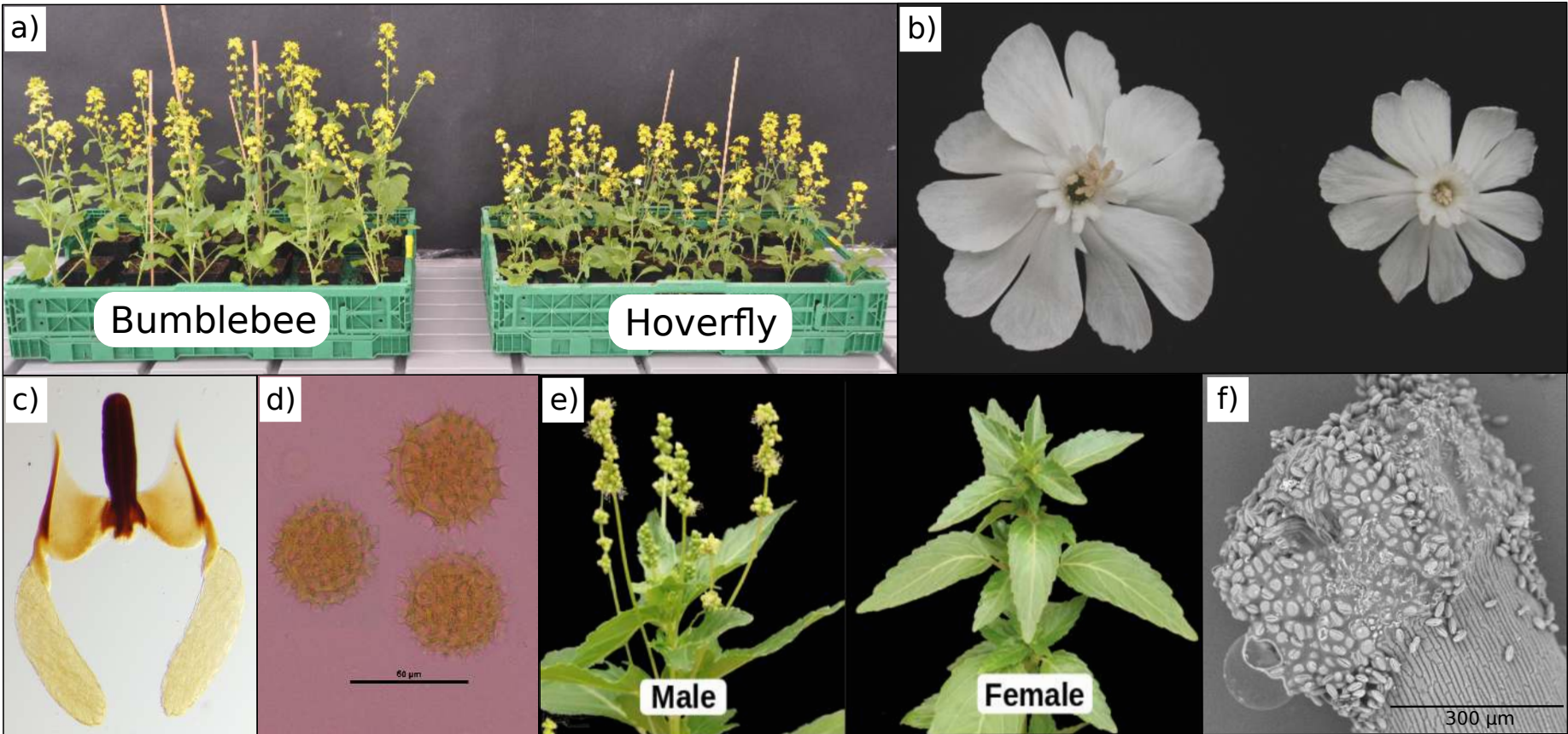
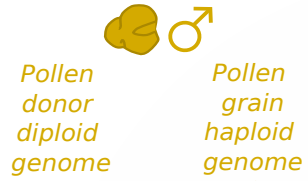


Figure 1

Opportunities for sexual selection during pollen-pistil interactions

Hypothetical source of variance in paternity

Male function



Pollen traits
(morphological, cytological, molecular)

Known complex molecular and cellular interactions

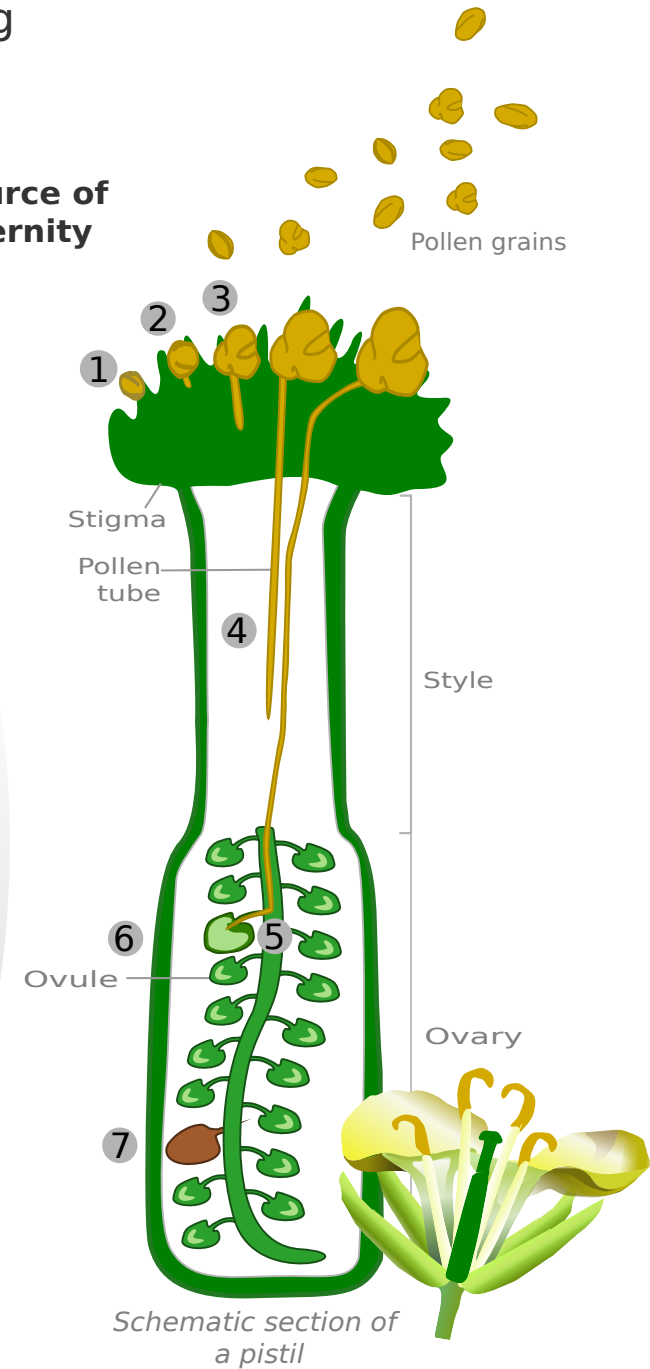
- 1 Pollen adhesion to dry stigma
 - 2 Pollen re-hydration
 - 3 Pollen germination and growth in stigma
 - 4 Pollen growth in style
 - 5 Ovule penetration
 - 6 Fertilisation
Zygotic diploid genome
Zygotic traits
 - 7 Seed development
- Male reproductive success

Hypothetical source of variance in paternity

Female function



Pistil traits
(morphological, cytological, molecular)



EVOLUTIONARY BIOLOGY

MOLECULAR BIOLOGY

EVOLUTIONARY BIOLOGY

Figure 2

MODELS PREDICTING FEMALE CHOICE

Testing predictions

RESEARCH AGENDA

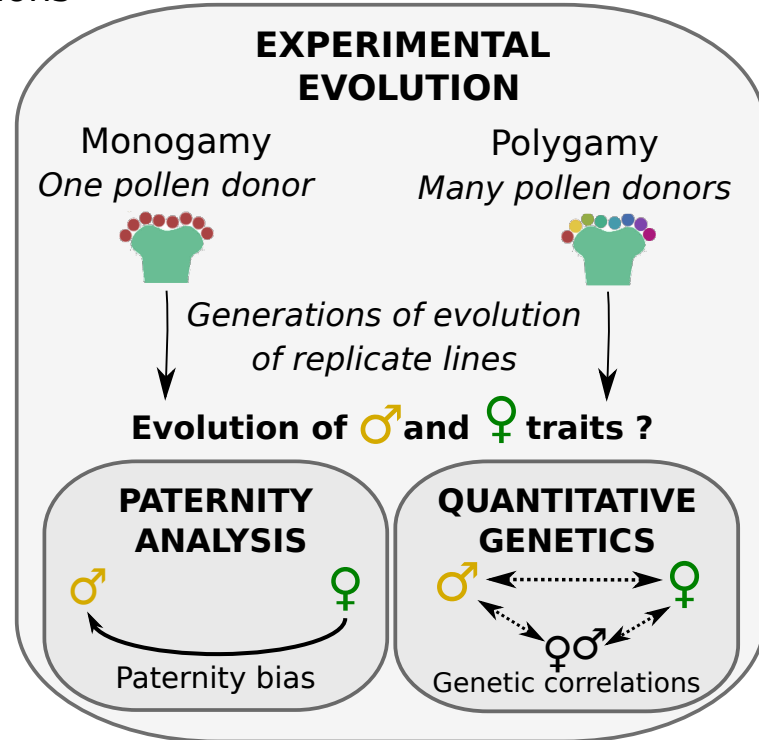
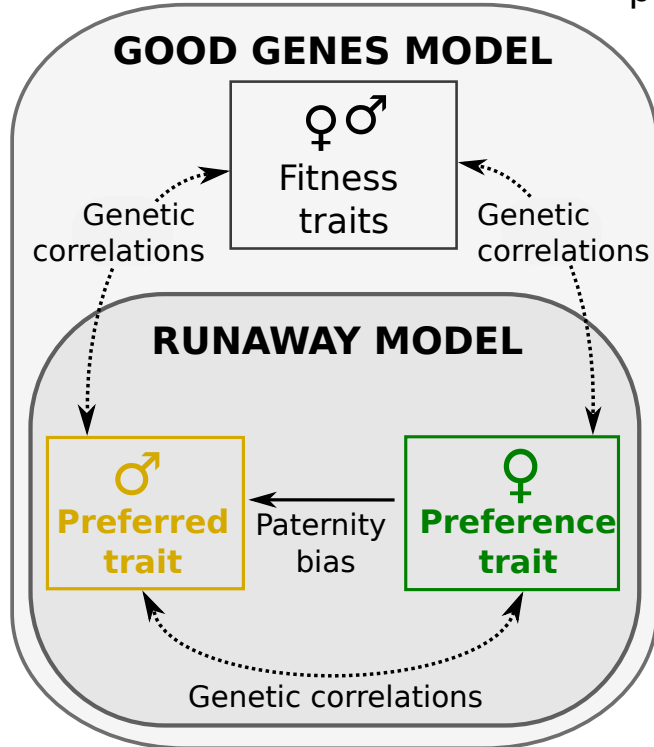


Figure 3

Supplementary Material

The scope for post-mating sexual selection in plants

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Table S1 Summary of the studies investigating the possibility of male-male competition occurring in the post-pollination phase

Methodology	Main result testing for male-male competition	Reference and species
Comparison of seed siring success after mixed donor hand-pollination	Positive correlation between pollen donor seed siring success and pollen tube growth rate and number of pollen tubes reaching different section of the style	[S1] <i>Prunus avium</i>
Comparison of pollen tube growth rates of two pollen donors in hand-pollinations on two pistil ramification and estimation of siring success through paternity analyses	Positive correlation between pollen donor seed siring success and pollen tube growth rate	[S2] <i>Hibiscus moscheutos</i>
<i>In vivo</i> and <i>in vitro</i> pollen tube growth rate assessment and estimation of seed siring success following two-donor hand-pollinations	Significant variation among pollen donors in pollen tube growth rate which was positively correlated to the seed siring ability following mixed pollen donor pollination	[S3] <i>Betula pendula</i>
Comparison of within fruit paternity by different pollen donor in maternal stressed and non-stressed plants	Pollen donor variation in abilities to sire seeds at different depth within the maternal ovary leading to variance in seed size between pollen donors because of a gradient of increasing seed size with ovary depth.	[S4] <i>Raphanus sativus</i>
Comparison of seed siring success of different pollen donors with different S-alleles than the pollen recipient	Significant variation in seed siring success among pollen donors but which was not related to pollen performances perhaps because the latter was measured in single pollen donor crosses thus excluding pollen-pollen interactions	[S5] <i>Raphanus sativus</i>
Comparison of seed siring success of self and outcrossed pollen donors in relation with their pollen tube growth	Significant variation in seed siring success among pollen donors but that was not related to pollen performances perhaps because the latter were measured in single pollen donor crosses thus excluding the pollen-pollen interactions	[S6] <i>Echium vulgare</i>
Comparison of seed siring success after two-donor pollination; artificial selection on seed siring success	Pollen tube growth rate had a strong effect on seed siring success, which, led to an increased seed production by offspring. Artificial selection of offspring sired by superior pollen donors also resulted in reduced variation in seed production and pollen tube growth rate.	[S7] <i>Viola tricolor</i>
Comparison of seed siring success after mixed pollinations among pollen donors with high <i>versus</i> low selfing history	Significant among pollen donors variation in seed siring success which was not determined by the selfing history of pollen donors; but, pollen donors producing smaller pollen grains did sire more seeds.	[S8] <i>Pseudotsuga menziesii</i>
Comparison of seed siring success after controlled pollination with varying quantity of fertile pollen	Significant variation in paternal success between pollen donors; pollen size was positively related to faster pollen tube growth rates and greater paternal success in one of the two orchards studied.	[S9] <i>Pseudotsuga menziesii</i>
Comparison of fertilization ability and post-fertilization ability of pollen from different donors following mixed pollination	Seed siring ability was positively correlated with pollen size and larger seed abortion for ovules sired by a second pollen donor was found when the first pollen donor showed large pollen size.	[S10] <i>Erythronium grandiflorum</i>

Comparison of *in vivo* siring success between pollen expressing more than three aperture and pollen from mutant plants without aperture

Larger seed siring success of pollen possessing aperture in mixed hand-pollination with pollen expressing no aperture.

[S11] *Arabidopsis thaliana*

Table S2 Main candidate molecules produced by different sections of pistil tissues reported to be involved in the pollen-pistil molecular interactions, which may be involved in sexual selection for a putative mate choice process.

Localization	Molecule	Type of molecule	Putative function to support to microgametophytes	Some references
Stigma	S-locus Receptor Kinase (SRK), S-locus Glycoprotein (SLG)	Protein, Glycoprotein	Female determinants in sporophytic self-incompatibility in Brassicaceae	[S12,S13]
Stigma	Expansins	Protein	Cell wall remodeling facilitating pollen tube penetration	[S14,S15]
Stigma	Lipid transfer protein (Tobacco LTP2)	Protein	Facilitating pollen tube growth and cell wall loosening	[S16]
Stigma	Phytocyanin (Chemocyanins, Plantacyanins)	Protein	Pollen tube guidance and growth	[S17,S18]
Stigma	Calcium	Mineral	Spikes of calcium after adhesion, hydration and pollen germination within the papilla cell wall	[S19]
Stigma	H2O2	Reactive Oxygen Species (ROS)	Accumulation in the stigma and decrease upon pollination concomitantly with NO production by the pollen: stigma-pollen interaction	[S20, S21, S22, S23]
Stigma Style	S-RNases	Glycoprotein	Female determinant in gamatophytic Self-Incompatibility in Solanaceae	[S24]
Stigma Style	PrsS, 14kDa	Protein	Female determinant in gamatophytic Self-Incompatibility in <i>Papaver rhoeas</i>	[S25]
Stigma Style	Cell wall remodeling enzymes and Glycoside hydrolases	Protein	Pollen tube cell wall extension, softening of the stigma and transmitting tract cells for pollen penetration.	[reviewed in S26, S14]
Stigma Style	Arabinogalactan proteins (AGP) (TTS1, TTS2, NaTTS, PELPIII)	Glycoprotein	Pollen grain germination Pollen tube nutritive support and attraction Reproductive barriers (for PELPIII : Translocated from the pistil to the pollen tube callose wall to concur in pollen tube growth Essential for interspecific incompatibility	[S27, S28, S29, S30, S31, S32, S33, S34, S35]
Style	Pectin (weakly methylesterified)	Polysaccharide	Pollen tube adhesion to the stilar tissues with SCA, facilitation of pollen tube growth in <i>Lilium longiflorum</i>	[S36]
Style	Lipid Transfer Protein: Stigma/stylar Cystein-rich adhesin (SCA)	Protein	Pollen tube adhesion to the stilar tissues with pectins, facilitating pollen tube growth in <i>Lilium longiflorum</i>	[S37, S38, S39, S40]
Style	AMOR (Methyl-glucuronosyl Disaccharide		Methyl-glucuronosyl galactose renders competent pollen	[S41]

	arabinogalactan)		tube for LURE attraction in <i>Torenia fournieri</i>	
Ovary	D-serine	Amino acid	Regulate pollen tube growth via a modulation of pollen glutamate receptors-like that form calcium channels	[S42]
Ovary Ovule	Sugar transporter (AtSTP8, 12)	Protein	Ensure sugars uptake in ovules	[S43]
Integument	GABA	Amino acid	Integument pollen tube guidance	[S44]
Synergid cells	Transcription factor MYB98	Protein	Pollen tube guidance and synergid cell differentiation	[S45]
Synergid cells	T/LUREs AtLUREs	Peptide	Micropylar attraction of pollen tubes Reproductive barrier and isolation	[S46, S47]
Synergid cells	Rapid Alkalinization Factor (RALF34)	Peptide	Replace the pollen RALF4 & 19 on the receptor causing rupture of the pollen tube	[S48]
Synergid cells	Egg-apparatus-secreted polymorphic peptides (ZmEA1)	Peptide	Micropylar guidance of pollen tubes in <i>Zea mays</i> Reproductive barrier	[S49,S50]
Synergid cells	FERONIA	Protein	Receptor-like kinase required for pollen tube reception	[S51]
Synergid cells	TURAN EVAN	Protein	Uridine diphosphate (UDP)-glycosyltransferase and dolichol kinase involved in protein N-glycosylation required for pollen tube reception	[S52]
Synergid cells	LORELEI	GPI-anchored protein	Pollen tube reception	[S53]
Synergid cells	NORTIA	Protein	A mildew-resistance locus O family involved in FERONIA-dependent pollen tube reception	[S54]

Table S3 Main candidate molecules produced by the gametophytes reported to be involved in the pollen-pistil molecular interactions, which may be involved in sexual selection through male-male competition and/or female choice.

Localization	Molecule Name	Type of molecule	Putative function to support pollen germination and growth	References
Pollen grain	S-locus Cystein-Rich, S-locus protein 11 (SCR/SP11)	Protein	Male determinant in sporophytic Self-Incompatibility in Brassicaceae	[S55, S56]
Pollen grain	NO	Reactive Nitrogen Species (RNS)	NO emission by the pollen grain through apertural regions concomitantly decreasing H ₂ O ₂ levels in the stigma : stigma-pollen interaction	[S20, S21]
Pollen grain Pollen tube	Calcium	Mineral	Spike of calcium after hydration at the potential germination site and oscillation during pollen tube growth	[S19, S57]
Pollen grain Pollen tube	<i>AtABCG28</i> (ABC transporter)	Protein	ROS accumulation at the pollen tube tip. Involvement in accumulating secretory vesicles containing polyamines, precursors of ROS	[S58]
Pollen grain Pollen tube	H ₂ O ₂	Reactive Oxygen Species (ROS)	Accumulation of ROS at the site of pollen tube emergence and oscillation during pollen tube growth	[S59, S60, S61, S62]
Pollen grain Pollen tube	Putrescine, spermine, spermidine	Polyamines	Modulation of ROS homeostasis, cytoskeleton assembly and cell wall remodeling	[S63]
Pollen grain Pollen tube	<i>PrpS</i> , 20kDa	Protein	Male determinant in gamatophytic Self-Incompatibility in <i>Papaver rhoeas</i>	[S64]
Pollen grain Pollen tube	Phosphatidic acid (PA) and Phosphoinositides : PtdIns3P (Phosphatidylinositol 3-phosphate); PtdIns(3,5)P ₂ (Phosphatidylinositol 3,5-bisphosphate); PtdIns(4,5)P ₂ (Phosphatidylinositol (4,5)-bisphosphate)	Phospholipids	Membrane and vesicle components influencing the biophysical properties. Involved in lipid-mediated signaling, exocytosis, orientation of tip growth and recycling endosomes in association with exocyst complex (SEC and EXO). PtdIns(4,5)P ₂ acts upstream of ROP by promoting plasma membrane localisation of GTP-Rop	[S65, S66, S67, S68, S69]

Pollen grain Pollen tube	Serine/threonine kinase	Protein	Pollen germination and pollen tube growth	[S70]
Pollen grain Pollen tube	Rho Family small GTPase (ROP) and ROP-interactive proteins (RIP)	Protein	Marks pollen germination sites and leads the oscillatory polarized tube growth	[S71]
Pollen grain Pollen tube	Exocyst complex (SEC3A)	Protein	Fundamental role in spatial regulation of polar exocytosis. Ensure correct delivery of cell wall material during pollen germination and growth.	[S72]
Pollen grain Pollen tube	Vacuolar Protein sorting 41 (VSP41)	Protein	Mediated late stage of the endocytic pathway is essential for male–female interaction in <i>Arabidopsis</i>	[S73]
Pollen grain Pollen tube	Aquaporins: NODULIN 26-like Intrinsic Proteins (NIP4), Tonoplast Intrinsic Proteins (TIP1 & 5), Small and basic intrinsic proteins (SIP2)	Protein	Water intake channels involved in self-incompatibility response, pollen hydration, germination and pollen tube growth	[S74, S75, S76, S77, S78]
Pollen grain Pollen tube	Expansins	Protein	Remodeling proteins that soften stigma cell walls for pollen tube penetration	[S79]
Pollen grain Pollen tube	VANGUARD, PPME1, PME48	Protein	Pectin methylesterases control the cell wall plasticity and rigidity (via calcium bridging between deesterified pectins) to ensure pollen grain germination and pollen tube growth	[S80, S81, S82]
Pollen grain Pollen tube	Pectin methylesterase Inhibitors (BoPMEI1)	Protein	Regulation of Pectin methylesterase activity influencing cell wall plasticity during growth.	[S83]
Pollen grain Pollen tube	Glycoside Hydrolase	Protein	Cell wall remodeling enzymes controlling the pollen tube cell wall mechanical properties to ensure growth.	[reviewed in S26]
Pollen tube	Skp1-Cullin1-F-box protein S-locus F-box (SCF ^{SLF})	Proteins	Male determinant in gametophytic Self-Incompatibility in Solanaceae	[S84, S85]
Pollen tube	Leucine rich repeat extensins (LRX)/ RLK	Proteins	Pollen germination and pollen tube growth. Control cell wall integrity and interact with RALF	[S86, S87, S88]
Pollen tube	Rapid Alkalinization Factors (RALF4 &19)	Peptide	Regulate pollen tube cell wall integrity and growth. Interact with LRX or BUPS (Buddha’s Paper Seal)	[S86, S89, S48]

Pollen tube	Ions, small osmolytes and mechanosensitive channels	Protein	Pollen tube growth	[S90, S91, S92, S93, S94, S95, S96]
Pollen tube	Glutamate receptors-like	Protein	Form calcium channels that regulate pollen tube growth in response to D-Serine originating from the pistil	[S42]
Pollen tube	Alkaline ceramidase (TOD1)	Protein	Regulation of turgor pressures	[S97]
Pollen tube	O-fucosyltransferases (<i>AtOFT1</i>)	Protein	Facilitate penetration of pollen tubes through the stigma style interface	[S98]
Pollen tube	<i>AtLTP5</i>	Protein	Pollen tube growth	[S99]
Pollen tube	Receptor-Like Kinases (RLKs): PRK, ANXUR, MARIS, Male discoverer (MDIS), Male discoverer-interacting receptor-like kinase (MIK), Lost in pollen tube guidance (LIP), Buddha's Paper Seal (BUPS)	Protein	Pollen pistil interaction, pollen tube growth and guidance. Perception of the signaling micropylar guidance of LURE peptides or pollen and ovule RALF peptides, maintain cell wall integrity	[S100, S101, S102, S103, S104, S105, S48]
Pollen tube	TURAN	Protein	Uridine diphosphate (UDP)-glycosyltransferase involved in protein <i>N</i> -glycosylation. TURAN is involved in pollen tube integrity and targets ANXUR.	[S52]
Pollen tube	Respiratory burst oxidative homologs (NADPH oxidases)	Protein	Participate in regulating Redox signaling during polarized growth of pollen tube. Act together with Receptor like Kinase and calcium channels	[S60, S61]
Pollen tube	Sugar transporter (<i>AtSTP2</i> , 4, 6, 7, 8, 9, 10, 11, <i>CsHT1</i>)	Protein	Ensure sugars intake during pollen tube growth	[S106, S107, S43]

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