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1 **Sidestepping Darwin: horizontal gene transfer from plants to insects**

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6 **Abstract**

7 Horizontal transfer of genetic material (HT) is the passage of DNA between organisms by means other
8 than reproduction. Increasing numbers of HT are reported in insects, with bacteria, fungi, plants and
9 insects acting as the main sources of these transfers. Here, we provide a detailed account of plant-to-
10 insect HT events. At least 14 insect species belonging to 6 orders are known to have received plant
11 genetic material through HT. One of them, the whitefly *Bemisia tabaci* (MEAM1), concentrates most
12 of these transfers, with no less than 28 HT events yielding 55 plant-derived genes in this species.
13 Several plant-to-insect HT events reported so far involve gene families known to play a role in plant-
14 parasite interactions. We highlight methodological approaches that may further help characterize
15 these transfers. We argue that plant-to-insect HT is likely more frequent than currently appreciated
16 and that in-depth studies of these transfers will shed new light on plant-insect interactions.

17

18 **Highlights**

- 19
- Recent HGT detection workflows enable large-scale studies of HGT among eukaryotes
 - At least 14 insect species belonging to 6 orders contain plant-derived genes
 - Many plant-derived genes have putative functions involved in plant-parasite interactions
 - The impact of plant-to-insect HGT on insect evolution remains to be characterized
- 20
21
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23

24 Introduction

25 Darwin proposed that evolution occurs through natural selection of intraspecific variations transmitted
26 across generations [1]. But he was unable to provide a satisfactory explanation for the origin of these
27 variations and the mechanism underlying their transmission. Darwin and Mendel were
28 contemporaries, but they never met and Mendel's work was ignored by Darwin [2]. About 50 years
29 after Darwin and Mendel died, Darwin's natural selection and Mendelian inheritance, which posits that
30 individuals inherit a combination of alleles from their parents, became two pillars of the modern
31 synthesis. Remarkably, observations made in bacteria as early as 1928 – *i.e.*, before the modern
32 synthesis was initiated – suggested that genetic information could also be transmitted between
33 individuals through horizontal transfer (HT), *i.e.*, through means other than vertical, parent-to-
34 offspring, inheritance [3]. In the second half of the 20^{ie}th century it became apparent that HT of genes
35 was rampant in prokaryotes and that it was a major source of bacterial innovation [4]. The first hint
36 that HT of genetic material was not restricted to prokaryotes but could also occur in eukaryotes may
37 correspond to the discovery of endogenous retroviruses in vertebrate genomes during the late 1960s
38 and early 1970s [5]. It was then suggested that the endosymbiotic origin of eukaryotes was
39 accompanied by the relocation (through HT) of many organellar genes to the nuclear genome [6], and
40 that transposable elements (TEs) [7,8], as well as non-organellar genes [9,10] could be acquired
41 horizontally in these taxa. These pioneering works were followed by the observation that the genome
42 of phagotrophic single-cell eukaryotes contained many genes captured from their prokaryote and
43 microbial eukaryote preys [11–13]. Today, the importance of HT of genes in recent eukaryote evolution
44 remains a matter of debate [14–18]. But as a matter of fact, we are witnessing an increasing number
45 of HT reports in both uni- and multi-cellular eukaryotes, largely fueled by the many high-quality new
46 whole genome sequences that are deposited on a daily basis in public databases [19–24]. Importantly,
47 many of these transfers likely facilitated the adaptation of the receiving species to a new ecological
48 niche [25–27]. In multicellular eukaryotes, most HT of genes reported so far involve genes of bacterial,
49 fungi, or viral origin [23,25,28–31]. Aside from HT of TEs which are not rare [32], relatively few HT of
50 genes between multicellular eukaryotes have so far been uncovered. This trend is seemingly changing
51 in plants, in which numerous recent cases of plant-to-plant HT have been characterized [33–36]. In
52 vertebrates, a single such event is known so far, which involves transfer of a gene coding an antifreeze
53 protein between the Atlantic herring and the rainbow smelt [37]. Here, we provide a comprehensive
54 account of another type of eukaryote-to-eukaryote HT, namely plant-to-insect HT, highlight
55 methodological challenges inherent to the detection of such transfers, and discuss the possible
56 mechanisms underlying these HT as well as their impact on insect genome evolution and plant insect
57 interactions.

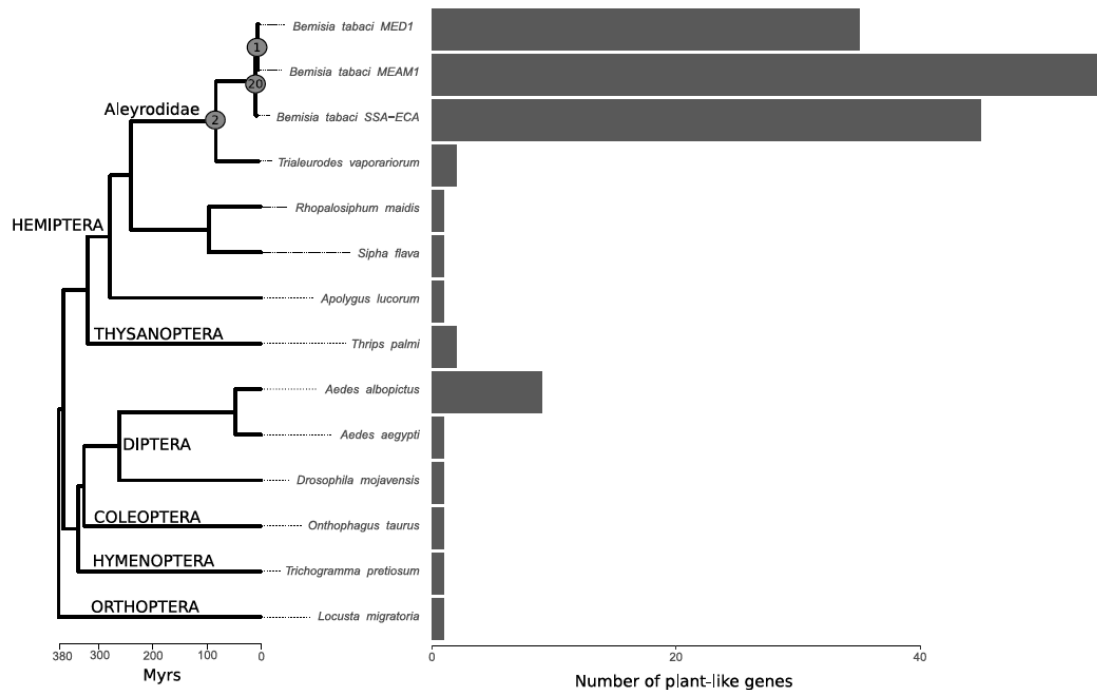
58 **How many genes of plant origin in insect genomes?**

59 The first claim of plant-to-insect HT was published in a 2015 article in which hundreds of transcripts
60 from the mosquito *Anopheles culicifacies* were reported to encode proteins 100% identical to proteins
61 found in plants [38]. However, using plant proteins listed in supplementary table 1 of Sharma et al.,
62 (2015) [38], we were unable to recover plant-derived genes in the genome of *A. culicifacies*, which is
63 now available in Genbank (accession number: AXCM00000000.1). Two cases of TE transfer between
64 plants and arthropods have been described but in both studies, HT was deemed more likely to have
65 occurred from arthropod to plants rather than in the opposite direction [39,40]. The first robust case
66 of plant-to-insect HT is thus the one reported in Lapadula et al., (2020) [41], in which a gene of plant
67 origin encoding a ribosome inactivating protein (RIP) has been acquired at least 80 million years ago
68 by an ancestor of two whitefly species (*Bemisia tabaci* and *Trialeurodes vaporariorum*). Whiteflies
69 (family Aleyrodidae; Hemiptera) are important agricultural pests as they are able to feed upon a large
70 spectrum of host plants and they can transmit many viruses to plants [42]. After transfer from an
71 unknown plant donor, the RIP gene was duplicated once and twice in the lineage leading to *B. tabaci*
72 and *T. vaporariorum*, respectively. Quickly following this report, two other plant-derived genes
73 encoding BAHD acyltransferases were characterized, again in the whitefly *B. tabaci* [43].

74 These studies prompted us to perform a systematic search for plant-to-*B. tabaci* HT, which yielded no
75 less than 49 plant-derived genes in the genome of the Middle East Asia Minor 1 (MEAM1) whitefly
76 [44]. We found that these genes could be clustered in 24 orthogroups, 20 of which have members in
77 another whitefly cryptic species (Sub-Saharan Africa - East and Central Africa [SSA-ECA]), which
78 diverged at least five MYA from the MEAM1 whitefly [45]. We uncovered another two plant-derived
79 genes in *T. vaporariorum*, which diverged several dozens of MYA from *B. tabaci* [46], but we were
80 unable to firmly conclude on whether these genes were acquired from plants independently in this
81 species or whether they were transferred in an ancestor of *B. tabaci* and *T. vaporariorum*.

82 In parallel to our study, a large-scale, systematic survey of HT performed by Li et al. (2022) [31] in 218
83 insect species uncovered no less than 1410 foreign genes. While the vast majority of these genes have
84 a bacterial source, many were transferred from fungi and viruses and a total of 43 were assigned a
85 plant origin. Just by itself, *B. tabaci* accounts for 24 of these 43 genes, most of them being also
86 reported in our study (see next section). The reason why *B. tabaci* has a much higher number of plant-
87 derived genes than other insects is not immediately evident but we note that this species also has a
88 higher number of genes transferred from bacteria and the higher overall number of horizontally
89 acquired genes (170 versus 68 in *Contarinia nasturtii*, the species with the second higher number of
90 foreign genes). Whether horizontal gene flux is higher in *B. tabaci* or whether it is similar to other

91 insects but foreign genes have a higher chance to be retained in *B. tabaci* remains to be assessed.
 92 Interestingly, Li et al. (2022) [31] also uncovered plant-derived genes in three other species of
 93 Hemiptera, one Coleoptera, three Diptera, one Hymenoptera, one Orthoptera and two Thysanoptera.
 94 In total, and accounting for the redundancy between our results [44] and those of Li et al. (2022) [31]
 95 for *B. tabaci*, a total of 156 genes of plant origin have been so far uncovered in the genome of 14 insect
 96 species belonging to six orders (Figure 1). It is noteworthy that nine plant-derived genes are annotated
 97 as plant transposons in *Aedes* mosquitoes [31], begging the question of whether these genes
 98 correspond to recently acquired TEs that may still be able to transpose or whether they arise from
 99 molecular domestication of ancient plant TEs horizontally acquired by an ancestor of *Aedes*
 100 mosquitoes.



101
 102 **Figure 1. Number of plant-derived genes identified in insect genomes.** The number of plant-derived
 103 genes in *Bemisia tabaci* MEAM1 results from our merging of results from [31] and [44]. Details
 104 regarding which genes were found in which study and on the predicted function of these genes are
 105 given in Supplementary Table 1. The tree and divergence times were taken from REF. 46 and 79.
 106 Numbers at nodes in Aleyrodidae correspond to putative numbers of horizontal transfer events that
 107 took place in the ancestors of Aleyrodidae, as inferred in [44] based on the delineation of orthogroups.
 108 Nine of the plant-derived genes from *Aedes* mosquitoes are annotated as encoding plant transposon
 109 proteins in supplementary table 2 of [31].

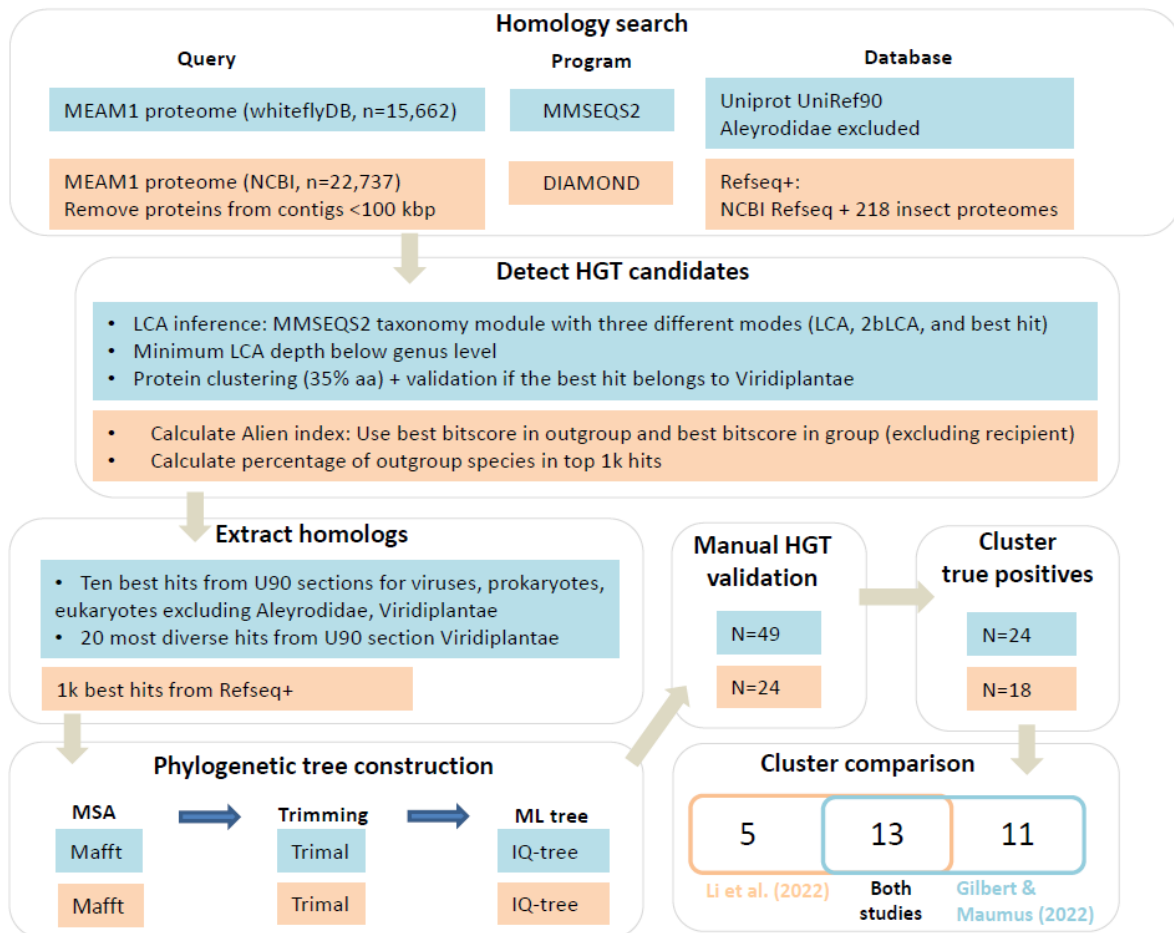
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111 **Methodological challenges to detect horizontal gene transfer**

112 Inferences of HGT are plagued by methodological issues and several hypotheses alternative to HGT
113 must be considered before HGT is favored [44,47,48]. It is for example essential to check that what
114 looks like a horizontally acquired gene is not instead a contaminant. This may be done using fluorescent
115 *in situ* hybridization, as in Dunning Hotopp et al. (2007) [49] or PCR as in Li et al. (2022) [31]. Another
116 way to discard the possibility of contamination is to find orthologs of horizontally acquired genes in a
117 group of species, the genome assembly of which were produced independently in different labs. Other
118 recommendations on HGT validation have been discussed in previous papers [44,47,48,50]. Yet, even
119 when greatest care is taken, large-scale studies of HGT may yield different results due to differences
120 in the bioinformatics approach being implemented. This is particularly well-illustrated by the two
121 recent reports of HGT from plants in *B. tabaci* (MEAM1) [31,44]. Both studies used overall similar
122 workflows, being based on sequence similarity search between *B. tabaci* query proteins and a target
123 database followed by the analysis of the taxonomic distribution of hits to identify candidate HT
124 proteins. Homologs of each candidate were then retrieved and used to build phylogenetic trees that
125 were manually examined for HGT validation. However, the two workflows present key differences
126 (Figure 2). First, they rely on different target databases. Li et al. (2022) [31] used Refseq proteins from
127 NCBI (approx. 240 million proteins as of September 2022,
128 <https://www.ncbi.nlm.nih.gov/refseq/statistics/>) combined with the proteomes from the 218 insects
129 they studied. Instead, Gilbert & Maumus (2022) [44] used UniRef90 from Uniprot
130 (<https://www.ebi.ac.uk/uniprot/TrEMBLstats>), which is composed of representative proteins from
131 UniRef100 clustered at 90% (152 million proteins as of November 2022 being representative of 318
132 millions).

133 Furthermore, the two studies differ in how they call HGT candidates from the result of similarity
134 searches. In Li et al. (2022) [31], an « alien index » (AI) is calculated, which was first introduced in
135 Koutsovoulos et al. (2022) [51], and broadly used to select HGT candidates [e.g. 50]. The AI, computed
136 for each HGT candidate, measures the extent to which the best hit against targets from the query
137 taxonomic group (ingroups) differs from that obtained against targets from other groups (outgroups).
138 To limit the number of false positives, Li et al. (2022) [31] also calculated the percentage of outgroup
139 species among the top hits. This percentage will be low if the homolog is not conserved in outgroups
140 or if the gene family is comparably distant to homologs across several taxa. By contrast, Gilbert &
141 Maumus (2022) [44] have used an original approach in which the UniRef90 target database is depleted
142 of ingroup proteins (here Aleyrodidae) to infer the last common ancestor (LCA) of each query protein.
143 Using this taxonomic exclusion, the placement of a protein LCA in Viridiplantae (plants) occurs when a
144 significant proportion of its best homologs are plant proteins, suggesting a plant origin. The study

145 applied three different modes of LCA inference implemented in the taxonomy module of the MMseqs2
 146 program [52], in which the taxonomical assignment of the LCA can be inferred using two methods
 147 derived from the 2bLCA protocol [53] or using lowest common ancestor of equal-scoring top hits (this
 148 last mode being theoretically similar to AI-based measures). To focus on most robust HGT candidates,
 149 only the proteins with LCA in Viridiplantae below the genus level were considered as a filter attesting
 150 for their conservation in plants.



151

152 **Figure 2. Graphical comparison of the HT detection workflows used in Li et al. (2022) [31] and Gilbert**
 153 **& Maumus (2022) [44].** The main steps of the workflows are separated in grey boxes and the methods
 154 used at each step by REF. 31 and REF. 44 are indicated in salmon and blue rectangles, respectively.

155

156 Using deep protein clustering (35% identity), Gilbert & Maumus (2022) [44] found that the 49 plant-
 157 derived proteins from *B. tabaci* MEAM1 correspond to 24 clusters. Here, we applied the same
 158 clustering to the 24 plant-derived proteins from Li et al. (2022) [31], which resulted in 18 clusters. We
 159 found that only 13 clusters comprise proteins from the two studies while 11 and 5 are unique to REF.
 160 44 or REF. 31, respectively (Figure 2 and Supplementary Table 1). One cluster unique to REF. 31

161 comprises two genes (XP_018917389.1 and XP_018909952.1) for which we could not confirm plant
162 origin. Two other clusters unique to REF. 31 have no homolog in the MEAM1 proteome used in REF.
163 44. This comparison shows that the HT detection workflow we used in REF. 44 is more sensitive, but it
164 is not entirely comprehensive. Understanding the causes of reciprocal false negatives will help
165 improving the sensitivity of HT detection. This comparison also shows that the number of insect HGT
166 reported in REF. 31 may be largely underestimated and that HGT, including from plants, may have had
167 an even stronger impact on insects than what is apparent from this study.

168 **Functional impact of plant genes in insects**

169 Only one experimental study characterized the function of a plant-derived gene in insect [43]. Together
170 with the predicted function of all plant-derived genes in *B. tabaci*, it suggests that much like bacteria-
171 to-insect HGT [54], plant-to-insect HGT was a source of important new functions to insects, which may
172 have facilitated adaptation to their environment. REF. 43 showed that the protein encoded by the
173 *BtPMat1* plant-derived gene in *B. tabaci* has malonyl-transferase activity, that is, it catalyzes the
174 transfer of a malonyl group onto several phenolic glucosides, which are secondary compounds
175 produced by many plants to defend themselves against herbivorous insects. Malonylation detoxifies
176 phenolic glucosides and renders them harmless to whiteflies. In agreement with this, whiteflies feeding
177 on transgenic tomato plants that express small interfering RNAs targeting *BtPMat1* are unable to
178 survive [43]. Thus, whiteflies harnessed a plant gene which allows them to thwart plant defenses and
179 was perhaps essential in the evolution of these hemipterans towards becoming generalist herbivores
180 [43,55].

181 In addition to this functional study, indirect evidence including evolution under purifying selection and
182 expression suggests that most if not all other plant-derived genes in *B. tabaci* encode important
183 functions [41,44]. To help explore these putative functions, we provide a table compiling predicted
184 functions of all *B. tabaci* plant-derived proteins reported in Li et al. (2022) [31] and Gilbert & Maumus
185 [44] (Supplementary Table 1). Several of these proteins have predicted functions previously shown to
186 play a role in plant-parasite interactions and response to pathogens, not necessarily insects but rather
187 fungi and oomycetes. It remains unclear however if and how these genes enabled whiteflies to adapt
188 to different host plants. The protein functions inferred are based on the annotation of homologs and
189 only speculative. Only three plant-derived gene clusters have a potentially evident role in helping the
190 insect bypassing host defenses. These include *BtPMat1* [43] as well as a predicted plant cell wall
191 degrading enzyme (PCWDE) and a predicted alpha-(1,4)-fucosyltransferase which could be involved in
192 cell wall patterning [56]. Perhaps more surprisingly, many plant-derived genes have putative functions
193 linked to the production and activation of plant defenses. For instance, plant-derived genes annotated

194 as BAHD acyltransferase and phenylalanine ammonialyase have putative functions in the production
195 of phenolic secondary metabolites [57], many being defense compounds. That said, the *B. tabaci* plant-
196 derived BAHD acyltransferase has best BLAST hits against Dcr-like (Defective in Cuticular Ridges)
197 homologs. Dcr is not involved in production of phenolic compounds but is instead required for the
198 assembly of cutin polymers, which are the major components of the outermost layer of plant defense,
199 the cuticle [58,59]. The whitefly plant-derived genes also comprise homologs of pathogen-related
200 proteins (which are produced by plants upon biotic attack) and proteins that have known roles in plants
201 in pathogen recognition and/or defense signaling pathways including Thaumatin [60], subtilisin-like
202 protease [61] or glucan endo-1,3-beta-glucosidase [62]. An advantage to herbivory could generally
203 make sense if the encoded proteins are inactive and simply tether plant enzymes or occupy receptors
204 to limit the defense response. It is also possible that some plant-derived genes may be recycled by
205 insects to protect themselves against pathogens, parasites or predators. In agreement with this
206 scenario, the RIP genes reported in REF. 41 are toxic N-glycosidases playing a role in plant defense
207 against pathogens and insect predators [63]. As pointed out by Lapadula et al., the whitefly RIPs might
208 play a role similar to those produced by *Spiroplasma* endosymbionts in *Drosophila*, known to protect
209 their host against nematodes [64] and parasitic wasps [65].

210 Other plant-derived genes in *B. tabaci* may have predicted functions in nutrient and micronutrient
211 assimilation, glycoprotein secondary modifications, and fatty-acid desaturation including a large family
212 of delta(12) fatty acid desaturases (Supplementary Table 1). It will be interesting to develop
213 experimental approaches to characterize these genes and how they may have been beneficial to
214 whiteflies compared to genes acquired from bacteria [54]. In this context, testing the function of the
215 *B. tabaci* plant-derived pectinesterase should be relatively straightforward as it has a clear predictable
216 function in degrading plant cell walls. It would also be worth addressing whether the catalytic sites in
217 predicted plant-derived enzymes are conserved to assess their catalytic potential and which plant-
218 derived genes are specifically expressed in the insect saliva or gut to suggest a direct link with
219 herbivory.

220 **How can plant DNA be transferred to insects?**

221 The mechanisms underlying HT in eukaryotes remain poorly understood. That most foreign genes so
222 far reported in eukaryotes are from prokaryotes (this is especially true for insects [31,66]) may in part
223 be due to the capacity of several bacteria to transfer their DNA to eukaryotic cells through conjugation
224 [67]. Furthermore, many arthropod and other metazoan species harbor obligate or facultative
225 intracellular symbionts [68], some of which are in close contact with the host germline genome,
226 facilitating HT [30]. The higher proportion of foreign prokaryotic versus eukaryotic genes so far

227 uncovered in eukaryote genomes may also have methodological underpinnings. Transfers are easier
228 to infer between distantly related species (*e.g.* between prokaryotes and eukaryotes) than between
229 more closely related ones (*e.g.* between two eukaryotes). Systematic studies focusing on detecting
230 eukaryote-to-eukaryote HT remain scarce. In any case, this later type of transfer is more difficult to
231 explain than prokaryote-to-eukaryote transfers because no mechanism dedicated to HT is known in
232 eukaryotes (but see [69]). Plant-to-plant HTs have been proposed to occur accidentally through whole
233 genome transfer in heterospecific grafts [70], illegitimate pollination, haustoria in parasitic plants [71],
234 or root-to-rhizome contact [33]. Regarding plant-to-insect transfers, one might argue that the close
235 ecological interactions existing between plants and most insects facilitate HT. Indeed, all insect species
236 in which plant-derived genes have been found so far (Figure 1) are herbivorous or nectarivores.
237 Whether DNA can be transferred from plants to insects through feeding, as proposed in the case of
238 bacteria-to-single cell eukaryotes HT [11] remains to be tested. In this context, it is noteworthy that
239 insects can internalize dsRNA produced by plants through feeding [43,72], so one could speculate that
240 DNA from their food may also occasionally penetrate into insect cells. However, the « you are what
241 you eat » hypothesis may not be fully sufficient to explain plant-to-insect HT as the majority of
242 herbivorous insects included in REF. 31 are devoid of plant-derived genes. Another, non-mutually
243 exclusive hypothesis is that vectors such as exosomes or viruses are involved in plant-to-insect HT
244 [73,74]. If true, the known exposure of *B. tabaci* to a very large diversity of plant viruses, several of
245 which are known to replicate in whitefly cells [75], may in part explain the higher number of foreign
246 genes found in this, compared to other insect species [31,44]. In this context, it is noteworthy that
247 whiteflies are the main insect vectors of dozens of Begomovirus species, which are highly successful
248 plant viruses. Some of these circular single-stranded DNA viruses are able to replicate in insect cells,
249 persist during the entire lifetime in the insect and can undergo transovarial transmission [76].
250 Acquisition of foreign genes by *B. tabaci* under the form of DNA, rather than RNA, through the
251 intermediate of DNA viruses is consistent with the fact that most plant-like genes uncovered in
252 whiteflies contain at least one intron [44]. However, it is also possible that these genes were
253 transferred through an RNA-mediated mechanism and later acquired introns once in the *B. tabaci*
254 genome.

255 **Conclusions and outstanding questions**

256 The first plant-to-insect HGT was reported recently [41] and since then 156 plant-derived genes have
257 been found in 14 insect species from six orders. The reasons why the whitefly *B. tabaci* concentrates
258 most of these genes, as well as most non-plant foreign genes among insects, are unknown. Based on
259 a comparison between two recent studies [31,44], we contend that the number of horizontally
260 acquired genes in insects, including those acquired from plants, is likely strongly underestimated. In

261 addition to improve current HGT pipelines that rely on the use of annotated protein-coding sequences,
262 it would be interesting to perform more comprehensive HGT searches using whole genomes. This
263 would allow assessing whether the currently observed higher number of horizontally acquired plant
264 genes versus plant TEs in insect genomes has biological underpinnings or is merely due to
265 methodological limitations. Should the current trend hold, it would be in striking contrast with the
266 trend observed for insect-to-insect HTs, as most if not all currently known such events involve TEs and
267 not genes [77]. Future large-scale examination of plant-to-insect HGT may also shed light on the factors
268 possibly influencing such transfers and on whether some plant and/or insect life history traits correlate
269 with HT numbers. Of particular relevance will be to identify recent plant-to-insect HGT events, as this
270 may help identifying donor plants species and the mechanisms underlying transfer. A deeper
271 understanding of the impact of plant-to-insect HGT will only be reachable through multiple functional
272 studies of insect plant-derived genes, such as the one performed in REF. 43. In addition to help
273 decipher the intricacy of plant-insect interactions, such studies have the potential to unveil new targets
274 for controlling insect pests, which may in some contexts be less problematic than pesticide-based
275 strategies [78].

276

277

278 **Legends of additional elements**

279 **Supplementary Table 1. Annotation of MEAM1 plant-derived proteins found in REF. 31 and REF. 44.**

280 The alternating shades of grey distinguish the clusters established at 35% amino-acid sequence identity
281 using MMseqs2. The false positive cluster from Li et al. (2022) is not indicated. The Genbank protein
282 identifiers begin with "XP" while the WhiteflyDB identifiers begin with "Bta". The annotations
283 correspond to the transfer of annotations of the best hits obtained by BLAST against Genbank. The
284 functional category and putative function are only speculative.

285

286 **Acknowledgements**

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325

326

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