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**Most diverse, most neglected: weevils (Coleoptera: Curculionoidea) are ubiquitous specialized brood-site pollinators of tropical flora**

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31 **Abstract**

32 In tropical environments, and especially tropical rainforests, a major part of pollination services  
33 is provided by diverse insect lineages. Unbeknownst to most, beetles, and more specifically  
34 hyperdiverse weevils (Coleoptera: Curculionoidea), play a substantial role there as specialist  
35 mutualist brood pollinators. The latter contrasts with a common view where they are only  
36 regarded as plant antagonists. This study aims at giving a comprehensive understanding of  
37 what is known on plant-weevil brood-site mutualistic interactions, through a review of the  
38 known behavioral, morphological and physiological features found in these systems, and the  
39 identification of potential knowledge gaps to fill. To date, plant-weevil associations have been  
40 described or indicated in no less than 600 instances. Representatives of major plant lineages  
41 are involved in these interactions, which have emerged independently at least a dozen times.  
42 Strikingly, these mutualistic interactions are associated with a range of convergent traits in  
43 plants and weevils. Plants engaged in weevil-mediated pollination are generally of typical  
44 cantharophilous type exhibiting large, white and fragrant flowers or inflorescences and they  
45 also show specific structures to host the larval stages of their specialist pollinators. Another  
46 characteristic feature is that flowers often perform thermogenesis and exhibit a range of  
47 strategies to separate sexual phases, either spatially or temporally. Conversely, lineages of  
48 brood-site weevil pollinators present numerous shared behavioral and physiological traits, and  
49 often form multispecific assemblages of closely related species on a single host; recent studies  
50 also revealed that they generally display a high degree of phylogenetic niche conservatism.  
51 This pollination mutualism occurs in all tropical regions, and the contrasts between the known  
52 and expected diversity of these systems suggests that a wide range of interactions remain to  
53 be described globally. Our early estimates of the species richness of the corresponding weevil  
54 clades and the marked pattern of phylogenetic niche conservatism of host use further suggest  
55 that weevil-based pollination far exceeds the diversity of other brood-site mutualistic systems,  
56 which are generally restricted to one or a few groups of plants. As such, weevil pollinators  
57 constitute a relevant model to explore the emergence and evolution of specialized brood-site  
58 pollination systems in the tropics.

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61 **Keywords**

62 Cantharophily, entomophily, mutualism, nursery pollination, plant-insect interactions, tropical  
63 rainforests

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## 102 Introduction

103 Most of the extant biodiversity in tropical regions is concentrated in tropical rainforests, which  
104 were the first biomes to be coined as 'biodiversity hotspots' (Myers 1988). The outstanding  
105 diversity of pollinating systems in these ecosystems offers unique opportunities to study the  
106 evolution of reciprocally beneficial interactions among organisms. Pollination ecology in  
107 tropical rainforests indeed presents unique characteristics due to specific constraints. For  
108 instance, anemophily (wind pollination) is considered to be infrequent and potentially limited  
109 because of a combination of marked spatial constraints (evergreen canopy, structural  
110 heterogeneity and complexity) associated with frequent periods of high rainfall preventing  
111 pollen dispersal (Regal 1982; Williams & Adam 1994). Anemophilous plants are also  
112 presumably disadvantaged whenever they are over-dispersed (Regal 1982; see also below).  
113 Hence, pollination by animal vectors is predominant and can concern up to 100% of the plant  
114 species in some tropical rainforests (Bawa 1990; Ollerton et al. 2011; Rech et al. 2016). The  
115 high level of plant diversity that characterizes tropical rainforests is also associated with a  
116 spatial trend where the distribution of conspecific individuals is usually patchy (Bawa 1990;  
117 Williams & Adam 1994). The latter limits the efficiency of generalist pollinators, as they are not  
118 constrained to actively seeking out specific plants (Whitehead 1968; Bawa 1990; but see  
119 Wolowski et al. 2014). To cope with these major constraints, the reliance on more intricate  
120 pollination mechanisms, involving specialist pollinators (especially insects), is a hallmark of  
121 tropical rainforests (Bawa 1990; Renner & Feil 1993; Vizentin-Bugoni et al. 2018) and also  
122 widespread in all tropical or subtropical biomes (e.g., Gottsberger 1986; Ramirez 2004;  
123 Maruyama et al. 2013; Guy et al. 2021).

124 A mode of specialized pollination that particularly stands out is brood-site pollination  
125 (or nursery pollination; hereafter called BSPM for brood-site pollination mutualism), a system  
126 where immature stages of a pollinator develop within tissues (either flowers, ovules or pollen;  
127 Sakai 2002) of a plant as a reward for its pollination. It has independently evolved several  
128 times, mostly in tropical and subtropical biomes (Sakai 2002; Dufaÿ & Anstett 2003). These  
129 specialized mutualistic systems have been unequivocally documented in at least a dozen plant  
130 families and five insect orders (Coleoptera, Diptera, Hymenoptera, Lepidoptera and  
131 Thysanoptera) (Sakai 2002; Dufaÿ & Anstett 2003; Kawakita & Kato 2009; Hembry & Althoff  
132 2016). Textbook examples of brood-site pollination are traditionally exemplified by the highly  
133 specialized fig/fig-wasp and yucca/yucca-moth models (Janzen 1979; Wiebes 1979; Pellmyr  
134 2003; Herre et al. 2008); studies on these models have yielded important discoveries on the  
135 origin and maintenance of mutualisms and on the degree of co-evolution, with obligatory  
136 interactions possibly leading to evolutionary co-diversifications (e.g., Hembry & Althoff 2016).  
137 However, the number of insect and plant lineages engaging in brood-site pollination likely goes  
138 well beyond the few iconic interactions typically studied. Here we advocate the need to  
139 consider other systems to obtain a broader and more complete view of the ecology and  
140 evolution of biological interactions in general, and pollination in particular.

141 Among the neglected insect lineages involved in BSPM, the weevils (Coleoptera:  
142 Curculionoidea) are probably the most overlooked. Weevils contain over 62,000 described  
143 species and a colossal amount of unknown diversity (Oberprieler et al. 2007). This clade of  
144 beetle is exclusively phytophagous and is the most speciose lineage of phytophagous insects,  
145 usually only depicted as antagonistic to plants (Anderson 1995). Indeed, brood-site pollination

146 by weevils is generally considered anecdotal and is often overlooked in reviews on brood-site  
147 pollination (Dufayé et al. 2003; Hembry & Althoff 2016; Toon et al. 2020). Weevils are not even  
148 mentioned as one of the most relevant groups of beetle pollinators in some studies (e.g.,  
149 Kevan & Baker 1983; Wardhaugh 2015; IPBES 2016). However, in recent decades, a number  
150 of plant-weevil interactions involving brood-site pollination have been progressively  
151 documented and described in detail (Franz & Valente 2005, Caldara et al. 2014; Nunes et al.  
152 2018; de Medeiros et al. 2019; Saunders 2020; Toon et al. 2020). Moreover, recent plant-  
153 focused studies on tropical pollinators have recovered weevils as one of the most important  
154 pollinator groups (Krimse & Chaboo 2020; Paz et al. 2021). Taken altogether, all these studies  
155 suggest that these associations may be more widespread than previously thought (Caldara et  
156 al. 2014); it also contradicts the common view that weevils are not pollinators, and suggests  
157 that much of the global insect pollinator diversity is currently left unnoticed. For example, the  
158 combined species diversity of the three weevil families containing brood-site pollinator  
159 lineages (ca. 350, 4400 and 51,000 species, for Belidae, Brentidae and Curculionidae,  
160 respectively; Marvaldi & Ferrer 2014; Oberprieler 2014a, 2014b) is at least twice as large as  
161 the diversity of bees (ca. 20,000 species; Zattara & Aizen 2021), which are usually considered  
162 to be the most important group of insect pollinators (Potts et al. 2016). As we detail in this  
163 review, multiple and diverse weevil lineages commonly visit flowers, and an ever-increasing  
164 number of them can be considered true pollinators. This broad reassessment of the potential  
165 role of weevils as pollinators is highly relevant for the understanding of ecosystem functioning  
166 (including for agroecosystems), especially in tropical regions where bees are much less  
167 diverse than weevils (Oberprieler et al. 2007; Orr et al. 2021; Freitas et al. 2022).

168 The aim of this review is to provide a synthetic overview of all plant-weevil brood-site  
169 pollination mutualisms described to date. We begin by aggregating available data about weevil  
170 flower visitors and detail the extent of plant and weevil lineages known to be engaged in such  
171 interactions. We further summarize known reciprocal adaptations or traits and evolutionary  
172 trends to highlight both common patterns and specificities within these interactions. Finally,  
173 we investigate possible reasons why weevils have been previously overlooked in the  
174 pollination literature, estimate the extent of potential undescribed interactions, and conclude  
175 with a road map for future research on plant-weevil pollination mutualisms.

## 176 1. A wide spectrum of mutualistic interactions

177 Weevils are the most diverse group of insects that visit flowers and develop in reproductive  
178 structures (Oberprieler et al. 2007; Kirmse & Chaboo 2020). This close interaction with the  
179 reproductive structures of plants probably preceded the colonization and diversification of  
180 weevils on angiosperms. The oldest weevil fossils (such as †*Belonotaris punctatissimus*) were  
181 found in the Karabastau Formation (ranging from the Oxfordian to Callovian stages, 166.1 to  
182 157.3 million years ago (Mya); Walker et al. 2018); at that time they were likely associated  
183 with gymnosperm-dominated floras (e.g., see Oberprieler & Oberprieler 2012 for slightly  
184 younger weevil fossils from the Tithonian stage, 150.8 to 145.5 Mya). Their origin therefore  
185 clearly predates the rise to dominance of angiosperms during the Cretaceous Terrestrial  
186 Revolution, from 125 to 80 Mya (Dilcher 2000; Magallón & Castillo 2009; Benton 2010). In  
187 addition, several early diverging weevil lineages, such as Caridae or Nemonychidae, typically  
188 breed on gymnosperm male or female reproductive structures (Oberprieler et al. 2007).  
189 Associations with angiosperm flowers and seeds evolved both within these early-diverging

190 lineages (Ferrer et al. 2011; Kuschel & Leschen 2011) but also in more derived lineages  
191 belonging to the two most speciose weevil families (Brentidae and Curculionidae). Weevils in  
192 these clades generally visit flowers when feeding on pollen and ovipositing in buds, ovaries  
193 and fruits where larval development occurs (Oberprieler et al. 2007; Caldara et al. 2014).  
194 When adults fly between flowers to mate or oviposit on one or on a fairly narrow range of  
195 hosts, they can carry pollen between conspecific plant species, thereby pollinating them.  
196 Therefore, the flower-visiting and plant oviposition behaviors of several weevil lineages create  
197 the context for the evolution of BSPM from antagonistic to mutualistic interactions, or  
198 conversely (Figure 1). Interestingly, the ever-growing body of accumulated knowledge on  
199 plant-weevil interactions suggests that increasingly diverse and complex specialized plant-  
200 weevil BSPM interactions are to be expected (Franz & Valente 2005; Franz 2006; Saunders  
201 2020; Toon et al. 2020).

202 The first report of weevil pollination activity refers to a palm-weevil interaction and  
203 dates back to the 19<sup>th</sup> century (Von Martius 1823). Since then, most efforts to describe and  
204 document weevil pollination have focused on palm-weevil and cycad-weevil mutualisms  
205 (Franz & Valente 2005; Toon et al. 2020). This focus on cycads and palms can be explained  
206 by their characteristic conspicuous inflorescences which attract massive gatherings of weevils,  
207 so much so that they have triggered specific research. To date, weevil BSPM has been  
208 reported for at least 87 palm species (Arecaceae) belonging to 26 genera (Table 1). Weevils  
209 pollinating palms consist of about 200 species from 17 genera, mostly belonging to the  
210 pantropical tribes Acalyptini and Derelomini (Curculionidae: Curculioninae) *sensu* Caldara et  
211 al. (2014), hereafter called Derelomini or derelomine weevils; see also Franz (2006) and  
212 Alonso-Zarazaga (2007) for nomenclatural uncertainties. Among the cycads, weevil BSPM  
213 has been reported for 91 cycad species belonging to seven genera from all three extant cycad  
214 families (Cycadaceae, Stangeriaceae and Zamiaceae). Weevils pollinating cycads belong to  
215 a diverse range of lineages; they are predominantly found within Curculioninae and Molytinae  
216 among the Curculionidae (ca. 50 species in six Paleotropical genera), but also within Belidae  
217 (24 species in six Neotropical genera) and Brentidae (12 species in two Afrotropical genera).

218 The study of these interactions, their mechanisms and their patterns of associations  
219 with palms and cycads has stimulated the discovery of similar cases among several monocot  
220 families of angiosperms. For instance, in Neotropical *Anthurium* (Araceae), 10 species are  
221 engaged in BSPM with *Cyclanthura* weevils (Derelomini, seven species; Franz 2003, 2006).  
222 In the same region, 34 species from eight genera of cyclanths (Cyclanthaceae) are pollinated  
223 by 27 weevil species belonging to six genera of Derelomini (Franz 2007a, 2008). In  
224 Neotropical Orchidaceae, three weevil species belonging to two genera of Baridinae  
225 (Curculionidae, alternatively classified as the supertribe Bariditae among Conoderinae)  
226 ensure their pollination (Nunes et al. 2018). More anecdotally, *Strelitzia nicolai* (Strelitziaceae)  
227 from southern Africa appears to be co-pollinated by two derelomine species belonging to two  
228 distinct genera (Haran et al. 2022a; Haran unpublished). Importantly, the majority of weevils  
229 engaged in BSPM show a marked pattern of phylogenetic niche conservatism (PNC) at the  
230 genus level (Table 1, Table S1 & Appendix 1; Franz & Valente 2005; Toon et al. 2020; Haran  
231 et al. 2021, 2022b, see section 2.3.5 for details). Such a pattern is far from unusual among  
232 groups of internal feeding insects, such as seed beetles (Kergoat et al. 2007, 2015) or noctuid  
233 stem borers (Kergoat et al. 2018). Therefore, we postulate that, in the absence of direct  
234 experimental evidence for a weevil species, knowledge about other species in a genus may  
235 provide an indication of pollination activity. This generalization can produce hypotheses to be



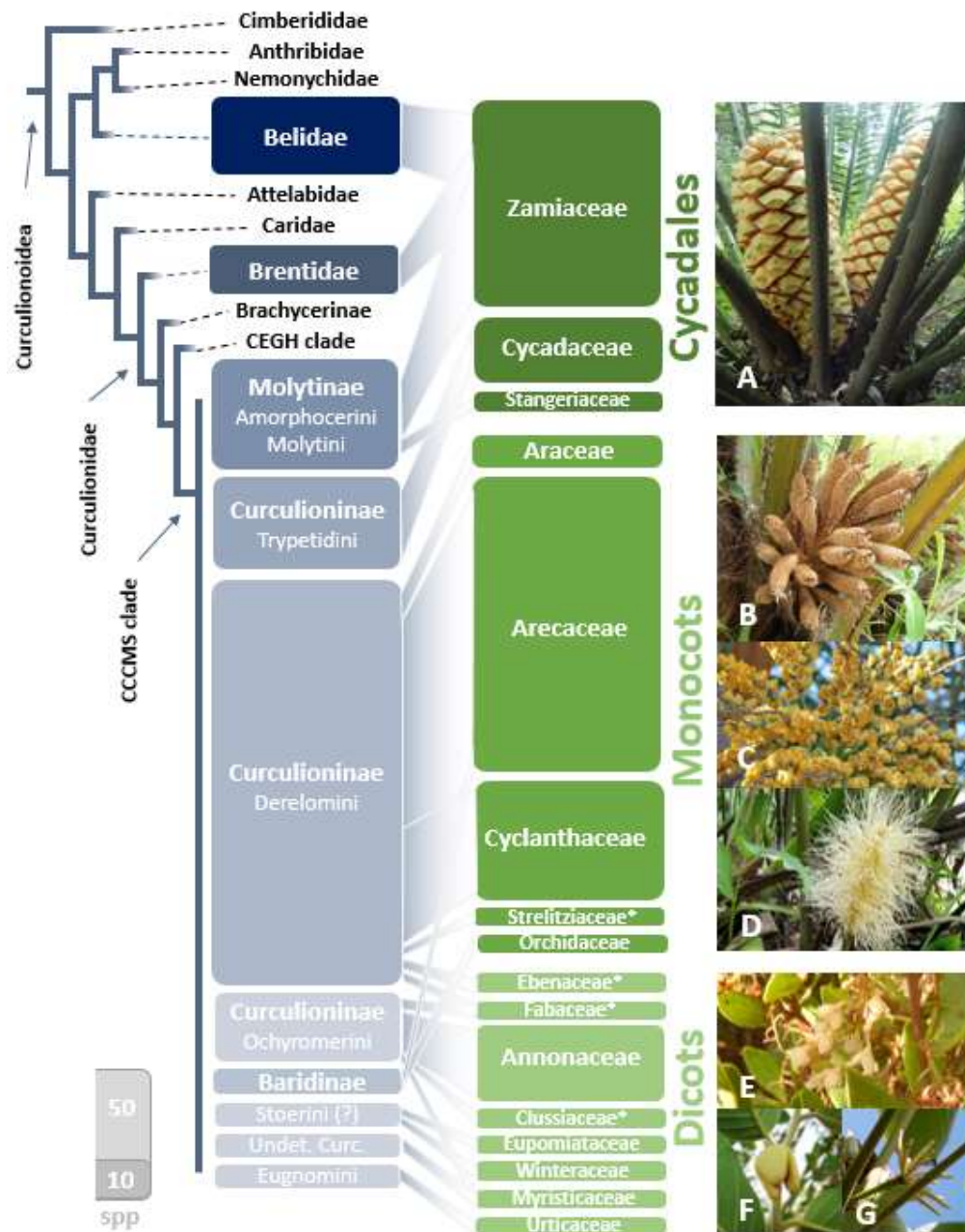
236 tested and also provide a first assessment of the extent of plant-weevil BSPM in overlooked  
237 tropical biomes (Toon et al. 2020).

238 Several dicot families have been also increasingly reported to be engaged in BSPM  
239 with weevils. In the Australasian region, some species of *Eupomatia* (Eupomatiaceae),  
240 *Myristica* (Myristicaceae) and *Exospermum* (Winteraceae) are pollinated by specific weevil  
241 lineages (*Elleschodes* spp., indet. genus (see Caldara et al. 2014) and *Palontus* spp.  
242 respectively; Armstrong & Irvine 1989a, 1989b, 1990; Pellmyr et al. 1990; Armstrong 1997).  
243 In African Ebenaceae (*Euclea*), Lecythidaceae (*Napoleonaea*) and Malvaceae (*Thespesia*)  
244 weevil pollination can be inferred on the basis of PNC since congeneric weevil species  
245 associated with other plant groups are brood pollinators (Haran et al. 2022a, 2022b; Haran  
246 pers. obs.). In the Neotropics, most species of *Cecropia* (Urticaceae) surveyed to date are  
247 associated with weevils belonging to the genus *Udeus* (Curculioninae: Eugnomini), which visit  
248 male inflorescences in all species (Lira et al. unpublished) and female inflorescences in at  
249 least one case (Mendonça 2004). In the speciose pantropical family Annonaceae, at least 22  
250 species in 13 genera are associated with 30 species of weevils pollinators belonging to two  
251 Ochyromerini genera (Curculionidae: Curculioninae) and other unidentified weevil groups  
252 (Momose et al. 1998; Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020; Dao et al. 2023;  
253 B. de Medeiros unpublished).

254 All in all, the extensive literature search conducted in this review underlines that no  
255 less than 600 instances of plant-weevils species-species BSPM interactions have been  
256 recorded to date or suggested based on the marked trend of PNC for brood pollination (Table  
257 1; see Table S1 and Appendix 1 for details). Overall, BSPM with weevils has been  
258 demonstrated experimentally in 12 of the 22 plant families involved in this mutualistic system,  
259 with the remaining 10 families suggested based on both PNC of weevil genera and traits of  
260 floral structures associated with cantharophily. Representatives of all major plant lineages,  
261 gymnosperms, monocots and dicots, are engaged in BSPM with weevils; collectively  
262 representing ca. 250 species belonging to 72 genera (Figure 1) associated with about 300  
263 species of weevils. In this regard, weevils are by far the most ecologically successful group of  
264 insects engaged in BSPM interactions with the plant kingdom. Our review shows that weevil-  
265 based BSPM has emerged several times independently with plants involved in these  
266 interactions typically belonging to groups considered to be ancient lineages (Pant 1987; Franz  
267 2004; Saunders 2020; Baker & Couvreur 2013). We also show that this type of interaction is  
268 currently predominantly found in tropical and subtropical regions of the eastern and western  
269 hemisphere, with only a few cases under Mediterranean climates (Figure 2).

270

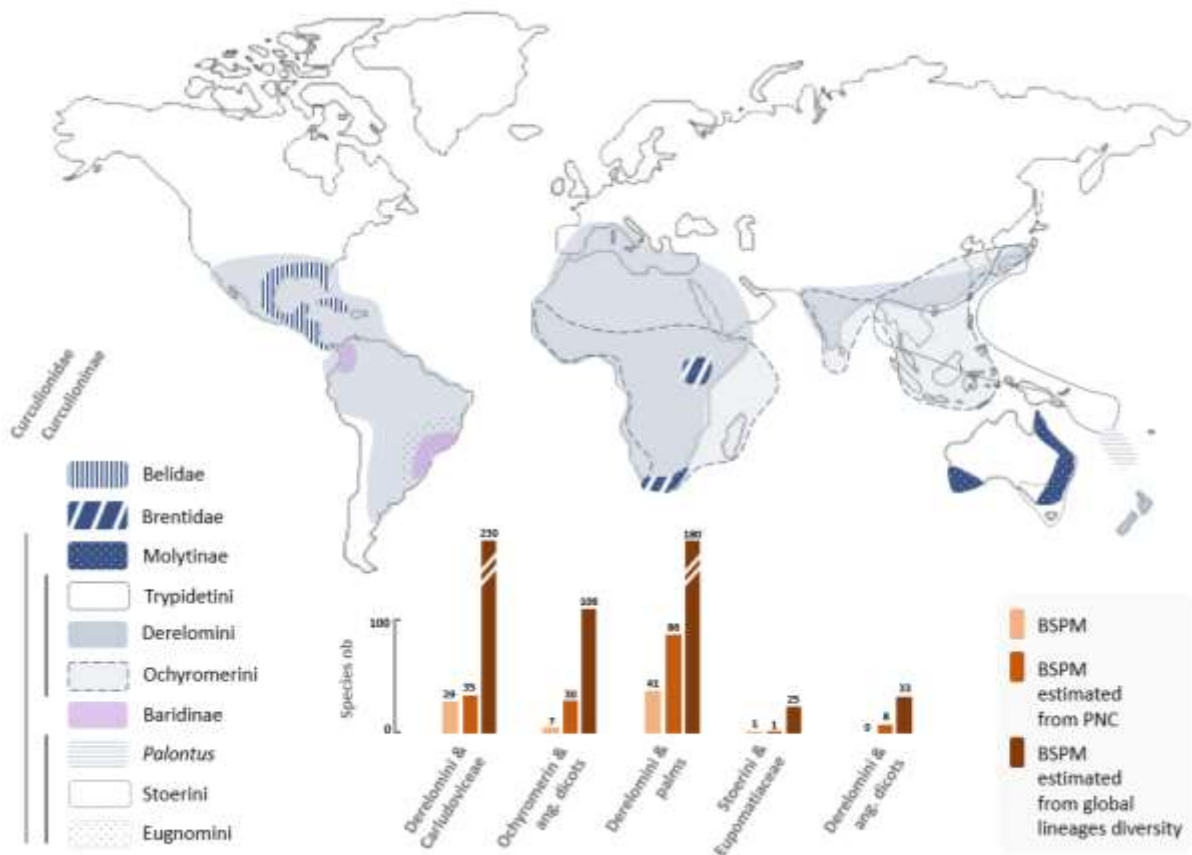




271

272 **Figure 1.** Summary of known and expected brood-site pollination mutualisms (BSPM) between plants  
 273 and weevils (Coleoptera: Curculionoidea). The boxes in blue and green refer respectively to the weevil  
 274 and plant lineages involved (the size of boxes is correlated to the number of species involved; see also  
 275 the approximate scale at the bottom left). The phylogenetic tree on the left presents a synthetic view of  
 276 phylogenetic relationships among weevils based on the phylogenomic study of [Shin et al. \(2018\)](#). The  
 277 relationships among the so-called CCCMS clade (for Baridinae, Cossoninae, Curculioninae, Molytinae  
 278 and Scolytinae) are unresolved; several subfamilies belonging to this clade and not involved in BSPM  
 279 (e.g., Scolytinae, Lixinae) are not shown. Most of the plant families reported here contain at least one  
 280 experimentally verified case of BSPM; however, for the plant families highlighted with an “\*”, BSPM  
 281 interactions are postulated based on the phylogenetic niche conservatism of the weevil genera involved  
 282 (see Methods in Appendix 1). Some minor interactions between several lineages of Curculioninae and  
 283 dicots are not shown for clarity; see Table S1 for details. Pictures of selected examples of inflorescences  
 284 of plant lineages involved: **A.** *Encephalartos* sp. (Zamiaceae) pollinated by weevils from the Brentidae  
 285 family and Curculionidae Molytinae. **B.** *Elaeis guineensis* (Arecaceae) pollinated by Derelomini. **C.**

286 *Syagrus coronata* (Arecaceae) pollinated by Derelomini. **D.** *Carludovica palmata* (Cyclanthaceae)  
 287 pollinated by Derelomini. **E.** *Euclea racemosa* (Ebenaceae) associated with Derelomini. **F.** *Annona*  
 288 *senegalensis* (Annonaceae) pollinated by Ochyromerini. **G.** *Cecropia peltata* (Urticaceae), a genus  
 289 including species pollinated by Eugnomini. (credits: A-B, E: J. Haran; C-D, G: B. de Medeiros, F: M.  
 290 Gueye).



291

292 **Figure 2.** Geographical distribution of brood-site pollination mutualism (BSPM) involving weevil  
 293 lineages and estimates of knowledge gaps. Distribution data collated from [Alonso-Zarazaga & Lyal](#)  
 294 [\(1999\)](#), articles listed in this review, and unpublished observations by the authors (note that the  
 295 distribution of an unidentified weevil genus associated with Myristicaceae is not shown). Bars show the  
 296 relative number of known and estimated BSPM interactions for a selection of plant-weevil interactions.  
 297 Beige: number of plant species involved in verified interactions (involving brood-site and/or  
 298 synchronization of weevil and flower phenology and/or pollen transfer observed). Light brown: number  
 299 of plant species involved estimated based on floral visitors, including weevils and PNC of weevils  
 300 involved. Dark brown: global diversity of interaction estimated from the diversity of plant lineages  
 301 engaged in BSPM with weevils (Derelomini-Carludoviceae; [Franz & Valente 2005](#); [Franz 2006](#); see  
 302 [details on Methods in Appendix 1](#)) and the diversity of weevil genera engaged in these interactions  
 303 (other interactions; Table S1, GBIF data and unpublished authors observations, see section 4.2). y-  
 304 axis: species number.

305

Plant lineage: Genera (number of species engaged)		Yeevil lineages : Genera (approximate number of species engaged or with indications of it)		Selected references	
<b>Gymnosperms</b>					
Cycadaceae	<i>Cycas</i> (18)	<b>Curculionidae: Curculioninae:</b> <i>Mancoplexus</i> (7), <i>Tychiodex</i> (11)		Toon et al. 2020	
Stangeriaceae	<i>Ewarotis</i> (2)	<b>Curculionidae: Molytinae:</b> <i>Milichtranes</i> (3)		Hsiao & Oberprieler 2020; 2022	
Zamiaceae	<i>Zamia</i> (13), <i>Encephalartos</i> (23), <i>Lepidozamia</i> (2), <i>Macrozamia</i> (12), <i>Zamia</i> (20)	<b>Belidae:</b> <i>Allocegnus</i> (2), <i>Microcephalotus</i> (4), <i>Olycegnus</i> (1), <i>Paralobocorynus</i> (11), <i>Rhiphalotus</i> (4) <b>Brentidae:</b> <i>Antilathinus</i> (6), <i>Plagionemus</i> (5) <b>Curculionidae: Molytinae:</b> <i>Amaurophoberus</i> (5), <i>Penthetes</i> (16), <i>Tranes</i> (7)		Toon et al. 2020	
<b>Angiosperms</b>					
<b>Monocots</b>					
Aitaceae	<i>Anthurium</i> (10)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Cyclanthura</i> (10)		Franz 2003; 2007; 2008	
Arecaceae	<i>Acoronmia</i> (1), <i>Alagoptera</i> (2), <i>Aphelandra</i> (1), <i>Arenge</i> (1), <i>Astrocaryum</i> (5), <i>Atrakea</i> (13), <i>Eactis</i> (14), <i>Eulia</i> (6), <i>Cercydon</i> (3), <i>Chamaerops</i> (1), <i>Conos</i> (1), <i>Desmoncus</i> (2), <i>Eleais</i> (2), <i>Euterpe</i> (3), <i>Geonoma</i> (3), <i>Musa</i> (1), <i>Musonilla</i> (1), <i>Nyssa</i> (1), <i>Oreocaryum</i> (6), <i>Phoenix</i> (2), <i>Phytelephas</i> (3), <i>Prentea</i> (1), <i>Psophodesiphellum</i> (1), <i>Rhapis</i> (1), <i>Sabal</i> (2), <i>Salacca</i> (1), <i>Socratea</i> (1), <i>Syagrus</i> (22), <i>Tritchinia</i> (1), <i>Thrypsan</i> (1), <i>Yretinia</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Anoxybolyanthus</i> (24), <i>Anoxybolyanthus</i> (9), <i>Celetes</i> (62), <i>Derelomachus</i> (1), <i>Derelomus</i> (13), <i>Diplothermichus</i> (1), <i>Elaeodius</i> (8), <i>Procelestus</i> (2), <i>Grasidius</i> (1), <i>Neotolomus</i> (2), <i>Pavimera</i> (1), <i>Perelioschus</i> (2), <i>Phyllanthus</i> (21), <i>Phyllocolus</i> (25), <i>Tentres</i> (3) <b>Curculionidae: Molytinae:</b> <i>Chobus</i> (3), <i>Hemalimnatus</i> (2), <i>Cobanoideres</i> (2) <b>Curculionidae: Baridinae:</b> <i>Argelocentrus</i> (1), <i>Anthemus</i> (1), gen. n. et sp. n. (4), <i>Gracetus</i> (1), <i>Austrochea</i> (2), <i>Limnancetus</i> (1), <i>Microrostratus</i> (3), <i>Motesia</i> (4), <i>Pariscocochaenus</i> (3), <i>Tonestia</i> (1), <i>Zazyzia</i> (1) <b>Dryophthoridae: Dryophthorinae:</b> <i>Beigocneus</i> (4), <i>Foveolus</i> (2), <i>Merlamastus</i> (1) <b>Curculionidae: Curculioninae: Derelomini:</b> <i>Colthene</i> (1), <i>Cyclanthura</i> (4), gen. 2 (3) <i>Gangliconus</i> (5), <i>Perelioschus</i> (8) <b>Curculionidae: Baridinae:</b> <i>Montella</i> (2), gen. n. (1) <b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (1), gen. n. (1)	Franz & Valente 2005 De Medeiros & Vanin 2020 De Medeiros et al. 2018; Nunes et al. 2015 Ervik & Feil 1997 Nunes et al. 2018 Küchmeister et al. 1998; Vaurie 1968 Franz & O'Brien 2001; Franz & Valente 2005		
Cyclanthaceae	<i>Asplundia</i> (18), <i>Caribbeevia</i> (4), <i>Chorizanthe</i> (1), <i>Cyclanthus</i> (1), <i>Zoanacarpium</i> (4), <i>Evodianthus</i> (1), <i>Sphaerandina</i> (3), <i>Thoreocarpus</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Colthene</i> (1), <i>Cyclanthura</i> (4), gen. 2 (3)			
Orobanchaceae	<i>Chochiaea</i> (2), <i>Grodia</i> (1)			Nunes et al. 2018	
Strelitziaceae	<i>Strelitzia</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (1), gen. n. (1)		J. Haran unpublished	
<b>Angiosperms Dicots</b>					
Anacardiaceae	<i>Scaevola</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (1)		Haran et al. 2022b	
Annonaeeae	<i>Annona</i> (1), <i>Cathacostemma</i> (1), <i>Dasymachalon</i> (1), <i>Enicocanthum</i> (2), <i>Ficusignata</i> (1), <i>Ficuscolletia</i> (3), <i>Goniobothalamus</i> (1), <i>Huteranthia</i> (2), <i>Melicogone</i> (1), <i>Miconiacarpis</i> (1), <i>Monocan</i> (4), <i>Polyalthia</i> (5), <i>Uvatis</i> (1), <i>Xylocopa</i> (1)	<b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (2), <i>Endaeoidius</i> (?) <b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (2), <i>Endaeoidius</i> (?) <b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (1), <i>Ethenacobius</i> (2) <b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Derelomus</i> (1), <i>Ethenacobius</i> (7) <b>Curculionidae: Curculioninae: Stoerini:</b> <i>Elleschodes</i> (3) <b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (2), <i>Lomeiderus</i> (1), <i>Ochyromerini:</i> <i>Endaeus</i> (2) <b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (2) <b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (1) <b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (1), undescribed genus (?) <b>Curculionidae: Curculioninae: Derelomini:</b> <i>Ethenacobius</i> (1) <b>Curculionidae: Curculioninae: Eugnomini: <i>Uebus</i> (2) <b>Curculionidae: Curculioninae: Stoerini: <i>Falcatus</i> (1)</b></b>	Haran et al. 2022a; 2022b J. Haran unpublished Haran et al. 2022a; 2022b Armstrong & Irvine 1990 Haran et al. 2022b; J. Haran unpublished J. Haran unpublished J. Haran unpublished Armstrong & Irvine 1989a; 1989b Haran et al. 2022a; 2022b Mendonça 2004 Pellmyr et al. 1990		
Apiaceae	<i>Acaulanthus</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Ethenacobius</i> (2)		Haran et al. 2022a; 2022b	
Clusiaceae	<i>Euclea</i> (3-4)	<b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (1)		J. Haran unpublished	
Ebenaceae	<i>Euclea</i> (3-4)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (1), <i>Ethenacobius</i> (7)		Haran et al. 2022a; 2022b	
Eupomatiaceae	<i>Eupomatia</i> (1)	<b>Curculionidae: Curculioninae: Stoerini:</b> <i>Elleschodes</i> (3)		Armstrong & Irvine 1990	
Fabaceae	<i>Estaliera</i> (1), <i>Pilicostigma</i> (1), <i>Yachella</i> (2)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (2), <i>Lomeiderus</i> (1), <i>Ochyromerini:</i> <i>Endaeus</i> (2) <b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (2) <b>Curculionidae: Curculioninae: Ochyromerini: <i>Endaeus</i> (1) <b>Curculionidae: Curculioninae: Ochyromerini: <i>Endaeus</i> (1) <b>Curculionidae: Curculioninae: Ochyromerini: <i>Endaeus</i> (1), undescribed genus (?) <b>Curculionidae: Curculioninae: Derelomini:</b> <i>Ethenacobius</i> (1) <b>Curculionidae: Curculioninae: Eugnomini: <i>Uebus</i> (2) <b>Curculionidae: Curculioninae: Stoerini: <i>Falcatus</i> (1)</b></b></b></b></b>		Haran et al. 2022b; J. Haran unpublished J. Haran unpublished J. Haran unpublished Armstrong & Irvine 1989a; 1989b Haran et al. 2022a; 2022b Mendonça 2004 Pellmyr et al. 1990	
Leguminosae	<i>Magnolonea</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Derelomus</i> (2)		J. Haran unpublished	
Malvaceae	<i>Thespesia</i> (1)	<b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (1)		J. Haran unpublished	
Mylristicaceae	<i>Atropa</i> (1), <i>Allypsitica</i> (1)	<b>Curculionidae: Curculioninae: Ochyromerini:</b> <i>Endaeus</i> (1), undescribed genus (?)		Armstrong & Irvine 1989a; 1989b	
Sapotaceae	<i>Mimusops</i> (1)	<b>Curculionidae: Curculioninae: Derelomini:</b> <i>Ethenacobius</i> (1)		Haran et al. 2022a; 2022b	
Urticaceae	<i>Cercopsis</i> (1)	<b>Curculionidae: Curculioninae: Eugnomini:</b> <i>Uebus</i> (2)		Mendonça 2004	
Winteraceae	<i>Excelspernum</i> (?)	<b>Curculionidae: Curculioninae: Stoerini:</b> <i>Falcatus</i> (1)		Pellmyr et al. 1990	

307 **Table 1.** Synthetic list of known plant-weevils BSPM systems. See Table S1 for details on species-specific  
308 interactions, species authorship, tissues for larval development, presence of cryptic lineages and corresponding  
309 reference list. See Figure 2 for information on the geographic distribution of weevil lineages involved in BSPM.

## 310 2. Traits related to BSPM by weevils

### 311 2.1 Plant traits

312 Flowers and inflorescences of plants engaged in BSPM with weevils generally display typical  
313 traits related to cantharophily (beetle pollination) and remarkable convergent morphologies,  
314 physiologies, phenology and reproductive strategies. Some of the traits in these flowers are  
315 associated with beetle pollination more generally and not specifically with brood pollination.  
316 Disentangling the role of each trait in the interaction is a task that remains to be done in most  
317 cases. Here we point out features that have been proposed to increase the attractiveness of  
318 flowers to weevils engaged in BSPM, provide them with food rewards and sometimes protect  
319 them from predators. They also may improve pollen transfer to weevil integuments and play a  
320 role in weevil pollinator selection and retention, thereby improving pollination efficiency.

321 A first major characteristic for weevil-pollinated plant lineages is that they tend to  
322 display **large flowers or inflorescences** (Figure 1). In cycads and most monocot lineages  
323 involved in BSPM (Araceae, Cyclanthaceae, some Arecaceae), flowers or female ovules are  
324 clustered in large compact cones or inflorescences (Franz & Valente 2005; Toon et al. 2020).  
325 Individual flowers can also reach substantial sizes in Annonaceae or Lecythidaceae (Prance  
326 & Jongkind 2015; Saunders 2020). In contrast, other plant lineages producing smaller  
327 individual flowers form either dense inflorescences (most Arecaceae) or synchronized blooms  
328 (Ebenaceae – *Euclea*, Orchidaceae – *Dichaea*, *Grobya* etc). Field observations and  
329 experiments on various Annonaceae flowers and Cyclanthaceae inflorescences show that  
330 larger floral structures attract greater number of pollinators (Gottsberger 1999; Franz 2007a),  
331 revealing that this floral trait has been independently selected to increase weevil attraction and  
332 pollination.

333 The main characteristic of weevil-based cantharophily is the transformation of floral  
334 structures to host the weevil larval stages. Two main types of floral morphology are typical of  
335 weevil-pollinated plants: (i) **clustered inflorescences** (in cycads and all monocots involved in  
336 BSPM except Orchidaceae and Strelitziaceae), and (ii) **individual floral chambers, bowls  
337 or claws** (in most dicots involved in BSPM; Gottsberger 1999; Prance & Jongkind 2015;  
338 Saunders 2020). Clustered inflorescences provide fleshy and nutrient-rich tissues for the  
339 development of weevil larvae, generally in male inflorescences (flower capsules,  
340 microsporophylls and rachises; Anstett 1999; Downie et al. 2008; Teichert et al. 2018; Haran  
341 et al. 2020). Within individual floral chambers, tissues for larval development include anthers,  
342 or fleshy petals (Saunders 2020; Haran et al. 2022a; Dao et al. 2023). In clustered  
343 inflorescences as in floral chambers, the modified structures effectively filter access to specific  
344 pollinators and sometimes further retain and protect them. For instance, in Cyclanthaceae, the  
345 inflorescences of *Asplundia*, *Evodianthus* and *Ludivia* exhibit narrow interfloral entrances  
346 allowing only a specific weevil pollinator to reach the hidden floral reproductive structures  
347 (Franz 2007a; Teichert et al. 2018), while larger, non-pollinating species are prevented from  
348 reaching them. Narrow interfloral openings can also promote the transfer of pollen from

349 anthers to the integuments of pollinators as they exit the floral chambers (Teichert et al. 2018).  
350 The Annonaceae provide the most striking examples of enclosed floral chambers, which are  
351 used to retain and protect *Endaeus* weevil pollinators and also ward reproductive tissues from  
352 predation (Gottsberger 1999; Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020). Other  
353 structures associated with weevil pollination include staminodes (in Cyclanthaceae and  
354 Eupomatiaceae), which are stamen-like structures that do not produce pollen but rather sticky  
355 secretions or odoriferous oils (elongated projections in Fig. 1D). They increase attraction,  
356 provide food, shelter or protection for weevil pollinators (Armstrong & Irvine 1990; Franz  
357 2007a; Teichert et al. 2018). In Annonaceae sticky pollenkitt and short pollen-connecting  
358 threads create large aggregates of pollen grains that are considered specific adaptations to  
359 improve the efficiency of pollen transfer onto weevils integuments (Ratnayake et al. 2006).  
360 The fleshy petals and other floral tissues of plants implicated in BSPM with weevils typically  
361 show extensive feeding damages (Ratnayake et al. 2006; Saunder 2020; Haran et al. 2022a;  
362 Dao et al. 2023; Figure 3F), indicating that these structures are also food sources for the adult  
363 pollinators.

364 The flowers of plant lineages engaged in BSPM with weevils are **predominantly white**  
365 **or creamy white** (Figure 1), but pale red, pale yellow and pale green flowers are occasionally  
366 encountered (Franz & Valente 2005; Ratnayake et al. 2006; Saunders 2020; Toon et al. 2020).  
367 In Cyclanthaceae, weevils show a preference for natural white inflorescences in contrast to  
368 those experimentally shaded by an opaque fabric (but letting the fragrance to be emitted;  
369 Franz 2007a). It should be noted that many weevils lineages involved in BSPM have nocturnal  
370 or crepuscular activity (Franz 2007a; Auffray et al. 2017; Lau et al. 2017; Auffray et al. 2022;  
371 Haran et al. 2022a), where light intensity is low. Under these conditions, the pale colors were  
372 hypothesized to provide better contrast with the surrounding environment in a way that likely  
373 enhances their visual recognition by weevils (Franz 2007a; Saunders 2020). This suggests  
374 that visual recognition of inflorescences is an important dimension of weevil attraction, at least  
375 as important as olfaction (see below), and that white or pale colors are more attractive to  
376 weevils.

377 All major plant lineages engaged in BSPM with weevils include representatives with  
378 **thermogenic** activity, allowing inflorescence or flower temperatures to rise several degrees  
379 above ambient temperature (Franz 2007a; Teichert et al. 2018; Saunders 2020; Toon et al.  
380 2020). This phenomenon is postulated to act as an attractant for weevil and other beetle  
381 pollinators, by increasing the emission of volatiles or infrared radiation itself. It has also been  
382 hypothesized to provide an energy reward to individuals reaching floral tissues (Rands &  
383 Whitney 2008), but this is likely not the case for weevils since thermogenic activity is usually  
384 correlated with short phases of attraction and is not maintained during an 'interim' phase when  
385 individuals stand on flowers or are enclosed in floral chambers (Teichert et al. 2018; Toon et  
386 al. 2020). In Annonaceae, thermogenesis is identified as typical of flowers pollinated by  
387 beetles, and weevils in particular (Gottsberger 1999). The temperature reached appears to be  
388 positively correlated with inflorescence size (Franz 2007a), which may explain why large  
389 flowers and inflorescences evolved convergently in weevil-pollinated plants. In several  
390 systems (Carludovicoideae-Derelomini; Zamiaceae-Belidae), the first peak of thermogenesis  
391 associated with the attraction phase of the weevils is followed, after an 'interim' phase of  
392 several hours, by a second peak where weevils leave the inflorescences (Franz 2007a;  
393 Teichert et al. 2018; Salzman et al. 2020). These second peaks of thermogenesis coincide  
394 with the staminate phase and probably act as repellent or as an aid for improved take-off that



395 favors weevil departure once they are covered with pollen (Teichert et al. 2018). This kind of  
396 push-pull mechanism where weevils are successively attracted and then repelled during the  
397 circadian flowering cycle promotes pollinator movement between plant congeners and thus  
398 cross-pollination (Salzman et al. 2020).

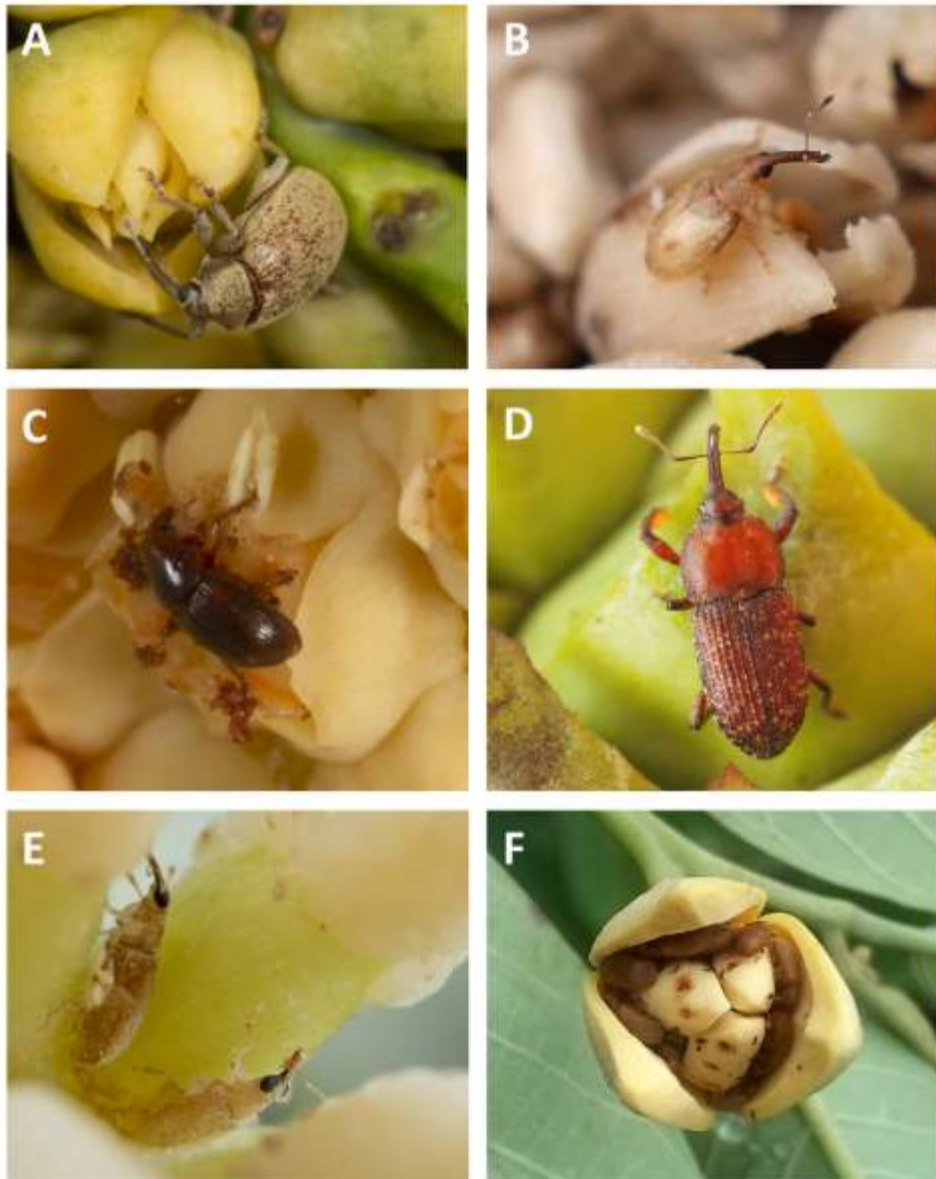
399 The **fragrances** produced by weevil-pollinated flowers during anthesis are strong and  
400 detectable by human olfactory senses, and are commonly associated with fruity or floral  
401 fragrances. In most genera of weevil-pollinated Cyclanthaceae (*Asplundia*, *Carludovica*,  
402 *Chorigyne*, *Dicranopygium* and *Evodianthus*), production of aromas reminiscent of various  
403 fruits and flowers has been reported (Franz 2007a). Similarly, in *Polyalthia* (Annonaceae), a  
404 fruity odor is produced during anthesis (Ratnayake et al. 2006). In *Elaeis guineensis*  
405 (Arecaceae), anthesis is correlated with the production of estragol (Lajis et al. 1985), while in  
406 *Attalea phalerata* (Arecaceae), weevils and other beetle pollinators are attracted by a strong  
407 emission of methyl acetate (Maia et al. 2021). In *Macrozamia* and *Zamia* (Zamiaceae) the  
408 emission of linalool or methyl salicylate has been recorded (Toon et al. 2020; Salzman et al.  
409 2021). Overall, the emission in large amount of one or a few compounds that are specific to  
410 the interaction seems to be a signature of chemical communication in BSPM involving weevils  
411 (Ervik et al. 1999; Teichert et al. 2018; Salzman et al. 2021; T. Auffray pers. com.). Notable  
412 exceptions of floral odor emission are found in *Chamaerops humilis* (Arecaceae), which  
413 attracts *Derelomus* species via the volatiles emitted from the leaves (Dufayé et al. 2003), and  
414 in *Syagrus coronata* (Arecaceae), where the volatiles are given off by a persistent peduncular  
415 bract (Barbosa et al. 2020).

416 The morphological and physiological features described above are generally  
417 organized into **timed phenological sequences** that coincide with **phases of flower and**  
418 **inflorescence receptivity**. In most plant lineages producing large inflorescences (e.g.,  
419 Araceae, Arecaceae, Zamiaceae), anthesis occurs over several days and is accompanied by  
420 circadian thermogenic cycles and emission of volatiles (Franz 2007a; Auffray et al. 2017; Toon  
421 et al. 2020). When flowers are isolated (in Annonaceae and Eupomatiaceae), but also in  
422 Cyclanthaceae, each individual flower or inflorescence goes through one cycle of anthesis  
423 with the following stages: (i) a phase of thermogenesis/attraction associated with the  
424 receptivity of female reproductive structures (pistillate phase), (ii) an interim period when  
425 weevils can be trapped in the floral chamber for a variable time, and (iii) a phase when  
426 pollinators are released with exposure to male reproductive structures (stamen and pollen,  
427 staminate phase), which can be achieved by abscission of the floral chamber petals and/or by  
428 a second peak of thermogenesis (Armstrong & Irvine 1990; Franz 2007a; Lau et al. 2017;  
429 Teichert et al. 2018; Saunders 2020). In the first case, the anthesis lasts between several days  
430 and two weeks (Toon et al. 2020), while in the second case, the complete cycle of anthesis is  
431 short and usually lasts at most 48h (Franz 2007a; Saunders 2020). Interestingly, the pistillate  
432 and staminate phase cycles found in some Cyclanthaceae (*Asplundia*; Franz 2007a) are very  
433 similar to those found in some Annonaceae (Saunders 2020), indicating a remarkable  
434 convergent evolution of plant-weevil pollination systems. With the notable exception of cycads,  
435 orchids and some palms, in all plant-weevil BSPM systems, the **pistillate and staminate**  
436 **phases coincide with peaks of crepuscular or nocturnal peaks in pollinator activity**  
437 (Armstrong & Irvine 1990; K uchmeister et al. 1998; Franz 2007a; Auffray et al. 2017; Saunders  
438 2020; Auffray et al. 2022). These converging nocturnal phenology suggest that nocturnal  
439 conditions improve pollination efficiency, possibly through increased attraction of weevil  
440 pollinators. It has been also hypothesized that the movement of pollinators and the dispersal

441 of floral fragrances are facilitated at night because there is less wind; lower temperatures also  
442 potentially improve the detection of thermogenic flowers (Borges et al. 2016; Auffray et al.  
443 2022).

444 A remarkable feature of plant lineages engaged in BSPM with weevils is the  
445 **separation of sexes**. About 95% of the species recorded in this review show physical or  
446 functional dioecy, a rare feature in the plant kingdom in general. In cycads, all species are  
447 dioecious, with male plants producing pollen cones and female plants ovulate cones (Toon et  
448 al. 2020). Weevil-pollinated palms may be dioecious or monoecious, but anthesis of male and  
449 female flowers are always separated in time in the latter case (Barfod et al. 2011). One  
450 example is the monoecious palm genus *Elaeis* (Arecaceae), in which individuals cyclically  
451 produce functionally unisexual male and female inflorescences, resulting in an allogamous  
452 mode of reproduction called temporal dioecy (Adam et al. 2011). In other genera, such as  
453 *Acrocomia* and *Bactris* the pistillate and staminate phases of the **protogynous**  
454 **inflorescences** are separated by a short interim phase resulting in circadian dioecy  
455 (Henderson et al. 2000; Carreño-Barrera et al. 2021). Similar patterns are observed in other  
456 monoecious plant lineages such as Annonaceae and Cyclanthaceae (Franz 2007a, 2007b;  
457 Saunders 2020). In Annonaceae in particular, several other types of monoecy that may result  
458 in functional dioecy have been reported (i.e. separate pistillate and staminate flowers on the  
459 same plant, with a few flowers per individual at a time; Saunders 2020). Finally, a number of  
460 palms exhibit **protandrous inflorescences** with very extended interim phases, also resulting  
461 in functional dioecy (Silberbauer-Gottsberger et al, 2013; Núñez-Avellaneda et al, 2008, 2015;  
462 de Medeiros et al. 2019). Another striking feature of systems involving Arecaceae,  
463 Annonaceae and Cyclanthaceae is the small number of flowering inflorescences per individual  
464 or the small number of flowering individuals at time, a strategy that also likely promotes cross-  
465 pollination (Saunders 2020). The resulting low number of propagules available at a certain  
466 time may be balanced by the long flowering periods of the plants engaged in these BSPM  
467 interactions, for instance up to seven-months in *Asplundia* (Cyclanthaceae; Franz 2007a) and  
468 many species of *Syagrus* (Arecaceae; Noblick 2017). These long flowering periods have also  
469 been proposed as a strategy for constant breeding of specialized brood pollinators (Carreño-  
470 Barrera et al. 2020).  
471





472  
 473 **Figure 3.** Examples of weevils and plants engaged in brood-site pollination mutualisms. **A.** *Anchylorhynchus*  
 474 *trapezicollis* (Derelomini) on pistillate flowers of *Syagrus coronata* (Arecaceae) in South America. **B.** *Derelomus*  
 475 sp. (*costiger* group; Derelomini) pollinator of *Phoenix reclinata* (Arecaceae) in southern Africa. **C.** *Perellesschus*  
 476 *evelynae* (Derelomini) on pistillate flowers of *Carludovica palmata* (Cyclanthaceae) in Central America. **D.** *Tranes*  
 477 *lyterioides* (Molytinae) on sporophylls of *Macrozamia communis* (Zamiaceae) in Australia. **E.** *Udeus eugnomoides*  
 478 (Eugnomini) on pistillate flowers of *Cecropia peltata* (Urticaceae) in Central America. **F.** Flowers of the African  
 479 custard apple (*Annona senegalensis*; Annonaceae) with aggregation of *Endaeus* spp. pollinators (Ochrymerini)  
 480 in tropical Africa. (credits: A/C/E: B, E: B. de Medeiros, B: J. Haran, D: R. Oberprieler, F: Z. Dao).  
 481

## 482 **2.2 Weevil morphology and behavior**

483 Like plants involved in BSPM, weevil pollinators display a series of morphological,  
 484 physiological and behavioral features that may constitute adaptations to pollination  
 485 mutualisms. Weevil pollinators have been less studied than the plants they pollinate, so not  
 486 only their shared morphological features have been scarcely reported, but also the function  
 487 and adaptive significance of these features are generally unexplored. This section provides a

488 summary of what is known to date, with the aim of identifying general trends associated with  
489 BSPM pollination, as well as pointing out more peculiar cases.

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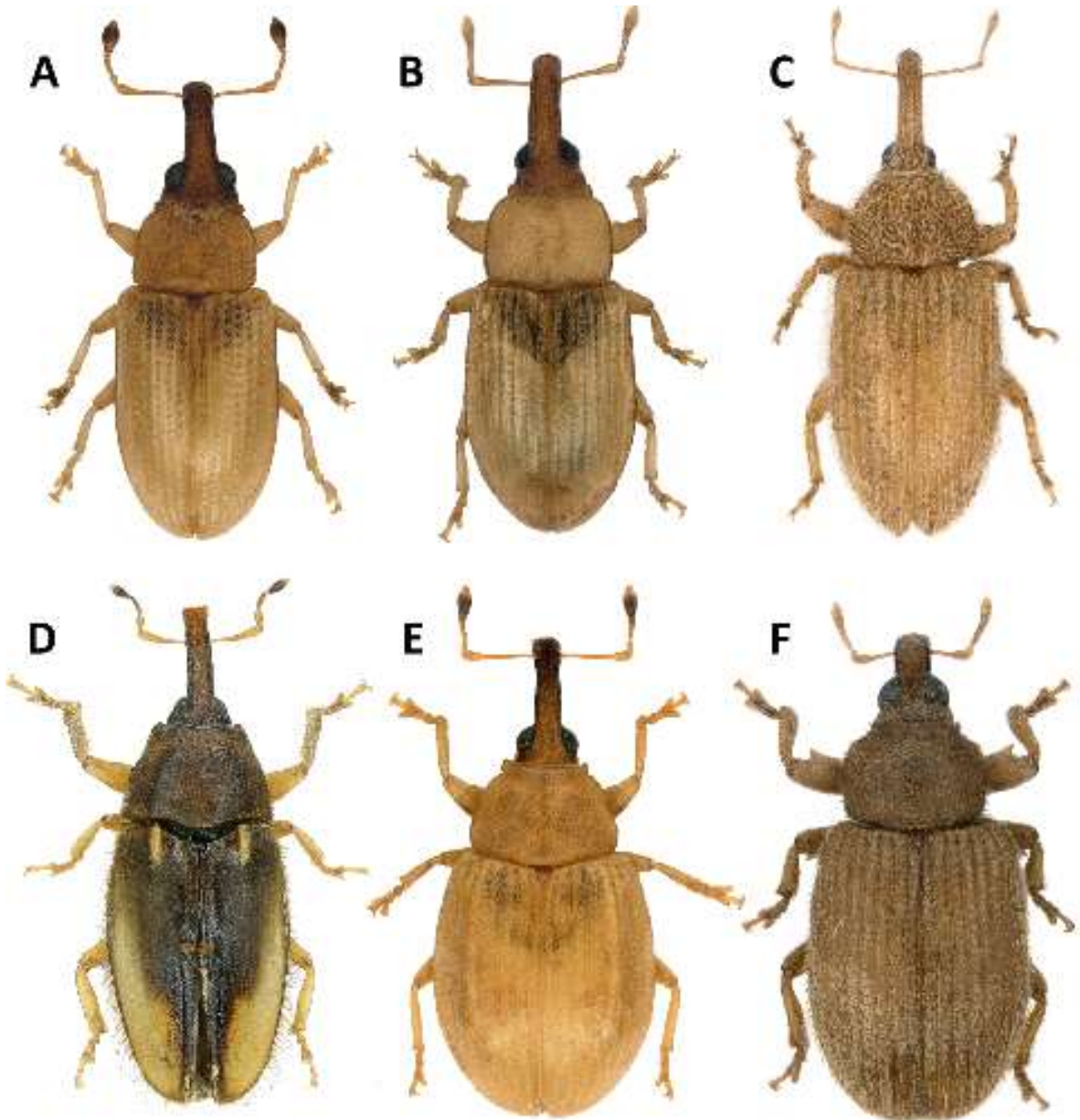
491 Known weevil species involved in BSPM are **small-sized beetles**, with body size  
492 ranging from a few millimeters to about one centimeter (1.1 mm, *Staminodeus inermis* (Franz  
493 2001); 8.6 mm in *Anchylorhynchus burmeisteri* (de Medeiros & Vanin 2020), rostrum  
494 excluded). Body shape is often consistent with floral morphology; for example, the body of  
495 weevils associated with cycads in Belidae and Brentidae is very flat and allows individuals to  
496 enter the cracks of megasporophylls. In most species, the body colors are **pale yellow,**  
497 **reddish or brown**; they usually match the color or shape of their floral substrates, probably  
498 to limit predation (Figures 3, 4). The matching colors are either obtained due to the color of  
499 the integument itself (e.g., in *Andranthobius*, *Cotithene*, *Derelomus*, *Ebenacobius*,  
500 *Elaeidobius*, *Prosoestus*) or due to the colors of the integument and scales covering it (e.g.,  
501 in *Anchylorhynchus*; Valente & da Silva 2014; de Medeiros & Vanin 2020; Haran et al. 2020,  
502 2022a). In some species, the shape of the elytra forms an angled surface mimicking the shape  
503 of the petals of the host plant (e.g., *Derelomus subcostatus*, *D. costiger* and *D. piriformis*; see  
504 Figure 4E). Overall, there seems to be a selective pressure to mimic floral substrates as  
505 suggested by the various examples of strongly converging phenotypes among unrelated  
506 species associated with the same host plant (e.g., *Derelomus pallidus* and *Ebenacobius*  
507 *rectirostris* on *Euclea racemosa*; Haran et al. 2022b; Figure 4A, B), but whether these  
508 phenotypes really provide an advantage in escaping predation has not been formally explored.  
509 Interestingly, patterns of mimicry are generally found in species active during the day on  
510 inflorescences, with little or no space to hide (i.e. most Derelomini associated with Arecaceae  
511 or Ebenaceae). Conversely, in weevil lineages that remain hidden in floral chambers or  
512 inflorescences during the day, the integuments are usually pale brown or reddish in color, and  
513 they do not specifically match floral substrates (e.g., in *Cyclanthura*; Ochyromerini; Figure 4C,  
514 F). Notable exceptions to this pattern include *Montella* weevils (Baridinae), which exhibit a  
515 dark body integument contrasting with the color of its host's flowers (Nunes et al. 2018) and  
516 some species of *Anchylorhynchus* weevils with extreme polymorphism showing disruptive  
517 patterns such as black and yellow stripes (de Medeiros & Vanin 2020).

518

519 A series of putative pollen-carrying morphologies are found in weevils engaged in  
520 BSPM. Most of these lineages have species with **erect setae** on their body surface (Haran et  
521 al. 2020, 2022a; Dao et al. 2023). Hair or scale cover on the integument are widespread in  
522 weevils, so these may represent instances of exaptation. However, their peculiar size or  
523 arrangement in some lineages acting as brood-site pollinators led to suggestions that they  
524 may improve pollen transport (Syed et al. 1982). The erect setae can cover the entire body  
525 surface (in Ochyromerini or in some *Ebenacobius* and *Celetes*; Valente 2005; Ratnayake et  
526 al. 2006; Haran et al. 2022b; Figure 4C, F), or form combs on the edge of the elytra (in some  
527 *Elaeidobius*; Figure 4D), or on the tibiae (in some *Derelomus*); setae may also be found on  
528 the ventral region (in some *Elaeidobius* and *Anchylorhynchus*). In *Anchylorhynchus*, a genus  
529 that breeds on female flowers and thus may benefit directly from pollination, these ventral  
530 setae may be highly branched in some species, reminiscent of setae found in bee corbiculae  
531 (de Medeiros et al. 2019; de Medeiros & Vanin 2020). Interestingly, in some weevil species,  
532 the presence of setae is a dimorphic feature, with only males exhibiting long setae, suggesting  
533 that they may play a differential role in pollen transport (Haran et al. 2020; Hsiao & Oberprieler  
534 2022). That said, even weevil species without specific setae (e.g., *Derelomus chamaeropsis*,  
535 *Andranthobius* spp., Baridinae and Belidae) are known to be effective pollinators (Anstett

536 1999; Nunes et al. 2018; Salzman et al. 2020; Carreño-Barrera et al. 2021), suggesting that  
537 integuments alone can efficiently transport pollen. Several unrelated lineages of weevils  
538 engaged in BSPM also exhibit prosternal processes or tubercles (in *Andranthobius*,  
539 *Diplothemobius*, *Ebenacobius*, *Elaeidobius*, *Miltotranes*, *Porthetes*, *Prosoestus*, *Tranes*;  
540 Bondar 1941; Valente & da Silva 2014; Haran et al. 2020, 2022a; Hsiao & Oberprieler 2022;  
541 Haran pers. obs.) consisting of cuticular apophyses located near the procoxae of males. In  
542 some Baridinae not involved in BSPM, such structures grow allometrically and have been  
543 shown to be used in interspecific fights to dislodge competing males (Eberhard & Garcia 2000;  
544 Eberhard et al. 2000; Davis & Engel 2010). Since fights between males have been described  
545 in Derelomini (Franz 2003, 2006), it can be postulated that these prosternal processes or  
546 tubercles probably have a similar function for the aforementioned genera. Finally, in some  
547 weevil lineages, structural complexity and dense cover of setae in these structures have been  
548 hypothesized to possibly improve pollen transport (see Hsiao & Oberprieler 2022). It is not  
549 known why the weevils evolved these pollen-carrying structures, except in the rare cases  
550 where the weevils directly benefit from the pollination of their hosts. Indeed, there are only two  
551 known cases where weevils breed on tissues that result from their direct pollination: in the  
552 genus *Montella* (Nunes et al. 2018) and in the genus *Anchylorhynchus* (de Medeiros & Vanin  
553 2020). *Montella* weevils display active pollination behavior (carrying orchid pollinaries; Nunes  
554 et al. (2018), which is consistent with other cases of specialized pollinating seed predators  
555 such as fig-wasps (Jousselin et al. 2003) and yucca moths (Pellmyr 1997). For  
556 *Anchylorhynchus* the evidence is more ambiguous; females rub their bodies against female  
557 flowers after oviposition, but it remains to be shown whether this behavior serves to mark  
558 oviposition and avoid competition, increases the likelihood of pollen deposition, or both (de  
559 Medeiros et al. 2014).

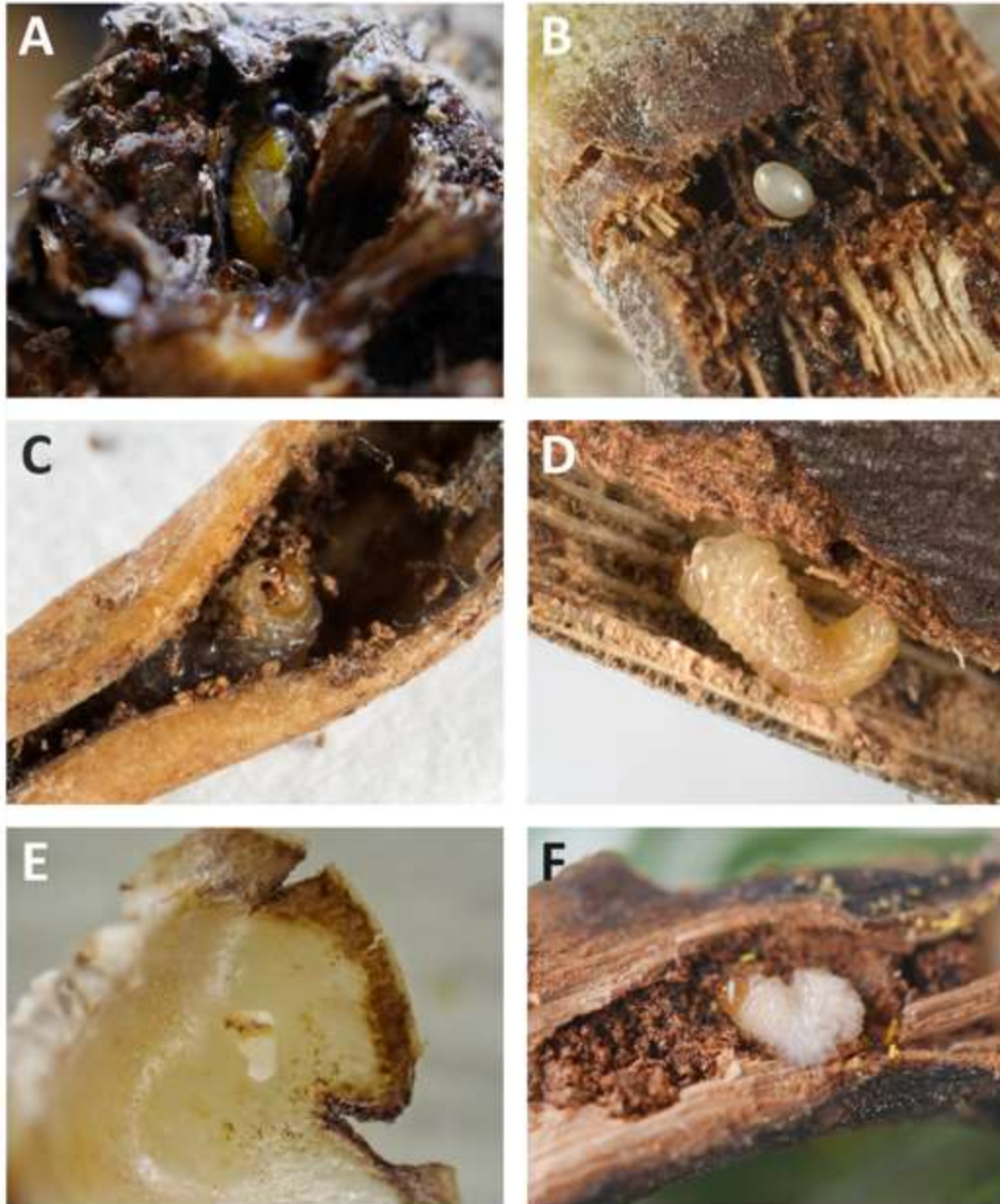
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**Figure 4.** Dorsal habitus of weevils involved in BSPM. **A-B.** *Derelomus pallidus* and *Ebenacobius rectirostris* (Derelomini), two species associated with inflorescences of *Euclea* bushes (Ebenaceae) showing a marked morphological convergence. **C.** *Ebenacobius curvistetis* (Derelomini), a species with body surface covered with erect setae, thought to be an adaptation to pollen transportation. **D.** *Elaeidobius kamerunicus* (Derelomini) pollinator of *Elaeis guineensis* (Arecaceae) with combs of setae on edge of elytra in males. **E.** *Derelomus costiger* (Derelomini) with shape of elytra mimicking the structure of petals of its host *Phoenix reclinata* (Arecaceae). **F.** *Endaeus floralis* (Ochyromerini) pollinator of *Annona senegalensis* (Annonaceae) with body surface covered by setae. (credits: A-F: J. Haran).



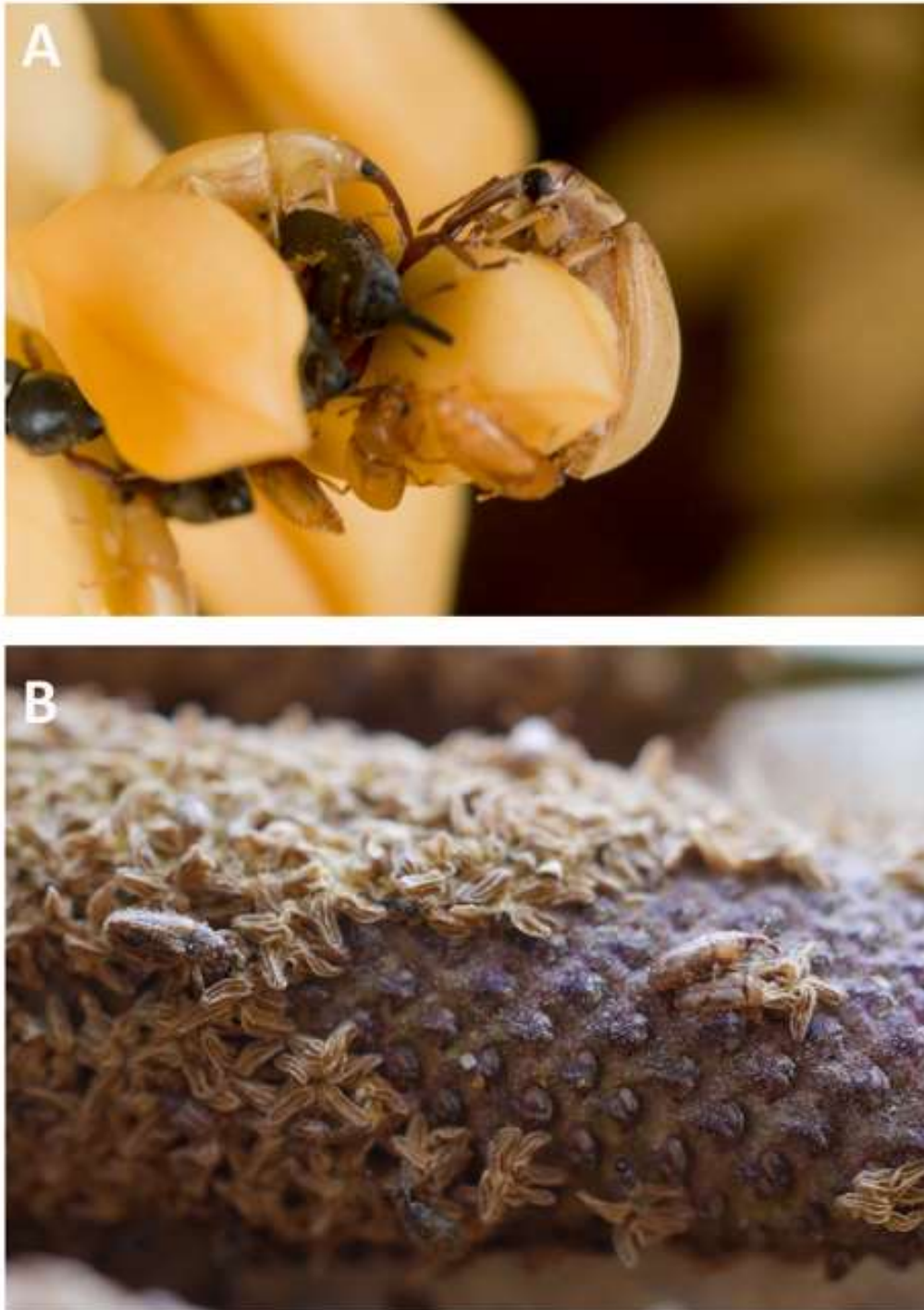


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573 **Figure 5.** Breeding sites of weevils engaged in BSPM. **A.** Pupa of *Elaeidobius plagiatus* (Derelomini) in flower  
 574 capsules of male inflorescences of *Elaeis guineensis* (Arecaceae). **B.** Egg of *Phytotribus platyrhinus* (Derelomini)  
 575 inside rachis of inflorescence of *Syagrus coronata* (Arecaceae). **C.** Larva of *Andranthobius bondari* (Derelomini) in  
 576 aborted staminate flower of *Syagrus coronata* (Arecaceae). **D.** Larva of *Celetes impar* (Derelomini) in a spathe of  
 577 *Syagrus coronata* (Arecaceae). **E.** Larvae of *Anchylorhynchus bicarinatus* (Derelomini) inside a pistillate flower  
 578 petal of *Oenocarpus mapora* (Arecaceae). **F.** Larva of *Derelomus chamaeropsis* (Derelomini) inside a rachis of male  
 579 inflorescence of *Chamaerops humilis* (Arecaceae). (credits: A, F: J. Haran, B-E: B. de Medeiros).

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582

583 **Figure 6.** Example of sympatric species assemblage of weevils of a host including species from other beetle  
 584 lineages. **A.** Inflorescence of *Syagrus coronata* (Arecaceae) with *Anchylorhynchus trapezicollis* (Derelomini, top  
 585 right), *Andranthobius bondari* (Derelomini, top left), *Microstrates ypsilon* (Baridinae, black weevils) and sap beetles  
 586 (Nitidulidae, *Mystrops palmarum*). **B.** Inflorescences in anthesis of *Elaeis guineensis* (Arecaceae) with multiple  
 587 specific pollinators including weevils (*Elaeidobius plagiatus* (left), *E. piliventris* (right) and *E. subvittatus* (bottom  
 588 left), Derelomini). (credits: A: B. de Medeiros, B: J. Haran).

589

590 Weevils engaged in BSPM likely have good **flight abilities**, which allow them to fly  
 591 actively between inflorescences of distant hosts ([Auffray et al. 2017](#); [Lau et al. 2017](#); [Saunders](#)

2020; Toon et al. 2020). This is supported by experimental data in other small weevils, which are capable to fly up to kilometers in flight mills (McKibben et al. 1998; Evenden et al. 2014) and by our own experience in collecting specimens on isolated hosts, suggesting that they can move over long distances (J. Haran and B. de Medeiros pers. obs.). Moreover, unlike social insects such as bees, the home range of pollinator weevils is not constrained by the location of a nest. Adult weevils feed on pollen or nectar produced by flowers (de Medeiros et al. 2014; Lau et al. 2017; de Medeiros et al. 2019) but also often on floral structures themselves (*Elaeidobius*, *Ebenacobius*, *Endaeus*; Haran et al. 2022a; Dao et al. 2023). The active behavior of adults is not surprising, since weevils **respond well to host specific floral volatiles**. This has, for example, been demonstrated in several cycad specialists, with electroantennography experiments and pheromone traps (Salzman et al. 2021). Several weevil lineages have also developed specific olfactory globules in their antennae which are considered to be adaptations for the detection of these volatiles (Crowson 1991; Oberprieler 2004). Following olfactory stimuli, weevils can reach or leave the flowers and inflorescences of their hosts, according to circadian cycles remarkably synchronized with flowering cycles (Franz 2007a; Auffray et al. 2017; Mendeléz-Jácome et al. 2019; Saunders 2020; Salzman et al. 2021). The weevil's reaction to a volatile can be concentration-dependent, with the same molecule acting as either an attractant or a repellent depending on the amount emitted from the floral structures. This change in behavior in turn creates a push-pull effect enhancing their movement between flowers and therefore pollination (Franz 2007a; Salzman et al. 2021). When floral structures do not produce peaks of volatiles (the so-called 'interim' phase'; Saunder 2020), weevils may simply remain on the inflorescences (in cycads and palms; Auffray et al. 2017; de Medeiros et al. 2019; Toon et al. 2020), be hidden or trapped there (in Araceae and Annonaceae; Franz 2007b; Saunders 2020; Dao et al. 2023), or leave inflorescences (Ratnayake et al. 2006; de Medeiros et al. 2019). In the genus *Ebenacobius*, many species have only been collected from the leaf litter during the day, which suggests that they hide there between their crepuscular and night phases of movements (Haran et al. 2022a). Weevils are fairly long-lived insects, with an adult lifespan of up to 79 days (mean 31 days) in *Elaeidobius subvittatus* (Syed et al. 1982). As the anthesis of the host inflorescence lasts only a few hours or a few days (five days in the case of *Elaeis guineensis*), the same individual can visit many flowers or inflorescences during its lifespan.

The **larval stages** of weevils **develop on the various types of substrates** provided by their hosts. In all the weevil lineages engaged in BSPM, the larvae are generally endophagous, developing either in live tissues or as detritivores on decaying plant material, in more or less woody tissues (Figure 5; Anstett 1999; Franz 2007a,b; Nunes et al. 2018; Toon et al. 2020; Dao et al. 2023). In Ebenaceae, which have small individual flowers, larvae of pollinators are ectophagous and feed at the base of the anthers (Haran et al. 2022a). In *Anchylorhynchus*, eggs are deposited externally between petals (Figure 5E) and first instars drill into female flowers to continue their development internally (de Medeiros et al. 2014). When larvae feed on limited spaces such as individual flowers or fruits, some species have developed a cannibalistic behavior (Figure 5E) and morphology to cope with a potential overpopulation in the brood site (de Medeiros et al. 2014). For most plant-weevil BSPM, the interplay between the presence of secondary compounds in plant tissues and a potential adaptation of associated weevil lineages has not been yet investigated, although they may drive specialization patterns (Wang et al. 2021). For example in weevils associated with cycads (Belidae), the larvae of some species have been found associated with specific bacteria involved in the control of toxic compounds from their host (Salzman et al. 2018).



640

## 641 **2.3 Evolutionary trends**

### 642 **2.3.1 Larval host specificity**

643 The vast majority of weevils engaged in brood-site pollination appear to be strictly  
644 monophagous as larvae (Franz & Valente 2005; de Medeiros & Núñez-Avellaneda 2013;  
645 Valente & de Medeiros 2013; Toon et al. 2020; de Medeiros & Farrell 2020; de Medeiros &  
646 Vanin 2020; Haran et al. 2021; Hsiao & Oberprieler 2022). Such a level of specialization is  
647 rare for weevils and phytophagous insects in general, even when considering other groups of  
648 endophagous feeders, which are known to be generally highly specialized (e.g., Gaston et al.  
649 1992; Anderson 1993; Bernays & Chapman 1994; Kergoat et al. 2008, 2018). One of the most  
650 striking case reflecting this host specificity is the pollination ecology of sympatric palms  
651 belonging to the genus *Oenocarpus* in the Amazon (Núñez-Avellaneda et al. 2015). The three  
652 species studied have a very similar floral structure and phenology, but each has a specific  
653 assemblage of weevil pollinators, only a few of which are able to visit several *Oenocarpus*  
654 species. Also, in *Montella* weevils actively pollinating *Dichaea cogniauxiana*, adults visit the  
655 flowers of another orchid species (*D. pendula*), but can only complete their life cycle in the  
656 former due differences in self-compatibility of the reproductive system (Nunes et al. 2016).  
657 Cases of oligophagy or polyphagy in weevil pollinators have been suggested in several  
658 systems based on general observations of inflorescences visitors, but these have never been  
659 formally tested (Franz & Valente 2005; Ratnayake et al. 2006; Saunders 2020). In the  
660 Annonaceae – Ochyromerini system, a species of *Endaeus* has been identified as the  
661 pollinator of two congeneric and sympatric *Polyalthia* species (Ratnayake et al. 2006). In the  
662 Araceae – Derelomini and Cyclanthaceae – Derelomini systems, a few intriguing cases of  
663 oligophagy or even polyphagy have been reported for weevil species acting as effective  
664 pollinators (Franz & O'Brien 2001a,b; Franz 2006, 2007); however, most of these accounts  
665 should be viewed with caution as they are based on observations of adult stages only. Weevils  
666 can be slightly eclectic in the selection of flowers visited at the adult stages (Haran et al. 2022a)  
667 and over-interpretation of these visits can lead to erroneous conclusions about larval host  
668 specificity. The complexity of the host plant taxonomy can also make it difficult to interpret  
669 historical records and blur patterns of host-associations (de Medeiros & Vanin 2020). All of  
670 this highlights that understanding the level of species-specificity in these systems is primarily  
671 hampered by the lack of actual host plant data for the larval stages (Franz 2004). More  
672 generally, integrative and detailed studies are needed to accurately assess plant-weevil BSPM  
673 interactions. All detailed studies of host plant associations using molecular data have found a  
674 higher than previously thought weevil diversity and a very high degree of specialization on  
675 their hosts (Downie & Williams 2009; Brookes et al. 2015; de Medeiros & Farrell 2020; Haran  
676 et al. 2021).

### 677 **2.3.2 Sympatric species assemblages**

678 While most weevils engaged in pollination mutualism are specialized and dependent on a  
679 single host, the reciprocal condition does not apply to plants, which are usually pollinated by  
680 various insect guilds. This imbalanced pattern, also referred to as mutualism asymmetry, is a

681 well-known trend in mutualistic associations as a whole, and it has been hypothesized that it  
682 could potentially determine the stability of associations over time and their level of specificity  
683 (Chomicki et al. 2020).

684 With respect to weevil specialists, plants involved in BSPM are often pollinated by  
685 diverse multi-species assemblages of weevil pollinators living in sympatry (Figures 3F, 6;  
686 Hotchkiss 1958; Ervik et al. 1999; Franz & Valente 2005; Núñez-Avellaneda et al. 2015; de  
687 Medeiros et al. 2019; Saunders 2020; Toon et al. 2020; Haran et al. 2021; 2022b; Auffray et  
688 al. 2022; Dao et al. 2023). A remarkable aspect of these assemblages is their stability over  
689 the range of their hosts (Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019; Haran et al.  
690 2020), in stark contrast to other brood-site pollination systems (Jousselin et al. 2008; McLeish  
691 & van Noort 2012). Sympatric weevil assemblages may coexist on the same host as they often  
692 develop on distinct ecological niches such as male or female inflorescences, as observed in  
693 the genera *Elaeidobius* and *Prosoestus* on *Elaeis guineensis* (Syed 1979; Alibert 1938) or in  
694 several cycad-associated weevils (Toon et al. 2020). Niche partitioning can also be observed  
695 within monoecious inflorescences, either on different tissues (de Medeiros et al. 2019; Figure  
696 6) or in relation to distinct phenological anthesis stages (Haran et al. in prep.). Unexpectedly,  
697 these sympatric multi-species assemblages have been described in all plant-weevil mutualism  
698 systems, suggesting that they may be the rule rather than the exception. The prevalence of  
699 these assemblages seems specific to weevil pollinators; in other BSPM systems such as the  
700 fig/fig-wasp model, instances of multispecific assemblages of pollinators are only reported in  
701 about 10% of associations (Cruaud et al. 2012), even though usage of molecular data for wasp  
702 species delimitation has been increasing this number (Satler et al. 2022; Su et al. 2022). In  
703 comparison with other brood-site pollinator systems, weevils also present the greatest  
704 diversity of congeneric species associated with the same host: this is the case of the African  
705 oil Palm (*Elaeis guineensis*), which hosts no less than eight species of *Elaeidobius* on its male  
706 inflorescences (Compton et al. 2009; Haran et al. 2020a, 2021; Figure 6B). The exact role of  
707 these assemblages is not yet elucidated and several potential evolutionary processes have  
708 been proposed to explain their emergence. A first process is the lineage duplication induced  
709 by the fragmentation of the host range in relation to past environmental changes (such as  
710 climate oscillations), followed by the reconnection of host populations. This case has been  
711 highlighted in the *Elaeis*-derelomine system where past cycles of fragmentation of *Elaeis*  
712 *guineensis* populations into the upper and lower Guinean forest blocks would have led to the  
713 diversification of *Elaeidobius* and *Prosoestus* species (Haran et al. 2021). When populations  
714 reconnect after isolation, differences in generation times between the host plant and its  
715 pollinators appear to allow palm populations to exchange genes again while weevil  
716 populations are already too divergent and already correspond to distinct species. A second  
717 process results from independent past colonizations (historical host shifts) of a host by multiple  
718 lineages of weevils. This process is suggested by the structure of sympatric assemblages  
719 themselves, where weevil species in an assemblage belong to distinct and phylogenetically  
720 unrelated genera (Franz 2007a; de Medeiros et al. 2019; Toon et al. 2020; Haran et al. 2022b).  
721 Interestingly these two processes are not mutually exclusive, as underlined by the example of  
722 the weevil community associated with the inflorescences of *Phoenix reclinata* (Arecaceae).  
723 Here, lineage duplication and independent colonizations led to the emergence of a sympatric  
724 assemblage of six species of brood-site pollinators (Haran et al. 2022b).

725 In plant-weevil BSPM, multi-species assemblages are not limited to weevils but also  
726 include a range of insects of various orders that develop on host inflorescences (Desmier de

727 [Chenon 1981](#); [Búrquez et al. 1987](#); [Ervik et al. 1999](#); [Gottsberger 1999](#); [Núñez-Avellaneda et](#)  
728 [al. 2015](#); [de Medeiros et al. 2019](#); [Toon et al. 2020](#); [Auffray et al. 2022](#)). It is very common, for  
729 example, that weevil-pollinated plants are also visited by sap beetles (Nitidulidae, Figure 6A).  
730 In Annonaceae they belong to the genus *Carpophilus*, in Arecaceae the most common genera  
731 are *Carpophilus*, *Microporum* and *Mystrops*, in cycads they belong to the genus *Carpophilus*,  
732 and in Cyclanthaceae they belong to the genus *Mystrops* ([Desmier de Chenon 1981](#); [Knudsen](#)  
733 [et al. 2001](#); [Núñez-Avellaneda et al. 2005](#); [Ratnayake et al. 2006](#); [Franz 2007a](#); [Núñez-](#)  
734 [Avellaneda et al. 2015](#); [Toon et al. 2020](#)). Sap beetles range from the most important  
735 pollinators in some plants to negligible in others ([Ratnayake et al. 2006](#); [Núñez-Avellaneda et](#)  
736 [al. 2015](#); [Lau et al. 2017](#); [de Medeiros et al. 2019](#); [Toon et al. 2020](#); [Carreño-Barrera et al.](#)  
737 [2021](#)). Indeed, the patterns observed in cycad-associated brood-site pollinators show that sap  
738 beetles, but also certain lineages belonging to other families of beetles (Boganiidae, Erotylidae  
739 and Tenebrionidae) or even other orders of insects (Lepidoptera and Thysanoptera) may have  
740 become brood-site pollinators of cycads ([Toon et al. 2020](#)). It is therefore not surprising that  
741 species of various groups of insects have independently colonized the same host and co-exist  
742 on it. In palms, multi-species assemblages sometimes even include generalist insects that  
743 have also been identified as pollinators. In some cases, bees are the most important  
744 pollinators with weevils being accessory ([Núñez & Carreño, 2017](#); [Bezerra et al. 2020](#)), but  
745 more commonly generalist pollinators play a minor role ([Desmier de Chenon 1981](#); [Núñez-](#)  
746 [Avellaneda et al. 2015](#); [de Medeiros et al. 2019](#)). The latter echoes the fact that, whenever  
747 weevils are involved in these diverse assemblages, they generally play a predominant role in  
748 host pollination ([Desmier de Chenon 1981](#); [Ratnayake et al. 2006](#); [Núñez-Avellaneda et al.](#)  
749 [2015](#); [Toon et al. 2020](#)). The precise role of these secondary pollinators (brood site or not) is  
750 not clear, but a reduction of extinction risk by limiting dependence on a specialized mutualist  
751 has been suggested ([Silberbauer-Gottsberger 1990](#); [Chomicki et al. 2020](#)).

### 752 **2.3.3 Cryptic and closely related weevil species**

753 The evolution of plant-weevil BSPM is a dynamic system with many instances of recent or  
754 ongoing speciation processes. This trend was first suggested thanks to the results of several  
755 morphological studies, which revealed that BSPM weevil genera often consist of diverse  
756 closely related species ([Oberprieler 1996](#); [Oberprieler 2004](#); [Valente 2005](#); [Franz & Valente](#)  
757 [2005](#); [de Medeiros & Vanin 2020](#); [Hsiao & Oberprieler 2022](#)). This trend has been confirmed  
758 by molecular studies, which have revealed additional layers of hidden diversity in the form of  
759 cryptic and closely related species often co-occurring on a single host ([Downie & Williams](#)  
760 [2009](#); [Brookes et al. 2015](#); [Nunes et al. 2018](#); [de Medeiros & Farrell 2020](#); [Haran et al. 2021,](#)  
761 [2022b,b](#)). All of these cryptic and closely related weevil species (Table S1) likely reflect recent  
762 speciation events. For example, dating analyses from two recent molecular studies have  
763 recovered numerous instances of recent speciation events (1.2 to 0.2 Mya old), which may be  
764 associated with recent changes in paleoenvironments ([Haran et al. 2021, 2022b](#)).  
765 Morphological features enabling to distinguish these closely related species include subtle  
766 differences such as the location and size of certain setae on the male ventrites, the  
767 arrangement of setae on the elytra or the ratios on the male genitalia. The repeated occurrence  
768 of these cases of cryptic and closely related species highlight the need for detailed taxonomic  
769 studies to properly estimate the levels of specificity of plant-weevil BSPM systems.

#### 770 2.3.4 Trade offs in cost-benefit of interactions

771 The balance between costs and benefits in plant-weevil BSPM interactions has been  
772 investigated in several systems (e.g., [Dufay & Anstett 2004](#); [Franz 2004](#); [Franz & Valente](#)  
773 [2005](#); [Nunes et al. 2018](#); [Saunders 2020](#); [Toon et al. 2020](#)). Plants engaged in BSPM with  
774 weevils require cross-pollination for a large fruit set. Therefore, a major pressure they have  
775 experienced is pollen limitation, linked to inadequate pollen quality and/or quantity ([Franz](#)  
776 [2007a](#); [Nunes et al. 2018](#)), a widely observed condition for tropical flora ([Tremblay et al. 2005](#);  
777 [Wolowski et al. 2014](#)). Under this pressure, the advantage of having specialized pollinators is  
778 believed to be high ([Silberbauer-Gottsberger 1990](#)), especially in the understory where small  
779 plants do not compete well for generalist pollinators because their floral displays are less  
780 conspicuous ([Turner 2001](#)). The benefit to the plant is clear when weevils develop only on  
781 male flowers or on non-reproductive tissues (e.g., live or decaying stems, bracts and petals),  
782 and therefore do not affect propagule production ([Dufay & Anstett 2003](#); [Dao et al. 2023](#)). This  
783 case is widely encountered in “pollination by deceit” systems ([Dufay & Anstett 2003](#)) described  
784 in many palms (Arecaceae), where adult weevils search for male inflorescences where  
785 development of larval stages take place but are misled by female inflorescences producing  
786 similar attractants but no rewards. Such a benefit is, however, less evident when the flower  
787 buds or seeds are destroyed during the larval development of the weevils, and sometimes it  
788 even results in a sharp reduction in the fitness of the host. For example, brentids in the genus  
789 *Antliarhinus* are ovule parasites that can destroy up to 80% of the seeds of their cycad host  
790 *Encephalartos*. Despite this damage, it has been shown that adults contribute up to 10% to  
791 the cross-pollination of their host ([Donaldson 1997](#)). Similarly, the main pollinator of the palm  
792 *Syagrus coronata* is a specialist weevil of the genus *Anchylorhynchus* (Derelomini), which are  
793 known to be seed predators ([de Medeiros et al. 2019](#)). However, it has been recently shown  
794 that there is variation in the genus, with some species only being able to develop on aborted  
795 female flowers and therefore harmless to the plant ([de Medeiros 2022 in press](#)). Studies on  
796 these peculiar cases can reveal why such costly pollination systems are maintained when less  
797 costly ones, involving other specialist or generalist pollinators, are potentially available and  
798 how interactions evolve along the mutualism-antagonism spectrum ([Fenster et al. 2004](#); [de](#)  
799 [Medeiros et al. 2019](#)).

800

801 In some cases, the detrimental effect of the larval development of weevil pollinators is  
802 mitigated by specific plant adaptations. In the dwarf palm (*Chamaerops humilis*), the process  
803 associated with fruit development leads to the termination of larval development on female  
804 inflorescences of *Derelomus chamaeropsis*. Thus, the maintenance of the populations of this  
805 obligate pollinator relies solely on male inflorescence tissues, with no impact on seed sets  
806 ([Dufay & Anstett 2004](#)). Control of the detrimental effects of larval development may also  
807 include other organisms. For example, in the orchid *Dichaea cogniauxiana*, pollination  
808 depends heavily on the activity of a baridine weevil developing as an ovule parasite. Normally,  
809 about 20% of fruits are lost to weevil larvae, but the activity of a parasitic wasp killing weevil  
810 larvae at an early stage can significantly reduce the fraction of seeds lost to the weevil ([Nunes](#)  
811 [et al. 2018](#)). Such tripartite interactions involving a plant, a pollinator and a parasitoid are  
812 probably overlooked, although they potentially play an important role in weevil-based BSPM  
813 systems.

814

815 Entirely detrimental interactions for the plants have also emerged within weevil  
816 lineages generally recognized as pollinators. The species involved have been labeled as

817 'cheaters' because they develop in the tissues of their hosts without providing pollination  
818 service (Franz, 2003, 2004; Franz & Valente, 2005; de Medeiros et al., 2019; de Medeiros &  
819 Farrell, 2020). In several plant-weevil BSPM, beneficial and detrimental weevil lineages  
820 coexist on the host inflorescence. For example, in the cyclanths (genus *Carludovica*) – weevil  
821 BSPM system, pollination is ensured by *Ganglionus* weevils (Derelomini) developing in the  
822 male flowers of the monoecious inflorescences. However, they coexist with another genus of  
823 derelomine weevils (genus *Systemotelus*), which predates *Carludovica* seeds while providing  
824 no pollination service. Since most derelomine weevils are brood pollinators, this cheater habit  
825 has therefore been inferred as a transformation from a beneficial to a detrimental one (Franz  
826 & Valente 2005). Such transitions of beneficial to detrimental life habits are a common feature  
827 of brood-pollinators system, and have been extensively documented in fig/fig-wasp and  
828 yucca/yucca-moth systems (e.g., Pellmyr et al. 1996; West et al. 1996; Segraves et al. 2005).

### 829 2.3.5 Evolutionary dynamics of host use

830 Since most of the plant groups actually associated with weevil brood pollinators are  
831 categorized as ancient tropical lineages (Annonaceae, Araceae, Arecaceae, cycads,  
832 Cyclanthaceae, Ebenaceae and Strelitziaceae; Franz & Valente 2005; Kress & Specht 2006;  
833 Toon et al. 2020), extant plant-weevil associations have sometimes been assumed to be  
834 ancient and possibly concurrent with the origin of plant lineages (Brenner et al. 2003;  
835 Oberprieler 2004; Franz 2006). However, such a pattern has not been backed up by any solid  
836 evidence, as all studies integrating knowledge of the fossil record and the results of molecular  
837 dating analyses support the hypothesis that weevil brood pollinator lineages began to diversify  
838 long after the origin of the plant lineages on which they specialize. For example, the estimated  
839 origin of palm-specialists from the Derelomini tribe (ca. 40 Mya; Haran et al. 2022b)  
840 significantly postdate the well-documented appearance of palms ca. 100 Mya (Baker &  
841 Couvreur 2013). Likewise, the phylogenetically diverse lineages of weevils that shifted on  
842 cycads (Oberprieler 2004) colonized them relatively recently (Downie et al. 2008; Hsiao &  
843 Oberprieler 2022), well after their origin more than 250 Mya (Condamine et al. 2015).

844 Weevils show a marked pattern of phylogenetic niche conservatism for the specific  
845 plant lineages they pollinate. Consistency of association with plant clades is observed at the  
846 tribe, genus or species-group level (Franz & Valente 2005; de Medeiros & Vanin 2020; Haran  
847 et al. 2021, 2022b; Figure 1). This consistency is particularly strong at the genus level for  
848 BSPM interactions (Table S1). In other words, when a BSPM interaction is established for a  
849 weevil species, it is very likely that congeneric species are also involved in such an interaction.  
850 An exception to this pattern has been reported in the genus *Cotithene* (Derelomini) associated  
851 with *Evodianthus* (Cyclanthaceae) in Amazonia: only one weevil species in this genus is a  
852 brood site pollinator., Congeners visiting this cyclanth are not engaged in such relationship  
853 due to a size mismatch with the host flower morphology (Valente et al. 2019).

854 Unlike other brood-pollinators, weevils display a remarkable ability to shift to unrelated  
855 plant lineages at various evolutionary scales. A striking example of this pattern is seen in  
856 eastern hemisphere Derelomini with two parallel instances of secondary shifts from palms  
857 (Arecaceae) to Ebenaceae (genus *Euclea*; Haran et al. 2022b). Interestingly, such secondary  
858 shifts did not necessarily constitute evolutionary dead ends since they are sometimes followed  
859 by lineage diversification and even additional secondary shifts (Haran et al. 2022b). Other  
860 notable examples of host shifts include the parallel and independent colonization of the closely



861 related palms *Elaeis guineensis* and *Elaeis oleifera* by two distinct lineages of derelomine  
862 weevils (Haran et al. 2021) and the independent colonization of the legume tree *Baikiaea*  
863 *insignis* (Fabaceae) by both Ochyromerini (two species of *Endaeus*) and Derelomini  
864 (*Lomederus ghesquieri*) (Marshall 1932, 1933). Overall, the evolutionary pattern of host use  
865 in weevils engaged in BSPM is much more dynamic than what is reported in other brood  
866 pollinators systems (Pellmyr 2003; Herre et al. 2008) and thus reinforces the interest of using  
867 weevils as an additional model system to investigate evolutionary dynamics of pollination  
868 mutualism in the tropics (Haran et al. 2022b).

### 869 3. Economic importance and conservation

870 Many plants engaged in BSPM with weevils have economic, cultural or ornamental values,  
871 features that have sometimes triggered the discovery and study of these mutualistic systems.  
872 Thanks to a better understanding of the plant-weevil BSPM systems, it was possible to achieve  
873 practical objectives. For example, a classic application in agriculture is the introduction of the  
874 derelomine weevil *Elaeidobius kamerunicus* from Africa to Asia, to improve pollination of  
875 cultivated African oil palm (*Elaeis guineensis*; Syed et al. 1982). The successful establishment  
876 of this weevil, also known as the 'million dollar weevil', has resulted in a dramatic increase in  
877 pollination rates and yields (Krantz & Poinar 2004; Li et al. 2019).

878  
879 Many weevil pollinated palms are an important source of food, goods and building  
880 materials (e.g., *Acrocomia*, *Cocos*, *Euterpe*, *Oenocarpus*, *Phytelephas*, *Syagrus*; Núñez-  
881 Avellaneda et al. 2015; de Medeiros et al. 2019; Bezerra et al 2020; Carreño-Barrera et al  
882 2021; Auffray et al. 2022). In tropical and subtropical regions, wild fruits and leaves of  
883 Annonaceae (e.g., *Annona senegalensis*), Clusiaceae (e.g., *Pentadesma butyracea*) and  
884 Fabaceae (e.g., *Piliostigma reticulatum*) for which pollination by weevils is indicated based on  
885 PNC are commonly consumed by local populations or have a cosmetic or medical use (e.g.,  
886 Babajide et al. 2008; Traoré et al. 2011; Dao et al. 2023). In cycad lineages primarily pollinated  
887 by weevils (Toon et al. 2020), the high ornamental and subsequent economic value of many  
888 cycad species has also led to over-collection (Mankga & Yessoufou 2017). In these groups,  
889 reproductive failure, among habitat loss and medicinal use, has been identified as one of the  
890 main drivers of population decline, highlighting the importance of detailed investigations of  
891 their pollination ecology. More generally, while plant-weevil BSPM probably emerged to  
892 balance some pollination constraints in tropical biomes, it is also a risky evolutionary path if  
893 the specialized pollinators become rare or extinct. Yet too little is known about the impact of  
894 pollinator population dynamics on the reproductive success and long-term survival of the  
895 plants involved (Toon et al. 2020).

### 896 4. Oversights and estimates of global richness

#### 897 4.1 The inconspicuousness of plant-weevils pollination 898 interaction

899 One may wonder why such widespread mutualistic interactions have taken so long to be  
900 described and recognized. Pollination ecology is a dynamic discipline and pollination

901 syndromes have been explored for a significant range of tropical flora (Momose et al. 1998;  
902 Schleuning et al. 2012; Vizentin-Bugoni et al. 2018), several causes may be invoked for the  
903 delays in description of plant-weevil BSPM systems.

904 First, it can be explained by common misconceptions about plant and weevil biology.  
905 For example, in the cycad/molytine and palm/derelomine systems, massive aggregations of  
906 weevils on inflorescences are highly suggestive of pollination activity. Although these  
907 associations have been known for a long time (e.g., von Martius 1823), the common  
908 misconception that palms and cycads are primarily anemophilous groups has hampered  
909 research on brood-site mutualism in these systems for decades (Von Martius 1823; Lepesme  
910 1947; Bondar 1943; Henderson 1986; Dufaÿ & Anstett 2003; Barfod et al 2011; Toon et al.  
911 2020). These flower visitors have long been considered parasites, providing no pollination  
912 service (Bondar 1943; Lepesme 1947), consistent with antagonistic interactions generally  
913 reported in weevils (Oberprieler et al. 2007). In a striking example of how prior misconceptions  
914 can prevent discovery, a study characterizing floral visitors of *Butia catarinensis* by collecting  
915 only during the day and using sweep nets failed to find a relevant number of beetles in female  
916 flowers (Rosa 2000). However, B. de Medeiros visited the same locality less than 10 years  
917 later and found hundreds of individuals of *Anchylorhynchus eriospathae* hiding at the base of  
918 inflorescences during the day (de Medeiros & Vanin 2020). These weevils breed on female  
919 flowers (de Medeiros et al. 2014) and adequate collection and observation methods could  
920 have recorded them visiting active female flowers for oviposition. To date, the cycad and palm-  
921 weevil associations remain by far the best studied plant-weevil BSPM systems, in particular  
922 because the abundance of these insects on the inflorescences and their specialized nature  
923 greatly facilitates the identification of the interactions (Franz & Valente 2005).

924 Second, the inconspicuous nature of many interactions hampered and slowed down  
925 the discovery of several plant-weevil BSPM interactions. For example, in the case of the  
926 Annonaceae – *Endaeus* mutualisms, the flowers are isolated and therefore the interactions  
927 are thus far less conspicuous. In these systems, weevils typically reach flowers in very low  
928 numbers, sometimes at a very specific time of the circadian flowering cycle (early in the  
929 morning or late in the evening), and may be hidden or “enclosed” in floral chambers during  
930 most of the day (Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020) or present on the  
931 flower only at night and notably absent during the day (Ratnayake et al. 2006). When not  
932 enclosed in flowers, *Endaeus* weevils and related weevil genera are usually collected while  
933 flying over the canopy (Kojima & Morimoto 1995; Sprick and Florent 2018), using light traps  
934 (Kojima & Morimoto 1995; Haran et al. 2022a) or by beating plants only used as shelters,  
935 generally in low numbers (Kojima & Morimoto 1995). Therefore, unraveling BSPM interactions  
936 between weevils and their host plants is usually a difficult task. To illustrate this point, a striking  
937 example of inconspicuous interactions is found in the *Anthurium* (Araceae) / Derelomini  
938 mutualism. In this system, only a few individuals of the derelomine *Cyclanthura carinata* reach  
939 *Anthurium* inflorescences at night during the 1-2 weeks of anthesis, and further remain hidden  
940 in areas protected by the spathe, leaving the inflorescences apparently empty. This  
941 inconspicuousness probably explains why this obligate pollination mutualistic system has  
942 been overlooked for decades (Franz and Valente 2005; Franz 2007b).

## 943 **4.2 An underestimated diversity of species and interactions**



944 How much of the diversity of weevil-based pollination is still unknown? A basic calculation of  
945 the discrepancies between the number of species whose biology is reported and the total  
946 richness of their clade suggests that only a small portion of the interactions are at least  
947 superficially known (Figure 2). There is also a strong geographic and taxonomic bias in the  
948 description of plant-weevil BSPM systems.

949 For example, host plant identity information is available for most Neotropical  
950 derelomine genera (Franz & Valente 2005). By comparison, host records are only available  
951 for five of the 13 Paleotropical genera of Derelomini (Alonso-Zarazaga & Lyal 1999; Franz &  
952 Valente 2005). The estimated number of derelomine species overall (ca. 300 species; Caldara  
953 et al. 2014; de Medeiros & Vanin 2020; Haran et al. 2020, 2022a) pales in comparison with  
954 the diversity estimates of their main hosts, because the species diversity in the palm family  
955 (Arecaceae) is estimated at about 2500 species (Dransfield et al. 2008; Baker & Couvreur  
956 2013). Since pollination ecology and pollinators have only been identified for a small fraction  
957 of extant palm species, we can hypothesize that dozens – if not hundreds – of palm-weevil  
958 BSPM systems remain to be discovered. Additionally, even though Derelomini are best known  
959 for their associations with palms, recent research has unraveled that some of them are also  
960 associated with plants other than palms. For example, in the Southern African derelomine  
961 fauna, the recently described genus *Ebenacobius* has been found associated with Ebenaceae  
962 and other basal angiosperms. In this genus, no less than 14 new species have been recently  
963 described (Haran et al. 2022a) and at least four others are awaiting description. Moreover,  
964 based on the inferred pattern of PNC in BSPM weevils, Franz & Valente (2005) and Franz  
965 (2006) suggested that most of the ca. 230 species of Carludovicoideae (Cyclanthaceae) and  
966 a significant part of the ca. 800 known *Anthurium* (Araceae) species in the Neotropical region  
967 are pollinated by derelomine weevils. In cycad-weevil BSPM systems, the range of interactions  
968 reported here only reflects our current state of knowledge, and many cycads species have  
969 been insufficiently studied and many interactions remain to be described (Toon et al. 2020).

970 The general lack of knowledge on plant-weevil BSPM systems can be exemplified by  
971 our understanding of Ochyromerini. Pollination activity in this tribe has been only reported  
972 between a few species of *Endaenidius* and *Endaeus* and their Annonaceae hosts and BSPM  
973 has been only formerly identified in one system (*Annona senegalensis* - *Endaeus* spp.; Lau et  
974 al. 2017; Saunders 2020; Dao et al. 2023). Importantly, Ochyromerini has been determined to  
975 be the dominant weevil guild circulating above the canopy in a Southeast Asian dipterocarp  
976 forest (Sprick & Floren 2018), with over 130 undescribed ochyromerine species recorded on  
977 Borneo island alone. Similar species richness was also observed in Cameroon using light  
978 traps (Haran unpublished). Finally, a multitude of undescribed Ochyromerini species (mostly  
979 belonging to the genus *Endaeus*) have been reported by several authors in Asia and Africa  
980 (Hustache 1924; Marshall 1926; Oberprieler 1993; Momose et al. 1998), and it can be  
981 suspected that this group could play an important role in the pollination of Paleotropical  
982 rainforests.

983 In the Annonaceae, a pantropical clade with more than 2400 species, cantharophily  
984 seems to be the most common pollination syndrome (Momose et al. 1998; Gottsberger 1999;  
985 Saunders 2020). The Neotropical species in this plant family sum up to more than 950 species  
986 (Maas et al. 2011), and it is in this region that cantharophilous flowers involving weevil  
987 pollination are the most widespread (Gottsberger 1999; Silberbauer-Gottsberger et al. 2003;  
988 Saravy et al. 2021). This set of interactions requires further investigations in this region since

989 the weevil lineages involved remain unidentified and possibly include undescribed lineages  
990 (the pollinators of Annonaceae reported (Ochyromerini) are exclusively paleotropical; [Alonso-](#)  
991 [Zarazaga & Lyal 1999](#)).

992 Our general overview of weevil-based pollination shows that several additional  
993 pantropical families of angiosperms are – or at least can be considered as partially – pollinated  
994 by weevils (Table S1), with only a small fraction of these interactions having been uncovered  
995 so far. For example, in Clusiaceae, Ebenaceae, Lecythidaceae, Myristicaceae and  
996 Sapotaceae, BSPM by weevils have been only indicated for a small number of species;  
997 however there are likely many more of such interactions because cantharophilous flowers are  
998 known in several genera of these families and the associated weevil lineages also contain a  
999 significant number of undescribed species ([Oberprieler 1993](#); [Caldara et al. 2014](#); [Haran et al.](#)  
1000 [2022b](#)). In some cases, the weevil diversity also exceeds that of the known potential hosts; for  
1001 example, 25 species of the Australian weevil genus *Elleschodes* are known ([Armstrong &](#)  
1002 [Irvine 1990](#); [Caldara et al. 2014](#); [Pullen et al. 2014](#)), of which several species are known to  
1003 pollinate the only three species of *Eupomatia* (Eupomatiaceae) so it is likely that this genus  
1004 also pollinates other plant families. Going further, the Orchidaceae-Baridinae system  
1005 highlights the fact that even weevils lineages that are not known to be pollinators and that lack  
1006 the associated typical morphological features can also be engaged in BSPM ([Nunes et al.](#)  
1007 [2018](#)), with a potential rich array of interactions ([van der Cingel 2001](#)). From the host plant  
1008 perspective, the orchid species studied (*Dichaea cogniauxiana*) also lacks features associated  
1009 with weevil pollination in other groups (i.e., it has a standard orchid floral morphology and  
1010 phenology; [Nunes et al. 2018](#)). Such examples greatly expand the potential spectrum of  
1011 brood-site mutualistic interactions between weevils and plants in tropical biomes and call for  
1012 a complete shift in our perception of the role of these beetles in the functioning of tropical  
1013 ecosystems.

1014 A preliminary estimate of the expected diversity of plant-weevil BSPM systems can be  
1015 made based on the discrepancies between the number of systems described and inferred  
1016 based on PNC (Figure 2; see Appendix 1). The calculation of the ratios for a selection of  
1017 systems (see figure 2) shows that the expected total diversity of species involved is on average  
1018 eight times richer than the number of species inferred from PNC and about 17 times richer  
1019 than the number of species with experimentally-verified BSPM. Based on the species counts  
1020 obtained in this review (see section 1), it is estimated that ca. 2000 plant species could be  
1021 engaged in BSPM with weevils globally. Similarly, the species richness of weevils involved in  
1022 these interactions could be around 2500 species. Thus, plant-weevil interactions probably  
1023 represent the most speciose case of brood-site pollination mutualism, exceeding the diversity  
1024 of other BSPM species-rich groups (e.g., [Lopez-Vaamonde et al. 2009](#); [Cruaud et al. 2010](#)).

## 1025 **5. Concluding remarks: a road map for future** 1026 **research**

### 1027 **5.1 Searching for new plant-weevil BSPM systems**

1028 Accumulating evidence for the role of weevils as specialized brood-pollinators of plants is  
1029 changing our perspective on the role of this super-diverse group of beetles in tropical

1030 ecosystems and beyond. As such, it is time to expand our understanding of pollination ecology  
1031 and to research and test this mutualism in a range of plant and weevil groups that have been  
1032 overlooked. We show in this review that some common features associated with BSPM  
1033 between plants and weevils can help identify novel systems. That said, we also show that  
1034 these mutualistic interactions can exist between lineages that do not exhibit these  
1035 characteristics at all. In this regard, we should also change our perception of the structure of  
1036 these interactions themselves. In light of this reasoning, a wide range of plant-weevil  
1037 interactions should be re-evaluated. A few selected “priority” examples include the potential  
1038 role of several ancient weevil groups (Belidae, Caridae, Cimberididae and Nemonychidae)  
1039 that visit and breed in gymnosperm cones. With the exception of cycads, they are not  
1040 considered pollinators (Oberprieler et al. 2007), but these cases have never been verified in  
1041 detail. In the Neotropics, *Oxycorynus* species (Belidae, Oxycoryninae) are known to visit the  
1042 male and female flowers of parasitic plants of the genus *Lophophytum* (Balanophoraceae),  
1043 the larvae developing in the inflorescences (Ferrer et al. 2011).

1044 Plant-weevil BSPM systems can also be expected in temperate regions, where the  
1045 predominance of anemophily and entomophily based on generalist pollinators might have  
1046 precluded investigations of more specialized systems. In some Western Palearctic willows  
1047 (Salicaceae), flowering cycles show intriguing spikes of volatiles which are not correlated with  
1048 the visits of pollinators considered as efficient (Jürgens et al. 2014). Interestingly, a part of  
1049 these compounds (4-1 dimetoxybenzène) is also produced by several South American palms  
1050 for the specific attraction of beetles, including weevils (Knudsen et al. 2001; Núñez-Avellaneda  
1051 et al. 2005). This case deserves special attention since the male and female inflorescences of  
1052 these dioecious trees also harbor the larval stages of several typical genera of flower weevils  
1053 (*Acalyptus*, *Dorytomus*, *Ellescus*; Hoffmann 1958).

1054 While this review focuses specifically on BSPM, it is also important to highlight that  
1055 weevils may be involved in the pollination of generalist plants, and may not necessarily use  
1056 breeding sites as rewards. One group within Curculionidae that deserves attention is the  
1057 subfamily Baridinae. Here we found only one example of a demonstrated effective pollinator  
1058 (*Montella*, a brood-site pollinator of orchids; Nunes et al. 2018), but this mainly Neotropical  
1059 taxon harbors an extreme diversity with more than 4,000 described species, many of which  
1060 are found in flowers as adults (Prena et al. 2014; B. de Medeiros pers. obs.). Due to their  
1061 unresolved phylogeny, complex taxonomy and very high number of undescribed taxa (Davis  
1062 2011), they are rarely identified beyond the subfamily or tribe level in pollination studies,  
1063 preventing accumulation of knowledge. A great diversity of baridine pollinators, with or without  
1064 brood sites as rewards, remains to be discovered. Interactions may also occur in even more  
1065 unexpected groups of flower-associated weevils. In orchids, a species endemic to the Cayman  
1066 Islands (*Myrmecophila thomsoniana*) is apparently pollinated by the weevil *Lachnopus*  
1067 *vanessablockae* (Curculionidae: Entiminae; Girón et al. 2018) with pollinia transferred by  
1068 contact of the elytra on the stigmatic surface of flowers. As typical for entimines, the larvae of  
1069 this species reproduce in the soil on the root systems of plants (Girón et al. 2018), so it is  
1070 unlikely to be a case of BSPM. These cases demonstrate the need for a better understanding  
1071 of the evolution of pollinators in weevils more broadly, and the contexts leading to BSPM more  
1072 specifically.

1073

## 1074 **5.2 Priority research axes**

### 1075 5.2.1 A plea for description of systems

1076 A better understanding of the diversity and functioning of plant-weevil BSPM systems requires  
1077 detailed studies of the corresponding interactions ([Fenster et al. 2004](#)), but also of the identity  
1078 and boundaries of the species involved. To date, too many plant-weevil BSPM studies have a  
1079 focus on plants and poorly account for pollinator identity. This is partly due to the complexity  
1080 of the taxonomy in these groups (species complexes, small sized species) but also to  
1081 taxonomic shortfalls. As [Franz & Engel \(2010\)](#) pointed out, there are no shortcuts to  
1082 understanding the evolution and diversification of plant-weevil interactions and only detailed  
1083 case studies can provide relevant insights. Taxonomic descriptions are essential prerequisites  
1084 for any study of pollination in the highly specialized plant-weevil BSPM systems, and this effort  
1085 must be made with the relevant expertise of trained taxonomists using integrative approaches  
1086 based on morphology and molecular tools ([Toon et al. 2020](#); [Engel et al. 2021](#)). When  
1087 expertise is not available, we strongly recommend producing at least one DNA barcode  
1088 sequence for each weevil morphospecies involved in a system and depositing it on  
1089 international databases (e.g., [de Medeiros et al. 2019](#)), and using images in addition to names  
1090 to document weevil flower visitors (e.g., [Núñez-Avellaneda & Rojas-Robles, 2008](#); [Núñez et al. 2015](#);  
1091 [Guerrero-Olaya 2017](#); [de Medeiros et al. 2019](#)). The associated voucher specimens  
1092 should also be deposited in permanent collections of museums or institutions. These two  
1093 procedures will make it possible to considerably improve species description rates, but also  
1094 the knowledge on their ecology and distribution.

### 1095 5.2.2 Evolutionary trajectories : when, why and how?

1096 Although preliminary insights on the emergence and maintenance of plant-weevil BSPM are  
1097 readily available, a significant number of evolutionary aspects of these interactions remain to  
1098 be investigated. A first aspect lies in the age of these interactions. Reliable fossils of weevil  
1099 lineages engaged in BSPM are noticeably absent, precluding making precise inferences about  
1100 the ages of these mutualisms. The reasons why so many ancient and more derived plant  
1101 lineages have engaged in BSPM with weevils can be elucidated if their emergence coincides  
1102 with specific past biogeographical or climatic events. More generally, plant-weevil BSPM  
1103 systems offer a rich and diverse range of systems considered as potential models for  
1104 understanding the conditions favoring: (i) the shift from detrimental to beneficial interactions,  
1105 and the role of tripartite interactions in driving these interactions, (ii) transitions between  
1106 pollination syndromes such as between BSPM, other kinds of entomophily, anemophily,  
1107 intermediate or ambophilous systems, and (iii) whether there is a general trend towards higher  
1108 frequency of specialized pollinators engaging in BSPM in tropical biomes. Interestingly, almost  
1109 all plant lineages exhibiting cantharophilous and thermogenic flowers are widely associated  
1110 with weevils. It remains to be determined to what extent the association with weevils  
1111 specifically was a key factor in the emergence of cantharophily in general ([Bernhardt 2000](#)).  
1112 Other poorly documented aspects of these interactions include the potential association with  
1113 specific microorganisms for colonization of breeding sites and whether plants alter their  
1114 physiology to favor the development of the hosted pollinators. Finally, an unexplored aspect  
1115 of these specialized interactions lies in their evolution in the context of current human-induced  
1116 ecosystem disruption. The present multifaceted changes affecting the biosphere and insects  
1117 in particular ([Potts et al. 2016](#); [Vanderplanck et al. 2021](#); [Wagner et al. 2021](#)) provide a context  
1118 for an assessment of the resilience or vulnerability of these systems.

1119

1120

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## 1131 **Conflict of interest disclosure**

1132 The authors of this article declare that they have no financial conflict of interest with the content  
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## 1978 **Supplementary information**

1979 **Table S1.** List of plant-weevil brood-site pollination mutualism obtained through literature  
1980 review completed by unpublished observations. Weevil names and authorship follows the  
1981 Weevil taxa database (accessed January 2023) otherwise stated. Plant names have been  
1982 updated according to the World Flora Online (<http://www.worldfloraonline.org/>, accessed  
1983 August 2022).

## 1985 **Appendix 1**

### 1987 **Material and Methods**

1988 The literature review was conducted directly through search of keywords on Web of Science  
1989 and indirectly through reference cited in review papers on specific plant-weevil pollination  
1990 systems. About 110 articles, including five review papers were screened to search for species-  
1991 specific plant weevil interactions, but also the ecological, phenological and physiological traits  
1992 associated with these interactions. These published data were completed by unpublished field  
1993 observations provided by colleagues or the authors themselves. For each species-species  
1994 interaction, we compiled an indication of classification (family rank), the location of the  
1995 breeding site of larval stages and the known evidence of pollination mutualism. The  
1996 experimental demonstration of an effective brood-site pollination mutualism requires the  
1997 observation of breeding sites of larval stage of the putative pollinator and the investigation of  
1998 pollination efficacy of the adults by a pollinator exclusion method. This time consuming  
1999 process is rarely conducted, except for a few model systems. In order to integrate a consistent  
2000 number of interactions without risk of overestimation, we followed the following rationale:  
2001 BSPM interactions were reported only when, 1) the weevil species is identified at least at the  
2002 tribal level, 2) BSPM interactions has been shown in a congeneric plant or weevil species  
2003 (phylogenetic niche conservatism, see sections 1 and 2.3.5) and/or 3) plants and/or weevils  
2004 show typical traits associated with BSPM (see sections 1 and 2). We explicitly excluded cases  
2005 of flower visitors reported in one publication that were demonstrated not to be relevant  
2006 pollinators in another one. This strategy has limitations but reflects the current state of  
2007 knowledge on these systems and should be seen as a first assessment of their extent in  
2008 overlooked tropical biomes. When relevant, details or a discussion on knowledge gaps were  
2009 added (see column "notes" in Table S1).

2010  
2011 A subset of plant-weevil interactions was used to estimate the extent of undescribed  
2012 interactions (Derelomini-angiosperms dicots/palms/Carludovicoideae, Ochyromerini-  
2013 angiosperms dicots, Storerini-Eupomatiaceae). All these types of interactions have in common  
2014 (except in the Derelomini-angiosperms dicots): effective BSPM has been reported at least in  
2015 one system; highly similar interactions are known in closely related genera and species; and  
2016 an estimate of the global diversity of the weevil of plant clade is available (published records  
2017 or author unpublished observations, see section 4 and Table S1). For these five groups, we  
2018 reported the number of effective BSPM interactions reported, the expected number of BSPM  
2019 expected based on phylogenetic niche conservatism (see section 1 and above) and an  
2020 estimate of the full diversity (of the weevil except for the Carludovicoideae) of the clade  
2021 involved in the interactions (see statistics in figure 2). Based on these values obtained from  
2022 the literature we computed the ratios between experimentally-verified BSPM and expected  
2023 BSPM based on PNC, and also between experimentally-verified BSPM and the full diversity

2024 of the lineages included (ratio of 8 and 17 respectively). Considering the species counts  
2025 obtained in this review (see section 1) and these ratios, we estimated that about 2000 plants  
2026 (250 x 8) and around 2500 weevil species (300 x 8) could be engaged in BSPM globally. We  
2027 chose the lower range estimates to avoid any overstatement.

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