

A review of the biology, ecology and control of saddle gall midge, *Haplodiplosis marginata* (Diptera: Cecidomyiidae) with a focus on phenological forecasting

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4

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10

11 Running title: Biology, ecology and control of *H. marginata*

12

13 **Abstract**

14

15 Saddle gall midge *Haplodiplosis marginata* (Diptera: Cecidomyiidae) is a pest of cereals
16 across Europe. The occasional nature of this pest has resulted in limited and sporadic
17 research activity. There remain important gaps in knowledge due either to a genuine lack of
18 research or to previous research being difficult to access. These knowledge gaps make the
19 development of effective control options difficult. Here, we review the existing literature in an
20 attempt to consolidate the information on *H. marginata* from research which spans several
21 decades and encompasses many different countries. The current distribution and pest
22 status of this insect are updated, along with the methods of cultural and chemical control
23 available to growers. The biology and life history of the insect are described in detail and the
24 ecological processes governing them are discussed. A forecasting model is presented which
25 allows the emergence of this pest in the UK to be predicted from degree day data, and the
26 potential application of this model in management decisions is discussed. Finally, the areas
27 in most need of further research are identified, along with suggestions of how this

28 information can be used to help develop effective and sustainable management solutions for
29 this pest.

30

31 **Keywords**

32 Cecidomyiidae, *Haplodiplosis marginata*, wheat, IPM, gall midge, phenological forecasting

33

34 **Introduction**

35

36 Saddle gall midge (*Haplodiplosis marginata* von Roser; *Haplodiplosis equestris* Wagner) is a
37 polyphagous pest of cereal crops across Europe. The first reference to this species in the
38 UK is by Omerod (1890), who received samples of injured barley stems from Lincolnshire
39 exhibiting the characteristic galling of *H. marginata*. Identification was confirmed in 1909
40 when adults were reared from larvae found in infested wheat stems in Pembrokeshire
41 (Enock, 1909). *Haplodiplosis marginata* has since become a sporadic pest of wheat, barley
42 and rye crops in the UK, particularly in central and eastern areas of England. In the mid-
43 1960s, a survey of the main cereal growing areas showed the species to be prevalent at low
44 levels but of no economic interest (Empson, 1965). Between 1967 and 1972 however,
45 severe outbreaks were reported in isolated areas across the country (Golightly & Woodville,
46 1974; Woodville, 1968, 1970, 1973). The pest was not considered to be a problem again
47 until 2010, when localised outbreaks were reported in central England (Allison, 2010; Case,
48 2011). Reports of the midge being present at lower levels have continued since this time
49 (HGCA, 2012).

50

51 The 40-year interval between economically damaging outbreaks of *H. marginata* in the UK
52 and other European countries has resulted in a lack of continuity in research into this pest.
53 For example, in the UK, prior to 2012 there had been no research published on *H. marginata*
54 since 1974. A similar pattern can be observed in other European countries in which *H.*
55 *marginata* has historically been economically damaging, with the last decade seeing an

56 increase in research activity. The sporadic nature of this pest has frustrated research efforts
57 as studies rarely coincide with serious outbreaks and long term information is sparse.
58 Additionally, existing research on *H. marginata* is fragmented across several countries and
59 several languages which, in combination with the age of the publications, can make
60 accessing and translating them difficult, particularly where there is no digital copy available.
61 The resulting knowledge gap has hampered attempts to respond to this re-emerging pest.
62 This review aims to consolidate existing information available on this insect so that a
63 consensus may be reached on key aspects of *H. marginata* biology and ecology, in
64 particular the effect of environmental conditions on insect development. This will then
65 provide a comprehensive source of information to inform and shape current and future
66 research and management of *H. marginata*. A phenological forecasting model aimed at
67 predicting the emergence of *H. marginata* in the UK is presented. Using data collected in
68 recent years, a degree-day based model is proposed that demonstrates the feasibility of
69 generating an early warning system for the pest based on environmental conditions. It is
70 hoped that with further research, the model could be used as a reliable tool to determine
71 appropriate dates for in-field monitoring as part of an integrated pest management
72 programme.

73

74 1.1 Geographical distribution

75 There is a long history of saddle gall midge attacking cereal crops in Europe. Reports of 'red
76 vernicules' on wheat and barley in Bavaria in 1692 are thought to refer to *H. marginata*
77 larvae (Weidner, 1985). The first economically important attack was reported in the former
78 Yugoslavia in 1956 (Skuhravý *et al.*, 1983), with further serious outbreaks occurring across
79 Europe over several decades in many countries including Belgium (Latteur, 1972), Romania
80 (Popov *et al.*, 1998), Poland (Walczak, 1982), Hungary (Racz, 1973), the Netherlands
81 (Nijveldt & Hulshoff, 1968), Sweden (Eklund *et al.*, 2005) and the Czech Republic (Skuhravý
82 *et al.*, 1983) (Figure 1).

83

84 A survey of growers and agronomists in 2011 by HGCA (known as AHDB Cereals &
85 Oilseeds from June 2015) in conjunction with ADAS, AICC, Dow AgroSciences, and NIAB
86 TAG, demonstrated that the current UK distribution of *H. marginata* ranges from East
87 Lothian to Cornwall (Caroline Nicholls, AHDB Cereals & Oilseeds, Pers. Comm., Figure 2).
88 The known distribution of this pest is primarily based on reports following outbreaks and as
89 such is likely to under-represent its range.

90

91

92 **2. Taxonomy and morphology**

93 2.1 Species history

94 The saddle gall midge belongs to the family Cecidomyiidae within the order Diptera and
95 suborder Nematocera. This family is distinguished by the presence of a sclerotized sternal
96 spatula in the larva and abdominal colouration that ranges from yellow to red. The subfamily
97 Cecidomyiinae, to which *H. marginata* belongs, is characterised by reduced wing venation,
98 antennae with fewer than 14 flagellomeres and larvae with only two dorsal papillae on the
99 eighth abdominal segment (Harris, 1966; Gagné, 2004). Within the Cecidomyiinae, *H.*
100 *marginata* belongs to the supertribe Cecidomyiidi, distinguished by the unique bi-nodal
101 flagellomeres and many-looped circumfila on the male antennae (Gagné, 1994; Gagné,
102 2004).

103

104 *Diplosis marginata* was first described in 1840 by von Roser from specimens found on barley
105 stems (Nijveldt & Hulshoff, 1968; Skuhrový *et al.*, 1993). In 1871, Wagner described
106 *Diplosis equestris* found on wheat in Germany, giving it the common name "sattelmücke"
107 (saddle midge) to make it easier for farmers to identify (Wagner, 1871). In 1900 *D. equestris*
108 was moved into the genus *Clinodiplosis* by Kieffer and it was again moved in 1910 into the
109 newly-created genus *Haplodiplosis* by Rübsaamen (Rübsaamen, 1910; Nijveldt, 1967).
110 *Diplosis marginata* and *Haplodiplosis equestris* were later determined to be the same

111 species by Nijveldt (1967), who concluded that *H. marginata* (von Roser) should be taken as
112 the accepted name. *Diplosis equestris* (Wagner) is now listed as a synonym.

113

114 2.2 Descriptions of stages

115 2.2.1 Eggs and larval stages

116 The eggs of *H. marginata* are smooth and oval-shaped, normally 0.32 - 0.50 mm in length,
117 with a slight red colouration that turns orange-red over time (Nijveldt & Hulshoff, 1968).
118 Skuhravý *et al.* (1993) describe the morphology of the different developmental stages of *H.*
119 *marginata*. As with other Cecidomyiidae, there are three larval instars. First instar larvae
120 are 0.6 – 1.0 mm in length, ranging from white to pale red. The second instar larvae are up
121 to 1.5 mm long and dark yellow in colour with a visible gastrointestinal tract. Third instar
122 larvae are between 2.5 mm and 4.0 mm long, 1.0 - 1.3 mm wide, pale red to red in colour,
123 and have the characteristic sternal spatula on the ventral part of the third thoracic segment.
124 The pupae are 3.5 - 4.5 mm long and are initially red, however as they develop, the terminal
125 section gradually turns black. Two pairs of horn-like protrusions are located at the anterior
126 end, the largest of which are thought to serve as respiratory organs (Nijveldt & Hulshoff,
127 1968). The abdominal areas of the pupae are orange-red in males and bright red in females
128 (Skuhravý *et al.*, 1993).

129 3.2.2 Adults

130 Adult midges range in size from 2 – 5 mm depending on the nutrient availability to the
131 developing larvae. Females are generally larger than males. Egg numbers are correlated
132 with female size and can be as high as 260 per individual (Skuhravý *et al.*, 1993). Adults of
133 both sexes have a black head and thorax with a red-coloured abdomen, however, the
134 abdomen of the females is wider and more brightly coloured due to the eggs inside. The
135 wing length of the female averages 3 - 4 mm. Adults are sexed on the basis of antennal and
136 genital morphology, as well as the presence of eggs in the female. Both sexes have
137 antennae with two basal segments and 12 flagellomeres (Nijveldt & Hulshoff, 1968). All but

138 the terminal flagellomeres of the male antennae are binodose, having two swellings at either
139 end, with rings of short circumfilar loops on each node as well as simple circumfila. The
140 flagellar segments of the female are cylindrical and elongated with two rings of sensillary
141 hairs on each (Figure 4) (Harris, 1966; Nijveldt & Hulshoff, 1968; Skuhrový *et al.*, 1993). The
142 male copulatory organ is rod-shaped with a two-lobed upper lamella and shorter, lower
143 lamella. The female ovipositor comprises three lamellae, the upper two larger than the
144 lower, all with short sensory hairs (Nijveldt & Hulshoff, 1968).

145

146 **3. Life cycle and pest status**

147 3.1 Life Cycle

148 The life cycle of *H. marginata* was recently described in detail by Censier *et al.* (2015b).
149 *Haplodiplosis marginata* is a univoltine species with the flight period beginning as early as
150 mid-April and lasting until the beginning of July depending on environmental conditions
151 (Censier *et al.*, 2012). Adults are short-lived and have limited dispersal ability. Lifespan
152 estimates vary between 1 and 7 days (Nijveldt & Hulshoff, 1968, Popov *et al.*, 1998) and
153 flight distances average 18 m (Schütte, 1964a). Females may undertake several short
154 flights seeking a suitable oviposition site (Skuhrový *et al.*, 1983). Eggs are laid in a chain-
155 like or raft-like formation along the leaf veins of cereals and grasses (Dewar, 2012, Censier
156 *et al.*, 2015b). Hatching occurs 1 - 2 weeks after oviposition depending on environmental
157 conditions following which the larvae migrate down the leaf and begin to feed on the stem
158 from beneath the leaf sheath (Golightly & Woodville, 1974). Larval feeding on the stem
159 results in galls 2 - 5 mm in length which appear as the elongated 'saddle shaped'
160 depressions characteristic of this species. The larvae reach maturity between June and mid-
161 July and drop from the stem to enter diapause in chambers in the soil where they overwinter
162 (Golightly & Woodville, 1974; Skuhrový *et al.*, 1993). Pupation generally occurs the following
163 spring, however larvae can remain in diapause in the soil for several years (Nijveldt &

164 Hulshoff, 1968, Popov *et al.*, 1998; Dewar, 2012). Rarely, larvae can be found in cocoons in
165 the soil stage (Censier *et al.*, 2014a).

166

167 3.2 Outbreaks

168 The reasons for the recent resurgence of *H. marginata* as a pest are as yet unknown. This
169 species is thought to have benefitted in part from the intensification of farming methods,
170 particularly the continuous sowing of wheat and barley crops (Skuhrový *et al.*, 1983). The
171 HGCA survey, the results of which are summarised in Roberts *et al.*, 2014, showed that the
172 majority of crops (48%) displaying symptoms consistent with *H. marginata* infestation were
173 continuous cereal crops. A further 24% were however, first wheat crops, which can be
174 explained by observations that populations are able to persist in the soil for more than one
175 year (Nijveldt & Hulshoff, 1968, Popov *et al.*, 1998; Dewar, 2012). Given the relatively low
176 dispersal ability of this pest, localised outbreaks are more likely to occur where wheat is
177 being grown successively, or in close proximity to previously affected fields (Schütte, 1964b).
178 Since 1980 the continuous cropping of wheat has steadily declined in the UK according to
179 the Defra Winter Wheat Pest and Disease Survey (Judith Turner, Fera, Pers Comm)
180 suggesting that on a landscape scale, continuous wheat systems do not explain increases in
181 *H. marginata* outbreaks. It has been suggested that selectively breeding cereal varieties to
182 increase productivity may have increased the availability of food resources for developing
183 larvae and reduced levels of natural resistance to the pest (Skuhrový *et al.*, 1983), although
184 the mechanism of any such resistance is unknown. Other possible factors include increased
185 use of minimum tillage, which may allow better pupal survival as they are not buried as
186 deeply by cultivations. The reduced disturbance from minimum tillage would however, also
187 benefit natural enemies (Landis *et al.*, 2000), which could negate some of the benefit to pest
188 populations. Rates of predation of *H. marginata* by natural enemies in the field however, are
189 as yet unknown (see section 4.3). Pesticide usage is likely to have had an effect on *H.*
190 *marginata* populations. This includes long term changes in the active substances being
191 used and the rate of application. For example, the total weight of insecticides applied to

192 cereal crops in the UK has decreased by 54% since 1990 (Fera, 2016), although this will in
193 part have been due to improvements in the efficiency of the active substances. The total
194 percentage area of cereal crops treated with an insecticide has also declined since 1990,
195 with most crops only receiving a single treatment (Fera, 2016). Although it is a complex area
196 of study, it is possible that such trends have benefited *H. marginata* populations in the long
197 term. Changes in the abundance or diversity of grass species on arable land may also have
198 influenced *H. marginata* populations. For example, a survey of arable weeds in 2000
199 showed the abundance of some common species such as black-grass (*Alopecurus*
200 *myosuroides*) and couch grass (*Elymus repens*) had either increased or remained stable
201 since the 1960s (Sutcliffe & Kay, 2000). Black-grass in particular is now a serious problem
202 on arable land due to the increasing incidence of multi-herbicide resistance in this species
203 (Hull *et al.*, 2014). Both species have the potential to act as wild hosts to *H. marginata*
204 (Skuhrová & Skuhrový, 2014), allowing populations to persist in the absence of a cereal crop
205 (see below).

206

207 3.3 Host range

208 In a study of host plant preferences comparing 48 different species of cereals and grasses in
209 the field, *E. repens* was the most heavily attacked by *H. marginata* (Schütte, 1964b).
210 *Haplodiplosis marginata* also had the lowest levels of larval mortality on *E. repens* when
211 compared with other host plants such as wheat and barley (Skuhrový *et al.*, 1983). *Elymus*
212 *repens* and other wild grasses have the potential to act as alternate hosts but it is as yet
213 unclear whether increased availability of alternate hosts would facilitate pest populations or
214 reduce pressure on the crop (Schütte, 1964b, Skuhrový *et al.*, 1983; Woodville, 1968).
215 Variation in severity of attack, defined as the number of galls per stem, has been shown to
216 occur between different varieties of wheat, barley and rye (Skuhrový *et al.*, 1993) and
217 between countries in which the same variety is grown (Nijveldt & Hulshoff, 1968). Some
218 degree of resistance to *H. marginata* was found in 28 out of 400 wheat varieties trialled in
219 the Netherlands in 1966 as judged by a lack of gall formation (Nijveldt & Hulshoff, 1968), and

220 complete resistance has recently been found in an old Russian variety (Mike Taylor,
221 Limagrain, Pers. Comm.), although the exact mechanism of this resistance is currently
222 unknown. No modern variety has however, yet been identified that offers complete
223 resistance, possibly as a result of outbreeding of any resistance traits (Skuhravý *et al.*, 1993,
224 Censier *et al.*, 2015b). Oats are a poor host with data suggesting that only 2 - 5% of the
225 larvae survive following hatching (Skuhravý *et al.*, 1993). A more recent study found that
226 oats were a less attractive host when sown next to spring wheat, and potential resistance
227 was observed in one variety on which no galls were formed despite evidence of oviposition
228 on the leaves (Censier *et al.*, 2013). Unlike with cereal leaf beetle (*Oulema melanopus*), a
229 higher density of leaf pubescence does not reduce the rate of infestation of *H. marginata* on
230 wheat (Schillinger & Gallun, 1968; Lange & Jochensen, 1987).

231

232 3.4 Crop Damage

233 3.4.1 Primary crop damage

234 Crops most at risk are spring crops, particularly wheat and barley (Skuhravý *et al.*, 1983,
235 Skuhravý *et al.*, 1993) but damage has also occurred in late sown (after mid-November)
236 winter wheat and barley (Pope & Ellis, 2012; HGCA, 2012). Golightly and Woodville (1974)
237 observed that damage is most severe when egg-hatch coincides with stem extension, whilst
238 losses are incurred on crops that are in or beyond the booting stage at the time of larval
239 infestation are minimal. Cereal crops are therefore most vulnerable to attack between
240 growth stages 31-39 (Sylvester-Bradley *et al.*, 2008). Early sown spring crops appear to be
241 less susceptible as the plant tissue is more mature at the time of egg hatch, potentially
242 making it more difficult for the larvae to feed (Skuhravý *et al.*, 1993).

243 Where high population densities occur, there may be as many as 60 galls per stem
244 (Skuhrová & Skuhravý, 2014). Galls are generally formed on the top three internodes where
245 the plant tissue is least mature. A substance secreted by the larvae inhibits the development

246 of epidermal cells in the immediate vicinity of the insect, while the surrounding tissues
247 continue to develop, forming the gall (Nijveldt & Hulshoff, 1968). Development of vascular
248 tissue is disrupted around the site of the gall, which can restrict the flow of nutrients to the
249 ear. This can lead to shrivelled or underdeveloped grains (Golightly, 1979) and reductions in
250 stem length (De Clercq & D'Herde, 1972; Popov *et al.*, 1998), ear length (De Clercq &
251 D'Herde, 1972), and thousand grain weight (Woodville, 1968). Galling has been shown to
252 result in reductions in grain number and thousand grain weight in wheat by 63% and 64%
253 respectively (Popov *et al.*, 1998).

254 3.4.2 Secondary crop damage

255 Destruction of the plant cuticle in the area of the gall leaves the plant vulnerable to
256 secondary attack by bacteria or fungi, particularly in wet weather (Nijveldt & Hulshoff, 1968;
257 Skuhravý, 1993; Eklund, 2005). Gall formation can also weaken the stem which increases
258 the risk of lodging, where the stem breaks or bends so that the ear falls below the level of
259 the combine and cannot be harvested (Woodville, 1970; Golightly & Woodville, 1974;
260 Gratwick, 1992). This is of particular concern where attack coincides with a period of high
261 winds and can be responsible for substantial yield losses.

262

263 3.5 Economic consequences

264 3.5.1 Potential yield loss

265 Estimates suggest that when the percentage of infested wheat stems reaches 70%, losses
266 of 2.2 t/ha could occur (Skuhravá & Skuhravý, 2014). A recent study in Belgium showed a
267 correlation between number of galls and yield loss in winter wheat, in the most severe case
268 yields fell by 191 kg/ha (0.191 t/ha) for every increase of 100 galls per 100 stems (Censier *et*
269 *al.*, 2015a). Past outbreaks of saddle gall midge in the UK have resulted in losses of 0.6 t/ha
270 (Woodville, 1968). There are no published figures for yield losses incurred in the recent UK
271 outbreaks, however, the recent HGCA survey anecdotally reports that 52% of respondents

272 who observed saddle gall midge infestation observed subsequent yield loss. In the most
273 severe case, there was an estimated 70% decrease in yield as reported by an agronomist in
274 Buckinghamshire (Ellis *et al.*, 2014).

275 3.5.2 Economic thresholds

276 Estimates of thresholds of soil densities of larvae above which economic losses occur range
277 from 12.4 million per hectare (Golightly & Woodville, 1974) to as little as 300,000 per hectare
278 (Popov *et al.*, 1998). In terms of infestation, it has been estimated that more than three galls
279 per stem causes significant damage and loss of yield (Skuhravý, 1993). In Denmark, this
280 threshold rises to five galls per stem (Woodville, 1973), in the UK it is between 4.5 and nine
281 galls (Ellis *et al.*, 2014) and in Germany it is between five and ten (Schütte, 1983). The
282 variation in these estimates demonstrates the current uncertainty surrounding the economic
283 impact of this pest. Thresholds based on gall number are of limited use in pest management
284 however, as control measures are likely to be ineffective at this stage. It is acknowledged
285 that the actual damage caused depends on many factors such as crop type, growth stage
286 and weather conditions (De Clercq & D'Herde, 1972; Censier *et al.* 2015a).

287

288 **4. Control methods and IPM**

289 4.1 Cultural control

290 Agricultural systems in which cereal crops are grown continuously are particularly
291 susceptible to outbreaks of *H. marginata* as high densities of larvae accumulate in the soil.
292 Break crops are generally accepted as an effective means of reducing infestation by
293 depleting larval soil populations (Censier *et al.*, 2015b). Skuhravý *et al.* (1993) showed that
294 infestations of wheat varieties were greatly reduced when sown after non-susceptible crops
295 such as lucerne or potato rather than susceptible cereals. Even so, with the potential for *H.*
296 *marginata* larvae to enter extended diapause, breaks of one year may not always be enough
297 to reduce soil populations to below economically damaging levels. Field trials over six years

298 in the Netherlands showed that a two year break did not entirely eradicate *H. marginata*
299 populations, and oats were often not particularly effective as a break crop despite being a
300 relatively poor host plant (Nijveldt & Hulshoff, 1968). The introduction of the EU crop
301 diversification requirement as part of the 2013 CAP reform aims to encourage farmers to
302 grow a greater variety of crops by specifying a minimum number of crops and a maximum
303 land cover amount for the two main crops (Regulation (EU) 1307/2013, 2013). This may
304 result in a reduction in *H. marginata* outbreaks if continuous wheat systems are disrupted by
305 widespread use of rotations and break crops.

306

307 4.2 Chemical control

308 Chemical controls applied directly to the soil are of limited efficacy, probably owing to
309 insufficient penetration of the soil to the depths where overwintering larvae are found (Popov
310 *et al.*, 1998). Foliar applications of organophosphates such as malathion and dimethoate
311 applied to the crop have shown some efficacy against eggs and newly-hatched larvae of *H.*
312 *marginata* on wheat in Romania (Popov *et al.*, 1998); and in the UK chlorpyrifos effectively
313 reduced numbers of larvae and galls in wheat when applied at the visible flag leaf stage
314 (Zadoks GS 37) (Roberts *et al.*, 2014). Control has also been achieved with pyrethroids
315 such as alpha-cypermethrin (Popov *et al.*, 1998), and with deltamethrin, lambda-cyhalothrin
316 and tau-fluvalinate on winter wheat (Censier *et al.*, 2012; Ellis *et al.*, 2014; Censier *et al.*,
317 2015a).

318

319 Early recommendations for chemical control advised using persistent insecticides and to
320 time applications for three to five days after the first adults were recorded or when the eggs
321 were found on 20% of leaves (Skuhravý *et al.*, 1993). There is a limited timeframe for
322 application as once the larvae are beneath the leaf sheath they are protected from contact-
323 acting insecticides (Gratwick, 1992). Repeated applications may be warranted as adult flight
324 can persist for up to ten weeks (Censier *et al.*, 2012). Censier *et al.* (2012) found that

325 treating the crop with pyrethroid insecticides twice with a two week interval resulted in 75 -
326 87% efficacy based on reductions in the percentage of attacked stems and mean gall
327 number per stem. In a further study the authors recommended treating the crop to coincide
328 with peak adult flight (Censier *et al.*, 2015a) The authors, however, acknowledged that
329 phenological monitoring was essential in order to synchronise applications with vulnerable
330 life stages (Censier *et al.*, 2015a). Ellis *et al.* (2014) reported that chemical controls applied
331 at the start of adult emergence resulted in the lowest yield loss, although treatments applied
332 7 – 10 days post emergence or when the first eggs were seen also reduced midge
333 infestation. Ideally a forecasting model, such as the one presented here (see section 6),
334 would be used to predict the onset of adult emergence and used to time in-field monitoring
335 efforts on which chemical treatments may be based.

336

337 4.3 Natural enemies

338 Carabidae or Staphylinidae may offer some degree of control having been observed feeding
339 on larvae of *H. marginata* at the soil surface (Golightly & Woodville, 1974; Skuhrový *et al.*,
340 1993). Species from these families have similarly been shown to feed on orange wheat
341 blossom midge larvae (*S. mosellana*); a species that shares many characteristics with
342 saddle gall midge (Holland *et al.*, 1996). Larval stages may be parasitised by *Chrysocharis*
343 *amyite* and *Platygaster taras* (Baier, 1963; Skuhrový, 1982), although research suggests that
344 saddle gall midge mortality due to the latter is only 1 - 2% and the former only attacks larvae
345 found on wild grasses as females are unable to penetrate the leaf sheaths of cereals with
346 their short ovipositors (Nijveldt & Hulshoff, 1968; Woodville, 1968; DeClercq & D'Herde
347 1972). Parasitism of *H. marginata* eggs by a novel parasitic hymenopteran was found in
348 Belgium in 1965. The species was described as *Platygaster equestris* in reference to the
349 host's earlier name (*Haplodiplosis equestris*) and was found to parasitise up to 10% of *H.*
350 *marginata* eggs (Spittler, 1969). An unidentified Chalcidid in Austria was found to parasitise
351 up to 23% of *H. marginata* eggs according to Faber (1959 cited in Nijveldt & Hulshoff, 1968).
352 Another *Platygaster* species was observed in 1966 attacking *H. marginata* larvae in the

353 Netherlands, parasitising between 1 and 40 % of larvae. Within a year, populations of the
354 parasitoid overtook that of *H. marginata* although it is not clear whether declines in the latter
355 were because of parasitism alone (Nijveldt & Hulshoff, 1968). *Holarcticesa clinius* is also
356 recorded as a parasitoid of *H. marginata* in the Universal Chalcidoidea Database (Noyes,
357 2012). Although populations of such parasitoids may help to keep *H. marginata* numbers in
358 check, there is little evidence to suggest that any of these species would be appropriate for
359 use as biological controls.

360 **5. Influence of environmental conditions on *H. marginata***

361 Like many Cecidomyiidae, outbreaks of *H. marginata* are highly sporadic. Populations
362 fluctuate from year to year and in the absence of a single correlating biotic or abiotic factor,
363 predictions of future population size are difficult (Woodville, 1973; Basedow, 1986).
364 Numbers of larvae in the soil can increase gradually over several years or rapidly within a
365 generation (Basedow, 1986). High larval population densities in the soil can result in
366 outbreaks (Skuhrový *et al.* 1993), however, the level of damage further depends on
367 elements such as reproductive success, crop susceptibility and weather conditions

368

369 5.1 Effects of temperature and moisture on *H. marginata* development

370 Skuhrový *et al.* (1983) have reported high larval mortality in the soil stage after recording
371 emergence levels of just 5-12% in field experiments in Slovakia. It is not clear, however,
372 what proportion of the population remained in diapause. Population declines have also been
373 observed following unfavourable weather conditions such as cold temperatures and
374 extremes of soil moisture content, however, this is not always consistent (Woodville, 1973;
375 Popov *et al.* 1998; Skuhrový, 1983; Skuhrový *et al.* 1993, Pope & Ellis, 2012). There is
376 evidence of larval resilience in the soil stage. Cold tolerance was observed in a laboratory
377 experiment by Nijveldt and Hulshoff (1968), where 49% of larvae survived being in frozen
378 clay soil after 48 days, however, survival was zero after two weeks at -10 °C in further
379 experiments by De Clercq and D'Herde (1972). *Haplodiplosis marginata* larvae may also

380 survive periods of flooding: over 50% of 100 larvae were able to survive immersion in water
381 for 28 days. This supports field observations of larvae surviving in flooded soils (Nijveldt &
382 Hulshoff, 1968) but disagrees with a recent UK study by Pope and Ellis (2012) who observed
383 high levels of larval mortality following heavy rainfall. Additionally, very wet weather in
384 summer may cause eggs to be washed off the leaves before hatching (Gratwick, 1992).
385 Conversely, very hot and dry summers may result in egg or larval desiccation (Eklund,
386 2005). The prevalence of *H. marginata* in heavy soils that contain a high proportion of clay
387 (Golightly & Woodville, 1974) is thought to be due to the higher moisture content of heavy
388 soils protecting the larvae from desiccation (Andersson, 1969). Nonetheless, some drought
389 tolerance has been recorded in experiments by Nijveldt and Hulshoff (1968): after 14 days of
390 drought under controlled conditions, 52% of 600 larvae developed into adults while 15%
391 remained in diapause. Larval survival dropped to 11% after 60 days of drought (Nijveldt &
392 Hulshoff, 1968). It was thought that, as with the Cecidomyiid wheat blossom midges
393 *Sitodiplosis mosellana* (orange wheat blossom midge) and *Contarinia tritici* (yellow wheat
394 blossom midge) the larvae overwinter in cocoons, however cocoons have only ever been
395 found in three field populations; one each in the UK (Barnes, 1956), the Netherlands
396 (Nijveldt & Hulshoff, 1968) and Belgium (Censier *et al.*, 2014a). Cocoon formation is
397 therefore considered to be rare in this species and is likely to be a response to drought,
398 preventing desiccation (Nijveldt & Hulshoff, 1968; Censier *et al.*, 2014a).

399

400 Temperature and moisture are likely to be closely linked to the termination of diapause
401 (Gratwick, 1992). *Sitodiplosis mosellana*, *Contarinia tritici* and *Contarinia sorghicola*
402 (sorghum midge), also in the supertribe Cecidomyiidi, all require an interaction between
403 temperature and moisture for diapause termination and adult emergence (Basedow, 1977;
404 Baxendale & Teetes, 1983; Oakley, 2009, Jacquemin *et al.*, 2014). Increased soil moisture
405 may make it easier for larvae to move up through the soil profile to pupate whilst rising
406 temperatures are likely to trigger the end of diapause for this species. This is supported in
407 the literature, with numerous reports of warm, humid conditions prevailing shortly before an

408 outbreak (Gratwick, 1992). It has been observed that under laboratory conditions, diapause
409 in *H. marginata* is not terminated below 10°C (Baier, 1963) with larvae unable to survive
410 prolonged temperatures of 5°C or 30°C (Nijveldt & Hulshoff, 1968). If conditions are too dry,
411 about 75% of the larvae will remain in diapause for another year (Dewar, 2012) but even in
412 suitable conditions, some 20% of larvae may extend diapause (Popov *et al.*, 1998).
413 Extended larval diapause has been observed in other cecidomyiids (Harris & Foster, 1999).
414 The orange wheat blossom midge, *S. mosellana* can remain in the soil within cocoons for
415 ten years or more (Oakley, 2009). The duration of diapause in *H. marginata* has been
416 shown to extend to at least six years, and is like to vary according to both biotic and abiotic
417 factors (Nijveldt & Hulshoff, 1968).

418

419 **6. Developing a degree-day model for predicting *H. marginata* emergence**

420 A study was completed to assess the feasibility of developing a model to reliably predict the
421 emergence of *H. marginata* in the UK. Approximate dates of *H. marginata* emergence were
422 established for sites across the UK in the years 2014 (four sites) and 2015 (seven sites).
423 Emergence traps (2014) and pheromone traps (2015) were placed in the fields in mid-April
424 and monitored on a weekly basis. Emergence traps consisted of an upturned seedling tray
425 which was coated on the underside with insect barrier glue (Agralan Ltd, Ashton Keynes,
426 UK) and secured on the soil surface by wooden stakes. Pheromone traps comprised a
427 standard red delta trap with a removable sticky insert (Agralan Ltd, Ashton Keynes, UK),
428 onto which plastic vials of the *H. marginata* sex pheromone, 2-nonyl butyrate, were placed
429 (Censier *et al.*, 2014b). Traps were positioned at least 10 m into the crop and the
430 pheromone traps were hung at crop height. The date midway between when midge were
431 first found on the trap and when the trap was last checked was used as the emergence date.
432 Hourly soil temperatures and daily rainfall data were obtained from the Met Office MIDAS
433 network of weather stations (Met Office, 2012). Each station was within 20 km of each field
434 site. The distance of the meteorological stations to the emergence sites is likely to be a

435 source of error in the model, however the data is representative of that which would be
436 available to farmers in order to use the model.

437

438 6.1 Model development

439 Two models were produced based on degree day models previously developed for *S.*
440 *mosellana* in Canada (Elliott *et al.*, 2009) and Belgium (Jacquemin *et al.*, 2014). The first
441 model used hourly soil temperatures to calculate the accumulated degree days above a
442 base temperature from 1st March until the date of emergence for each site. Degree hours
443 were calculated by subtracting the base temperature from the mean hourly temperature and
444 summing all positive values. The total was then divided by 24 to convert it to degree days
445 (Cesaraccio *et al.*, 2001). The mean number of degree days was then used to predict
446 emergence dates for all sites. Base temperatures ranging from 0 – 10 °C were tested to
447 determine the best model. The 1st March was chosen as a date at which any diapause
448 requirements for this insect are likely to have been met, as is the case with *S. mosellana*,
449 and there are no references to post-larval development occurring prior to this date in the
450 field. The second model incorporated rainfall data as current evidence suggests that
451 moisture is important in the onset of *H. marginata* emergence (Nijveldt & Hulshoff, 1968;
452 Gratwick, 1992; Popov *et al.*, 1998). The first date on which rainfall occurred after the mean
453 daily soil temperature rose above a predetermined threshold was used as the date of biofix.
454 Here we are using the term 'biofix' to represent the estimated date at which pupation begins.
455 The date of biofix was then used to calculate accumulated degree days above a base
456 temperature until emergence as before. Mean daily soil temperature thresholds of 5 - 12 °C
457 were tested, along with degree day base temperatures of 0 – 10 °C to determine the best
458 model.

459

460 For both models, the predicted dates of emergence were compared against the observed
461 dates for the sites sampled in 2014 and 2015. The standard deviation of the differences
462 were calculated to determine the accuracy of each model as described by Elliott *et al.*

463 (2009). Previously recorded emergence dates were used for model validation. The models
464 were used to predict emergence dates for *H. marginata* in North Bedfordshire for sites
465 sampled in 1971 and 1972 (Woodville, 1973), although daily soil temperatures were used for
466 the degree day calculations due to the unavailability of hourly data. The models were further
467 validated against emergence data for the Aylesbury from sampling done in 2012 and 2013
468 (Pope & Ellis, 2012; Ellis *et al.*, 2014).

469

470 6.2 Results

471 Across all sites and years, the date of emergence varied from 30th April at the earliest, until
472 19th May at the latest. For the first model, the mean number of degree days accumulated
473 above 0 °C from 1st March until emergence was 588DD (\pm 9.7DD). A base temperature of 0
474 °C was chosen as it gave the best results in terms of predicted emergence date compared
475 with the observed emergence date. This base temperature is unlikely to have any
476 physiological relevance as the developmental threshold temperature for *H. marginata* has
477 previously been reported as 10 °C (Baier, 1963; Nijveldt & Hulshoff, 1968), although this is
478 possibly an overestimation as temperatures between 5 °C and 10 °C were apparently not
479 tested in either study. In an analysis of the limitations of using degree day units, Bonhomme
480 (2000) noted that, for plants at least, the threshold temperature used for degree day
481 calculations is only of statistical relevance and is often unrelated to threshold temperature at
482 which the rate of development is zero. Similarly, Snyder *et al.* (1999) reported good results
483 when using a 0 °C base temperature in degree day models compared to other
484 developmental thresholds estimated from field observations. For the second model, a
485 temperature of 6 °C gave the best modelled results for the onset of pupation, followed by
486 degree day accumulations above 0 °C for the completion of adult development. The mean
487 number of degree days calculated from the date of biofix until the date of emergence for
488 each site was 548DD (\pm 8.4DD). The first model was able to predict emergence at the
489 sampled sites to within 5 days (\pm 4days) and the second model to within 4 days (\pm 2 days).
490 The standard deviation of the differences between the observed dates and model predictions

491 was also smaller for the second model suggesting a higher degree of accuracy (Table 1).
492 From the historical data, predictions for the date of emergence from both models were within
493 5 days (± 3.5 days) for all sites (Table 2).

494

495 These data indicate that a simple degree day model is capable of predicting the emergence
496 of *H. marginata* adults. Additionally, the incorporation of rainfall provides a biofix date, which
497 improves the accuracy of the model. This method has previously been developed for *S.*
498 *mosellana* and fits with the current understanding of *H. marginata* biology. Further data will,
499 however, be required for improved accuracy and validation of the model before it can be
500 used reliably.

501 **7. Conclusions**

502 The models presented here demonstrate that simple degree day calculations can be used to
503 forecast the emergence of this pest. The incorporation of rainfall monitoring further improves
504 the accuracy of the model, as has been found with orange wheat blossom midge
505 (Jacquemin *et al.*, 2014). Models based on simple degree day calculations offer a means for
506 farmers to predict the date of emergence of this pest if they have had past evidence of
507 infestation. This will reduce the time required to monitor for this pest either by checking the
508 crop itself for adults and eggs or using pheromone traps such as those recently described by
509 Censier *et al.* (2014b). It is important, however, that any pest management decisions, take
510 into account factors such as the growth stage of the crop and population size. Careful crop
511 monitoring remains essential if chemical controls are to be timed appropriately (Ellis *et al.*,
512 2014; Censier *et al.*, 2015a). The use of degree day models and monitoring systems are an
513 important part of the principles of integrated pest management as described by the EU
514 Sustainable Use of Pesticides Directive (Council Directive 2009/128/EC, 2009).

515

516 Variation in susceptibility of different cereal crops and between wheat varieties indicates the
517 potential of breeding for full or partial resistance to this pest. Antibiotic resistance to *S.*

518 *mosellana* has been bred into some varieties of wheat, which prevents the larvae from
519 developing past the first instar (Lamb *et al.*, 2000; Oakley, 2005). However, such a
520 development would require an understanding of the mechanism(s) of resistance to *H.*
521 *marginata*, which is currently unknown. Research into the use of chemical controls against
522 *H. marginata* has focused on the use of broad spectrum insecticides, such as
523 organophosphates and pyrethroids. While potentially effective these broad spectrum
524 insecticides are harmful to beneficial insects, including natural enemies of *H. marginata*, and
525 if applications are not timed to target the vulnerable life stage of the pest the efficacy of
526 these chemical controls will be reduced. There is therefore a need to develop a more
527 integrated approach: exploiting improved monitoring techniques, breeding varietal
528 resistance, implementing effective crop rotations and conserving natural enemies, all of
529 which can play a role in the management of this most unpredictable pest.

530

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828 Table 1. Dates of observed and predicted emergence for years 2014 & 2015 from sampled
 829 sites, and difference in days for each model

Site	Observed emergence date	Model 1		Model 2	
		Predicted emergence date	Days difference (Obs – Pred)	Predicted emergence date	Days difference (Obs – Pred)
2014					
Royston (Herts)	30 th April (± 0 days)	29 th April	+1	27 th April	+3
Bicester (Oxs)	3 rd May (± 3.5 days)	2 nd May	+1	2 nd May	+1
High Wycombe (Bucks)	3 rd May (± 3.5 days)	3 rd May	0	4 th May	-1
Aylesbury (Bucks)	3 rd May (± 3.5 days)	3 rd May	0	6 th May	-3
2015					
Royston (Herts)	2 nd May (± 2 days)	4 th May	-2	2 nd May	0
Bicester (Oxs)	2 nd May (± 2 days)	6 th May	+4	3 rd May	-1
High Wycombe (Bucks)	2 nd May (± 2 days)	4 th May	-2	5 th May	-3
Aylesbury (Bucks)	9 th May (± 4 days)	4 th May	+5	8 th May	+1
Glemsford (Suffolk)	3 rd May (± 3 days)	5 th May	+2	2 nd May	+1

Thirsk (North Yorkshire)	9 th May (± 2 days)	12 th May	+3	13 th May	-4
Devizes (Wiltshire)	3 rd May (± 3 days)	4 th May	1	1 st May	+2
Max. difference			+5 (± 4 days)		-4 (± 2 days)
SD (observed-predicted)			2.43		2.17

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832 Table 2. Dates of observed and predicted emergence for years 2012 & 2013 and 1971 &

833 1972, and difference in days for each model

834

Site	Observed emergence date	Model 1		Model 2	
		Predicted emergence date	Days difference (Obs – Pred)	Predicted emergence date	Days difference (Obs – Pred)
2013					
Aylesbury (Bucks)	17 th May (± 3.5 days)	19 th May	-2	19 th May	-2
2012					
Aylesbury (Bucks)	10 th May (± 3.5 days)	6 th May	+4	5 th May	+5
1972					
N. Bedfordshire	19 th May	16 th May	+3	21 st May	-2
1971					
N. Bedfordshire	18 th May	19 th May	-1	16 th May	+2

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837 Figure 1. Map of European countries showing the decades in which *Haplodiplosis marginata*
838 was first recorded, from 1692 until present.

839

840 Figure 2. Map showing the 2011 areas with *Haplodiplosis marginata* infestation in the UK by
841 county based on a survey of farmers and agronomists; shaded areas represent counties with
842 at least one incidence of *H. marginata* infestation (Caroline Nicholls, AHDB Cereals &
843 Oilseeds).

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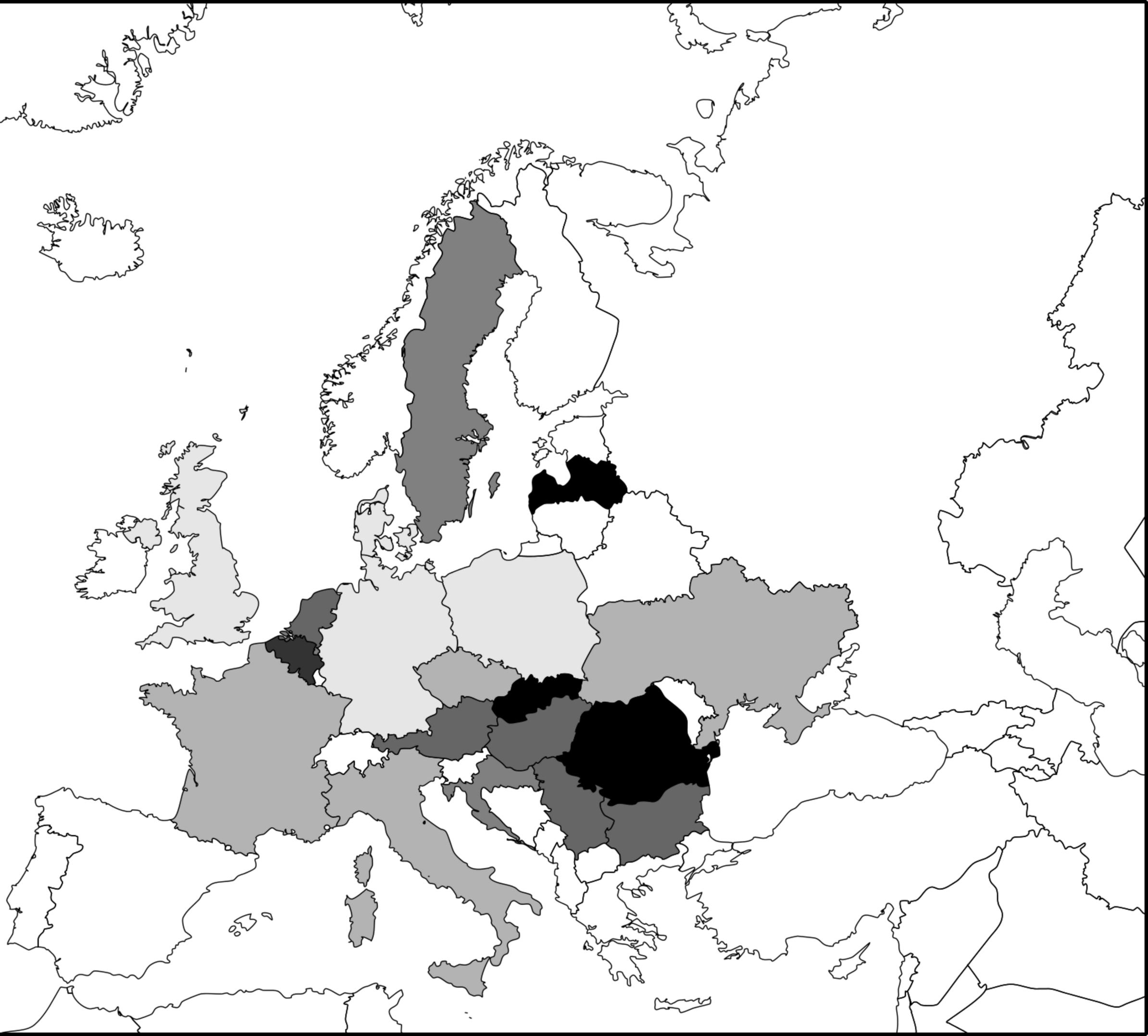
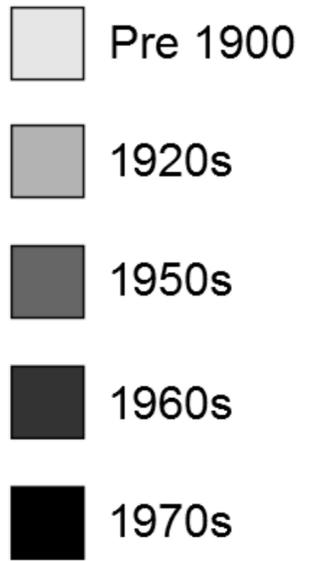
845 Figure 3. Life cycle of *Haplodiplosis marginata*; **A.** adult emergence, **B.** oviposition, **C.** gall
846 formation and larval maturation, **D.** larval diapause, **E.** pupation.

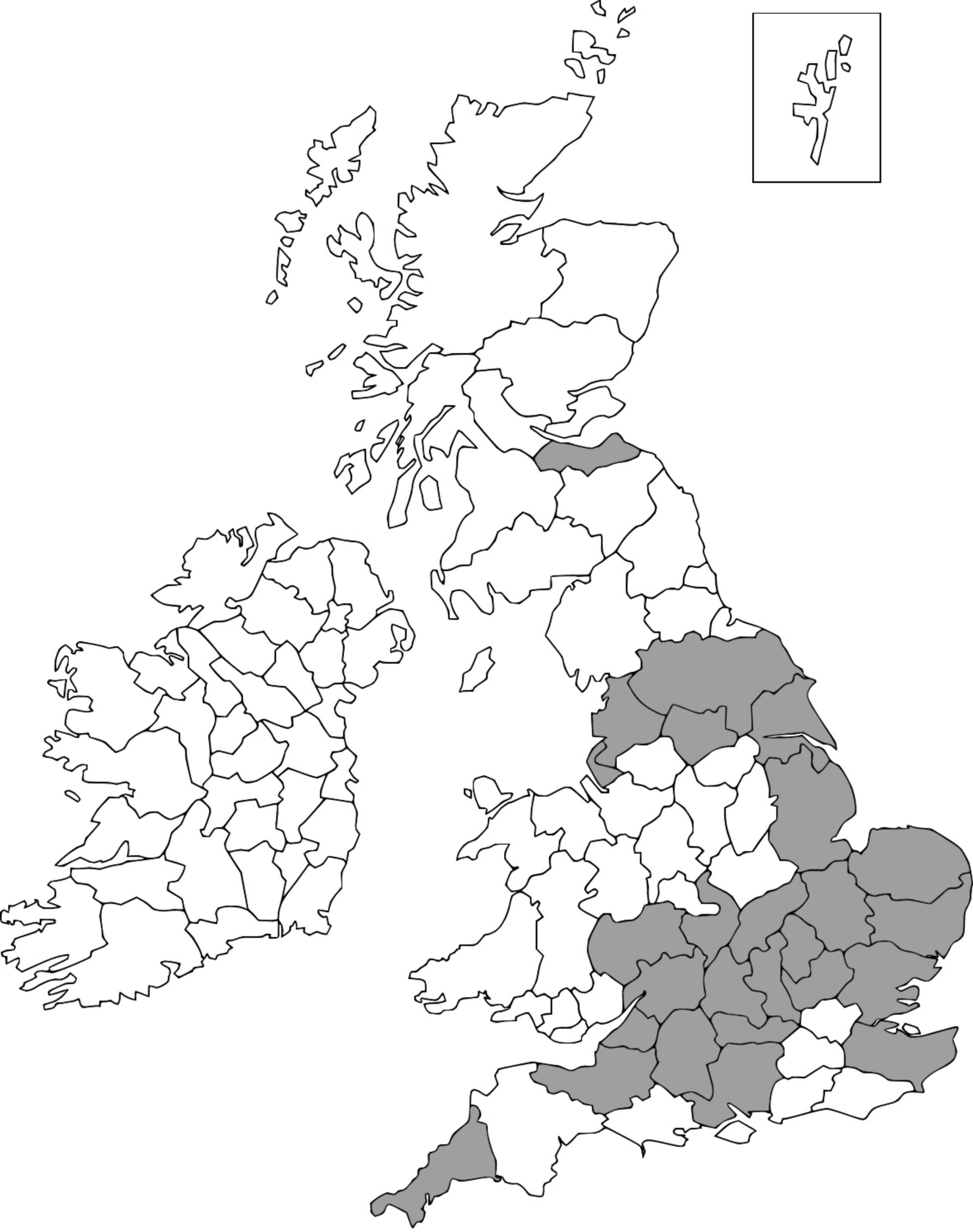
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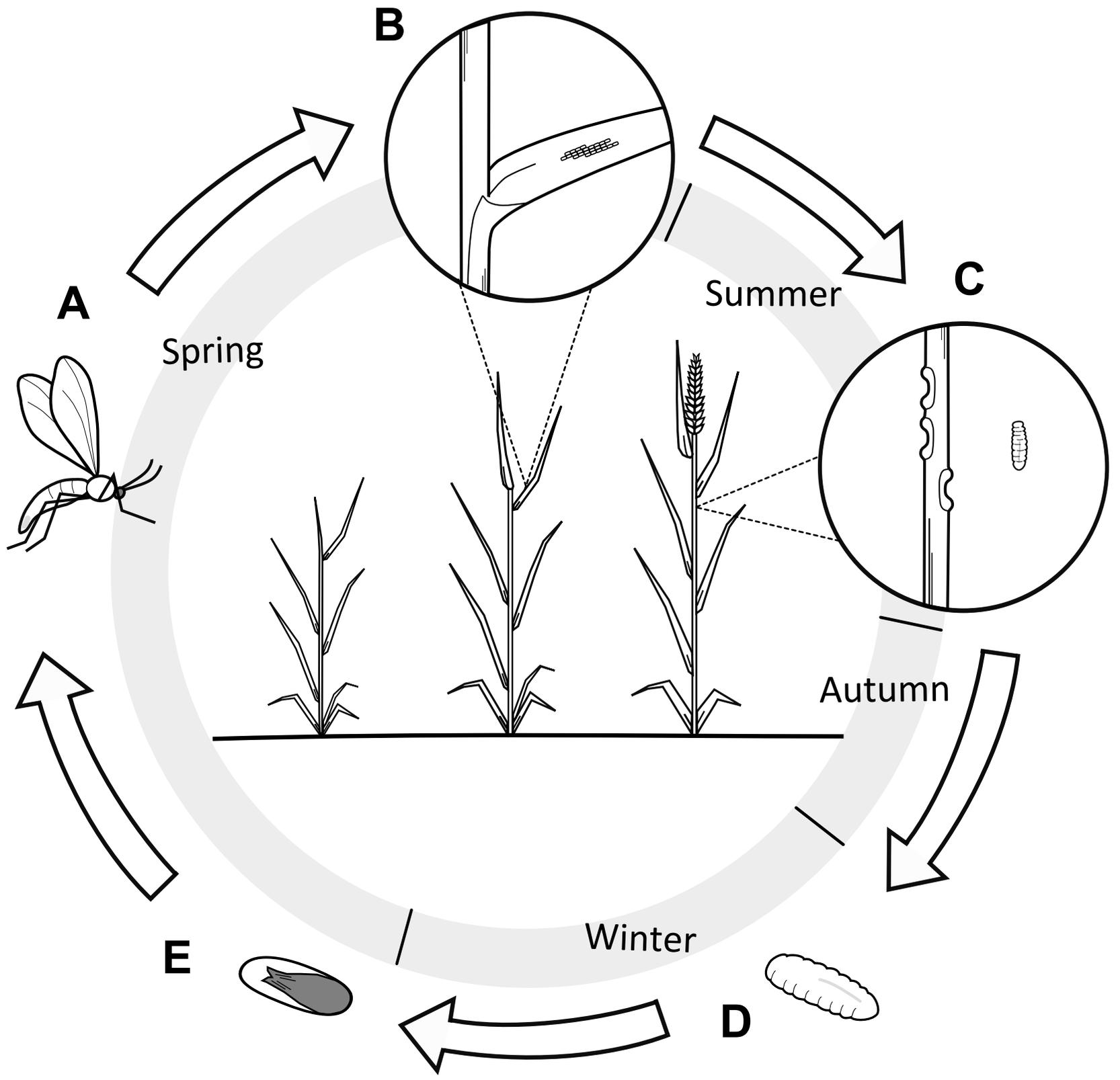
848 Figure 4. Scanning electron microscope images of antennal segments of *Haplodiplosis*
849 *marginata* **A.** female **B.** male

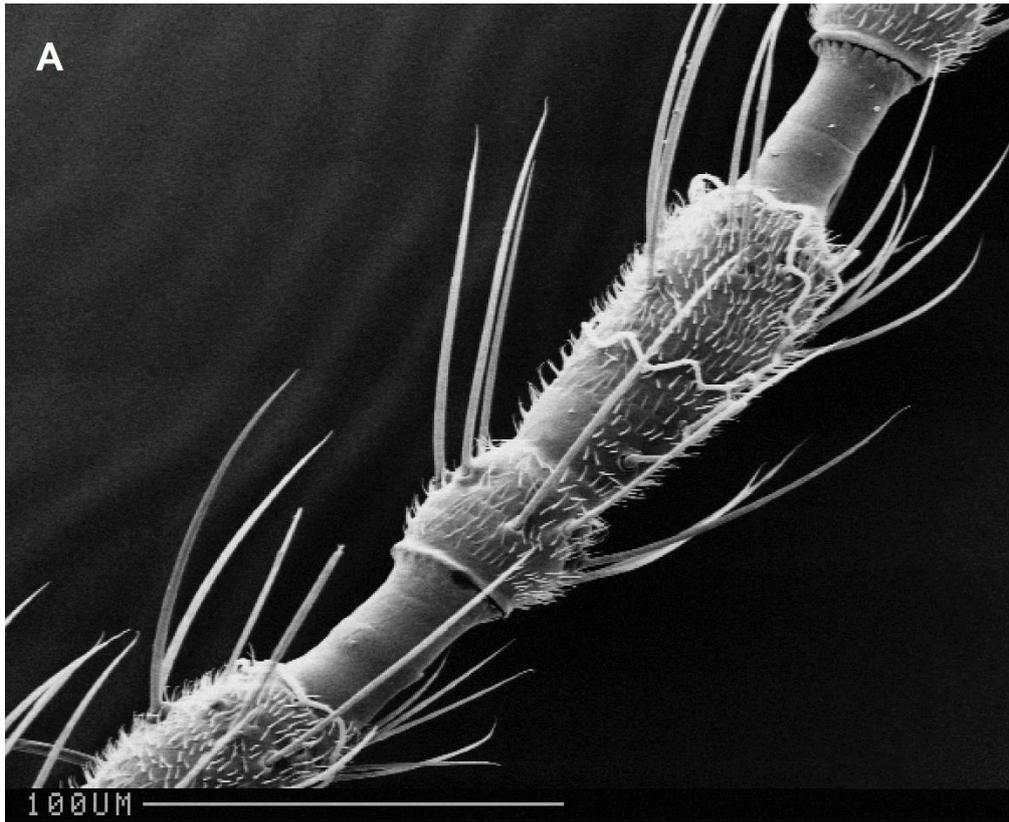
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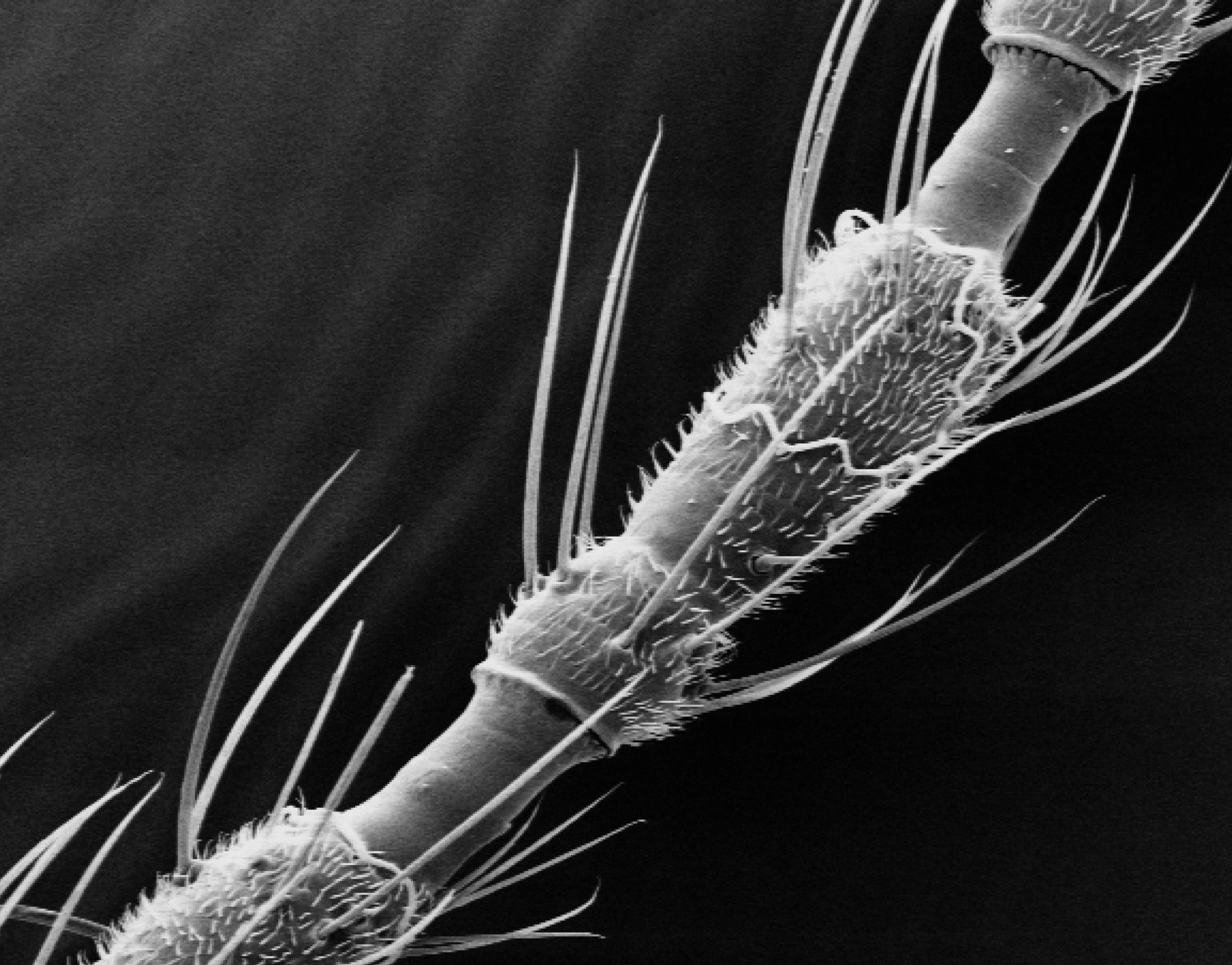
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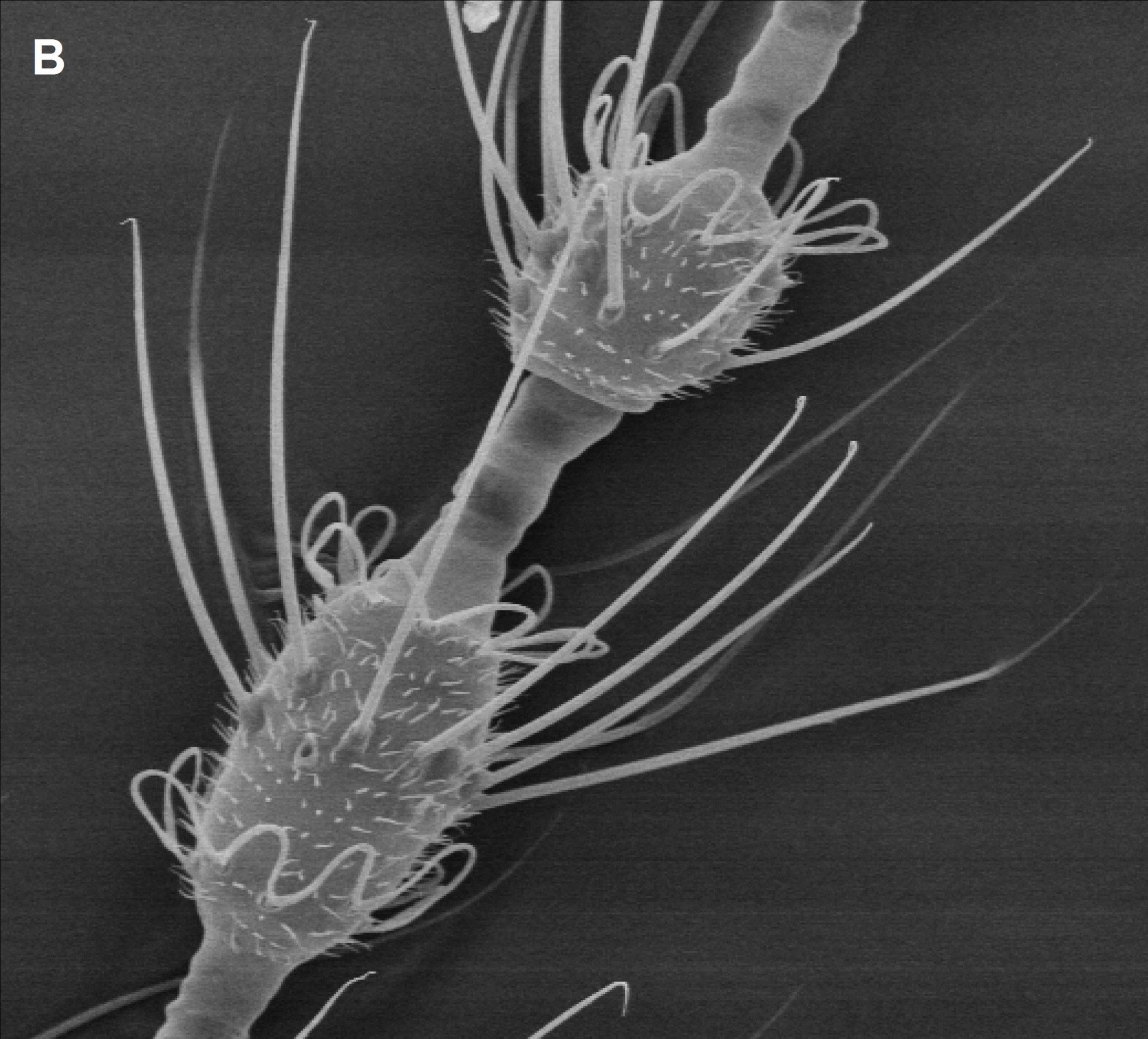






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