

1 **Invertebrate Community Associated with the Asexual Generation of *Bassettia***  
2 ***pallida* Ashmead (Hymenoptera: Cynipidae)**

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13  
14 **Abstract**

15 Cynipid gall wasps play an important role in structuring oak invertebrate communities.  
16 Wasps in the Cynipini tribe typically lay their eggs in oaks (*Quercus* L.), and induce the  
17 formation of a “gall”, which is a tumor-like growth of plant material that surrounds the  
18 developing wasp. As the wasp develops, the cynipid and its gall are attacked by a  
19 diverse community of natural enemies, including parasitoids, hyperparasitoids, and  
20 inquilines. Determining what structures these species-rich natural enemy communities  
21 across cynipid gall wasp species is a major question in gall wasp biology. Additionally,  
22 gall wasps are ecosystem engineers, as the abandoned gall is used by other  
23 invertebrates. The gall-associated insect communities residing on live oaks (*Quercus*

24 *geminata* Small and *Q. virginiana* Mill.) are emerging as a model system for answering  
25 ecological and evolutionary questions ranging from community ecology to the evolution  
26 of new species. Documenting the invertebrates associated with cynipids in this system  
27 will expand our understanding of the mechanisms influencing eco-evolutionary  
28 processes, record underexplored axes of biodiversity, and facilitate future work. Here,  
29 we present the community of natural enemies and other associates of the asexual  
30 generation of the crypt gall wasp, *Bassettia pallida* Ashmead. We compare the  
31 composition of this community to communities recently documented from two other  
32 cynipid gall wasps specializing on live oaks along the U.S. Gulf coast, *Disholcaspis*  
33 *quercusvirens* Ashmead and *Belonocnema treatae* Mayr. *B. pallida* and their crypts  
34 support a diverse arthropod community, including over 25 parasitoids, inquilines, and  
35 other associated invertebrates spanning 5 orders and 16 families.

36

37 **Key words:** oak gall, Natural Enemy Hypothesis, crypt gall wasp, crypt keeper wasp

38

39 Shelter-building insects (including gall formers, leaf rollers, leaf miners, and other  
40 insects that generate three-dimensional structures on their host plants) are ecosystem  
41 engineers, and are often associated with increases in arthropod richness and  
42 abundance on their host plants (reviewed in Cornelissen et al. 2016). While residing in  
43 their shelters, these insects are the target of parasitoids and predators, and are  
44 exploited by inquilines (i.e., organisms that typically do not make shelters themselves,  
45 but move into shelters with variable fitness implications for the shelter-maker) (Sanver  
46 and Hawkins 2000, Mendonça and Romanowski 2002, Hayward and Stone 2005,

47 Bailey et al. 2009). The shelters often remain after the ecosystem engineer has  
48 abandoned it, and are subsequently settled by other arthropods (Cornelissen et al.  
49 2016, Harvey et al. 2016, Wetzel et al. 2016).

50         Some of nature's most complex shelters are created by cynipid gall wasps  
51 (Stone et al. 2002, Stone and Schönrogge 2003). Members of the Cynipini tribe lay their  
52 eggs in *Quercus* oaks (or sometimes other trees in the family Fagaceae), and induce  
53 the plant to produce a structure called a "gall". The gall is lined with nutritious tissue,  
54 and will support the wasp while it feeds and develops (Rohfritsch 1992). Galls vary in  
55 appearance and structure, including those that exhibit exterior defenses that are sticky,  
56 hairy, or protruding spikes, or contain internal air sacs (Stone and Cook 1998, Csóka et  
57 al. 2005, Bailey et al. 2009), and those that are more cryptic (Melika and Abrahamson  
58 2007). The incredible structural diversity among galls is thought to be a defense against  
59 the speciose community of parasitoids and inquilines that are often associated with galls  
60 (Abe et al. 2007, Askew et al. 2013), and which can have dramatic impacts on cynipid  
61 population fitness (Price et al. 1987, Sanver and Hawkins 2000, Stone and Schönrogge  
62 2003, Csóka et al. 2005, Bailey et al. 2009). An estimated ~1,400 described species of  
63 cynipid gall wasps produce morphologically diverse galls in their respective host plants  
64 (Ronquist et al. 2015, Péntzes et al. 2018), making this system ideal for asking  
65 questions about the importance of factors such as host relatedness, phenology, and  
66 natural enemy defense strategies on the structure of natural enemy communities  
67 (Cornell 1985, Stone et al. 2002, Stone and Schönrogge 2003, Price et al. 2004, Csóka  
68 et al. 2005, Hayward and Stone 2005).

69 Many of the studies on the structuring of the communities of natural enemies  
70 attacking cynipid gall wasps have been done in the Palaearctic (e.g., Schönrogge et al.  
71 1996, Hayward and Stone 2005, Bailey et al. 2009, Nicholls et al. 2010, Stone et al.  
72 2012, Bunnefeld et al. 2018). In North America, groundwork is being laid to conduct  
73 similar studies on the communities associated with the cynipid gall wasps that infect the  
74 “live oaks” (subsection Virentes) - a monophyletic group of seven North American semi-  
75 evergreen oak species within the genus *Quercus* – where much of the focus has  
76 centered on two partially overlapping sister species along the U.S. Gulf coast, *Quercus*  
77 *virginiana* and *Quercus geminata* (Cavender-Bares and Pahlisch 2009, Cavender-Bares  
78 et al. 2015, Hipp et al. 2018). These live oaks are home to at least six (Egan et al. 2013)  
79 and potentially twelve (Egan, unpublished data) cynipid gall wasp species, which are in  
80 turn attacked by a community of parasitoids and inquilines (Bird et al. 2013, Forbes et  
81 al. 2016). The cynipid gall wasps and their communities of natural enemies associated  
82 with the live oak lineage are emerging as powerful systems for answering a broad set of  
83 ecological and evolutionary questions on local adaptation (Egan and Ott 2007), natural  
84 selection (Egan et al. 2011), speciation (Egan, Hood, and Ott 2012, Egan, Hood, Feder,  
85 et al. 2012, Egan et al. 2013, Zhang et al. 2017, 2019, Hood et al. 2019), developmental  
86 plasticity (Hood and Ott 2010), and novel species interactions (Egan et al. 2017,  
87 Weinersmith et al. 2017, Ward et al. 2019). However, the extent to which these species-  
88 rich natural enemy communities on gall wasp host species overlap is currently unclear,  
89 and even documentation of the species present in these communities is far from  
90 complete. Because of these limitations, the factors determining the overlap between the

91 natural enemy communities attacking cynipid gall wasps species residing on live oaks  
92 remains unexplored.

93         After the host and/or its various natural enemies have exited the gall, the gall  
94 itself often remains. Abandoned oak galls are settled by a variety of arthropods,  
95 including ants, spiders, mites, and beetles (e.g., Cooper and Rieske 2010, Wetzal et al.  
96 2016, Giannetti et al. 2019). While a recent review found that insect-made shelters are  
97 associated with increases in the abundance and diversity of arthropods that use the  
98 shelter once it is abandoned (Cornelissen et al. 2016), increases in density and diversity  
99 are not the rule. For example, the abandoned galls of the California gall wasp, *Andricus*  
100 *quercuscalifornicus* (Bassett), are associated with a *reduction* in herbivore invertebrate  
101 density and diversity, presumably because the galls are colonized by predatory spiders  
102 which attack herbivore invertebrates (Wetzal et al. 2016). Additional work is needed to  
103 better understand of the importance of abandoned galls on the local arthropod  
104 community.

105         Here we describe the community of natural enemies of the asexual generation of  
106 *Bassettia pallida* Ashmead (the crypt gall wasp), and discuss the overlap between the  
107 natural enemies of *B. pallida* and the previously described natural enemy communities  
108 of two gall wasps (*Belonocnema treatae* Mayr and *Disholcaspis quercusvirens*  
109 Ashmead) specializing on the same two live oak hosts, *Q. virginiana* and *Q. geminata*.  
110 The asexual generation of *B. treatae* creates leaf galls that contain one chamber, and  
111 was recently found to be associated with 24 invertebrate species (Forbes et al. 2016).  
112 The asexual generation of *D. quercusvirens* (which produces “bullet galls” on stems)  
113 was associated with nine species of parasitoids and inquilines (Bird et al. 2013).

114            Additionally, to stimulate future studies examining how *B. pallida* influences the  
115            diversity and abundance of the invertebrate community residing on live oaks, we report  
116            observations of associates of *B. pallida* that are likely benign and facultative, and use  
117            the crypt once it has been abandoned.

118

## 119    **Study System**

120

121    The asexual generation of wasps in the North American genus *Bassettia* Ashmead  
122    (Hymenoptera, Cynipidae, Cynipini) produce stem galls in twigs, in which compartments  
123    where the wasps develop run parallel to the bark (Melika and Abrahamson 2007). The  
124    sexual generations of this genus – when known – make their galls in leaves, where they  
125    produce swellings that are visible on both sides of the leaf (Melika and Abrahamson  
126    2007). The crypt gall wasp, *Bassettia pallida* (Hymenoptera: Cynipidae) (Fig. 1), infects  
127    both sand live oaks (*Q. geminata*) and southern live oaks (*Q. virginiana*) in the  
128    southeastern United States (Melika and Abrahamson 2007, Egan et al. 2013). The stem  
129    galls produced by the asexual generation of *B. pallida* are called “crypts”, and the  
130    sexual generation galls of this species have not been definitively identified. The  
131    community of natural enemies attacking *B. pallida* has not been described previously.

132

## 133    **Materials and Methods**

134

135    Collections and Characterization of Natural Enemy Community

136 The stem galls made by the asexual generation of *Bassettia* are concealed, and are  
137 typically identified by finding emergence holes made by *Bassettia* which emerged  
138 previously (Melika and Abrahamson 2007). We collected *Q. geminata* stems with  
139 evidence of *B. pallida* emergence holes from four locations in Florida: Inlet Beach  
140 (Lat/Long: 30.273663, -86.001911), Lake Lizzie (28.227718, -81.179641), Topsail Hill  
141 Preserve State Park (30.3675327, -86.2752784), and Camp Helen State Park  
142 (30.270194, -85.991833). Collections made at Florida State Parks were made under  
143 Scientific Research Collecting Permit #04301840 from the Florida Department of  
144 Environmental Protection. We also collected *B. pallida*-infected *Q. virginiana* stems from  
145 two locations in Texas: Humble (29.998392, -95.184455) and Rice University's Campus  
146 in Houston (29.717030, -95.401279). Collections occurred between August and March  
147 in 2015, 2016, 2018, and 2019. Tables 1 and 2 summarize collection years, locations  
148 sampled, host plant, and the number of invertebrates that emerged from each  
149 collection.

150 Stems collected in the field were placed in plastic bags and transported to either  
151 Rice University (Houston, Texas) or Charlottesville, Virginia. Leaves and non-target  
152 galls were removed from the stems, and stems were placed in clear plastic cups. The  
153 cups were covered with a coffee filter, which was secured in place with a rubber band.  
154 Cups were then placed outside, where they experienced natural light:dark cycles and  
155 ambient temperatures and humidity. The stems were misted with tap water periodically  
156 to mimic local precipitation. Abiotic differences between outdoor rearing conditions in  
157 Virginia and Texas may have influenced emergence success, but this is unlikely. After  
158 emergences ceased, haphazard dissections of stems suggested that most of the

159 associates from the samples sent to Virginia had indeed emerged, and that no particular  
160 natural enemy species remained in the crypts. Cups were checked for emergences five  
161 days a week. Emerged insects were placed in 95% ethanol, and stored at room  
162 temperature or -20°C until further analysis.

163 Most emergent insects were Hymenoptera, which we identified using keys by  
164 Mason (1993), Gibson et al. (1997), Weld (1952), Gillette (1896), and Wahl (2019). For  
165 a subset of the associates, we extracted DNA using the DNeasy Blood and Tissue Kit  
166 (Qiagen) in accordance to the manufacturer's protocol with the addition of a pestle  
167 crushing step prior to incubation. The mitochondrial cytochrome oxidase I (COI) region  
168 was amplified using the KAPA Taq ReadyMix (Sigma Aldrich) and the primers LEP F 5'  
169 TAAACTTCTGGATGTCCAAAAAATCA 3' and LEP R 5'  
170 ATTCAACCAATACATAAAGATATTGG 3' (Smith et al. 2008). Due to primer  
171 incompatibility, for the *Eurytoma* sample we used the following primers: COI\_P2 5'  
172 ACC WGT AAT RAT AGG DGG DTT TGG DAA 3' and COI\_2437d 5' CGT ART CAT  
173 CTA AAW AYT TTA ATW CCW G 3' (Kartinen et al. 2010). Thermocycling programs  
174 included 35 cycles with 48°C as the annealing temperature. We cleaned the resulting  
175 PCR products using the QIAquick PCR purification KIT (Qiagen) or an EXO1  
176 (exonuclease 1) and SAP (shrimp alkaline phosphatase) method (15 min at 37°C  
177 minutes and then 80°C for an additional 15 min) prior to Sanger sequencing on an ABI  
178 3730 (Applied Biosystems, Foster City, CA) in the University of Iowa's Roy J. Carver  
179 Center for Genomics.

180

181



182 **Results**

183

184 Host Collection

185 *B. pallida* emerged from crypts in five of our collections, and emerged from both *Q.*  
186 *geminata* in Florida and *Q. virginiana* in Texas (Table 1). The greatest number of *B.*  
187 *pallida* emerged from crypts collected at Camp Helen State Park in Florida. Two *B.*  
188 *pallida* sequences (MN935926, MN935927; Table S1) were obtained from this location.  
189 The sequences were 98.98% identical, and multiple Cynipidae were ~90-94% similar in  
190 GenBank. Most of the observed *B. pallida* emergences occurred in March, which is  
191 consistent with previous collections in Florida (Melika and Abrahamson 2007), and  
192 expectations from their natural history. Eight *B. pallida* emerged from late October  
193 through mid-December from collections made in the fall (August through October) and  
194 are likely responding to galled branches being removed from the tree.

195 Three specimens of an unidentified cynipid were found in the 2018-2019  
196 collection. This cynipid appears to make crypt-like galls on stems and keys to the genus  
197 *Callirhytis* Foerster using (Zimmerman 2018), but could not be identified or matched to  
198 any currently described species. Upon further inspection, this 'new' species emerges  
199 from a solitary crypt gall with little to no external and visible swelling found at branching  
200 points within new stems, which is distinct from the cluster of crypt galls that generate a  
201 subtle swelling of the lateral parts of new branches induced by *B. pallida* (Brandão et  
202 al., MS in prep). We cannot rule out the possibility that some of the natural enemies and  
203 associates we describe below emerged from this galler. However, only 3 of the 590  
204 (0.5%) cynipids that emerged from this collection were the non-target host species,

205 suggesting that the vast majority of the natural enemies we collected were likely  
206 associated with *B. pallida*.

207 Associates from five orders and 16 families were reared from *Q. geminata* and *Q.*  
208 *virginiana* stems infected by the asexual generation of *B. pallida*. We present the  
209 Hymenopteran associates (Table 1) first, as they were the most abundant and diverse  
210 order present in our samples.

211  
212 Hymenoptera  
213 We collected one specimen (Table 1) that keys to the family Encyrtidae (Chalcidoidea)  
214 using Grissell and Schauff (1997). The sequence from this specimen (MN935918, Table  
215 S1) was 97.7% similar to an unclassified Hymenopteran in GenBank. Encyrtid wasps  
216 can be parasitoids and hyperparasitoids, and many known host associations are with  
217 scale insects or mealybugs (Noyes 1988, Noyes and Woolley 1994). This wasp may be  
218 an associate of *B. pallida* galls, and not a direct parasitoid of the galler.

219 *Euderus set* Egan, Weinersmith, & Forbes (Chalcidoidea: Eulophidae; Fig 2A)  
220 emerged from *Q. virginiana* and *Q. geminata* at four sites. *E. set* is a recently described  
221 parasitoid of *B. pallida* (Egan et al. 2017), and manipulates its host into excavating an  
222 emergence hole from the crypt and then dying while plugging the hole with its head  
223 capsule (Fig. 1C, 2A) (Weinersmith et al. 2017). This behavior facilitates *E. set*'s escape  
224 from the crypt following completion of development (Weinersmith et al. 2017). Six other  
225 cynipid gall wasp hosts of *E. set* have recently been identified, all residing on different  
226 oak species than *B. pallida*, and all of which appear to be manipulated to facilitate  
227 parasitoid emergence (Ward et al. 2019).

228 Two species of Tetrastichinae (Chalcidoidea: Eulophidae) emerged in our  
229 collections. The first species keyed to the genus *Galeopsomyia* Girault (Fig. 2B) using  
230 Schauff et al. (1997). This species emerged from three of our collections (Table 1), with  
231 the majority emerging mid-March through mid-April from the stems collected from *Q.*  
232 *geminata* at Camp Helen State Park (FL). We acquired a COI sequence (MN935919;  
233 Table S1), which was ~84% similar to unclassified Eulophidae in GenBank. The second  
234 Tetrastichinae species was collected from *Q. virginiana* in Texas, and the sequence  
235 collected from this species (MN935910; Table S1) was only 79.9% similar to the  
236 *Galeopsomyia* species sequences. The tetrastichine wasp was 96.1% identical to an  
237 early release sequence from an Eulophidae in BOLD. In GenBank, this sequence was  
238 ~86% identical to *Eulophidae* specimens in the subfamily Tetrastichinae.

239 Forbes et al. (2016) observed *Galeopsomyia nigrocyanea* (Ashmead) emerging  
240 from *B. treatae* on *Q. virginiana* in Texas. Based on sequence data, we suspect that the  
241 *Galeopsomyia* emerging from *B. pallida* are not *G. nigrocyanea*. The two *G.*  
242 *nigrocyanea* sequences deposited in GenBank from Forbes et al. (2016) are 84%  
243 similar to our Camp Helen specimen (from *Q. geminata* in Florida), and our  
244 Tetrastichinae specimen from Rice University (from *Q. virginiana* in Texas) shares only  
245 ~83% similarity. Wasps in the genus *Galeopsomyia* are parasitoids of cynipid gall  
246 wasps (e.g., *Belonocnema treatae* (Forbes et al. 2016)), gall-forming dipterans (e.g.,  
247 Cecidomyiidae (Stiling et al. 1992)), and are hyperparasitoids of other wasps, including  
248 some genera represented in our samples (e.g., *Eurytoma* Illiger (Herting 1977)). The  
249 *Galeopsomyia* that emerged from our samples could be a parasitoid, hyperparasitoid, or  
250 both (i.e., a facultative hyperparasitoid).

251 *Brasema* Cameron (Chalcidoidea: Eupelmidae: Eupelminae; Fig. 2C) were  
252 reared in our collections (Table 1), and were identified according to Gibson (1997). We  
253 obtained one sequence (MN935905; Table S1), which was 97.7% similar to “*Brasema*  
254 sp. GG5” (GenBank Accession HQ930308.1), which was collected by freehand  
255 sampling from a mesic hammock at Kissimmee Prairie Preserve State Park in Florida  
256 (BOLD Barcode Index Number BOLD:AAN7976). Based on sequence identity, the two  
257 *Brasema* species collected by Forbes et al. (2016) may be different species than that  
258 emerging from *B. pallida*. The sequences for *Brasema* sp. 1 and *Brasema* sp. 2  
259 emerging from *B. treatae* (Forbes et al. 2016) are ~89% and ~91% similar to the  
260 sequence we collected from *Brasema* emerging from *B. pallida*. *Brasema* have a wide  
261 host range, with primary hosts including cynipid gall wasps, dipterans, and orthopterans,  
262 and a range of parasitoid hosts as well (including Pteromalids, Eurytomids, and  
263 Eulophids) (Noyes 2019). The exact relationship of *Brasema* to *B. pallida* is unknown.

264 *Eurytoma* (Chalcidoidea: Eurytomidae: Eurytominae; Fig. 3A) were reared from  
265 three collections (Table 1). Morphological ID of these specimens was done using  
266 DiGiulio (1997). We were unable to obtain sequence data for the one *Eurytoma* that  
267 emerged from two of the collections (one from *Q. virginiana* from Rice University in TX,  
268 and one from *Q. geminata* from Topsail Hill Preserve State Park in FL).

269 *Eurytoma* parasitoid species also emerge from galls of *B. treatae* and *D.*  
270 *quercusvirens*. Forbes et al. (2016) identified *Eurytoma furva* Bugbee and *Eurytoma*  
271 *bugbeei* Grissell, as well as one unidentified *Eurytoma* species emerging from *B.*  
272 *treatae*. Sequence comparisons between the *Eurytoma* specimen from *B. pallida*  
273 (MN935909; Table S1) and *E. furva* and *E. bugbeei* sequences collected from *B.*

274 *treatae* (Forbes et al. 2016) are an ~88% match, suggesting that the species collected  
275 from *B. pallida* is distinct. DNA could not be extracted from the unidentified *Eurytoma*  
276 species from *B. treatae*, so it is possible that this species emerges from both *B. pallida*  
277 and *B. treatae*. *Eurytoma hecale* Walker and an unidentified *Eurytoma* species were  
278 identified as parasitoids of *D. quercusvirens* by Bird et al. (2013). Our specimen is  
279 unlikely to be *E. hecale* based on morphology, and it is not possible to know if the  
280 unidentified *Eurytoma* species reported in Bird et al. (2013) is the same as that  
281 emerging from *B. pallida*.

282 Four morphospecies of *Sycophila* Walker (Chalcidoidea: Eurytomidae:  
283 Eurytominae, Fig. 3B-E) were reared from three collections (Table 1). The specimens  
284 were identified using Balduf (1923). The interpretation of the color variations in Balduf's  
285 key is problematic, and the current species concepts are dubious until the taxonomic  
286 revision of the genus is conducted (Zhang et al., unpublished data). The first *Sycophila*  
287 morphospecies in our samples keys to *S. foliatae* (Ashmead) (Fig. 3B), which has  
288 previously been recorded from "live oak" in Jacksonville, FL, and is associated with a  
289 variety of oak gall parasitoids (Balduf 1923). The female specimens have varying  
290 degrees of black and yellow across the body and a small forewing infumation band,  
291 while males are mostly black with similar wing band patterns (Fig. 3B). These coloration  
292 characters also fit the description of *S. quinqueseptae* (Balduf), but this species is  
293 currently only known from California and is associated with *Plagiotrochus*  
294 *quinqueseptum* Ashmead (Balduf 1923). The second species identified was *S. nr. dubia*  
295 (Fig. 3C), although this species might be a synonym of *S. varians* based on morphology  
296 (large angular forewing infumation band, body color mix of yellow and black) and

297 preliminary molecular studies (Zhang et al., unpublished data). *S. nr. nubilistigma* (Fig.  
298 3D) is reared from *Q. virginiana*. They can be identified by their mostly yellow coloration  
299 with a dorsal black band on the mesoma and metasoma. The wing band is rectangular  
300 with a constriction near stigma vein (Fig. 3D). Finally, *S. nr. disholcaspidis* (Fig. 3E) was  
301 reared. The specimen is orange in coloration, and has the characteristic jug-shaped  
302 wing band and a secondary band near the parastigma similar to that of *S. disholcaspidis*  
303 Balduf which are parasitoids of *Disholcaspis cinerosa* (Bassett) in Texas. However, one  
304 key difference from *S. disholcaspidis* is the presence of multiple setae radiating from the  
305 secondary band (Fig. 3E), but more specimens are needed to better understand the  
306 species limits.

307 Three species of *Sycophila* (*S. texana* (Balduf), *S. varians* (Walsh), and *S.*  
308 *dorsalis* (Fitch)) were recently reared from the asexual generation of *D. quercusvirens*  
309 (Forbes et al. 2016), and one unidentified *Sycophila* species was reared from the  
310 asexual generation of *B. treatae* (Bird et al. 2013). While more work is needed to clarify  
311 the identities of these *Sycophila* species, it seems likely based on morphology that very  
312 little overlap occurs between the *Sycophila* species attacking *B. pallida*, *B. treatae*, and  
313 *D. quercusvirens*.

314 Two species of *Ormyrus* Westwood (Chalcidoidea: Ormyridae: Ormyrinae; Fig.  
315 4A-B) emerged from crypts on *Q. geminata* from two of the Florida collections (Table 1),  
316 and were identified using the key in Hanson (1992). Two *Ormyrus nr. labotus* Walker  
317 (Fig. 4A) emerged from collections at Inlet Beach, FL. We obtained sequence data from  
318 one of these specimens (MN935904; Table S1), and the closest match in GenBank was  
319 to an unidentified Ormyridae. The sequence was also 91.5% to 93.6% identical to

320 sequences from four *O. labotus* infecting *B. treatae* galls (Forbes et al. 2016). *O.*  
321 *labotus* is a generalist parasitoid, reported from more than 15 species of cynipid gall  
322 wasps (Noyes 2019). Additionally, six *O. nr. thymus* emerged (Fig. 4B, Table 1). A  
323 sequence obtained from one of these specimens (MN935907; TableS1) was an ~89%  
324 match with an unidentified Ormyridae in BOLD. This sequence was only 86-87% similar  
325 to the *O. labotus* sequences associated with *B. treatae*. *Ormyrus hegeli* (Girault) was  
326 also reared from both the asexual and sexual generation of *D. quercusvirens* (Bird et al.  
327 2013), and based on morphology appears to be a different species from the two  
328 *Ormyrus* species reared from *B. pallida*. No known associates of *O. thymus* or *O. hegeli*  
329 are listed in Noyes (2019).

330 *Acaenacis* Girault (Chalcidoidea: Pteromalidae: Pteromalinae; Fig 4C) were  
331 reared from four sites, including stem galls from both *Q. virginiana* and *Q. geminata*  
332 (Table 1). These specimens keyed to the genus *Acaenacis* using Gibson et al. (1997).  
333 Three COI sequences (MN935908, MN935911, MN935912; TableS1) were 88.8% to  
334 92.67% identical to each other, and the top hit for all three sequences in GenBank were  
335 to an unidentified Pteromalidae (85.5 to 88.3% identical).

336 Species in the genus *Acaenacis* attack oak-dwelling insects. *Acaenacis agrili*  
337 (Rohwer) is a parasitoid of the oak twig girdler (*Agrilus angelicus* Horn), which infects  
338 stems of *Quercus agrifolia* Nee in California (Rohwer 1919). Live oaks in the  
339 southeastern U.S. also harbor twig girdling beetles (Egan, S.P., personal observation).  
340 While associates of *Acaenacis taciti* (Girault) have not been identified (Noyes 2019), all  
341 other known hosts of *Acaenacis* are cynipid gall wasps. An undescribed *Acaenacis*  
342 infects *Andricus quercuslanigera* (Ashmead) on *Quercus rugosa* Nee in Mexico

343 (Serrano-Muñoz et al. 2016). *Acaenacis lasus* (Walker) has been reared from leaf galls  
344 of *B. treatae* from *Quercus fusiformis* Small and *Q. virginiana* in Texas (Forbes et al.  
345 2016), and *D. quercusvirens* on *Q. virginiana* in Florida (Bird et al. 2013). The four *A.*  
346 *lausus* sequences in GenBank from Forbes et al. (2016) were only 80-86% similar to  
347 the three *Acaenacis* sequences obtained from our collections. While *A. lasus* is infecting  
348 cynipid gall wasps on the same host plant as *B. pallida*, sequence data suggests that *A.*  
349 *lausus* is a different species than that emerging from *B. pallida*.

350 One *Ceroptres* sp. Hartig (Cynipoidea: Ceroptresini; Fig. 5A) was reared from a  
351 crypt collected at Inlet Beach, FL (Table 1), as was one *Synergus walshii* Gillette  
352 (Cynipoidea: Synergini; Fig. 5B). The *Ceroptres* specimen (MN935928; Table S1) was  
353 90.4% similar to *Ceroptres* sp. FSU 399 (Accession: DQ012636.1), which was reared  
354 from an *Andricus quercuscornigera* gall from Kentucky (USA) (Ronquist et al. 2015).  
355 The sequence from *S. walshii* (MN935929; TableS1) was 97.1% similar to *Synergus* sp.  
356 1 from Forbes et al. (2016), which was one of three *Synergus* species associated with  
357 *B. treatae* in that study. Three *Synergus* are also associated with the asexual  
358 generation of *D. quercusvirens*, but it is unclear if the species in our study is the same  
359 as *Synergus* sp. 1 reported in Bird et al. (2013). Members of the genera *Synergus* and  
360 *Ceroptres* are inquilines of cynipid gall wasps, which are not able to initiate galls, but  
361 can maintain the production of nutritious tree tissue once inside a gall (Pénzes et al.  
362 2012, Ronquist et al. 2015). *S. walshii* was reared from galls of several species of  
363 *Andricus* on various white oaks in IA, MO, and KY (A.K.G.W and A.A.F, unpublished  
364 data). Previous *S. walshii* collections were from *Andricus quercusflocci* galls on white  
365 oaks (*Quercus alba*) (Gillette 1896).



366           Ants (Formicidae) were observed twice during our samplings (Fig. 6, Table 1),  
367 and were identified to genus using Fisher and Cover (2007). Ants in the genus  
368 *Brachymyrmex* Mayr were observed and collected (N = 4 individuals; Fig. 6A) three  
369 months after *B. pallida*-infected *Q. virginiana* stems were brought into the lab. The  
370 sequence data from the *Brachymyrmex* (MN935915; TableS1) were 100% identical to a  
371 *Brachymyrmex obscurior* Forel sequence in GenBank. *Brachymyrmex obscurior* is likely  
372 an introduced species in North America (Deyrup et al. 2000). We also collected  
373 *Crematogaster ashmeadi* (N = 8 individuals; Fig. 6B), which were identified using  
374 Morgan and MacKay (2017). Some cynipid gall wasps induce their plant host to produce  
375 honeydew, which is consumed by ants who subsequently tend the gall (reviewed in  
376 Pierce 2019). While other cynipid gall wasps infecting oaks are known to secrete  
377 honeydew from their galls (e.g., *D. quercusvirens* on sand live oaks (Nicholls et al.  
378 2017)), we did not observe honeydew on nor tending by ants of *B. pallida* crypts. Ants  
379 are also “secondary occupants” of galls, settling in the galls once cynipids have  
380 abandoned them (e.g., Giannetti et al. 2019). We suspect that *B. pallida*-abandoned  
381 crypts are occasionally settled by ants.

382           The genus *Allorhogas* Gahan (Ichneumonoidea: Braconidae: Doryctinae)  
383 includes both gall-formers and parasitoids or inquilines (Zaldívar-Riverón et al. 2014).  
384 Eight *Allorhogas* (Table 1, Fig 7A) were reared from *Q. geminata*-infected stems from  
385 Camp Helen State Park (FL). A sequence was obtained from one of these specimens  
386 (MN935913; TableS1), and the sequence was 99.5% similar to a private *Allorhogas*  
387 sequence in BOLD. In GenBank, this sequence was 91.6% similar to the *Allorhogas*  
388 species reported from *B. treatae* in Forbes et al. (2016), and was 90.6 to 91.1% similar

389 to an *Allorhogas* sp. 2 collected from South America (Zaldívar-Riverón et al. 2014). No  
390 *Allorhogas* were reported to infect *D. quercusvirens* in Bird et al. (2013). Whether this  
391 *Allorhogas* is a parasitoid, inquiline, or other associate of *B. pallida* is currently  
392 unknown, but the original description of the only *Allorhogas* species currently reported  
393 from the U.S. suggested that it might be a parasitoid of gall-associated lepidoptera  
394 burrowing through gall tissue (Gahan 1912).

395         Five Platygastroidea specimens (Fig. 7B-D, Table 1) were identified using Mason  
396 (1993) and by Elijah Talamas (Florida Department of Agriculture and Consumer  
397 Services) based on specimen images. Sequence data were obtained from one  
398 specimen (MN935906; TableS1; Fig. 7B), which was ~89% similar to an undescribed  
399 *Telenomus* Haliday species in BOLD and GenBank. The remaining four specimens  
400 belongs in the genus *Calotelea* Westwood and *Synopeas* Foerster (Scelionidae) (Fig.  
401 7C and D, respectively). No Platygastriidae or Scelionidae were observed emerging  
402 from the asexual generations of galls made by *B. treatae* (Forbes et al. 2016) or *D.*  
403 *quercusvirens* (Bird et al. 2013). Platygastroidea are typically egg parasitoids, and while  
404 specific Platygastroidea species often specialize, the range of hosts infected by  
405 parasitoids in this superfamily is broad (Murphy et al. 2007, Taekul et al. 2014). Both  
406 *Telenomus* and *Calotelea* may be egg parasitoids of *B. pallida* or other gall inhabitants,  
407 while *Synopeas* attacks the gall midge associate.

408

409 Coleoptera

410 One beetle emerged from a *Q. geminata* stem in 2019 (Table 2, Fig. 8A), one month  
411 after the stem was brought into the lab. The sequence obtained from this beetle

412 (MN935914; Table S1) was an ~93% match to three published *Petalium bistratum*  
413 (Ptinidae) sequences in BOLD. *Petalium* beetles are wood-boring (Ford 1973), and may  
414 not be directly associated with *B. pallida* crypts.

415

#### 416 Diptera

417 Two unidentified gall midge species in subfamily Cecidomyiinae (Sciaroidea:  
418 Cecidomyiidae) were reared in our collections (Table 2). The first species emerged from  
419 collections at Rice University's campus on *Q. virginiana*, and the one sequence  
420 (MN935916; TableS1) obtained from this species is 99.9% similar to the unidentified  
421 gall midge associated with *B. treatae* (Forbes et al. 2016). The second species  
422 (MN935917; TableS1; Fig. 8B) was 91.9% similar to the first, emerged from Inlet Beach,  
423 FL on *Q. geminata*, and is ~92% similar to *Asteromyia euthamiae* (subfamily  
424 Cecidomyiinae) sequences in GenBank. Gall midges are both gall formers and  
425 inquilines, including inquilines of cynipid gall wasps (Mamaev and Krivosheina 1992).

426

#### 427 Psocoptera

428 Thirty-six Psocopterans from at least three species emerged from the stems in our  
429 collections (Table 2, Fig 9). We sequenced six of these specimens, which we suspected  
430 represented two specimens for each of the three species. The rest of the Psocopterans  
431 we reared are reported as "Unidentified Psocoptera" in Table 2. Each pair of sequences  
432 from putative conspecifics were 99% similar to one another, and putative congener  
433 sequences were only ~77-81% similar. Sequence data thus supports the presence of  
434 three Psocopteran species associated with *B. pallida* crypts. The sequences from the

435 first species (MN935922 and MN935924; Table S1; Fig. 9A) were ~98% similar to  
436 *Peripsocus madidus* sequences in GenBank. Two sequences from the second species  
437 (MN935923 and MN935925; Table S1; Fig. 9B) were ~94% similar to an classified  
438 Psocodea in BOLD, and ~84% similar to an unclassified Psocidae in GenBank. Two  
439 sequences (MN935920 and MN935921; TableS1) from the third species (Fig. 9C) were  
440 ~97-99.7% similar to private Lachesillidae sequences in BOLD, and 83.1% similar to an  
441 unclassified Psocoptera in GenBank. These psocopterans colonize abandoned crypts  
442 and inhabit them for long periods of time. They move in and out of the crypts,  
443 sometimes partially sealing the emergence holes with detritus.

444

445 Thysanoptera

446 One thrips from the family Phlaeothripidae (Table 2, Fig. 8C) was associated with a  
447 stem collected in 2015 from *Q. geminata* at Inlet Beach, FL. We identified the specimen  
448 to family (Mound et al. 2009), but were unable to extract DNA.

449

## 450 **Discussion**

451 A diverse and species-rich community of invertebrates is associated with the asexual  
452 generation of the gall wasp, *B. pallida*, and the crypts they create. These included  
453 Hymenoptera (21 species) (Table 1), Diptera (2), Coleoptera (1), Psocoptera (3), and  
454 Thysanoptera (1) (Table 2). The associates included parasitoids, inquillines, and  
455 secondary colonist that utilize the crypt after the emergence of *B. pallida* and/or its  
456 natural enemies.

457

458 Putative Natural Enemies

459 Communities of natural enemies attacking cynipid gall wasps are structured by factors  
460 that include differences in gall structure and location on the host tree (e.g., leaf versus  
461 stem; Bailey et al. 2009). The natural enemy communities of three cynipid gall wasps  
462 residing on live oaks (*Q. geminata* and *Q. virginiana*) have been described recently (*D.*  
463 *quercusvirens*: Bird et al. 2013, *B. treatae*: Forbes et al. 2016, this study). The asexual  
464 generation of two of these wasps (*B. pallida* and *D. quercusvirens*) reside in similar  
465 locations (i.e., stems), while the asexual generation of *B. treatae* creates galls on  
466 leaves. The number of Hymenoptera that are likely parasitoids, hyperparasitoids, or  
467 inquilines was more similar between *B. pallida* (a stem-galler, ~19 Hymenopteran  
468 natural enemies; this study) and *B. treatae* (a leaf-galler, ~21 Hymenopteran natural  
469 enemies; (Forbes et al. 2016)), while the asexual generation of *D. quercusvirens* hosted  
470 only 9 natural enemies (Bird et al. 2013). While differences in sampling methods could  
471 explain this difference, it is also possible that *D. quercusvirens* had a low number of  
472 natural enemies due to its mutualism with ants. Some gall wasps attract ants by  
473 inducing the gall to produce honeydew, and these ants then defend the gall against  
474 inquilines and parasitoids (Washburn 1984, Abe 1992, Seibert 1993, Fernandes et al.  
475 1999, Inouye and Agrawal 2004). Bird et al. (2013) noted the presence of ants on bullet  
476 galls created by *D. quercusvirens*, and these ants could have either excluded particular  
477 parasitoid species or reduced parasitoid success to low enough levels that these natural  
478 enemies were not observed during the collections.

479         While *B. pallida*, *D. quercusvirens*, and *B. treatae* all reside on live oaks, none of  
480 the natural enemies identified to species were common across all three cynipid gall

481 wasp hosts. Additional natural enemies recorded for *D. quercusvirens* in Krombein et al.  
482 (1979) and for *B. treatae* in Peck (1963) overlap very little with natural enemies reported  
483 from the more recent studies. For *B. treatae*, only 1 of the 8 natural enemies reported in  
484 Peck (1963) was also reported by Forbes et al (2016), and, for *D. quercusvirens*, 7  
485 natural enemies reported in Krombein et al. (1979) were not observed by Bird et al  
486 (2013). This suggests either that community composition is changing over time, that  
487 species were misidentified or the use of synonyms is confounding comparisons, or that  
488 no study has yet to sample these cynipid hosts with enough temporal and spatial  
489 coverage to capture the entire natural enemy community. However, there is some  
490 overlap between pairs of cynipid hosts. For example, *Acaenacis lausus* infects both *B.*  
491 *treatae* and *D. quercusvirens* (Bird et al. 2013, Forbes et al. 2016), and the inquiline  
492 *Synergus walshii* may be infecting both *B. treatae* and *B. pallida* (Forbes et al. 2016,  
493 and this study). In general though, it is difficult to draw strong conclusions about the  
494 degree of natural enemy overlap in these communities due to differences in sampling  
495 effort (including sampling done at different sites in different years). What is clear is that  
496 these galls support a diverse community of Hymenopteran natural enemies. As a rough  
497 estimation, if we assume that each of the 12 cynipid species on live oaks harbor about  
498 15 host-specific natural enemies, that would yeild a community of 180 natural enemies  
499 in this system. Future work to quantify this diversity, and understand factors that  
500 influence the degree of overlap of these natural enemy communities across cynipid  
501 hosts is greatly needed.

502         One area of high interest is the association between *B. pallida* crypt galls and the  
503 recently described parasitoid *Euderus set*, which an example of a parasitoid species

504 that can manipulate the behavior of its insect host (Weinersmith 2019). Specifically, *E.*  
505 *set* manipulates *B. pallida* into excavating an emergence hole from the crypt, which *B.*  
506 *pallida* then plugs with its head before being consumed by the parasitoid (Egan et al.  
507 2017, Weinersmith et al. 2017). The parasitoid subsequently emerges from the host's  
508 head capsule (Weinersmith et al. 2017). *E. set* infects and manipulates at least six  
509 additional cynipid gall wasp hosts infecting other oak species (Ward et al. 2019). The  
510 finding that *E. set* manipulates a broad range of cynipid gall wasps (Ward et al. 2019),  
511 suggests that the mechanism *E. set* uses to manipulate its host either does not require  
512 extreme specialization on host physiology or involves a mechanism common to many  
513 gall wasp residents. A more careful look at the gallers, inquilines, and parasitoids  
514 residing in live oak galls is warranted to determine if *E. set* is infecting and manipulating  
515 more hosts than just *B. pallida* in this system. Additionally, it is unclear why *E. set* is the  
516 only parasitoid that has been documented manipulating its hosts in this manner, while  
517 none of the other parasitoids or inquilines attacking cynipid gall wasps appear to do the  
518 same. Future work putting *E. set* in context with the other parasitoids infecting cynipid  
519 gall wasps should address questions about the selective pressure for manipulation,  
520 constraints on the evolution of this trait (including the costs paid by *E. set* as it  
521 manipulates its host), and the fitness benefits accrued through manipulation.

522 Finally, one common natural enemy that often attacks live oak galls was not  
523 observed in our study. Birds often break open the galls of *D. quercusvirens*, *D. cinerosa*,  
524 and *Callirhytis quercusbatatoides* (Ashmead) on live oaks to consume the wasps  
525 developing within (Weaver et al. in revision). During our collections we did not directly  
526 observe birds attacking *B. pallida* galls, nor did we see indirect evidence of predation on

527 the stems. This suggests that the cryptic phenotype of *B. pallida* galls may to some  
528 extent protect the galler (and its natural enemy community) from bird predation.

529

530 Other Associates

531 Associates reported in this study, which likely colonize *B. pallida* crypts after the galler,  
532 inquilines, and parasitoids have emerged, included ants, a beetle, a thrips, and barklice.  
533 While barklice were fairly common (36 were observed over the course of the study), the  
534 other associates were quite rare. Other reported colonizers of live oak galls include  
535 spiny millipedes (*Polyxenus* sp), spiders, mites, and lepidopterans (Wheeler and  
536 Longino 1988, Forbes et al. 2016). The lack of these associates in *B. pallida* galls could  
537 be explained by our sampling procedure underestimating the number of associates  
538 present, or because the small size of *B. pallida* crypts make them undesirable habitats  
539 for would-be colonizers. Ants, for example, seem to prefer to colonize larger galls  
540 (Almeida et al. 2014, Santos et al. 2017, Giannetti et al. 2019). The stem galls made by  
541 *B. pallida* tend to be smaller than the other cynipid galls on live oaks, and invertebrates  
542 may choose to colonize larger abandoned galls first.

543 We anticipated seeing lepidopterans in *B. pallida* galls, as they are associates of  
544 many galls on oaks (Brown and Mizell III 1993), including *B. treatae* leaf galls (Forbes et  
545 al. 2016) and *C. quercusbatatoides* stem galls (Egan, personal observation). The lack of  
546 lepidopterans has possible implications for our understanding of the biology of the  
547 parasitoid *Allorhogas*, as the original description of *Allorhogas* postulated that this  
548 genus may be parasitoids of lepidopterans (Gahan 1912). While it is possible that the  
549 timing of our collections missed lepidopterans associated with *B. pallida* crypts, the



550 current data suggest that the *Allorhogas* observed in our system are not parasitoids of  
551 lepidopterans.

552

553 Conclusions

554 While more detailed work may reveal some the associates we collected resided within  
555 the infected stem without actually associating with the crypt (e.g., this may be the case  
556 with the wood-boring Ptinid beetle), it is likely that future work will also reveal additional  
557 associates. In fact, our sampling may underestimate associate diversity in a number of  
558 ways. First, we have not sampled the unknown sexual generation of *B. pallida*, which  
559 remains to be discovered. This gall wasp generation will likely harbor some known  
560 species that attack both generations, as well as some that are unique to the sexual  
561 generation – as was found to be the case with the community attacking *B. treatae* on  
562 these same host plants (Forbes et al. 2016). Second, we identified infected live oak  
563 stems by looking for abandoned crypts, where these emergence holes were most likely  
564 formed in current and previous years. This highlights an important and general  
565 challenge to sampling cynipid associated communities, which is that time of sampling  
566 matters. We may have missed some parasitoids that emerge earlier - prior to the  
567 emergence of *B. pallida* – and/or missed some that attack later. Third, our sampling did  
568 not include the entire geographic range of *B. pallida*, which matches the distribution of  
569 its known host plant associations within the live oaks (*Q. virginiana* throughout the entire  
570 coastal southeastern United States from Virginia to Texas, *Q. geminata* restricted to  
571 xeric soils in Alabama, Mississippi, Florida, and Georgia, and *Q. fusiformis* in central  
572 and south Texas; see detailed host plant distributions in Cavender-Bares et al. 2015).

573 We found that the asexual generation of *B. pallida* is associated with a diverse  
574 arthropod community, including over 25 parasitoids, inquilines, and other invertebrates  
575 spanning five orders and 16 families. There was very little overlap between the natural  
576 enemy communities infecting two other live-oak infecting cynipid gall wasp species,  
577 suggesting a species-rich community of parasitoids and inquilines attacking cynipid gall  
578 wasps on live oaks. Descriptive studies like this are a necessary first step towards  
579 addressing broader ecological and evolutionary questions. In the future, we will use the  
580 community of cynipid gall wasps residing on live oaks, and the communities of natural  
581 enemies associated with these gallers, to address questions about habitat  
582 fragmentation and diversity (Maldonado-López et al. 2015), and the structuring of  
583 natural enemy communities (e.g., Bailey et al. 2009). Additionally, studies which  
584 quantify natural enemy communities and quantify the host range of parasitoids are  
585 critical for more accurate estimates of species richness (Forbes et al. 2018)

586

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595

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844

#### 845 **TABLE LEGENDS**

846 **Table 1:** Hymenopteran associates (including putative parasitoids, hyperparasitoids, and  
847 inquilines) of the asexual generation of *Bassettia pallida*. The table presents the number of  
848 specimens reared from live oak stems infected by *B. pallida* at various collection sites in Florida  
849 and Texas from 2015 – 2019. Collection site abbreviations: IB = Inlet Beach, LL = Lake Lizzie,  
850 TH = Topsail Hill Preserve State Park, CH = Camp Helen State Park, Rice U. = Rice University  
851 in Houston.

852

853 **Table 2:** Associates of the asexual generation of *Bassettia pallida*. The table presents the  
854 number of specimens reared from live oak stems infected by *B. pallida* at various location sites  
855 in Florida (FL) and Texas (TX) from 2015 – 2019. Host tree abbreviations: *Qg* = *Quercus*  
856 *geminata*, *Qv* = *Quercus virginiana*. Collection site abbreviations: TH = Topsail Hill Preserve  
857 State Park, CH = Camp Helen State Park, Rice U. = Rice University in Houston.

858

#### 859 **FIGURE LEGENDS**

860 **Fig. 1.** The asexual generation of *Bassettia pallida*, and their stem galls. **(A)** Female *B. pallida*.  
861 **(B)** Male *B. pallida*. **(C)** A *Quercus geminata* stem infected by *B. pallida*, showing the  
862 emergence hole from a crypt concealed within the stem, and showing two *B. pallida* whose  
863 heads are plugging an incomplete emergence hole following manipulation by the parasitoid  
864 *Euderus set.* **(D)** Two crypt galls containing subadult *B. pallida*, revealed by removing the bark  
865 and some woody tissue using a razor blade. Photos A, B, and D originally appeared in  
866 Weinersmith et al. 2017, Proc Roy Soc B., and is available under a CC by 4.0 License.

867

868 **Fig. 2.** Natural enemies reared from *B. pallida* galls. **(A)** *Euderus set*, and examples of a *B.*  
869 *pallida* head capsule plugging an emergence hole (right) and a head-plugged emergence hole  
870 from which *E. set* has emerged (left). *E. set* photo originally appeared in Weinersmith et al.  
871 2017, Proc Roy Soc B., and is available under a CC by 4.0 License. Photos of *B. pallida* head  
872 capsules by Mattheau Comerford. **(B)** *Galeopsomyia* species. Female on the left, with wing  
873 inset in top center. Male on the right, with wing inset in bottom center. **(C)** Unidentified *Brasema*  
874 species. Female on the left, male on the right, with an inset of a male's wing in the center.  
875

876 **Fig. 3.** Eurytomidae natural enemies reared from galls made by the asexual generation of *B.*  
877 *pallida*. Males, when present, are on the right. Wings are from female specimens. **(A)**  
878 Unidentified *Eurytoma* species. **(B)** *Sycophila nr. foliatae*. **(C)** *Sycophila nr. dubia*, **(D)** *Sycophila*  
879 *nr. nubilistigma*. **(E)** *Sycophila nr. disholcaspidis*.  
880

881 **Fig. 4.** Natural enemies reared from *B. pallida* galls, with wing insets from female specimens.  
882 **(A)** *Ormyrus nr labotus*, **(B)** *Ormyrus nr thymus*, **(C)** Unidentified *Acaenacis* species, with  
883 female on left and male on right.  
884

885 **Fig. 5.** Inquilines reared from galls made by the the asexual generation of *B. pallida*. **(A)**  
886 Unidentified *Ceroptres*. **(B)** *Synergus walshii*, with inset showing detail of wing.  
887

888 **Fig. 6.** Ants (Formicidae) associated with *B. pallida* crypts. **(A)** *Brachymyrmex obscurior*. **(B)**  
889 *Crematogaster ashmeadi*.  
890

891 **Fig. 7.** Natural enemies reared from galls made by the asexual generation of *B. pallida*, with  
892 wing insets from female specimens when available. **(A)** Unidentified *Allorhogas* species, with

893 female on the left and male on the right, **(B)** Unidentified *Telenomus* species, **(C)** Unidentified  
894 *Calotelea* species, **(D)** Unidentified *Synopeas* species.

895

896 **Fig. 8.** Associates of galls made by the asexual generation of *Bassettia pallida*. **(A)** Unidentified  
897 Ptinidae beetle (Coleoptera: Bostrichoidea), **(B)** Unidentified Cecidomyiidae (Diptera), **(C)**  
898 Unidentified Phlaeothripidae (Thysanoptera).

899

900 **Fig. 9.** Psocopterans associated with galls made by the asexual generation of *Bassettia pallida*.  
901 **(A)** *Peripsocus madidus*. **(B)** Unidentified Psocidae. **(C)** Unidentified Lachesillidae.

902

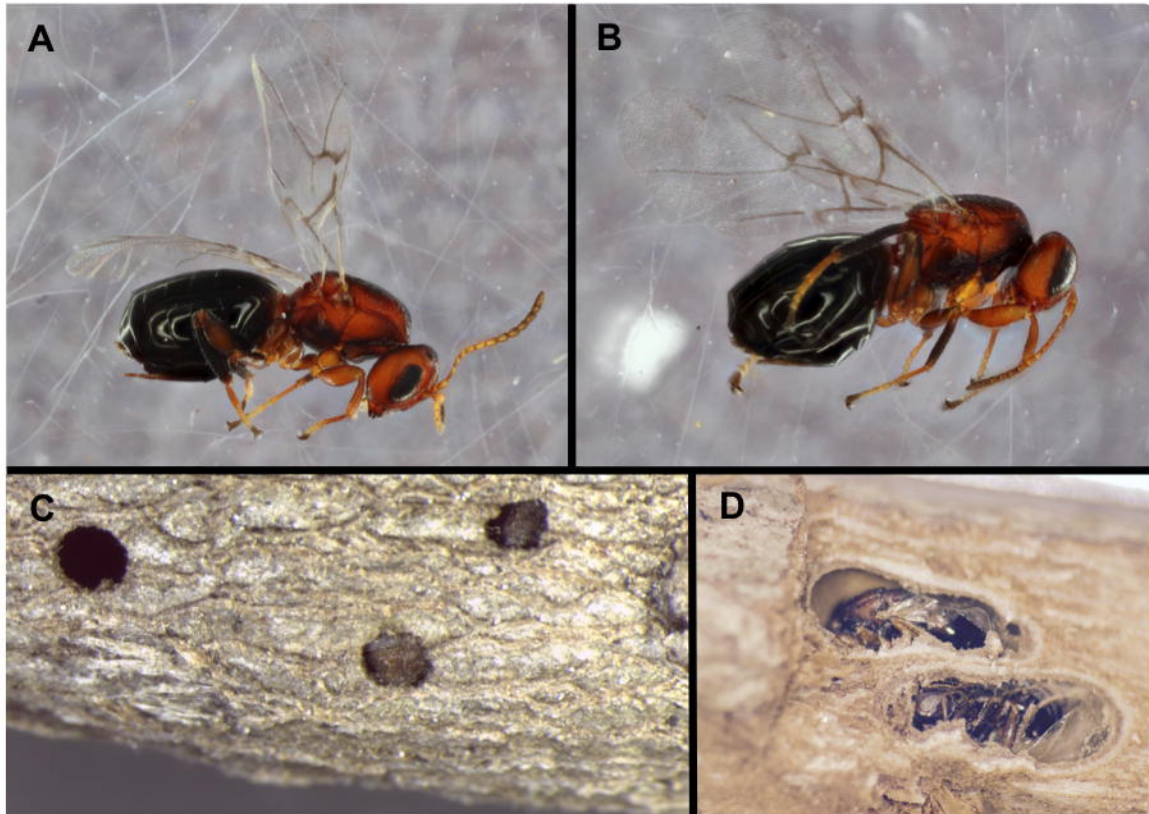
Collection State, Host Tree Collection Site Collection Year (20XX)		Florida, <i>Quercus geminata</i>					Texas, <i>Quercus virginiana</i>					
		IB		LL	TH		Humble			Rice U.		
		15	19	15	18	19	15	16	19	16	17	
<b>Family</b>	<b>Species or subfamily</b>											
Cynipidae	<i>Bassettia pallida</i> (galler)	4	11	4						5		
Encyrtidae	<i>Encyrtidae</i> sp.											1
Eulophidae	<i>Euderus set</i>	154			5				6			
	<i>Galeopsomyia</i> sp.	3										146
	<i>Tetrastichinae</i> sp.											3
Eupelmidae	<i>Brasema</i> sp.	2			1							
Eurytomidae	<i>Eurytoma</i> sp.	5			1							1
	<i>Sycophila</i> (4 morphotypes)	13						1			2	7
Ormyridae	<i>Ormyrus</i> nr. <i>thymus</i>	5										1
	<i>Ormyrus</i> nr. <i>labotus</i>	2										
Pteromalidae	<i>Acaenacis</i> sp.	8			1							43
Cynipidae	<i>Ceroptres</i> sp.	1										
	<i>Synergus walshii</i>	1										
Formicidae	<i>Brachymyrmex obscurior</i>											4
	<i>Crematogaster ashmeadi</i>			8								
Braconidae	<i>Allorhogas</i> sp.											8
Platygastridae	<i>Telenomus</i> sp.	1										
	<i>Calotelea</i> sp.				1							
	<i>Synopeas</i> sp.	3										

**Table 1:** Hymenopteran associates (including putative parasitoids, hyperparasitoids, and inquilines) of the asexual generation of *Bassettia pallida*. The table presents the number of specimens reared from live oak stems infected by *B. pallida* at various collection sites in Florida and Texas from 2015 – 2019. Collection site abbreviations: IB = Inlet Beach, LL = Lake Lizzie, TH = Topsail Hill Preserve State Park, CH = Camp Helen State Park, Rice U. = Rice University in Houston.

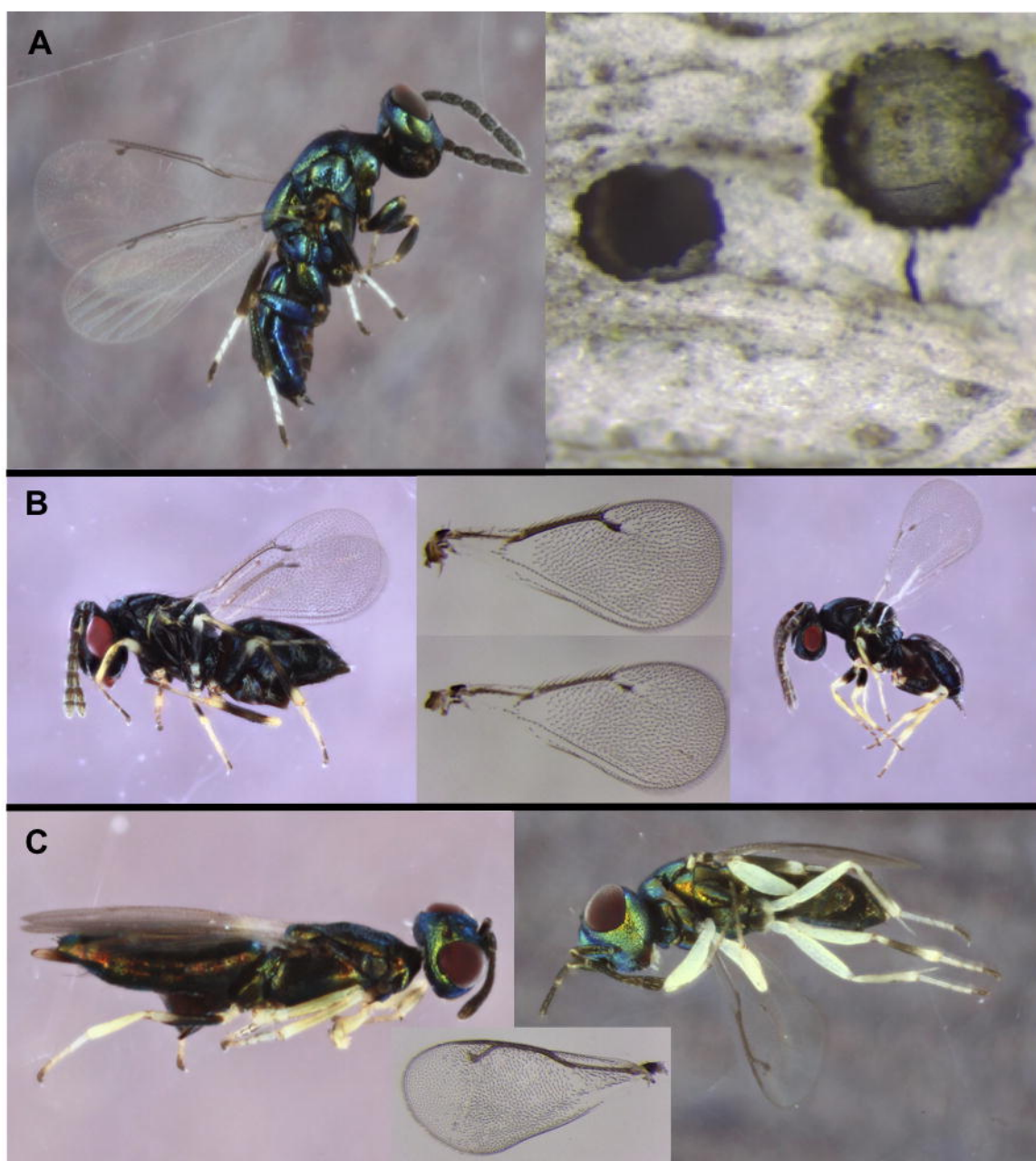


<b>Collection State, Host Tree</b>		<b>FL, Qg</b>					<b>TX, Qv</b>	
<b>Collection Site</b>		<b>Inlet Beach</b>			<b>TH</b>	<b>CH</b>	<b>Rice U.</b>	
<b>Collection Year (20XX)</b>		<b>15</b>	<b>18</b>	<b>19</b>	<b>18</b>	<b>19</b>	<b>16</b>	<b>17</b>
<b>Order</b>								
<b>Family</b>	<b>Subfamily/Species</b>							
Coleoptera								
Bostrichoidea	Ptinidae					1		
Diptera								
Cecidomyiidae	Cecidomyiinae sp 1	5		1				
	Cecidomyiinae sp 2							1
Psocoptera								
Peripsocidae	<i>Peripsocus madidus</i>			1	1			
Psocidae	Unknown					2		
Lachesillidae	Unknown	1						1
Various	UnIDed Psocoptera	3	2	7	13	2	2	1
Thysanoptera								
Phlaeothripidae	Unknown	1						

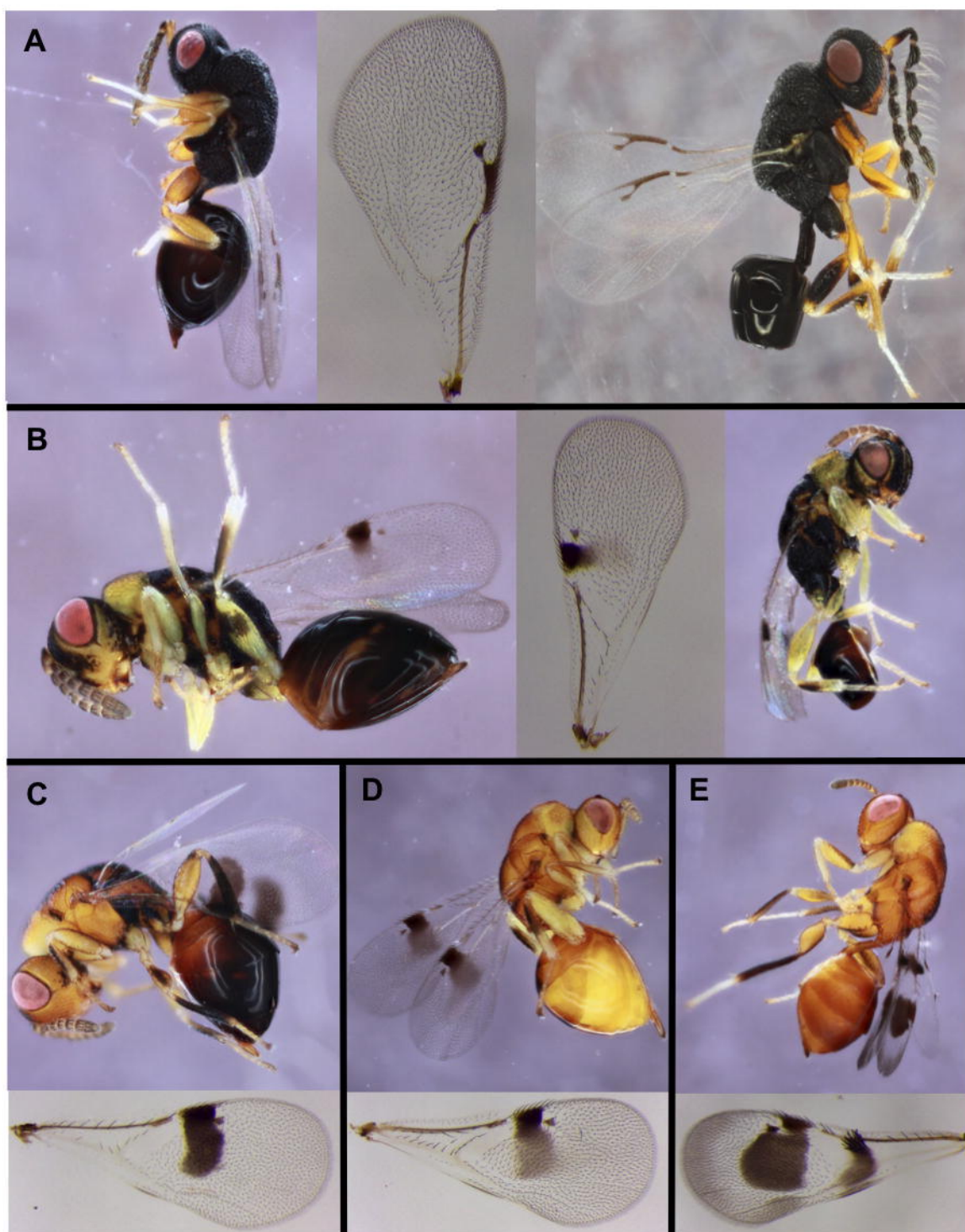
**Table 2:** Associates of the asexual generation of *Bassettia pallida*. The table presents the number of specimens reared from live oak stems infected by *B. pallida* at various location sites in Florida (FL) and Texas (TX) from 2015 – 2019. Host tree abbreviations: Qg = *Quercus geminata*, Qv = *Quercus virginiana*. Collection site abbreviations: TH = Topsail Hill Preserve State Park, CH = Camp Helen State Park, Rice U. = Rice University in Houston.



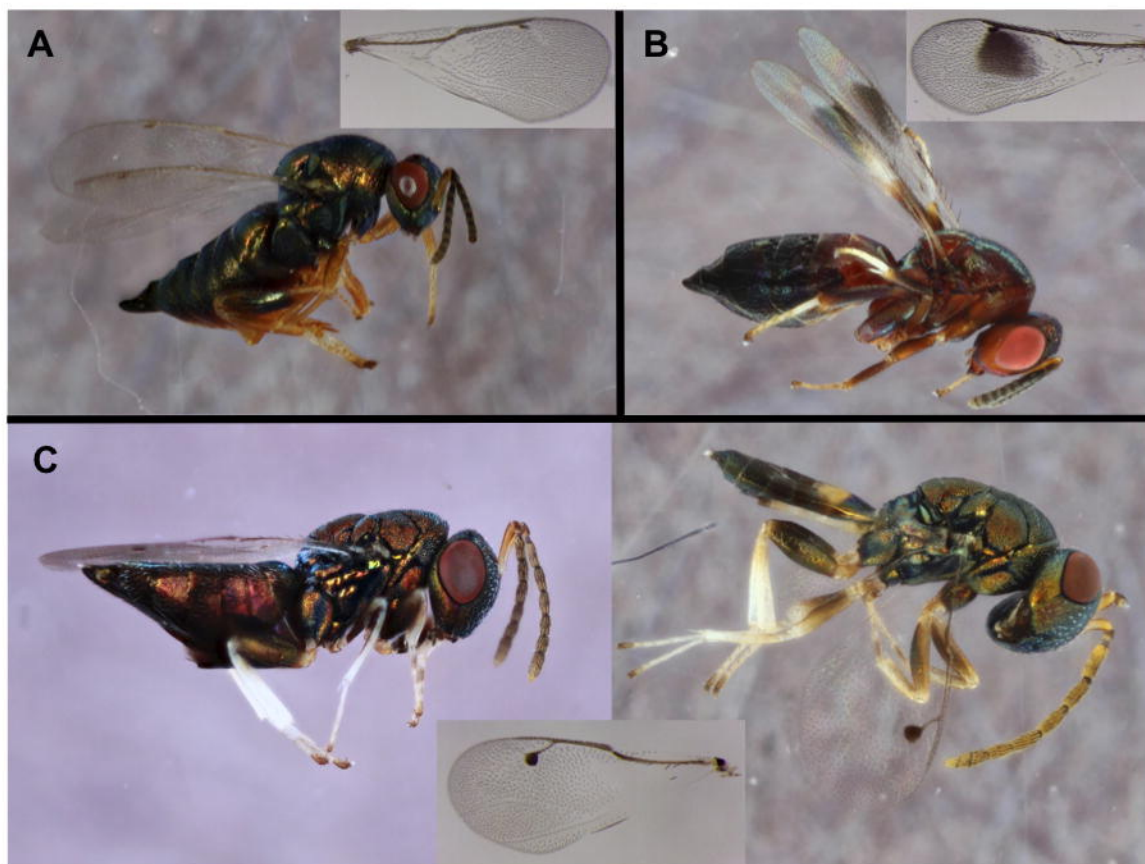
**Fig. 1.** The asexual generation of *Bassettia pallida*, and their stem galls. **(A)** Female *B. pallida*. **(B)** Male *B. pallida*. **(C)** A *Quercus geminata* stem infected by *B. pallida*, showing the emergence hole from a crypt concealed within the stem, and showing two *B. pallida* whose heads are plugging an incomplete emergence hole following manipulation by the parasitoid *Euderus set.* **(D)** Two crypt galls containing subadult *B. pallida*, revealed by removing the bark and some woody tissue using a razor blade. Photos A, B, and D originally appeared in Weinersmith et al. 2017, Proc Roy Soc B., and is available under a CC by 4.0 License.



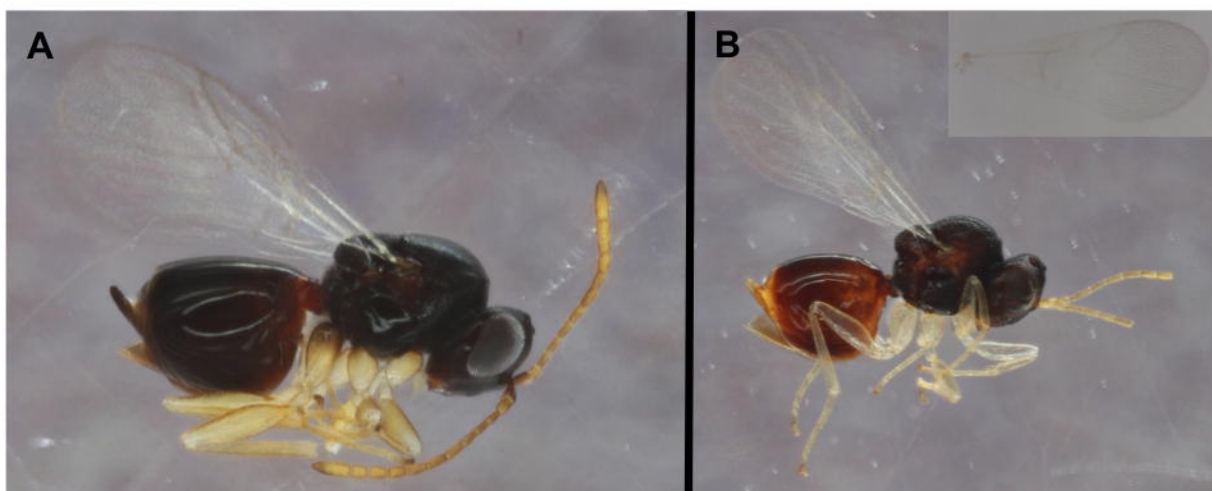
**Fig. 2.** Natural enemies reared from *B. pallida* galls. (A) *Euderus set*, and examples of a *B. pallida* head capsule plugging an emergence hole (right) and a head-plugged emergence hole from which *E. set* has emerged (left). *E. set* photo originally appeared in Weinersmith et al. 2017, Proc Roy Soc B., and is available under a CC by 4.0 License. Photos of *B. pallida* head capsules by Mattheau Comerford. (B) *Galeopsomyia* species. Female on the left, with wing inset in top center. Male on the right, with wing inset in bottom center. (C) Unidentified *Brasema* species. Female on the left, male on the right, with an inset of a male's wing in the center.



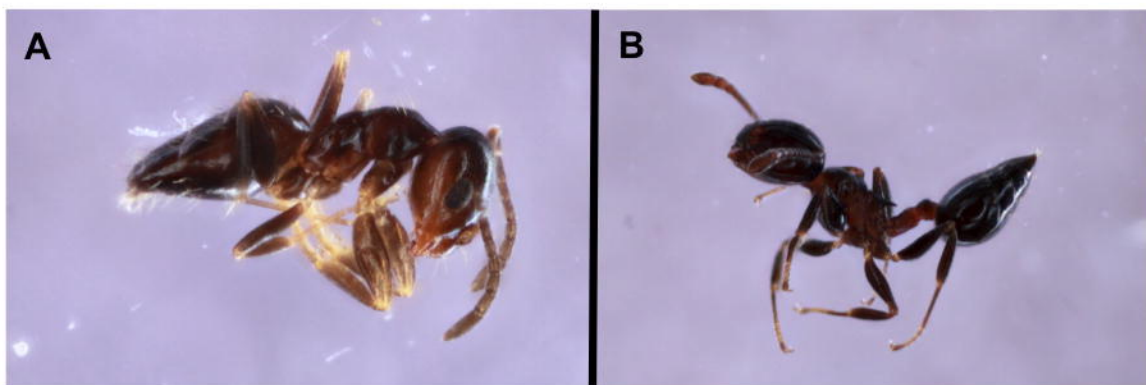
**Fig. 3.** Eurytomidae natural enemies reared from galls made by the asexual generation of *B. pallida*. Males, when present, are on the right. Wings are from female specimens. (A) Unidentified *Eurytoma* species. (B) *Sycophila* nr. *foliatae*. (C) *Sycophila* nr. *dubia*, (D) *Sycophila* nr. *nubilistigma*. (E) *Sycophila* nr. *disholcaspidis*.



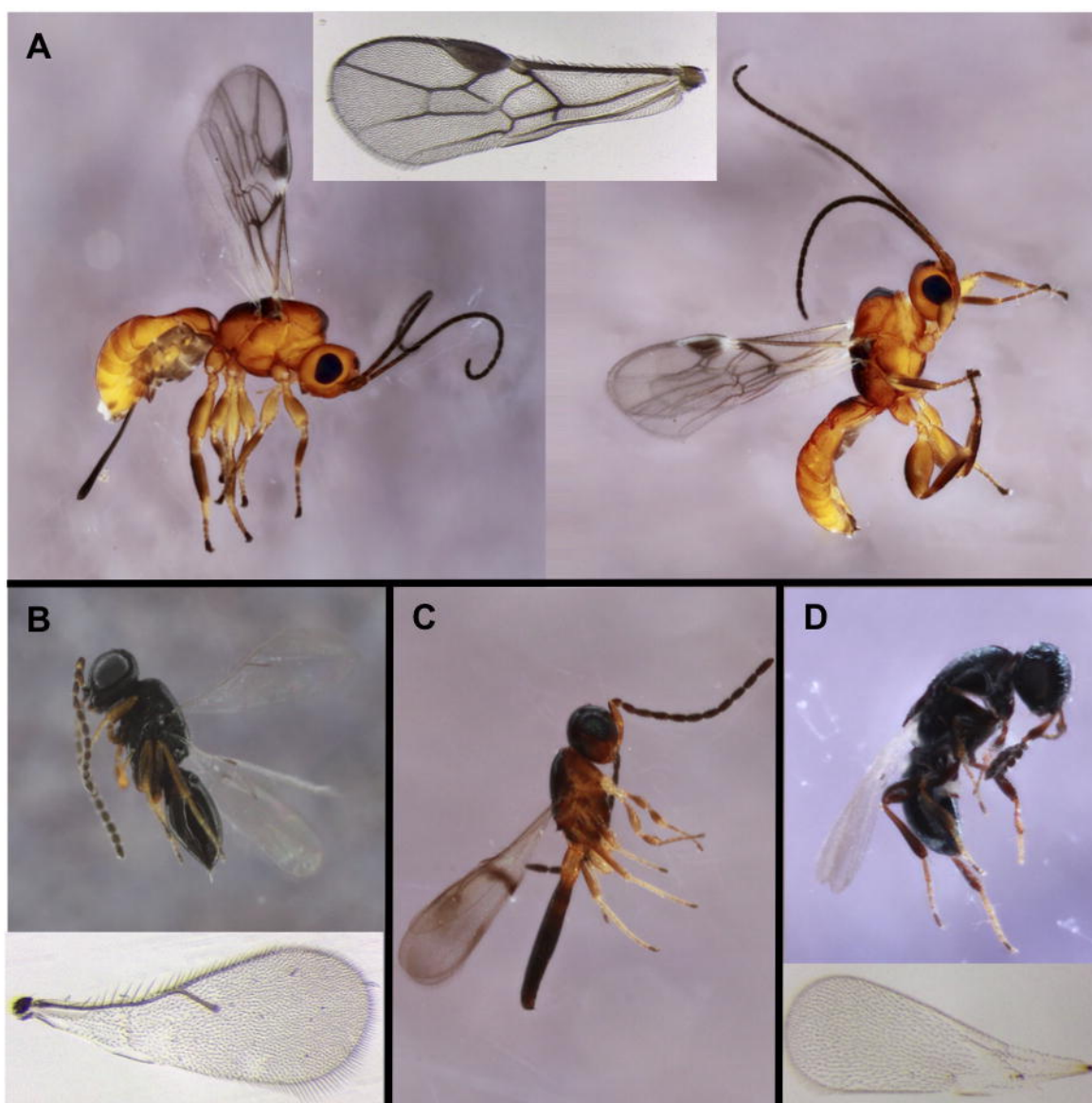
**Fig. 4.** Natural enemies reared from *B. pallida* galls, with wing insets from female specimens. **(A)** *Ormyrus nr labotus*, **(B)** *Ormyrus nr thymus*, **(C)** Unidentified *Acaenacis* species, with female on left and male on right.



**Fig. 5.** Inquilines reared from galls made by the the asexual generation of *B. pallida*. **(A)** Unidentified *Ceroptres*. **(B)** *Synergus walshii*, with inset showing detail of wing.

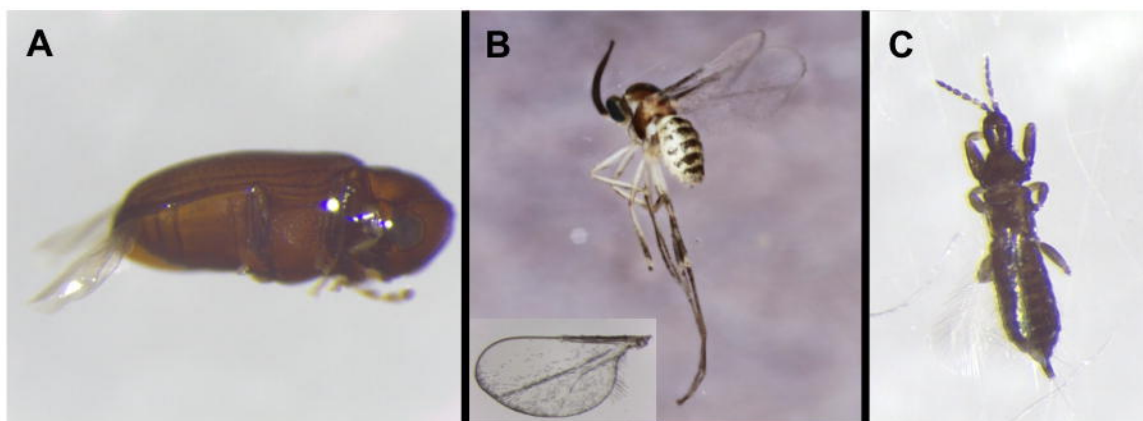


**Fig. 6.** Ants (Formicidae) associated with *B. pallida* crypts. **(A)** *Brachymyrmex obscurior*. **(B)** *Crematogaster ashmeadi*.

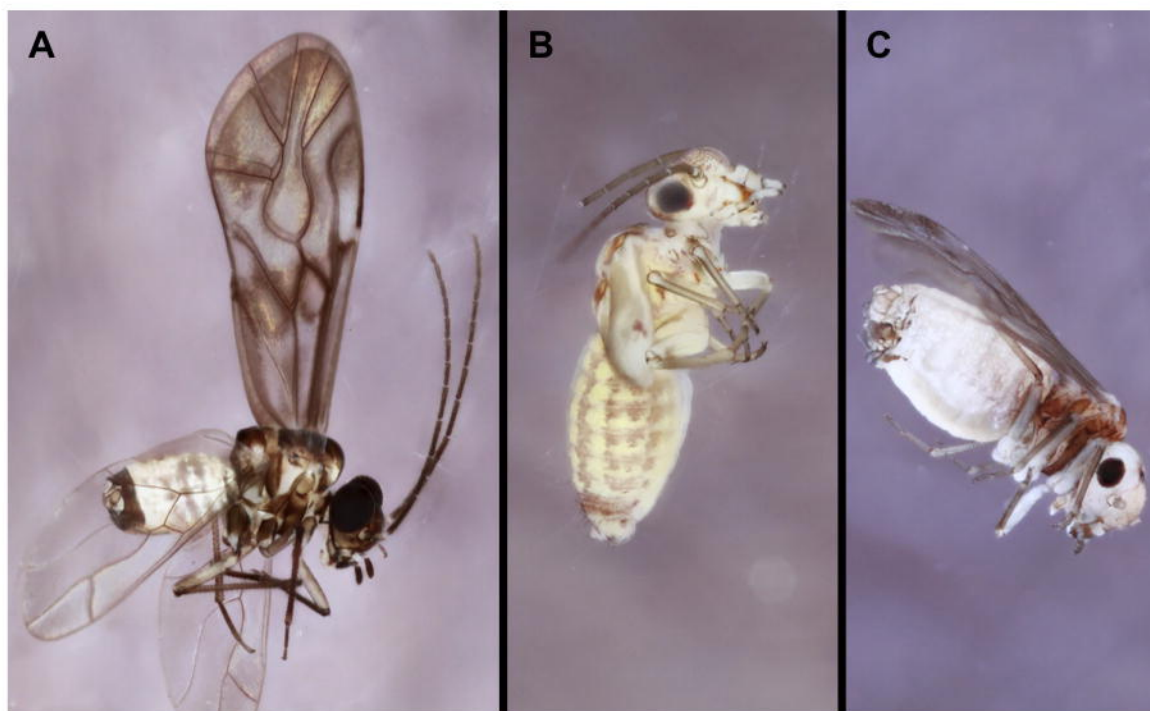


**Fig. 7.** Natural enemies reared from galls made by the asexual generation of *B. pallida*, with wing insets from female specimens when available. (A) Unidentified *Allorhogas* species, with female on the left and male on the right, (B) Unidentified *Telenomus* species, (C) Unidentified *Calotelea* species, (D) Unidentified *Synopeas* species.





**Fig. 8.** Associates of galls made by the asexual generation of *Bassettia pallida*. (A) Unidentified Ptinidae beetle (Coleoptera: Bostrichoidea), (B) Unidentified Cecidomyiidae (Diptera), (C) Unidentified Phlaeothripidae (Thysanoptera).



**Fig. 9.** Psocopterans associated with galls made by the asexual generation of *Bassettia pallida*. **(A)** *Peripsocus madidus*. **(B)** Unidentified Psocidae. **(C)** Unidentified Lachesillidae.