

Arthropod Community Associated With the Asexual Generation of *Bassettia pallida* (Hymenoptera: Cynipidae)

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Abstract

Cynipid gall wasps play an important role in structuring oak arthropod communities. Wasps in the Cynipini tribe typically lay their eggs in oaks (*Quercus* L.), and induce the formation of a ‘gall’, which is a tumor-like growth of plant material that surrounds the developing wasp. As the wasp develops, the cynipid and its gall are attacked by a diverse community of natural enemies, including parasitoids, hyperparasitoids, and inquilines. Determining what structures these species-rich natural enemy communities across cynipid gall wasp species is a major question in gall wasp biology. Additionally, gall wasps are ecosystem engineers, as the abandoned gall is used by other invertebrates. The gall-associated insect communities residing on live oaks (*Quercus geminata* Small and *Quercus virginiana* Mill.) are emerging as a model system for answering ecological and evolutionary questions ranging from community ecology to the evolution of new species. Documenting the arthropods associated with cynipids in this system will expand our understanding of the mechanisms influencing eco-evolutionary processes, record underexplored axes of biodiversity, and facilitate future work. Here, we present the community of natural enemies and other associates of the asexual generation of the crypt gall wasp, *Bassettia pallida* Ashmead. We compare the composition of this community to communities recently documented from two other cynipid gall wasps specializing on live oaks along the U.S. Gulf coast, *Disholcaspis quercusvirens* Ashmead and *Belonocnema treatae* Mayr. *B. pallida* and their galls support a diverse arthropod community, including over 25 parasitoids, inquilines, and other associated arthropods spanning 5 orders and 16 families.

Key words: oak gall, natural enemy hypothesis, crypt gall wasp, crypt keeper wasp, successors

Shelter-building insects, including gall formers, leaf rollers, leaf miners, and other insects that generate three-dimensional structures on their host plants, are ecosystem engineers, and are often associated with increases in arthropod richness and abundance on their host plants (reviewed in Cornelissen et al. 2016). While residing in their shelters, these insects are the target of parasitoids and predators, and are exploited by inquilines (i.e., organisms that typically do not make shelters themselves, but move into shelters with variable fitness implications for the shelter-maker; Sanver and Hawkins 2000, Mendonça and Romanowski 2002, Hayward and Stone 2005, Bailey et al. 2009). The shelters often remain after the ecosystem engineer has abandoned it, and are subsequently settled by arthropod ‘successors’ (Cornelissen et al. 2016, Harvey et al. 2016, Wetzel et al. 2016).

Some of nature’s most complex shelters are created by cynipid gall wasps (Stone et al. 2002, Stone and Schönrogge 2003). Members

of the tribe Cynipini lay their eggs in *Quercus* oaks (or sometimes other trees in the family Fagaceae), and induce the plant to produce a structure called a ‘gall’. The gall is lined with nutritious tissue, and will support the wasp while it feeds and develops (Rohfritsch 1992). Galls vary in appearance and structure, including those that exhibit exterior defenses, such as sticky, hairy, or protruding spikes, or contain internal air sacs (Stone and Cook 1998, Csóka et al. 2005, Bailey et al. 2009), and those that are more cryptic (Melika and Abrahamson 2007). The incredible structural diversity among galls is thought to be a defense against the speciose community of parasitoids and inquilines that attack the gall-makers (Abe et al. 2007, Askew et al. 2013), and can have dramatic impacts on cynipid population fitness (Price et al. 1987, Sanver and Hawkins 2000, Stone and Schönrogge 2003, Csóka et al. 2005, Bailey et al. 2009). An estimated ~1,400 described species of cynipid gall wasps produce morphologically diverse galls in their respective host plants (Ronquist

et al. 2015, Pénzes et al. 2018), making this system ideal for asking questions about the importance of factors such as host relatedness, phenology, and natural enemy defense strategies on the structure of natural enemy communities (Cornell 1985, Stone et al. 2002, Stone and Schönrogge 2003, Price et al. 2004, Csóka et al. 2005, Hayward and Stone 2005).

Many of the studies on the structuring of the communities of natural enemies attacking cynipid gall wasps have been done in the Palearctic (e.g., Schönrogge et al. 1996, Hayward and Stone 2005, Bailey et al. 2009, Nicholls et al. 2010, Stone et al. 2012, Bunnefeld et al. 2018). In North America, groundwork is being laid to conduct similar studies on the communities associated with the cynipid gall wasps that infect the ‘live oaks’ (subsection Virentes)—a monophyletic group of seven North American semievergreen oak species within the genus *Quercus*—where much of the focus has centered on two partially overlapping sister species along the U.S. Gulf coast, *Quercus virginiana* and *Quercus geminata* (Cavender-Bares and Pahlich 2009, Cavender-Bares et al. 2015, Hipp et al. 2018). These live oaks are home to at least six (Egan et al. 2013) and potentially twelve (S. P. Egan, unpublished data) cynipid gall wasp species, which are in turn attacked by a community of parasitoids and inquilines (Bird et al. 2013, Forbes et al. 2016). The cynipid gall wasps and their communities of natural enemies associated with the live oak lineage are emerging as powerful systems for answering a broad set of ecological and evolutionary questions on local adaptation (Egan and Ott 2007), natural selection (Egan et al. 2011), speciation (Egan et al. 2012a, Egan et al. 2012b, Egan et al. 2013, Zhang et al. 2017, Hood et al. 2019, Zhang et al. 2019), developmental plasticity (Hood and Ott 2010), and novel species interactions (Egan et al. 2017, Weinersmith et al. 2017, Ward et al. 2019). However, the extent to which these species-rich natural enemy communities on gall wasp host species overlap is currently unclear, and even documentation of the species present in these communities is far from complete. Because of these limitations, the factors determining the overlap between the natural enemy communities attacking cynipid gall wasps species residing on live oaks remains unexplored.

After the host and/or its various natural enemies have exited the gall, the gall itself often remains, which is particularly true for galls that are integral and woody. Abandoned oak galls are settled by a variety of arthropod successors, including ants, spiders, mites, and beetles (e.g., Cooper and Rieske 2010, Wetzel et al. 2016, Giannetti et al. 2019). While a recent review found that insect-made shelters are associated with increases in the abundance and diversity of arthropods that use the shelter once it is abandoned (Cornelissen et al. 2016), increases in successor density and diversity are not the rule. For example, the abandoned galls of the California gall wasp, *Andricus quercusalifornicus* (Bassett), are associated with a reduction in herbivore arthropod density and diversity, presumably because the gall successors included predatory spiders which attack herbivore invertebrates (Wetzel et al. 2016). Additional work is needed to better understand of the importance of abandoned galls on the local arthropod community.

Here, we describe the community of natural enemies of the asexual generation of *Bassettia pallida* Ashmead (the crypt gall wasp), and discuss the overlap between the natural enemies of *B. pallida* and the previously described natural enemy communities of two gall wasps (*Belonocnema treatae* Mayr and *Disholcaspis quercusvirens* Ashmead) specializing on the same two live oak hosts, *Q. virginiana* and *Q. geminata*. The asexual generation of *B. treatae* creates leaf galls that contain one chamber, and was recently found to be associated with 24 arthropod species (Forbes et al. 2016). The

asexual generation of *D. quercusvirens*, which produces ‘bullet galls’ on stems, was associated with nine species of parasitoids and inquilines (Bird et al. 2013).

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

Study System

The asexual generation of wasps in the North American genus *Bassettia* Ashmead (Hymenoptera, Cynipidae, Cynipini) produce stem galls in twigs, in which individual chambers, or crypts, where the wasps develop run parallel to the bark (Melika and Abrahamson 2007). The sexual generations of this genus—when known—make their galls in leaves, where they produce swellings that are visible on both sides of the leaf (Melika and Abrahamson 2007). The crypt gall wasp, *Bassettia pallida* (Fig. 1), infects both sand live oaks (*Q. geminata*) and southern live oaks (*Q. virginiana*) in the southeastern United States (Melika and Abrahamson 2007, Egan et al. 2013). The stem galls produced by the asexual generation of *B. pallida* come in groups or clusters of individual chambers, which we refer to as ‘crypts’, and emergence from these galls typically occurs in March and April (Melika and Abrahamson 2007). Each crypt contains one *B. pallida*, and the number of crypts in a stem varies from few to hundreds (S. P. Egan and K. L. Weinersmith, personal observations). The sexual generation galls of this species have not been definitively identified. The community of natural enemies attacking *B. pallida* has not been thoroughly described (Noyes 2019).

Materials and Methods

Collections and Characterization of Associates

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

Stems collected in the field were placed in plastic bags and transported to either Rice University (Houston, TX) or Charlottesville, VA. Leaves, nontarget galls, and any invertebrates found on the exterior of the stems were removed, and stems were placed in clear plastic cups. The cups were covered with a coffee filter secured in place with a rubber band. Cups were then placed outside, where they experienced natural light:dark cycles and ambient temperatures and humidity. The stems were misted with tap water periodically to mimic local precipitation. Abiotic differences between outdoor rearing conditions in Virginia and Texas may have influenced

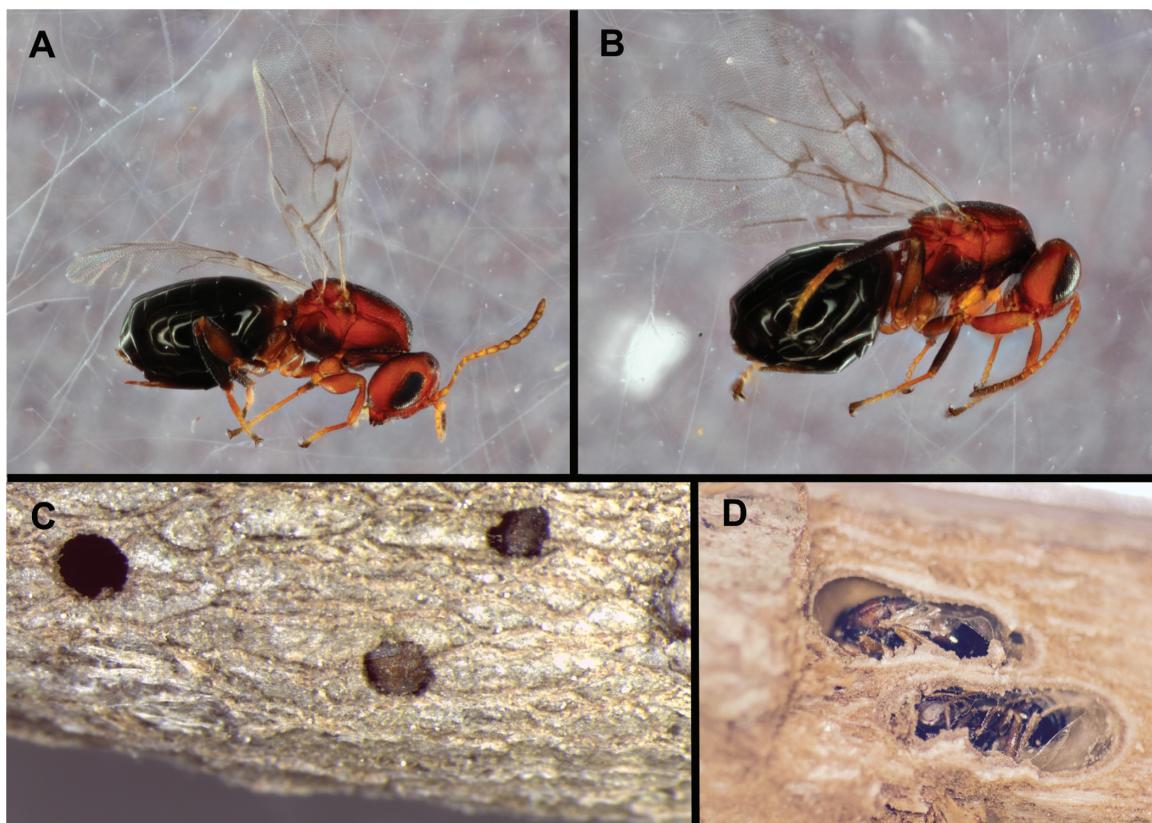


Fig. 1. The asexual generation of *Bassettia pallida*, and their stem galls. (A) Female *B. pallida*. (B) Male *B. pallida*. (C) A *Quercus geminata* stem infected by *B. pallida*, showing the emergence hole from one inner chamber, or crypt, concealed within the stem, and showing two *B. pallida* whose 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) and are available under a CC by 4.0 License.

Table 1. Hymenopteran associates (including putative parasitoids, hyperparasitoids, inquilines, and successors) of the asexual generation of *Bassettia pallida*

Family	Species or subfamily	Collection State, Host Tree				Florida, <i>Quercus geminata</i>			Texas, <i>Quercus virginiana</i>		
		Collection Site		IB	LL	TH	CH	Humble			Rice U.
		Collection Year (20XX)	15	19	15	18	19	15	16	19	16
Cynipidae	<i>Bassettia pallida</i> (galler)		4	11	4		590			5	
Encyrtidae	<i>Encyrtidae</i> sp.						1				
Eulophidae	<i>Euderus set</i> (Egan, Weinersmith, & Forbes)	154				5	19	6			
	<i>Galeopsomyia</i> sp.		3				146				
	Tetrastichinae 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 nr. thymus</i>		5								
	<i>Ormyrus nr. labotus</i>		2				1				
Pteromalidae	<i>Acaenacis</i> sp.		8			1	43			1	
Cynipidae	<i>Ceroptres lanigerae</i>		1								
	<i>Synergus walshii</i>		1								
Formicidae	<i>Brachymyrmex patagonicus</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								

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 to 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).

Table 2. Associates of the asexual generation of *Bassettia pallida*

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

The table presents the number of specimens reared from live oak stems infected by *B. pallida* at sites in Florida (FL) and Texas (TX) from 2015 to 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).

emergence success, but this is unlikely. After emergences ceased, haphazard dissections of stems suggested that most of the associates from the samples sent to Virginia had indeed emerged, and that no particular natural enemy species remained in the crypts. Cups were checked for emergences 5 d a week. Emerged insects were placed in 95% ethanol, and stored at room temperature or -20°C until further analysis.

We refrain from making quantitative comparisons between years and collection sites for a variety of reasons. First, although unlikely, rearing conditions in Virginia and Texas may have differed, favoring some associates over others. Second, because stems were collected based on evidence of prior emergences, and because these emergences may have happened in prior years, we could not know which galls were from this season and which were from previous seasons. Thus, we did not know the exact number of viable galls that were present on each stem. Additionally, due to constraints concerning when we were able to get to the field, collection dates are not standardized between years and sites. For these reasons, we do not report the total number of galls or stems examined. Because the crypt of each gall is highly cryptic, and often packed in quite tightly next to one another, we were unable to separate and maintain galls individually. Galls needed to be maintained in groups on stems, and the stems may have harbored additional arthropod diversity hidden beneath the bark. Our results focus on a qualitative examination of the arthropods we observed after bringing suspected viable galls into the lab, and removing all visible arthropods from the stem surface. A subset of the arthropods we report may be ‘associated’ with *B. pallida* in that they reside in a similar microhabitat under the bark, without directly interacting with *B. pallida*. For a subset of the associations we note below, future work is needed to clarify the exact relationships of these associations. We report all associations noted during our rearing observations to facilitate future work in this system.

Most emergent insects were Hymenoptera, which we identified using keys by [Gillette \(1896\)](#), [Balduf \(1923\)](#), [Weld \(1952\)](#), [Mason \(1993\)](#), [Gibson et al. \(1997\)](#), [Fisher and Cover \(2007\)](#), [Lobato-Vila and Pujade-Villar \(2019\)](#), and [Wahl \(2019\)](#). For a subset of the

associates, we extracted DNA using the DNeasy Blood and Tissue Kit (Qiagen) in accordance with the manufacturer’s protocol with the addition of a pestle crushing step prior to incubation. The mitochondrial cytochrome oxidase I (COI) region was amplified using the KAPA Taq ReadyMix (Sigma-Aldrich) and the primers LEP F 5'-TAACTTCTGGATGTCCAAAAATCA-3' and LEP R 5'-ATT CAACCAATACATAAAGATATTGG-3' ([Smith et al. 2008](#)). Due to primer incompatibility, for the *Eurytoma* sample we used the following primers: COI_PF2 5'-ACC WGT AAT RAT AGG DGG DTT TGG DAA-3' and COI_2437d 5'-CGT ART CAT CTA AAW AYT TTA ATW CCW G-3' ([Kaartinen et al. 2010](#)). Thermocycling programs included 35 cycles with 48°C as the annealing temperature. We cleaned the resulting PCR products using the QIAquick PCR purification KIT (Qiagen) or an EXO1 (exonuclease 1) and SAP (shrimp alkaline phosphatase) method (15 min at 37°C min and then 80°C for an additional 15 min) prior to Sanger sequencing on an ABI 3730 (Applied Biosystems, Foster City, CA) in the University of Iowa’s Roy J. Carver Center for Genomics. Sequence length varied from 408 to 703 base pairs. DNA sequences were then compared with available sequences in the Barcode of Life Database (BOLD, [Ratnasingham and Hebert 2007](#)) and the Basic Local Alignment Search Tool (BLAST) for nucleotides in GenBank. The sequences we obtained are registered in GenBank. GenBank accession numbers and additional information about the specimens are available in [Supp Table 1 \(online only\)](#). We present information about the percent similarity between the sequences we obtained and the sequences currently registered in BOLD and BLAST.

Results

Host Collection

Bassettia pallida emerged from crypts collected at four of the six collection sites, and emerged from both *Q. geminata* in Florida and *Q. virginiana* in Texas ([Table 1](#)). The greatest number of *B. pallida* emerged from crypts collected at Camp Helen State Park in Florida. Two *B. pallida* sequences (MN935926, MN935927; [Supp Table 1](#)

[online only]) were obtained from this location. The sequences were 98.98% identical, and multiple Cynipidae were ~90–94% similar in GenBank. Most of the observed *B. pallida* emergences occurred in March, which is consistent with previous collections in Florida (Melika and Abrahamson 2007), and expectations from their natural history. Eight *B. pallida* emerged from late October through mid-December from collections made in the fall (August through October) and are likely responding to removal of galled branches from the tree.

Three specimens of an unidentified cynipid were found in the 2018–2019 collection. This cynipid appears to make crypt-like galls on stems and keys to the genus *Callirhytis* Foerster using Zimmerman (2018), but could not be identified or matched to any currently described species. Upon further inspection, this ‘new’ species emerges from a solitary crypt gall with little to no visible swelling, found at branching points within new stems. This is distinct from the cluster of crypt galls that generate a subtle swelling of the lateral parts of new branches induced by *B. pallida* (P. F. P. Brandão-Dias et al., in preparation). We cannot rule out the possibility that a small number of the natural enemies and associates we describe below emerged from this galler. However, only 3 of the 590 (0.5%) cynipids that emerged from this collection were the nontarget host species, suggesting that the vast majority of the natural enemies we collected were associated with *B. pallida*.

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

Hymenoptera

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

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

Two species of Tetrastichinae (Chalcidoidea: Eulophidae) emerged in our collections. The first species keyed to the genus *Galeopsomyia* Girault (Fig. 2B) using Schauff et al. (1997). This species emerged from three of our collections (Table 1), with the majority emerging mid-March through mid-April from the stems collected from *Q. geminata* at Camp Helen State Park (FL). We acquired a COI sequence (MN935919; Supp Table 1 [online only]), which was ~84% similar to unclassified Eulophidae in GenBank. The second Tetrastichinae species was collected from *Q. virginiana* in Texas, and the sequence collected from this species (MN935910; Supp Table 1 [online only]) was only 79.9% similar to the *Galeopsomyia* species

sequences. The tetrastichine wasp was 96.1% identical to an early release sequence from an Eulophidae in BOLD. In GenBank, this sequence was ~86% identical to *Eulophidae* specimens in the subfamily Tetrastichinae.

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

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

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

Eurytoma parasitoid species also emerge from galls of *B. treatae* and *D. quercusvirens*. Forbes et al. (2016) identified *Eurytoma furva* Bugbee and *Eurytoma bugbee* Grissell, as well as one unidentified *Eurytoma* species emerging from *B. treatae*. Sequence comparisons between the *Eurytoma* specimen from *B. pallida* (MN935909; Supp Table 1 [online only]) and *E. furva* and *E. bugbee* sequences collected from *B. treatae* (Forbes et al. 2016) are an ~88% match, suggesting that the species collected from *B. pallida* is distinct. DNA could not be extracted from the unidentified *Eurytoma* species from *B. treatae*, so it is possible that this species emerges from both *B. pallida* and *B. treatae*. *Eurytoma hecale* Walker and an unidentified *Eurytoma* species were identified as parasitoids of *D. quercusvirens* by Bird et al. (2013). Our specimen is unlikely to be *E. hecale* based on morphology, and it is not possible to know if the unidentified *Eurytoma* species reported in Bird et al. (2013) is the same as that emerging from *B. pallida*.

Four morphospecies of *Sycophila* Walker (Chalcidoidea: Eurytomidae: Eurytominae, Fig. 3B–E) were reared from three collections (Table 1). The specimens were identified using Balduf

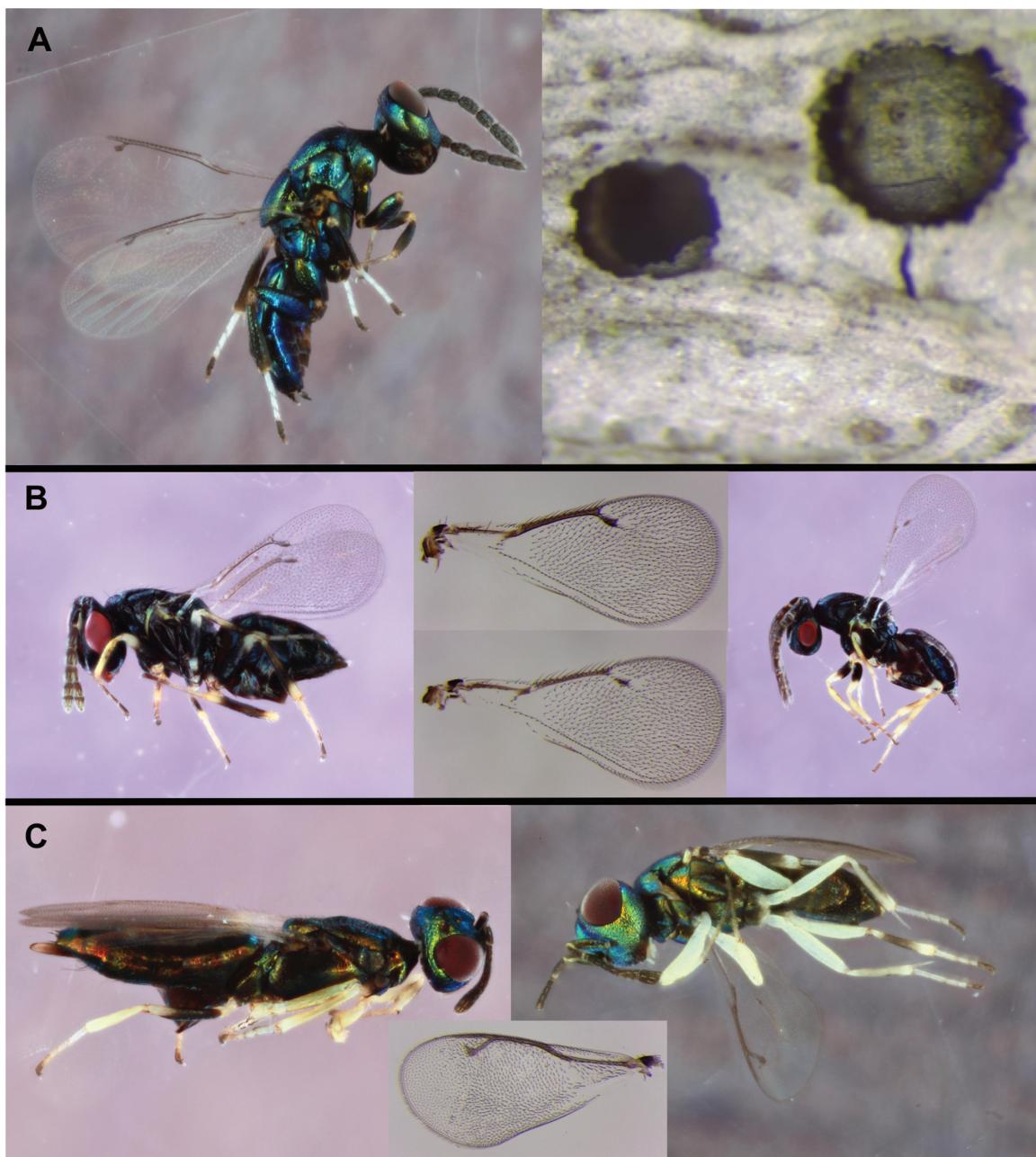


Fig. 2. Associates of galls made by the asexual generation of *Bassettia pallida*. (A) *Euderus set*, and examples of a *B. pallida* head capsule plugging an emergence hole (right) and a head-plugged emergence hole from which *E. set* has emerged (left). *Euderus set* photo originally appeared in Weinersmith et al. (2017) 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.

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(1923). The interpretation of the color variations in Balduf's key is problematic, and the current species concepts are dubious until the taxonomic revision of the genus is conducted (Y. M. Zhang, A. A. Forbes, M. W. Gates, S. I. Sheikh, A. K. G. Ward, and A. Lucky, unpublished data). The first *Sycophila* morphospecies in our samples keys to *Sycophila foliatae* (Ashmead; Fig. 3B), which has previously been recorded from 'live oak' in Jacksonville, FL, and is associated with a variety of oak gall parasitoids (Balduf 1923). The female specimens have varying degrees of black and yellow across the body and a small forewing infumation band, while males are mostly black with similar wing band patterns (Fig. 3B). These coloration characters

also fit the description of *S. quinqueseptae* (Balduf), but this species is currently only known from California and is associated with *Plagiotrochus quinqueseptum* Ashmead (Balduf 1923). The second species identified was *Sycophila nr. dubia* (Walsh) (Fig. 3C), although this species might be a synonym of *Sycophila varians* (Walsh) based on morphology (large angular forewing infumation band, body color mix of yellow and black) and preliminary molecular studies (Y. M. Zhang, A. A. Forbes, M. W. Gates, S. I. Sheikh, A. K. G. Ward, and A. Lucky, unpublished data). *Sycophila nr. nubilistigma* (Walsh) (Fig. 3D) was reared from *Q. virginiana*. They can be identified by their mostly yellow coloration with a dorsal black band

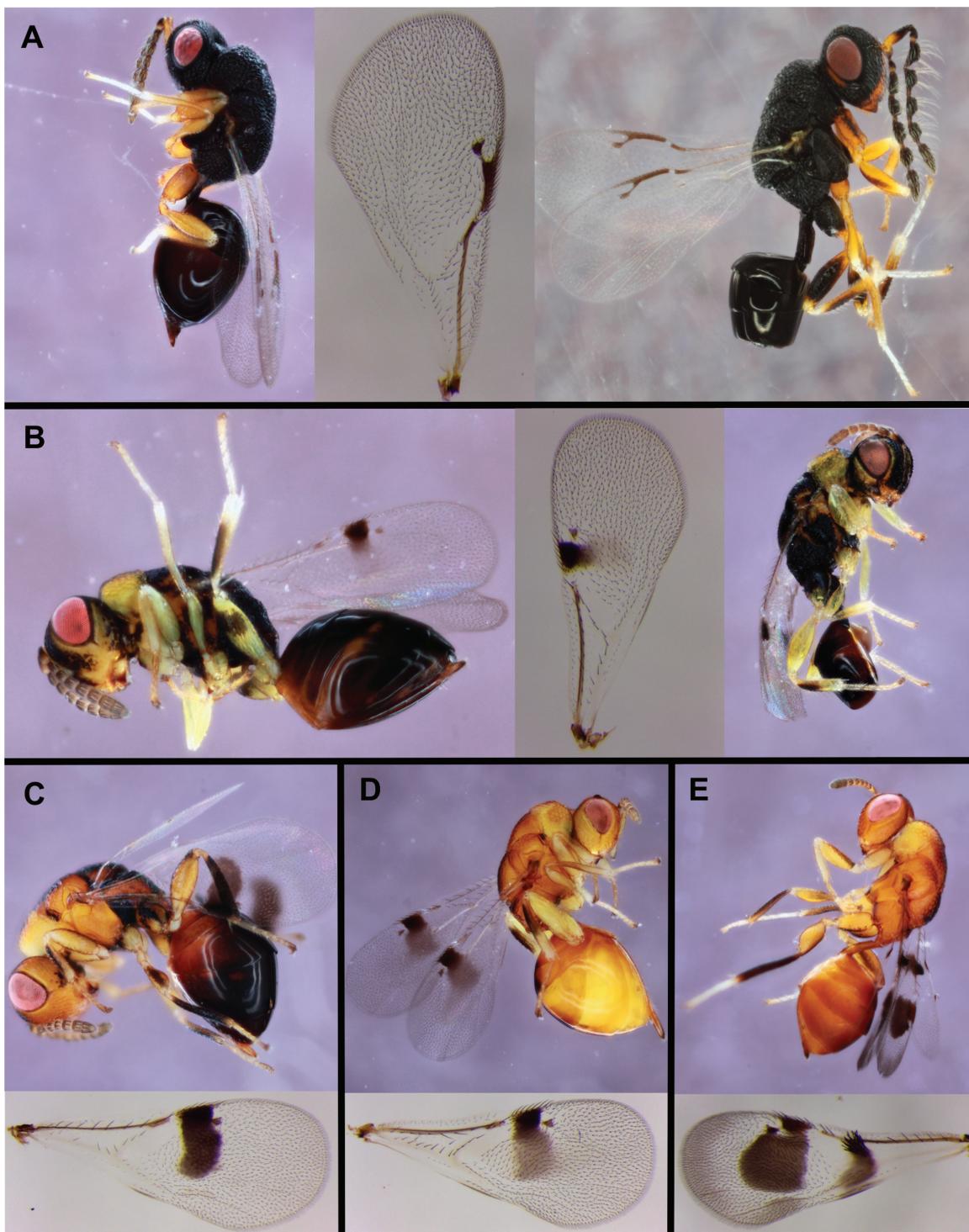


Fig. 3. Eurytomidae associates of galls made by the asexual generation of *Bassettia pallida*. Males, when present, are on the right. Wings are from female specimens. (A) Unidentified *Eurytoma* species. (B) *Sycophila* nr. *foliatae*. (C) *Sycophila* nr. *dubia*. (D) *Sycophila* nr. *nubilistigma*.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

on the mesosoma and metasoma. The wing band is rectangular with a constriction near stigma vein (Fig. 3D). Finally, *Sycophila* nr. *disholcaspidis* (Balduf) (Fig. 3E) was reared. The specimen is orange in coloration, and has the characteristic jug-shaped wing band and a secondary band near the parastigma similar to that of *S. disholcaspidis* which are parasitoids of *Disholcaspis cinerosa* (Bassett) in Texas. However, one key difference from *S. disholcaspidis* is the presence of multiple setae radiating from the secondary band

(Fig. 3E), but more specimens are needed to better understand the species limits.

Three species of *Sycophila* (*Sycophila texana* (Balduf), *S. varians*, and *Sycophila dorsalis* (Fitch)) were recently reared from the asexual generation of *B. treatae* (Forbes et al. 2016), and one unidentified *Sycophila* species was reared from the asexual generation of *D. quercusvirens* (Bird et al. 2013). While more work is needed to clarify the identities of these *Sycophila* species, it seems likely based

on morphology that very little overlap occurs between the *Sycophila* species attacking *B. pallida*, *B. treatae*, and *D. quercusvirens*. *Sycophila* are endoparasitoids of plant gall inhabitants (most often induced by cynipids) in temperate regions of the world (Balduf 1923, Gómez et al. 2013), therefore they are likely targeting *B. pallida* and/or their inquilines.

Two species of *Ormyrus* Westwood (Chalcidoidea: Ormyridae; Ormyrinae; Fig. 4A and B) emerged from crypts on *Q. geminata* from two of the Florida collections (Table 1), and were identified using the key in Hanson (1992). Two *Ormyrus nr. labotus* Walker (Fig. 4A) emerged from collections at Inlet Beach, FL. We obtained sequence data from one of these specimens (MN935904; Supp Table 1 [online only]), and the closest match in GenBank was to an unidentified Ormyridae. The sequence was also 91.5% to 93.6% identical to sequences from four *O. labotus* infecting *B. treatae* galls (Forbes et al. 2016). *Ormyrus labotus* is a generalist parasitoid, reported from more than 15 species of cynipid gall wasps (Noyes 2019). Additionally, six *Ormyrus nr. thymus* Girault emerged (Fig. 4B, Table 1). A sequence obtained from one of these specimens (MN935907; Supp Table 1 [online only]) was an ~89% match with an unidentified Ormyridae in BOLD. This sequence was only 86–87% similar to the *O. labotus* sequences associated with *B. treatae*. *Ormyrus hegeli* (Girault) was also reared from both the asexual and sexual generation of *D. quercusvirens* (Bird et al. 2013), and based on morphology appears to be a different species from the

two *Ormyrus* species reared from *B. pallida*. *Ormyrus hegeli* also infects *Discholcaspis bisethiae* Medianero & Nieves-Aldrey (Sánchez et al. 2017). No known associates of *O. thymus* or *O. hegeli* are listed in Noyes (2019).

Acaenacis Girault (Chalcidoidea: Pteromalidae: Pteromalinae; Fig. 4C) were reared from four sites, including stem galls from both *Q. virginiana* and *Q. geminata* (Table 1). These specimens keyed to the genus *Acaenacis* using Gibson et al. (1997). Three COI sequences (one sequence from each of the three Florida sites from which *Acaenacis* emerged; MN935908, MN935911, MN935912; Supp Table 1 [online only]) were 88.8–92.67% identical to each other, and the top hit for all three sequences in GenBank were to an unidentified Pteromalidae (85.5–88.3% identical).

Species in the genus *Acaenacis* attack oak-dwelling insects. *Acaenacis agrili* (Rohwer) is a parasitoid of the oak twig girdler (*Agrilus angelicus* Horn), which infects stems of *Quercus agrifolia* Nee in California (Rohwer 1919). Live oaks in the southeastern United States also harbor twig girdling beetles (S. P. Egan, personal observation). While associates of *Acaenacis taciti* (Girault) have not been identified (Noyes 2019), all other known hosts of *Acaenacis* are cynipid gall wasps. An undescribed *Acaenacis* infects *Andricus quercuslanigera* (Ashmead) on *Quercus rugosa* Nee in Mexico (Serrano-Muñoz et al. 2016). *Acaenacis lasus* (Walker) has been reared from leaf galls of *B. treatae* from *Quercus fusiformis* Small and *Q. virginiana* in Texas (Forbes et al. 2016), and *D. quercusvirens*

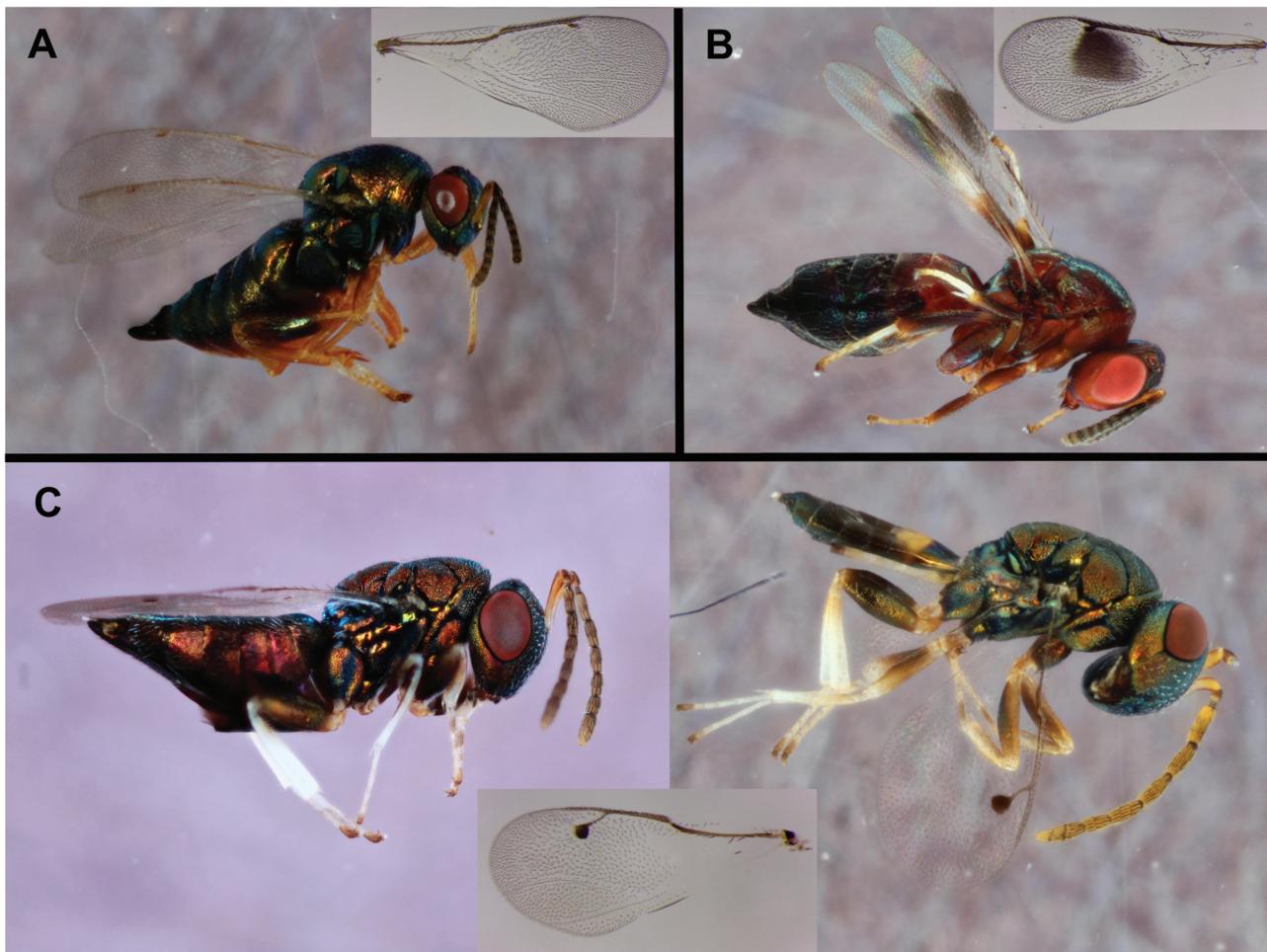


Fig. 4. Associates of galls made by the asexual generation of *Bassettia pallida*, with wing insets from female specimens. (A) *Ormyrus nr. labotus*, (B) *Ormyrus nr. thymus*, (C) unidentified *Acaenacis* species, with female on left and male on right.

on *Q. virginiana* in Florida (Bird et al. 2013). The four *Acaenacis lausus* sequences in GenBank from Forbes et al. (2016) were only 80–86% similar to the three *Acaenacis* sequences (MN935908, MN935911, MN935912; Supp Table 1 [online only]) obtained from our collections, suggesting that *A. lausus* is a different species than that emerging from *B. pallida*.

One *Ceroptres langeriae* Ashmead (Cynipoidea: Ceroptresini; Fig. 5A) was reared from a gall collected at Inlet Beach, FL (Table 1), as was one *Synergus walshii* Gillette (Cynipoidea: Synergini; Fig. 5B). Identifications were made using Lobato-Vila and Pujade-Villar (2019) and Gillette (1896), respectively. The *Ceroptres* specimen (MN935928; Supp Table 1 [online only]) was 90.4% similar to *Ceroptres* sp. FSU 399 (Accession: DQ012636.1), which was reared from an *Andricus quercuscornigera* gall from Kentucky (USA; Ronquist et al. 2015). The sequence from *S. walshii* (MN935929; Supp Table 1 [online only]) was 97.1% similar to *Synergus* sp. 1 from Forbes et al. (2016), which was one of three *Synergus* species associated with *B. treatae* in that study. Three *Synergus* are also associated with the asexual generation of *D. quercusvirens*, but it is unclear if the species in our study is the same as *Synergus* sp. 1 reported in Bird et al. (2013). Members of the genera *Synergus* and *Ceroptres* are inquilines of cynipid gall wasps, which are typically not able to initiate galls, but can maintain the production of nutritious tree tissue once

inside a gall (Péñez et al. 2012, Ronquist et al. 2015). *C. langeriae* was previously known from *A. quercuslanigera* reared from other live oak species in the United States and Mexico (Lobato-Vila and Pujade-Villar 2019). *Synergus walshii* was reared from galls of several species of *Andricus* on various white oaks in Iowa, Missouri, and Kentucky (A. K. G. Ward and A. A. Forbes, unpublished data). Previous *S. walshii* collections were from *Andricus quercusfloccif* galls on white oaks (*Quercus alba*; Gillette 1896).

Ants (Formicidae) were observed twice during our samplings (Fig. 6, Table 1), and were identified to genus using Fisher and Cover (2007). Ants in the genus *Brachymyrmex* Mayr were observed and collected ($n = 4$ individuals; Fig. 6A) 3 mo after *B. pallida*-infected *Q. virginiana* stems were brought into the lab. The sequence data from the *Brachymyrmex* (MN935915; Supp Table 1 [online only]) were 100% identical to a *Brachymyrmex patagonicus* Mayr and *Brachymyrmex obscurior* Mayr sequences in BOLD. Based on morphology (MacGown 2016), and geographic localities of collections, we suspect these specimens are *B. patagonicus*. We also collected *Crematogaster ashmeadi* ($n = 8$ individuals; Fig. 6B), which were identified using Morgan and MacKay (2017). Some cynipid gall wasps induce their plant host to produce honeydew, which is consumed by ants who subsequently tend the gall (reviewed in Pierce 2019). While other cynipid gall wasps infecting oaks are known to

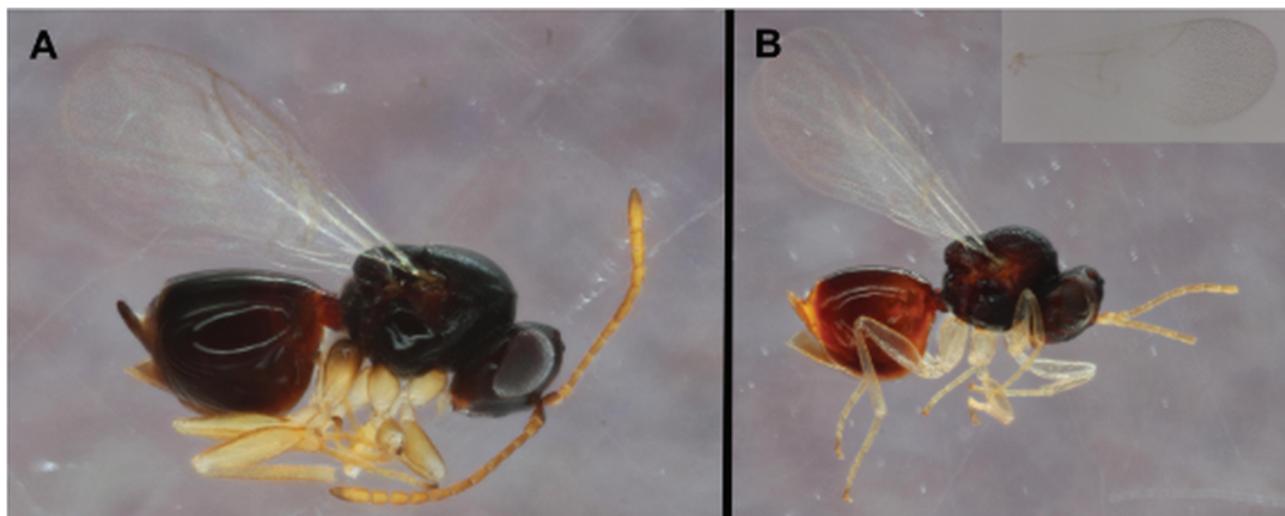


Fig. 5. Inquilines associated with galls made by the asexual generation of *Bassettia pallida*. (A) *Ceroptres langeriae*. (B) *Synergus walshii*, with inset showing detail of wing.



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

secrete honeydew from their galls (e.g., *D. quercusvirens* on sand live oaks; Nicholls et al. 2017), we did not observe honeydew on nor tending by ants of *B. pallida* crypts. Ants are also successors of galls, settling in the galls once cynipids have abandoned them (e.g., Giannetti et al. 2019). We suspect that *B. pallida*-abandoned crypts are occasionally settled by ants.

Eight *Allorhogas* (Table 1, Fig. 7A) were reared from infected *Q. geminata* stems from Camp Helen State Park (FL). A sequence was obtained from one of these specimens (MN935913; Supp Table 1 [online only]), and the sequence was 99.5% similar to a private *Allorhogas* sequence in BOLD. In GenBank, this sequence was 91.6% similar to the *Allorhogas* species reported from *B. treatae* in Forbes et al. (2016), and was 90.6 to 91.1% similar to an *Allorhogas*

sp. 2 collected from South America (Zaldívar-Riverón et al. 2014). No *Allorhogas* were reported to infect *D. quercusvirens* in Bird et al. (2013). The genus *Allorhogas* Gahan (Ichneumonoidea: Braconidae: Doryctinae) includes both gall-formers and parasitoids or inquilines (Zaldívar-Riverón et al. 2014). The original description of the only *Allorhogas* species currently reported from the United States suggested that it might be a parasitoid of gall-associated lepidoptera burrowing through gall tissue (Gahan 1912). Whether the *Allorhogas* we collected are parasitoids, inquilines, or other associates of *B. pallida* is currently unknown.

Five Platygastroidea specimens (Fig. 7B–D, Table 1) were identified using Mason (1993) and by Elijah Talamas (Florida Department of Agriculture and Consumer Services) based on specimen images.

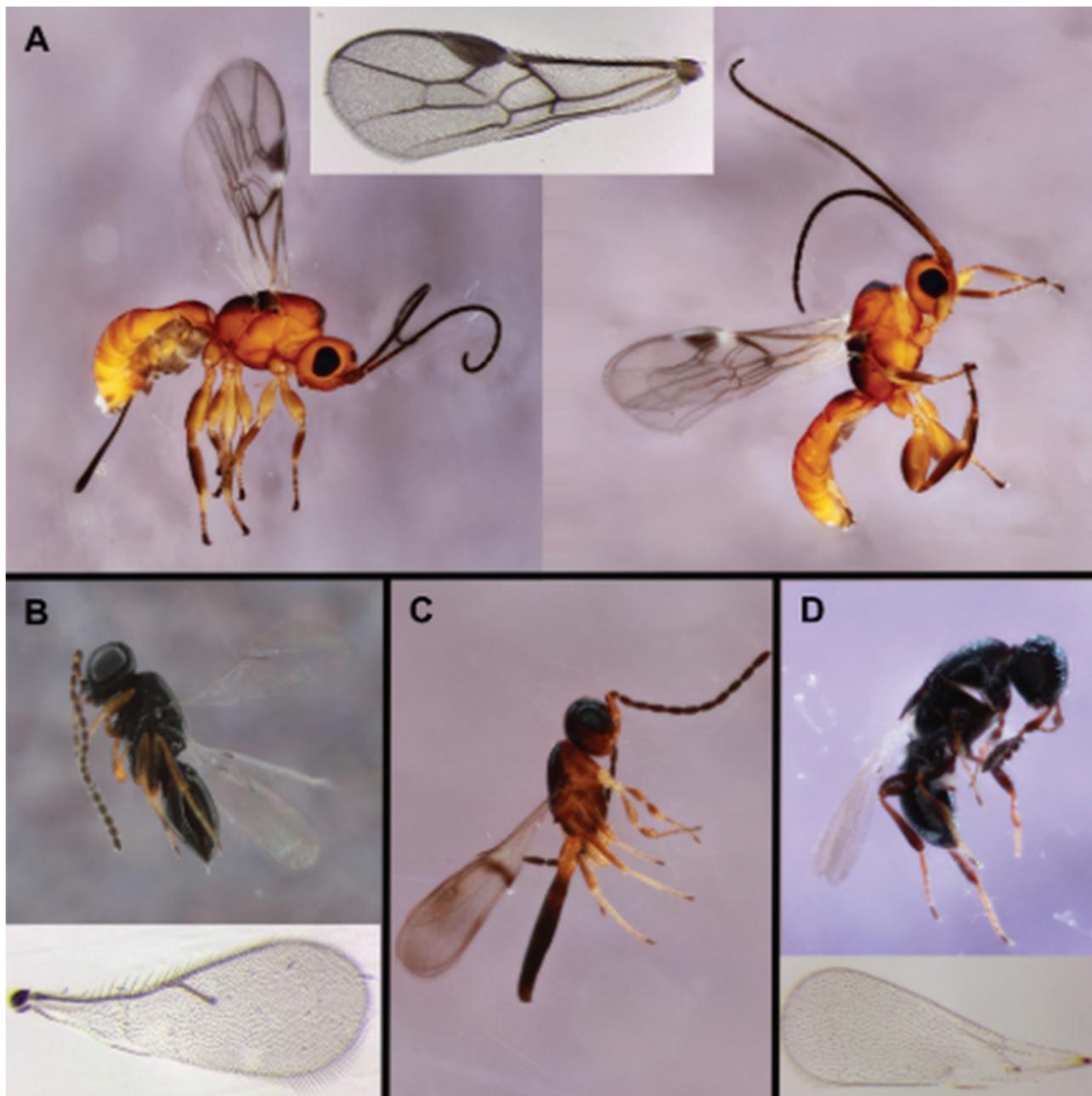


Fig. 7. Associates of galls made by the asexual generation of *Bassettia pallida*, with wing insets from female specimens when available. (A) Unidentified *Allorhogas* species, with female on the left and male on the right. (B) Unidentified *Telenomus* species. (C) Unidentified *Calotelea* species. (D)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

Sequence data were obtained from one specimen (MN935906; Supp Table 1 [online only]; Fig. 7B), which was ~89% similar to an undescribed *Telenomus* Haliday species in BOLD and GenBank. Of the four other specimens, one was from the genus *Calotelea* Westwood (Fig. 7C), and three were from the genus *Synopeas* Foerster (Scelionidae; Fig. 7D). No Platygastriidae or Scelionidae were observed emerging from the asexual generations of galls made by *B. treatae* (Forbes et al. 2016) or *D. quercusvirens* (Bird et al. 2013). Platygastroidea are typically egg parasitoids, and while specific Platygastroidea species often specialize, the range of hosts infected by parasitoids in this superfamily is broad (Murphy et al. 2007, Taekul et al. 2014). Both *Telenomus* and *Calotelea* may be egg parasitoids of *B. pallida* or other gall inhabitants, while *Synopeas* attacks the gall midge associate.

Coleoptera

One beetle emerged from a *Q. geminata* stem in 2019 (Table 2, Fig. 8A), 1 mo after the stem was brought into the lab. The sequence obtained from this beetle (MN935914; Supp Table 1 [online only]) was an ~93% match to three published *Petalium bistriatum* (Say) (Ptinidae) sequences in BOLD. *Petalium* beetles are wood-boring (Ford 1973), and may not be directly associated with *B. pallida* crypts, although we have observed wood-boring Ptinid beetles emerge from clearly defined gall tissue induced by *B. treatae* on live oaks (Forbes et al. 2016).

Diptera

Two unidentified gall midge species in subfamily Cecidomyiinae (Sciaroidea: Cecidomyiidae) were reared in our collections (Table 2). The first species emerged from collections at Rice University's campus on *Q. virginiana*, and the one sequence (MN935916; Supp Table 1 [online only]) obtained from this species is 99.9% similar to the unidentified gall midge associated with *B. treatae* (Forbes et al. 2016). The exact nature of the association between this gall midge and *B. treatae* and *B. pallida* is currently unclear. The second species (MN935917; Supp Table 1 [online only]; Fig. 8B) was 91.9% similar to the first, emerged from Inlet Beach, FL on *Q. geminata*, and is ~92% similar to *Asteromyia euthamiae* (Gagne) (subfamily Cecidomyiinae) sequences in GenBank. Gall midges are both gall formers and inquilines, including inquilines of cynipid gall wasps (Mamaev and Krivosheina 1992).

Psocoptera

Thirty-six Psocopterans from at least three species emerged from the stems in our collections (Table 2, Fig. 9). We sequenced six of these specimens, which we suspected based on morphology represented two specimens for each of the three species. The rest of the Psocopterans we reared are reported as 'Unidentified Psocoptera' in Table 2. Each pair of sequences from putative conspecifics were 99% similar to one another, and putative congeners sequences were only ~77–81% similar. Sequence data thus supports the presence of three Psocopteran species associated with *B. pallida* crypts. The sequences from the first species (MN935922 and MN935924; Supp Table 1 [online only]; Fig. 9A) were ~98% similar to *Peripsocus madidus* sequences in GenBank. Two sequences from the second species (MN935923 and MN935925; Supp Table 1 [online only]; Fig. 9B) were ~94% similar to an unclassified Psocidae in BOLD, and ~84% similar to an unclassified Psocidae in GenBank. Two sequences (MN935920 and MN935921; Supp Table 1 [online only]) from the third species (Fig. 9C) were ~97–99.7% similar to private Lachesillidae sequences in BOLD, and 83.1% similar to an unclassified Psocoptera in GenBank. These psocopterans colonize abandoned crypts and inhabit them for long periods of time. They move in and out of the crypts, sometimes partially sealing the emergence holes with detritus (S. P. Egan, personal observations).

Thysanoptera

One thrips from the family Phlaeothripidae (Table 2, Fig. 8C) was associated with a stem collected in 2015 from *Q. geminata* at Inlet Beach, FL. We identified the specimen to family (Mound et al. 2009), but were unable to extract DNA. The relationship between this thrips and the *B. pallida* galls is unclear.

Discussion

A diverse and species-rich community of arthropods is associated with the asexual generation of the gall wasp, *B. pallida*, and the crypt gall they create. These included Hymenoptera (21 species; Table 1), Diptera (2), Coleoptera (1), Psocoptera (3), and Thysanoptera (1; Table 2). The associates included parasitoids, inquilines, and successors that utilize the crypt after the emergence of *B. pallida* and/or its natural enemies. These associates also likely included some arthropods that reside in the same microhabitat as *B. pallida*, without

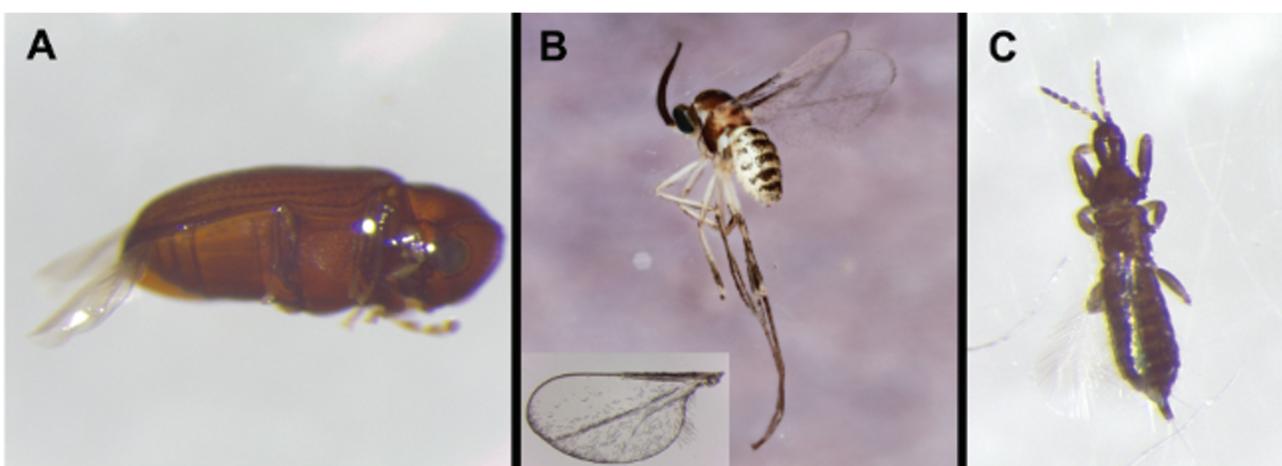


Fig. 8. Associates of galls made by the asexual generation of *Bassettia pallida*. (A) Unidentified Ptinidae beetle (Coleoptera: Bostrichoidea). (B) Unidentified Cecidomyiidae (Diptera). (C) Unidentified Phlaeothripidae (Thysanoptera).

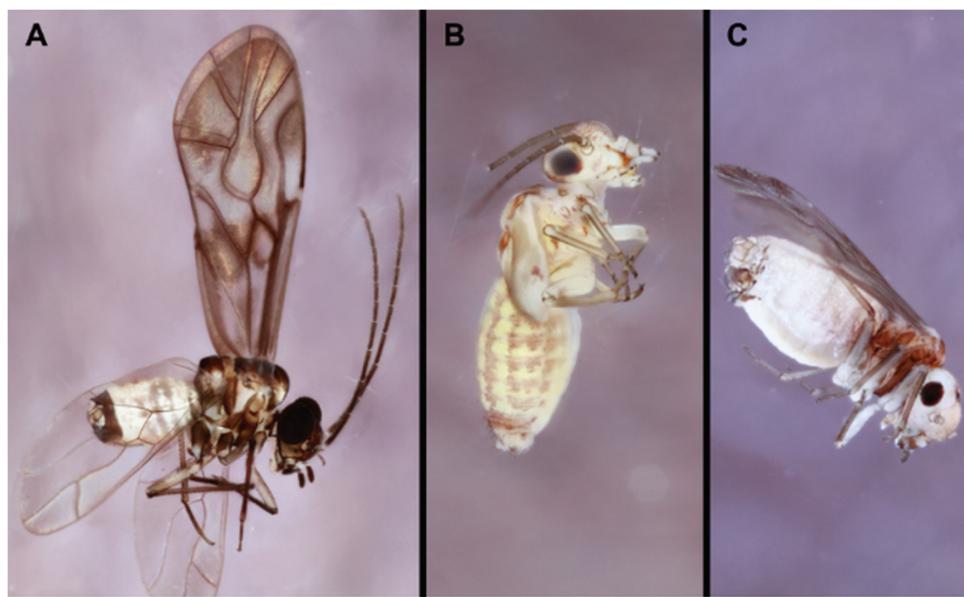


Fig. 9. Psocopterans associated with galls made by the asexual generation of *Bassettia pallida*. (A) *Peripsocus madidus*. (B) Unidentified Psocidae. (C) Unidentified Lachesillidae.

interacting with *B. pallida* directly (e.g., the beetle and thrips). More work is required to understand the nature of these interactions.

Putative Natural Enemies

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

While *B. pallida*, *D. quercusvirens*, and *B. treatae* all reside on live oaks, there appears to be little overlap in their natural enemy communities. Additionally, natural enemies recorded for *D. quercusvirens* in Krombein et al. (1979) and for *B. treatae* in Peck (1963) overlap very little with natural enemies reported from the more recent studies. For *B. treatae*, only 1 of the 8 natural enemies reported in Peck (1963) was also reported by Forbes et al.

(2016), and, for *D. quercusvirens*, 7 natural enemies reported in Krombein et al. (1979) were not observed by Bird et al. (2013). This suggests either that community composition is changing over time, that species were misidentified or the use of synonyms is confounding comparisons, or that no study has yet to sample these cynipid hosts with enough temporal and spatial coverage to capture the entire natural enemy community. However, there is some overlap between pairs of cynipid hosts. For example, *A. lausus* infects both *B. treatae* and *D. quercusvirens* (Bird et al. 2013, Forbes et al. 2016), and the inquiline *S. walshii* may be infecting both *B. treatae* and *B. pallida* (Forbes et al. 2016, and this study). In general though, it is difficult to draw strong conclusions about the degree of natural enemy overlap in these communities due to differences in sampling effort (including sampling done at different sites in different years). What is clear is that these galls support a diverse community of Hymenopteran natural enemies. As a rough estimation, if we assume that each of the 12 cynipid species on live oaks harbor about 10 host-specific natural enemies, that would yield a community of 120 natural enemies in this system. Future work to quantify this diversity, and understand factors that influence the degree of overlap of these natural enemy communities across cynipid hosts is greatly needed.

One area of high interest is the association between *B. pallida* crypt galls and the recently described parasitoid *Euderus set*, which is an example of a parasitoid species that can manipulate the behavior of its host (Weinersmith 2019). Specifically, *E. set* manipulates *B. pallida* into excavating an emergence hole from the crypt, which *B. pallida* then plugs with its head before being consumed by the parasitoid (Egan et al. 2017, Weinersmith et al. 2017). The parasitoid subsequently emerges from the host's head capsule (Weinersmith et al. 2017). *Euderus set* infects and manipulates at least six additional cynipid gall wasp hosts infecting other oak species (Ward et al. 2019). The finding that *E. set* manipulates a broad range of cynipid gall wasps (Ward et al. 2019), suggests that the mechanism *E. set* uses to manipulate its host either does not require extreme specialization on host physiology or involves a mechanism common to many gall wasp residents. A more

careful look at the gallers, inquiline, and parasitoids residing in live oak galls is warranted to determine whether *E. set* is infecting and manipulating more hosts than just *B. pallida* in this system. Additionally, it is unclear why *E. set* is the only parasitoid that has been documented manipulating its hosts in this manner, while none of the other parasitoids or inquiline attacking cynipid gall wasps appear to do the same. Future work putting *E. set* in context with the other parasitoids infecting cynipid gall wasps should address questions about the selective pressure for manipulation, constraints on the evolution of this trait (including the costs paid by *E. set* as it manipulates its host), and the fitness benefits accrued through manipulation.

Finally, one common natural enemy that often attacks live oak galls was not observed in our study. Birds often break open the galls of *D. quercusvirens*, *D. cinerosa*, and *Callirhytis quercusbatatooides* (Ashmead) on live oaks to consume the wasps developing within (A. K. Weaver, G. R. Hood, M. Foster, and S. P. Egan, unpublished data). During our collections we did not directly observe birds attacking *B. pallida* galls, nor did we see indirect evidence of predation on the stems (S. P. Egan and K. L. Weinersmith, personal observations). This suggests that the cryptic phenotype of *B. pallida* galls may to some extent protect the galler (and its natural enemy community) from bird predation.

Putative Successors

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

We anticipated seeing lepidopterans in *B. pallida* galls, as they are associates of many galls on oaks (Brown and Mizell III 1993), including *B. treatae* leaf galls (Forbes et al. 2016) and *C. quercusbatatooides* stem galls (S. P. Egan, personal observation). The lack of lepidopterans has possible implications for our understanding of the biology of the parasitoid *Allorhogas*, as the original description of *Allorhogas* postulated that this genus may be parasitoids of lepidopterans (Gahan 1912). While it is possible that the timing of our collections missed lepidopterans associated with *B. pallida* crypts, the current data suggest that the *Allorhogas* observed in our system are not parasitoids of lepidopterans.

Conclusions and Future Directions

While more detailed work may reveal that some the associates we collected resided within the infected stem without actually interacting with *B. pallida* or its crypt gall (e.g., this may be the case with the wood-boring Ptinid beetle), it is likely that future work will also reveal additional associates. In fact, our sampling may underestimate the diversity associated with *B. pallida* galls in a number of ways. First, we have not sampled the unknown sexual

generation of *B. pallida*, which remains to be discovered. This gall wasp generation will likely harbor some known species that attack both generations, as well as some that are unique to the sexual generation—as was found to be the case with the community attacking *B. treatae* on these same host plants (Forbes et al. 2016). Second, we identified infected live oak stems by looking for abandoned crypts, where these emergence holes were most likely formed in current and previous years. This highlights an important and general challenge to sampling cynipid associated communities, which is that time of sampling matters. We may have missed some parasitoids that emerge earlier—prior to the emergence of *B. pallida*—and/or missed some that attack later. Third, our sampling did not include the entire geographic range of *B. pallida*, which matches the distribution of its known host plant associations within the live oaks (*Q. virginiana* throughout the entire coastal southeastern United States from Virginia to Texas, *Q. geminata* restricted to xeric soils in Alabama, Mississippi, Florida, and Georgia, and *Q. fusiformis* in central and south Texas; see detailed host plant distributions in Cavender-Bares et al. 2015).

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

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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