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SHELTER BUILDING AND EXTRAFLORAL NECTAR EXPLOITATION BY A MEMBER OF THE ARISTOTELIA CORALLINA SPECIES COMPLEX (GELECHIIDAE) ON COSTA RICAN ACACIAS

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ABSTRACT. A new member of the unresolved Aristotelia corallina Walsingham species complex (Gelechiidae) from a Costa Rican dry forest (Parque Nacional Palo Verde) is reported. Its larval behavior and possible relationships to the rest of the complex are described and analyzed. Field and laboratory observations revealed that these caterpillars consumed the extrafloral nectar, Beltian bodies, and young foliage of two acacia species (Vachellia collinsii and Vachellia farnesiana; Fabaceae: Mimosoideae). The caterpillars were observed building individual silk webs surrounding a single stem node’s thorns and leaf rachises. If open domatia are included in shelters, the caterpillars reside in the domatia between feeding bouts and during pupation. These caterpillars are the only non-myrmecophilous caterpillars known to regularly exploit a host plant’s ant rewards. DNA barcoding of the Costa Rican specimens showed that they are significantly different from the United States members of A. corallina (12–13% difference in cox1 sequence). An examination of host plant herbarium material for caterpillar shelters demonstrated likely differences in host plant use, with webs consistent with A. corallina only found on specimens of United States Chamaecrista nictitans (Fabaceae: Caesalpinioideae), but not Vachellia farnesiana. By contrast, webs were found on V. collinsii, V. cornigera, and V. farnesiana from Central America (including Mexico), but not on Central American C. nictitans. This ecological evidence suggests that the Costa Rican populations of A. corallina may be more closely related to the Mexican populations than to the US populations.

Additional keywords: natural history; DNA barcoding; host plant; behavior

The species Aristotelia corallina (Gelechiidae) was first described by Walsingham in 1909 from three specimens collected in Guerrero, Mexico. Since then, adults have been reported from the southern United States (Kimball 1965, Hebbner et al. 2003, Moth Photographers Group 2016), and Puerto Rico (Moth Photographers Group 2016), and caterpillars have been found in Florida (Kimball 1965) and Mexico (Janzen 1967). Unfortunately, Aristotelia corallina has never been given a modern taxonomic treatment and recent DNA barcoding work has identified at least three distinct clades within the United States and Costa Rican specimens identified as A. corallina (Barcode of Life Data System [Ratsingham & Herbert 2007], unpublished data), suggesting it is an unresolved species complex.

Little is known of A. corallina biology or ecology beyond a few host plant records. There are two records of caterpillars feeding on Chamaecrista nictitans (L.) Moench (Fabaceae: Caesalpinioideae; Kimball 1965, Hebbner et al. 2003) in Florida and one record on Vachellia coriugera (L.) Seigler & Ebinger (Fabaceae: Mimosoideae; Janzen 1967) in Mexico. There is also a host plant database record for V. farnesiana (L.) Wight & Arn., but the original source has been elusive (Robinson et al. 2017). Here, another cryptic species within the A. corallina complex is reported, including description of its exploitation of acacias’ ant adaptations and its shelter-building behavior, and comparison to the other members of the A. corallina species complex.

To better understand these caterpillars, field and laboratory observations of over 40 individuals were collected, including video recordings of their shelter-building efforts. These observations were then supplemented with traditional natural history records, molecular data, and herbarium documentation of plant-insect interactions to understand how these caterpillars compare to the other members of the Aristotelia corallina species complex.

MATERIALS AND METHODS
Field and laboratory observations. The caterpillars were first found in May 2015 in the tropical dry forest at Palo Verde Biological Station (Parque Nacional Palo Verde, Guanacaste, Costa Rica). The caterpillars occurred on both Vachellia collinsii (Saff.) Seigler & Ebinger and V. farnesiana (L.) Wight & Arn. In May–August 2015 and 2016, caterpillar shelters were found, marked, and checked each morning for up to seven days. Caterpillars and their shelters were then collected and reared in the lab for adults and parasitoids. Each acacia stem was placed in a water-filled florist’s tube and kept in a plastic bag, while caterpillars were checked daily. The length, width, and height of shelters were also measured.

Shelter-building. To observe shelter construction, a freshly cut Vachellia collinsii stem with expanding foliage was placed in a water-filled florist’s tube, inside a beaker. A caterpillar collected from V. collinsii was removed from its shelter, placed on the new foliage,
Amplicons concentration were checked using gel electrophoresis. Reaction was amplified using the LCO1490 and HCO2198 primers designed by Folmer et al. (1994). Reaction conditions followed Levin and Parker (2013), except that 3 µL of template DNA were used for each 25 µL reaction because initial DNA concentrations were relatively low (~1–10 ng/µl). Amplicon length and sequence were preserved in 95% ethanol. In 2017, caterpillar head capsules were examined to determine if the ingestion of nectar was associated with any unique mouthpart morphology. Voucher specimens will be deposited at the Smithsonian National Museum of Natural History (Washington D.C., USA) and the Museo Nacional de Costa Rica (San José, Costa Rica). One immature specimen is in the collection of Steven Passoa (USDA-APHIS-PPQ).

Identification. Upon return from the field in 2015, specimens were identified using both morphological and molecular methods. A series of adults were sent to a gelechiid specialist (Sangmi Lee, Arizona State University) and she dissected the male genitalia. To extract DNA, tissue samples were frozen with liquid nitrogen and ground with plastic pestles before using Macherey-Nagel Tissue kits (Macherey-Nagel GmbH & Co. KG, Düren, Germany). The mitochondrial cytochrome c oxidase subunit 1 (cox1) barcoding region was amplified using the LCO1490 and HCO2198 primers designed by Folmer et al. (1994). Reaction conditions followed Levin and Parker (2013), except that 3 µL of template DNA were used for each 25 µL reaction because initial DNA concentrations were relatively low (~1–10 ng/µl). Amplicon length and concentration were checked using gel electrophoresis and UV spectrophotometry, respectively. Amplicons were then cleaned using a mixture of exonuclease I and antarctic phosphatase (#M0289S and #M0293S, New England Bio Labs Inc., Ipswich, MA), diluted to the appropriate concentrations, and sent to an outside company for sequencing (Beckmann Coulter Genomics in 2015). Sequences were then aligned using Geneious (Geneious 10, Biomatters Ltd.) and GenBank was searched for matching sequences using BLAST. The sequences are GenBank accessions MG700310-MG700314.

Herbarium search. To obtain more information on A. corallina host plants, plant specimens from the Missouri Botanical Garden herbarium (MO) were examined. Caterpillar shelters can be inadvertently preserved on herbarium specimens, particularly when many leaves are included on a herbarium sheet (i.e., the plant and/or the leaves are small). However, collectors may deliberately avoid damaged plants or collect specimens when caterpillar shelters are rare. For instance, if the caterpillars are most abundant when host plants are sterile, their shelters are unlikely to be sampled by collectors seeking fertile specimens. Shelters can also be damaged, discarded, or hidden during collection and mounting. Therefore, a major caveat of this method is that an absence of caterpillars or caterpillar shelters is not definitive proof that a plant species is not a host plant.

Accordingly, the United States, Central American (Mexico-Costa Rica), and Caribbean material of Chamaecrista nictitans and Vachellia barnesiana was examined, as well as the Central American material for V. collinsii and V. cornigera. Possible signs of A. corallina presence included silk webs or their remains on stems, EFNs, and/or domatia, small frass pellets and/or plant damage, and caterpillars or caterpillar exuviae of appropriate size and appearance. Specimens with possible A. corallina signs were photographed and annotated in the TROPICOS database (MBG 2017; see Table 1 for a full list of the specimens).

RESULTS

Identification. Based on the genitalia dissection, the adults were identified as Aristotelia corallina Walsingham, 1909 (S. Lee, pers. comm.). However, DNA barcoding shows that this identification is incomplete (Fig. 1). The BLAST search matched the DNA barcodes of the new specimens to adult moths collected in Costa Rica’s Area de Conservación Guanacaste and sequenced by Janzen and colleagues (<1% difference). These moths were only identified as barcode index number (BIN) BOLD:AAT9249 in the Barcode of Life Data System (BOLD). When these Costa Rican barcodes were compared to BOLD barcodes from 63 North American A. corallina specimens, they differed by 12–13%. Two sequences are generally considered to represent different species if they differ by more than 2% (Ratnasingham & Hebert 2007). Moreover, the barcodes in BOLD identified as A. corallina form three BINs (BOLD:AA8061, BOLD:AA8062, and BOLD:AAT9249) that correspond to their collection locations (Florida, the southern US, and Puerto Rico, respectively). Unfortunately, the type specimen of A. corallina originated from Guerrero, Mexico, and no Mexican specimens have been barcoded. As a result, it is currently impossible to determine with available barcodes which, if any, of these cryptic species is the true A. corallina.
Specimens and morphology. The caterpillar (Fig. 2e). Unknown number of instars; the final instar is ~15 mm long. **Head**: Light brown, with a lighter band across the middle. The front of the hypopharyngeal complex is dark brown. Examination of a slide-mounted head capsule revealed normal mouthparts with sharp mandibles probably used for scraping (S. Passoa, pers. comm.). **Thorax**: Coloration of alternating dark maroon and white rings. **Abdomen**: Anterior portion is dark maroon with three thin dark rings. Posterior portion has broad horizontal maroon and white stripes.

The adult (Fig. 2f). **Head**: Light yellow, with dark grey antennae. **Thorax**: Same color as the head, with yellow- and grey-striped legs and dark grey scales over the base of the wings. Forewing length ~5 mm. Forewing elongate and narrowly triangular, apex slightly curved and fringed, and margin straight. Dorsum ground color dark grey with light yellow shading to pink along the anal margin of the wing. Distal third of forewing speckled with yellow and pink spots. Ventrum dark grey. Hindwing triangular with a fringe approximately as broad as the rest of the hindwing. Dorsum greyish brown. Ventrum dark grey. **Abdomen**: Dark grey.

Field and laboratory observations. During the 2015 and 2016 field seasons, it became apparent that the caterpillars exploited the acacias’ ant adaptations in a variety of ways. Each caterpillar occupied its own shelter (Fig. 2a), a small web (mean dimensions $25 \times 15 \times 15$ mm, $N = 37$) surrounding a stem node. A web covered all expanding leaves at that node, but only reached the rachises of mature leaves. Caterpillars were frequently seen consuming nectar from the extrafloral nectaries (EFNs, Fig. 2a), but were not seen eating the foliage itself. However, shelter photographs taken days apart showed that young caterpillars were also consuming expanding foliage and Beltian bodies (Figs.
Fig. 2. a. Costa Rican *Aristotelia corallina* shelter, including the silk tunnel (red arrow) connecting the domatium entrance to the EFN and the caterpillar drinking EFN nectar. Scale bar = 1 mm. b. A shelter with an extended silk tunnel built on *Vachellia faren-esia*, which does not have domatia. Scale bar = 10 mm. c and d. The same shelter photographed five days apart, showing caterpillar damage to an expanding leaf (yellow circle) and past damage to now-mature leaves (red arrows). Note that the shelter was rotated 180° from its original orientation in d. Scale bar in both photos = 10 mm. e. Costa Rican *A. corallina* caterpillar. Scale bar = 5 mm. f. Adult. Scale bar = 1 mm.
Specifically, pinnae and associated Beltian bodies (nutrient-rich bodies on the tips of expanding pinnules, Belt 1874) were stripped from leaf rachises, or rachises were chewed off just above the EFNs. Less commonly, the shoot tip itself was chewed, or the expanding foliage was intact but yellowed and wilted. Chewing damage was only associated with early instars: in cases when a caterpillar built a second shelter, expanding foliage in or near that shelter remained intact and developed normally.

The caterpillars also exploited the acacia domatia. When opened domatia were available, the caterpillars took refuge in them and often incorporated the entrance holes into their shelter architecture (Fig. 2a). Before pupation, caterpillars entered domatia, sealed the entrance holes with silk, and pupated inside (Baer Video 2). In some cases, caterpillars travelled one or two nodes away from their shelters to find an open domatium for pupation. Occasionally, no domatium was available, either because none had been opened by ants or because the caterpillar was on V. farnesiana, which only produces small defensive thorns (Zamora 2010). In these cases, the caterpillar pupated within its web.

The caterpillars’ relationship with the ants themselves appears to be more complex. Caterpillars were only found on plants unoccupied by aggressive acacia ants (at Palo Verde, these are primarily Pseudomyrmex flavicornis F. Smith and P. spinicola Emery [Hymenoptera: Formicidae]). While non-specialist ants visited many of the host plants, they did not interact with the caterpillars. As the ants sometimes walked over the webs or fed at an EFN used by a caterpillar, it seems likely that the ants were exposed to caterpillar cues but did not respond to them. By contrast, Janzen (1967) reported that when a Mexican Aristotelia corallina caterpillar shelter was discovered by specialist acacia ants (P. ferrugineus F. Smith), the shelter was quickly disassembled and the caterpillar killed.

Observations during laboratory rearing provided further evidence that late instar caterpillars were not feeding directly on acacia foliage. Although many caterpillars pupated within a few days of collection, several caterpillars were reared for long periods (7–18 days) before successfully pupating. During rearing, no loss of leaf area was observed, no fresh foliage was added, and very little frass was produced by the caterpillars.

Shelter-building. Four successful shelter-building observations revealed a consistent pattern (Baer Video 3 shows an example). The caterpillar began by positioning itself on the domatium or stem and repeatedly stringing single strands of silk between anchor points (the stem, the rachis, and the thorns) by moving its head and

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thorax back and forth while its abdomen remained anchored to the substrate. Most strands were placed between adjacent anchors, forming a rough diamond, but some silk was placed along the diagonals. As building continued, strands were also run from anchor points to existing silk strands. Once there were enough intersecting strands to bear the caterpillar’s weight, the larva shifted to hanging upside-down on the silk. The caterpillar then built up both the exterior and the interior of the web. These reinforcements led to the caterpillar hanging from a relatively solid silk platform. At this point (~20–30 min), the basic structure of the web was established, and the caterpillar rested for several hours. The shelter was then completed during one or more additional building bouts (these occurred overnight, so the exact timing is unknown), with the caterpillar extending the outer webbing to the EFNs and completely enclosing the silk platform to form a tunnel.

Depending on foliage architecture, there was some variation in shelter construction. If there was an entry hole on the upper surfaces of the domatium, one end of the silk tunnel connected to the hole (Fig. 2a). If there was no conveniently located entry hole, the silk tunnel itself was used as a retreat. This was always true for shelters built on V. farnesiana, as this acacia species does not produce domatia. Instead, these shelters had a long silk tunnel running along the stem (Fig. 2b).

Unlike the other caterpillar species observed at Palo Verde, these caterpillars do not usually build additional shelters or significantly expand the original one. Only four unmanipulated caterpillars out of 33 built a second shelter and no unmanipulated caterpillar built more than two. This also supports the hypothesis that older caterpillars feed on a renewable resource (EFN).

Parasitism status may affect shelter-building behavior. During one shelter-building observation, the caterpillar built a simple web in the foliage, rather than the complex node-centered shelter described above. Two days later, a parasitoid larva emerged from the webbing, and the caterpillar pupated in the web.

Herbarium search. Evidence suggestive of A. corollina was found on 2 of 33 United States C. nictitans specimens, but no webs were found on any of the 82 Central American C. nictitans specimens. Only one specimen of Caribbean (Puerto Rican) C. nictitans was present in the herbarium. None of the 12 United States V. farnesiana specimens showed any evidence of A. corollina. A. corollina evidence was most abundant on Central American Vachellia farnesiana specimens, with 14 of 221 specimens showing webs. One Mexican specimen even had a clearly preserved A. corollina caterpillar in a flattened web (Fig. 3). Eight of 35 Caribbean V. farnesiana specimens, all from Puerto Rico, had possible A. corollina webs. Five of 239 Central American V. collinsii specimens had webs, as did four of 110 Central American V. cornigera specimens. For a full list of specimens with apparent A. corollina webs and caterpillars, see Table 1.

**Discussion**

During my field research in a Costa Rican tropical dry forest, a species of shelter-building gelechiid caterpillar was observed to exploit the domatia, EFN nectar and Beltian bodies acacias provide for their ant defenders. The caterpillars also build their silk webs by repetitively stringing silk strands between anchor points, but this apparently simple method is flexible enough to accommodate variations in plant architecture, such as the proximity of a domatium hole or EFN. The study species was identified morphologically as Aristotelia corollina Walsingham and genetically as a fourth member of the cryptic species complex currently represented by this name (BOLD:AAH5498). A search of known host plant species in the Missouri Botanical Garden herbarium revealed geographic variation in host plant use, as well as additional locations where A. corollina likely occurs.

Costa Rican BOLD:AAH5498 Aristotelia corollina caterpillars are not the only caterpillars to consume EFN nectar, but they differ in two respects from previously described nectar-drinking caterpillars. First,
all other known nectar-drinking caterpillars have close relationships with ants, that is, they are myrmecophilous. Many myrmecophilous riodinid caterpillars consume EFN nectar to supplement other food sources, including leaf tissue (DeVries and Baker 1989, DeVries 1997), floral parts (DeVries et al. 1992, Wagner & del Rio 1997), or membracois and/or their honeydew secretions (DeVries et al. 1992, DeVries 2000). Although several Australian lycaenid caterpillars have been observed drinking EFN nectar (N. E. Pierce, pers. comm.), I have been unable to find any published observations. Past reviews have cited three articles (Horvitz & Schemske 1984, Maschwitz et al. 1984, Pierce & Elgar 1985), but while they report lycaenid caterpillars near EFNs or food bodies, they do not contain direct observations of caterpillars consuming these resources. Belcher et al. (1983) reported that Heliothis virescens Fabricius (Lepidoptera: Noctuidae) caterpillars preferentially consumed the tissue of cotton EFNs, but found that the caterpillars were not attracted to the nectar itself. I have not found any reports of non-myrmecophilous caterpillars consistently consuming EFN nectar. This may simply mean that caterpillars that successfully consume EFN nectar and avoid ants are small and inconspicuous, or it may mean that the strategy is truly rare.

Second, while the caterpillars do feed on emerging foliage when young, they can successfully pupate after consuming EFN nectar for over two weeks, and the late instars may consume only nectar and Beltian bodies. This raises the question of how the caterpillars can fulfill all their dietary needs. While EFN nectar, especially from obligate myrmecophytes, contains relatively high concentrations of free amino acids in addition to sugars, the caterpillars must still successfully digest these nutrients (González-Teuber & Heil 2009, Shenoy et al. 2012). Research on specialist acacia ants and acacia rewards has shown that acacias generally “lock” their rewards by packaging nutrients in forms that require specific enzymes to digest them (Heil 2015). In the case of EFN nectar, acacias can make it unappealing to generalists by secreting EFN nectar with unusual sugar compositions (Heil et al. 2005). Beltian bodies are highly nutritious, but acacias also lock them by including enzymes that inactivate generalists’ digestive enzymes (Orona-Tamayo et al. 2013). This suggests that these Costa Rican BOLD:AAH5498 caterpillars must have one or more specific adaptations for feeding on acacia rewards, particularly if they successfully digest Beltian bodies.

The Costa Rican BOLD:AAH5498 caterpillars’ natural history is broadly similar to what is known for the Mexican A. corallina caterpillars. Janzen (1967) reported A. corallina caterpillars in Veracruz and Oaxaca, Mexico. These caterpillars spun webs on Vachellia cornigera shoots and emerged from them at night to feed on the shoot tips, often damaging them and preventing or slowing plant growth. This behavior seems consistent with the damage caused by the early instar Costa Rican BOLD:AAH5498 caterpillars, and nocturnal feeding would explain why folivory was never directly observed. No mention was made of caterpillars feeding at EFNs or consuming Beltian bodies, but since the EFNs would have been inside the shelters, visits to them may have been missed. Janzen’s surveys of other local mimosoid legumes, which included V. macracantha (Humb. & Bonpl. Ex Willd.) Seigler & Ebinger and V. chiapensis (Saff.) Seigler & Ebinger but not V. collinsii or V. farnesiana, did not find A. corallina caterpillars on any species but V. cornigera. V. cornigera occurs at Palo Verde, but no A. corallina caterpillars were found on them, possibly because the plants were always occupied by acacia ants.

Herbarium specimens of Vachellia farnesiana, V. collinsii, and V. cornigera from Central America suggest that A. corallina caterpillars can be found throughout Central American dry forests, with webs found on plants collected in Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica. One such specimen of V. cornigera (Janzen #1980) was collected in 1964 from Oaxaca, Mexico, apparently during the research described in Janzen (1967). Another V. cornigera specimen (Gentry #32254) had silk in a domatium entrance hole, suggesting that the Mexican caterpillars may also retreat into domatia. While many of the shelters have been somewhat distorted by pressing and mounting, and some may have been old when collected, they appear very similar to the shelters observed and collected at Palo Verde. These specimens suggest that there may be one cryptic species, or perhaps multiple species with similar larval behavior, throughout Central America.

The observed differences in the A. corallina complex appear to correspond to different geographic regions. For instance, information on the A. corallina complex in the continental United States presents a much different picture than that of the Central American A. corallina. First, while the non-myrmecophilic acacia Vachellia farnesiana is patchily distributed in the southern United States (USDA 2016), A. corallina adults have been reported in areas where there are no acacias, such as Tennessee and Oklahoma (Moth Photographers Group 2016). These moths likely belong to the ‘southern US’ BIN (BOLD:AAA8062). In Florida, this clade is joined by another (BOLD:AAA8061). Interestingly, Kimball (1965) reported two wing color forms for Florida A. corallina and suggested that these might represent two
V. collinsii needed to compare the morphologies and DNA sequences of all four groups to those of the Caribbean were far too few (2 specimens from North Carolina and Mississippi, suggesting that this may be the case. No webs were found on US V. farnesiana, although the sample size was small (N = 12).

Aristolotelia corallina have also been identified in Puerto Rico. One Puerto Rican specimen was included in the BOLD barcode data, and it was placed in its own BIN (BOLD:AAT9249). While there are no published Puerto Rican host records, both V. farnesiana and C. nictitans are native to the island. Several A. corallina-type webs were found on herbarium specimens of Puerto Rican V. farnesiana, suggesting that this acacia may be A. corallina's Puerto Rican host. There was only one Puerto Rican specimen of C. nictitans, so its potential as a Puerto Rican host plant could not be assessed. The herbarium specimens from the rest of the Caribbean were far too few (2 V. farnesiana; 0 C. nictitans) to give any insight into whether A. corallina might occur on other islands.

CONCLUSION

Aristolotelia corallina Walsingham is a currently unresolved species complex, containing at least four distinct clades. Complex members from different locations apparently feed on different host plants with different levels of ant association, ranging from the facultative C. nictitans to the obligate myrmecophytes V. collinsii and V. cornigera. Additional research is needed to compare the morphologies and DNA barcodes of all four groups to those of A. corallina from the type locality of Guerrero, Mexico. If the type specimen corresponds to any of the currently identified clades, it is most likely the Costa Rican one (BOLD:AAH5498), as both the Costa Rican and eastern Mexican caterpillars exploit obligate myrmecophytes by consuming young foliage and building shelters that provide access to both EFNs and domatia. Inspection of herbarium specimens also shows that there are likely populations of A. corallina throughout Central America. Whether these caterpillars belong to identified cryptic species remains to be determined. It may be possible to barcode caterpillars preserved in herbaria, although projects that have used herbarium insect material have required large sample sizes to successfully generate sequences (e.g., Lees et al. 2011). However, this report shows significant ecological differentiation between the Costa Rican clade and the two clades found in the United States, as the Costa Rican BOLD:AAH5498 caterpillars exploit several aspects of an elaborate ant-plant relationship, including Beltian bodies and extrafloral nectar. Due to these feeding and developmental behaviors, these caterpillars appear to be particularly reliant on ant-adapted plants. To my knowledge, this is the first reported instance of a non-myrmecophilous caterpillar exploiting these resources.

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LITERATURE CITED


