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DEFENSE MECHANISMS IN PYRALIDAE AND CHOREUTIDAE: FECAL STALACTITES AND ESCAPE HOLES, WITH REMARKS ABOUT COCOONS, CAMOUFLAGE AND APOSEMATISM

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ABSTRACT. A novel behavior, linking fecal pellets with silk on the underside of leaves, to form what look like slender brown stalactites, is reported in two species of Pyralidae and two species of Choreutidae from the Republic of Panama. These fecal stalactites, constructed in association with escape holes cut in leaves, may function as landmarks to locate those holes and/or as decoys or camouflage. We discuss fecal stalactites, camouflage and aposematism, and cocoons in these larvae as part of a multiple defense system. We provide the first larval description for *Monoloxis flavicinctalis*.

Additional key words: *Abaera, Brenthia, Monoloxis*, Panama, host plants.

Larvae of some lepidopterans living within enclosed spaces, e.g., leaf-eating species that roll leaves or cut and fold leaf shelters, remove fecal pellets, at times explosively, from their habitations (e.g., Friedlander 1987, Rawlins 1984, M. Weiss pers. com., AA pers. obs.). These behaviors may have evolved to avoid pathogens (Rawlins 1984) or to eliminate olfactory cues that might attract predators or parasitoids (Stamp & Wilkens 1993). Contrary to this, some larvae use and live with fecal pellets in their habitations, e.g., many pyraloid larvae, including stored product pests (MAS pers. obs.).

We document a novel use of fecal pellets by the larvae of four moth species. We use "fecula" and "fecal pellets" to refer to larval excrement, reserving "frass" for "The chips or particles cast aside by wood borers" (Frost 1959). The larvae of *Monoloxis flavicinctalis* (Sepp, [1852]) (Pyralidae: Chrysauginae) (Figs. 2–4), *Abaera nactalis* Walker, [1859] (Pyralidae: Chrysauginae) (Figs. 6, 7), and two species of *Brenthia* Clemens, 1860 (Choreutidae: Brenthiinae) chew one or more escape holes near the blade midvein, then link their fecal pellets using silk to form what look like slender brown stalactites suspended from the underside of the leaf (Figs. 4, 7, 8). In addition, *M. flavicinctalis* and *Brenthia* sp. 1 are here reported to construct cocoons of fecula.

We discuss the function of fecal stalactites and escape holes, briefly address the evolution of fecal stalactites in *Brenthia* species, in contrast to those species that do not construct them, and review other structures that appear similar to fecal stalactites, with similar or dissimilar functions. We also address the host plants of these four moth species and possible aposematism of their larvae.

MATERIALS AND METHODS

The four species were collected as larvae (representing various stadia), or pupae, on the dates and at the localities (all in the Republic of Panama) listed in Table 1. They were reared in petri dishes or in small cages fashioned from petri dishes and window screening, and placed in Ziploc® bags with folded, moistened paper towel strips to regulate humidity. Their behavior was observed and recorded daily (with few exceptions), and shed head capsules and pupal exuviae were collected and mounted. Larvae were preserved by bringing them to a boil in distilled water, then dropping them into 80% ethanol.

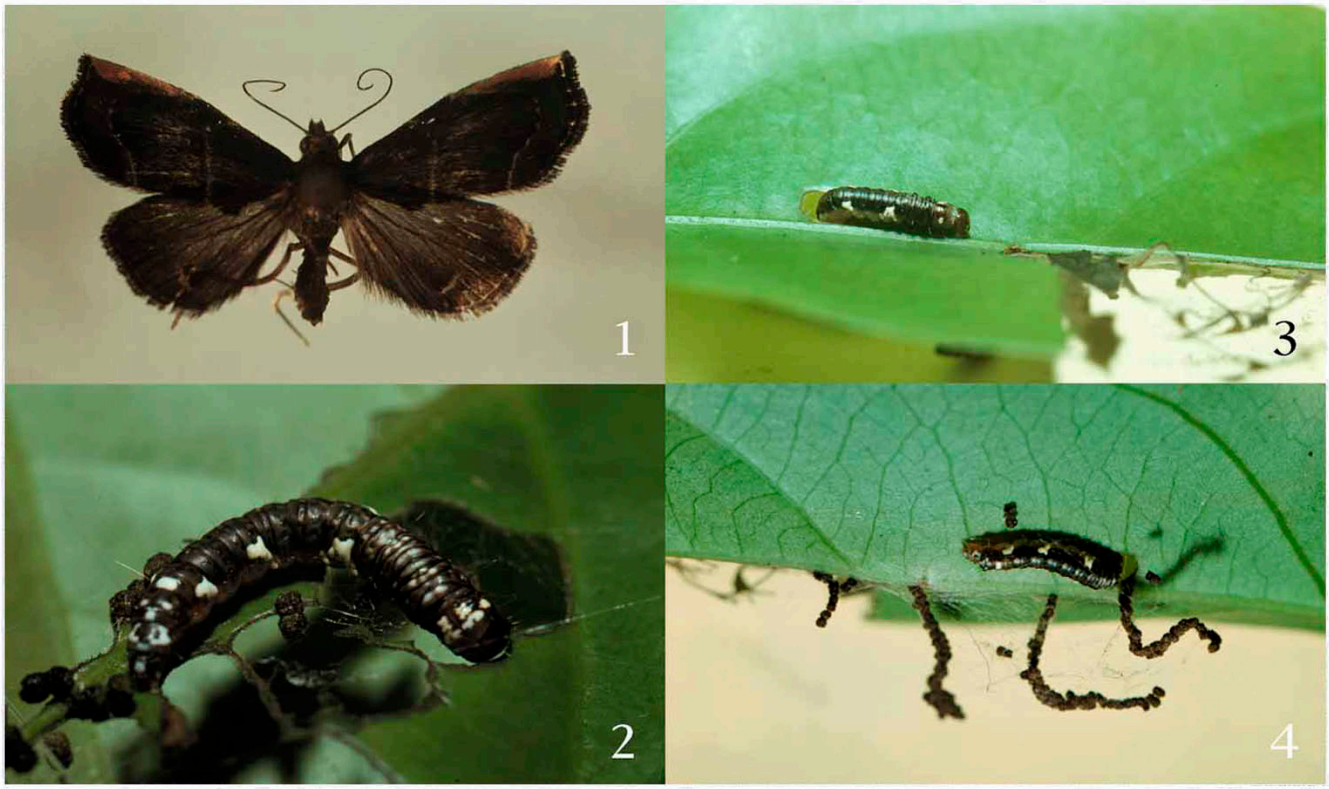
The two *Brenthia* are not identified to species. *Brenthia* species-level identifications are possible only with genitalic dissection of males and only if the specimen belongs to a species described by Meyrick and illustrated by Clarke (1969) (V. Becker in litt.).

Adult specimens and exuviae of *Maracayia chlorisalis* Walker (Aiello lot 1978-45) and *Monoloxis flavicinctalis* (Aiello lot 1979-73) are deposited at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., U.S.A. All material relating to the remaining rearings, including other specimens of *M. flavicinctalis*, and plant vouchers, are at the Smithsonian Tropical Research Institute (STRI), Republic of Panama.

In the accounts to follow, lot numbers are those of Aiello, and consist of the year plus a sequential number. When more than one individual is reared, an individual number (#) is appended. Thus "lot 1979-73 #2" refers to individual #2 of the 73rd lot for the year 1979. These numbers appear on the labels of all reared specimens

Table 1. Collection and developmental data (number of days in each stadium) and outcomes. Numbers include days spent preparing for molting or pupation, i.e., not eating. Final date is the date of eclosion, death, or preservation, and is not included in durations. If cocoon contents were not visible, only the duration in the cocoon is given. Eclosion dates are for the morning immediately following adult nocturnal emergence. Minimum durations (≥) are given for the stages collected or for stages cut short by preservation or natural death. A ≈ indicates a molt that may have occurred on a day when observations were not made. A lowercase "p" next to an individual indicates it was parasitized.

Name and collection data	Lot#	Indiv#	Instar a	Instar b	Instar c	Instar d	Instar e	Cocoon/ pupa	Final date	Outcome
PYRALIDAE (CHRYSAUGINAE):										
Monoloxis flavicinctalis, on *Lacistema aggregatum*										
Canal Area, Barro Colorado Island Snyder-Molino Trail-5.9 25 May 1979, A. Aiello										
	1979-73	1				≥2	18	≥12P	27 Jun	Pupa died, discarded
	1979-73	2				≥1	12	15P	23 Jun	Adult
Canal Area, Barro Colorado Island Brokaw Ridge (off Balboa Trail-10) 25 August 1988, A. Aiello & E. Leigh										
	1988-19	1					≥7	30C	1 Oct	Adult
	1988-19	2					≥7	—	1 Sep	Larva preserved
Panama Province, Arraiján Loma del Río 12 December 2001, A. Aiello										
	2001-44	1					≥5	39C + 15P	9 Feb	Pupa died, pointed
	2001-44	2					≥1	—	13 Dec	Larva preserved
Abaera nactalis, on *Cordia panamensis*										
Canal Area, Summit, Old Gamboa Road 27 June 1990, D. Windsor										
	1990-7	1	≥2	≈6	≈6	8	9	37C	3 Sep	Adult
CHOREUTIDAE (BRENTHIINAE):										
Brenthia sp. 1, on *Cojoba rufescens*										
Panama Province, Arraiján Loma del Río 12 January 1992, A. Aiello										
	1992-5	1						—	12 Jan	Empty cocoon
	1992-5	p2							27 Jan	Parasitized, wasp pupa died
	1992-5	3					≥5	2C + 11P	30 Jan	Adult
	1992-5	4						≥15C	27 Jan	Adult
Brenthia sp. 2, on *Calathea* sp.										
Canal Area, Barro Colorado Island 26 August 1993, D. Windsor										
	1993-70	1						≥12C	7 Sep	Adult
	1993-70	2						≥12C	7 Sep	Adult
	1993-70	3						≥12C	7 Sep	Adult
Brenthia sp. 2?, on *Calathea* sp.										
Panama Province, Cerro Jefe Conservation Trail 10 September 1993, A. Aiello, D. Windsor & J. Miller										
	1993-73	p1					≥1	1C + 8P	20 Sep	Parasitized, wasp adult
	1993-73	2					≥1	—	11 Sep	Larva preserved



FIGS. 1–4. *Monoloxis flavicinctalis* (Sepp) (Pyralidae: Chrysauginae), reared on *Lacistema aggregatum* (P. J. Bergius) Rusby (Flacourtiaceae), as Aiello lot 1979-73. **1,** Pinned adult. **2,** Mature larva, eating. **3,** Larva (anterior portion), moving to upper surface of leaf, through escape hole. **4,** Larva (posterior portion), returning to lower surface of leaf, by backing through escape hole. Photographs by A. Aiello.

and their associated parts, and correspond to numbers on daily data forms maintained by Aiello at STRI.

RESULTS

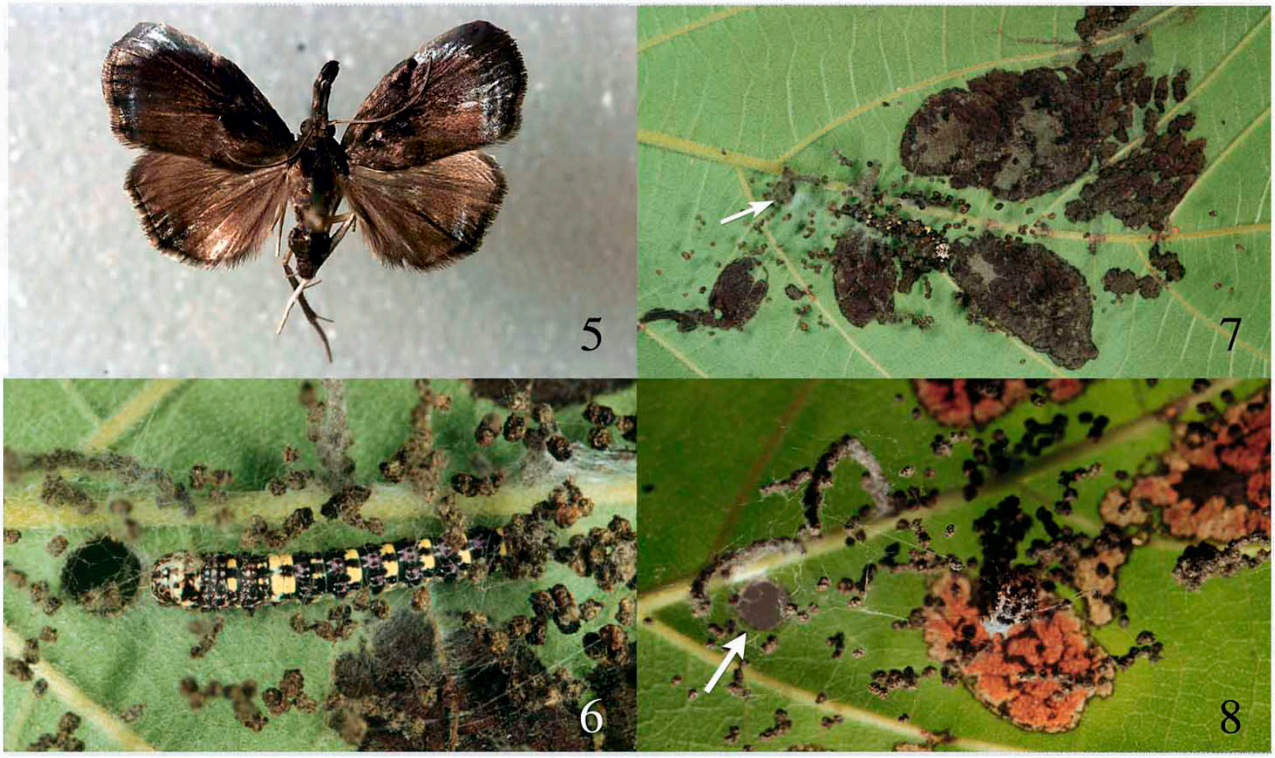
Monoloxis flavicinctalis (Sepp, [1852]) (Pyralidae: Chrysauginae) (Figs. 1–4, 9)

All six *Monoloxis flavicinctalis* larvae were found on mature leaves of *Lacistema aggregatum* (P. J. Bergius) Rusby (Flacourtiaceae). Table 1 gives collection and developmental data. Of these six individuals, two were preserved as larvae, two died as pupae, and two were reared to adults. In each larva the head was dark red and the body was purplish black, with white markings (dorsal and lateral on T1 and A7, and lateral on A2, A5, and A8–A10) (Fig. 2). The larvae lived on the undersurfaces of leaves, each within a wispy tangle of silk supported by a series of three or four, flexible, brown stalactites, several mm apart along one side of the midvein, and constructed by linking as many as 50 fecal pellets and securing them with silk. Each larva rested with its head near a small, neatly rounded hole located to one side of the midrib and near a fecal stalactite. When touched, the larva moved rapidly head first through the hole to the upper surface of the leaf, which was totally bare (Fig. 3). After a few seconds without further disturbance, it backed down through the hole into its silk tangle (Fig. 4). Except for these escape maneuvers, larvae remained within their silk tangles, extending out of them only to eat surrounding leaf tissue. In the only instance that new shelter construction was witnessed (lot 2001-44 #1), the larva produced the escape hole before anything else.

Molting took place within the silk tangles. Cocoons were constructed of fecula and silk on the leaf or on the container floor. The adults were brown, with orange forewing apices (Fig. 1), and rested with the forewings covering the hind wings, in a broad, flat, triangle. Plant vouchers for lot 2001-44 are Aiello 1582 and 1635.

Though the setal pattern of *M. flavicinctalis* is typical of the Chrysauginae, the larvae are distinctively patterned, an unusual trait within the Pyralidae. We provide the first larval description for the genus, together with an illustration (Fig. 9). A pupa was not available for description.

Larva (Fig. 9): Length: 18 mm (n = 1) (final instar). Head with reddish brown platelets; beige or white between platelets. Epicranial suture present. White between L1 and A3, medially across head and on frons dorsal to F1, on either side of epicranial suture,



FIGS. 5–8. *Abaera nactalis* Walker (Pyralidae: Chrysauginae), reared on *Cordia panamensis* L. Riley (Boraginaceae), as Aiello lot 1990-7. **5,** Pinned adult. **6,** Penultimate larva within fecula and silk tangle beneath leaf; the largest dorsal, yellow marks are on A1. **7,** Larva camouflaged within fecula and silk tangle; dark patches are feeding areas. **8,** Larval shelter back-lighted, showing fecal stalactites, escape hole (arrow), and scraped feeding areas. Photographs by Carl Hansen.

and ventroposterior to stemmata. Frontoclypeus area ventral to F1, including clypeus dark brown; anteclypeus white; labrum yellowish brown. Adfrontal area light brown. Mandibles yellowish brown with dark brown margins. T1–3 and A1–10 integument lightly rugose. With sclerotized rings at the bases of D2 on T3 and SD1 on A8. Prothoracic shield white, dark brown between D2 and SD2 along posterior margin and extending length of medial line. XD1, XD2, SD1 with small dark brown pinacula. T1 with lobes anterior to thoracic legs and prothorax; 2 L setae below and anterior to spiracle on brown pinaculum. T1–3 legs with basal segments sclerotized dark brown; tarsus white. T2–3 with D1–D2, SD1–SD2, and L1–L2 on same pinaculum; SV1 and L3 with one seta on separate pinacula. T1-3 and A1, light brown ventrally; A2–A10 white ventrally. A2, A5, and A7 with white areas anterior to spiracle and SD1 and extending dorsal to SD1, but ventral to D setae. A7 also with a white area joining D2 on both sides. A8 with white between SD1 and D1 and between both D2 setae. A9 primarily white; pinaculum dark brown. A10 primarily white with brown mottling between SD2, D2, and D1. A1–8 with L1 and L2 present on separate pinacula ventral to spiracle; SD1 on a large, brown pinaculum dorsal to spiracle, except A2, A5, and A7 where the pinaculum is small, dark brown, triangular; D1 and D2 setae on separate small, round, dark brown pinacula. A1–6 with three SV setae, A7–8 with two SV setae. A1–8 with one L3 seta. SD2 of A1 anterior to SD1, SD2 of A2, A3, A4, A6, and A8 anterodorsal to spiracle; SD2 not present on A2, A5, and A7. SD1 pinaculum on A8 protruding, seta at least 20 times the length of other setae. Spiracle on A8 at least twice as large and slightly more dorsal than other abdominal spiracles. A9 with three L setae on same pinacula; D1, D2, and SD1 on separate pinaculum. Prolegs with crochets biordinal in a circle.

Abaera nactalis Walker, [1859]
(Pyralidae: Chrysauginae)
(Figs. 5–8)

The single *Abaera nactalis* larva (lot 1990-7) was found on a mature leaf of *Cordia panamensis* L. Riley (Boraginaceae). Table 1 gives collection and developmental data. The head was patterned with white and dark brown, and the body was checkered dark brown, pale brown, and bright yellow (Fig. 6). Like *M. flavicinctalis*, it lived within a loose, silk tangle supported by flexible fecal stalactites, and had an escape hole (Figs. 6–8) through which it scooted to the upper surface of the leaf when we disturbed it. Unlike *M. flavicinctalis*, this larva decorated the silk tangle with numerous individual fecal pellets, which, in conjunction with the complex markings of the larva, provided messy but highly effective camouflage (Fig. 7). Early instars ate only the tissue of the leaf undersurface, producing extensive, brown scraped patches bounded by the secondary veins (Fig. 7). The final instar ate areas of leaf, veins and all.

Portions of three shelter-building efforts were observed. The first of these new shelter building events

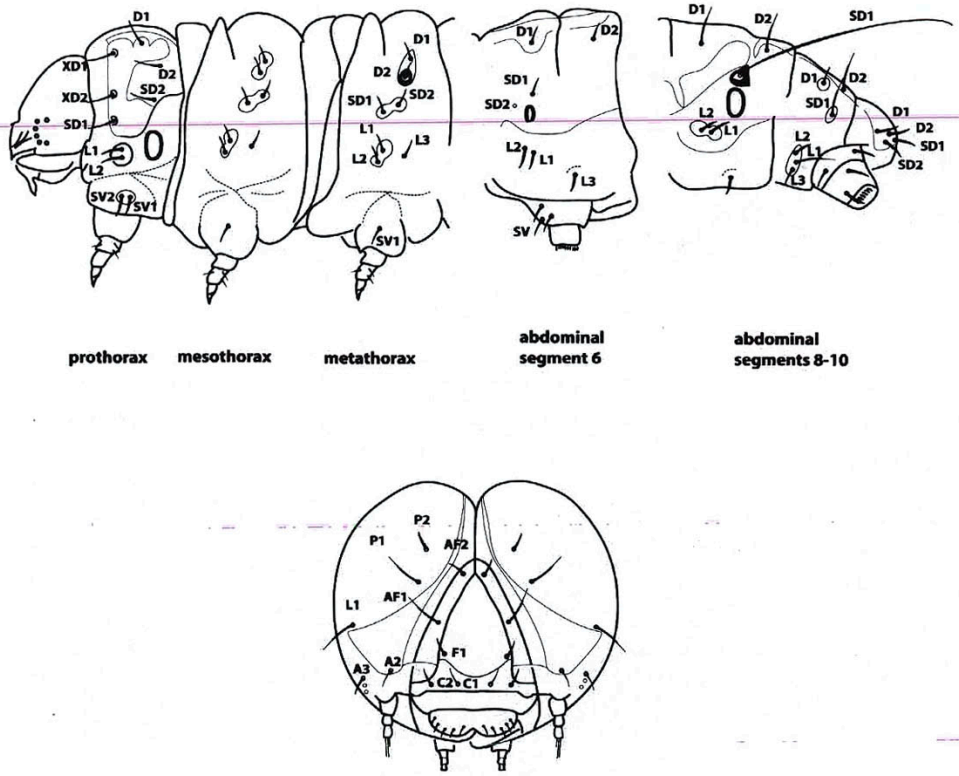


FIG. 9. *Monoloxis flavicinctalis* (Sepp) (Pyralidae: Chrysauginae), setal maps of larva body (above) and head (below). Illustrations by A. Solis.

took place 5 July on the original leaf, and consisted of an escape hole near the midrib, one fecal stalactite, a silk tangle sprinkled with fecula, and two scraped feeding areas. When the leaf began to turn black, the larva was prodded onto a fresh leaf, thus precipitating the second building episode. Within 30 minutes the larva had moved to the underside of the leaf and chewed an escape hole next to the midrib. During the next 45 minutes, it constructed a fecal stalactite (4 mm long) near the hole. The next morning a second fecal stalactite (10 mm long), a silk tangle, and a small feeding area had been added. And the day after that a third stalactite (17 mm long) appeared. The third new shelter effort took place 20 July, after the newly molted final instar was transferred to a fresh leaf. The larva first chewed a new escape hole, then constructed several fecal stalactites and a silk tangle. The following day (21 July), it fashioned a cocoon-like shelter of fecula and silk instead of more stalactites, and began eating whole leaf rather than simply scraping the blade surface.

The mature larva curled into an **O** next to the midrib at a leaf base and constructed a cocoon of silk and leaf material. The finished cocoon was cream color on the inside, dark brown on the outside, and was covered with tufts of leaf trichomes. The adult male, brown, with powder-blue forewing apices (Fig. 5), eclosed the night of 2–3 September. It held the wings in a slightly tented triangle.

Brenthia Clemens, 1860, sp. 1
(Choreutidae: Brenthiinae)

One larva and three fecula and silk cocoons (lot 1992-5) of a small species of *Brenthia* (6 mm wing span) were found on the undersurface of mature leaflets of *Cojoba* (=*Pithecellobium*) *rufescens* (Benth.) Britton & Rose (Fabaceae: Mimosoideae), in secondary growth. Table 1 gives collection and developmental data. The three cocoons were suspended horizontally among stalactites, within fecula-sprinkled silk webbing. Cocoon #1 contained only a cast larval skin. Cocoon #2 held a pupa, which protruded from its housing and within which a wasp pupa could be seen clearly; the wasp pupa failed to develop, then molded and was discarded.

The only larva (#3) was among fecula-sprinkled webbing and had made several neatly rounded holes in the leaflet, permitting rapid passage to the upper surface. Each hole had a flexible fecal stalactite next to it. The larva ate the undersurface leaf tissue only, producing small scraped patches. Cocoon #4 contained a healthy pupa. Individuals #3 and #4 yielded adults. Prior to eclosion, pupae protruded from their cocoons.

Adults displayed in their petri dishes. This and the next species are among the microlepidopteran "peacock moths" that are seen frequently in the Canal watershed area, performing a raised wing display (Aiello & Becker in prep.) on foliage, sometimes several individuals per leaf.

Brenthia Clemens, 1860, sp. 2
(Choreutidae: Brenthiinae)

Table 1 gives collection and developmental data. Three cocoons (lot 1993-70) of a larger *Brenthia* species (1 cm wing span, versus 0.7 cm) were found on the undersurface of *Calathea* sp. (Marantaceae) leaves. Escape holes, short fecal stalactites, silk tangles, and scraped feeding areas on the leaf undersurface indicated a larval life style similar to that of the preceding *Brenthia* species. However, this species was found on a monocotyledonous plant, and instead of constructing a cocoon of fecula and silk, it spun a white silk cocoon. The cocoon was composed of three parts. The main part, an elongate spindle-shaped structure that housed the pupa, rested suspended within a cloud of wispy silk between two silk sheets; the top sheet was flat and had numerous holes, especially towards its margins, and was anchored all around to the leaf; the bottom sheet was creased lengthwise to form a **V**-shaped trough, shorter than the top sheet, and anchored to it along its sides. The final larval skin had been pushed out of one end of the spindle and into the silk cloud. Prior to eclosion the pupae projected from their cocoons. All three cocoons yielded adult females. And all three moths dashed about their petri dishes displaying in the same manner as the smaller species.

One of two larvae found on Cerro Jefe (Table 1, lot 1993-73), also on the leaves of *Calathea* sp., spun a white, three-layered cocoon like those of lot 1993-70, and almost surely was *Brenthia*, very likely *Brenthia* sp. 2. Following pupation, it pushed its final larval skin out of one end of the spindle-shaped cocoon. On the mistaken conviction that an adult would be obtained from it, the other larva was preserved. Alas, a small braconid wasp emerged from the cocoon and no adults were obtained from this rearing.

DISCUSSION

The larval constructions, i.e., fecal stalactites and escape holes, and associated behavior described above are part of a complex defense system that includes camouflage and possibly aposematism. Fecal stalactites are always near an escape hole, and appear to act as landmarks to help larvae locate the holes and escape quickly. The escape hole and its accompanying stalactite were the first items to appear in the shelter construction sequences, underscoring their importance to larval survival. Unlike the larval behavior of the two *Brenthia* species described here, several other species of *Brenthia* fashion escape holes, but not stalactites. Specimen information and previous descriptions of *Brenthia* biology in two different parts of the World do not report the building of fecal stalactites. *Brenthia pavonacella* Clemens, reared by Busck in the United States (NMNH: specimens and leaf remains), lived among fecula-dotted silk tangles beneath leaves. In Japan, *B. japonica* Issiki (Arita 1971, Issiki et al. 1975) and *B. pileae* Arita (Arita 1971) have been reported to fashion escape holes and fecula-laden silk tangles; fig. 230 in Issiki et al. (1975) shows a larva that has "escaped" through its hole. Similar behavior is found in an unrelated, more primitive, microlepidopteran species, *Compsistis* Meyrick (Elachistidae: Depressariinae), whose larvae cut escape holes but do not construct fecal stalactites, beneath mature leaflets of *Pseudobombyx septenatum* (Jacq.) Dugand (Bombacaceae) (AA pers. obs. lot 1993-94). Because escape holes appeared before fecal stalactites in shelter construction and because some species of *Brenthia* create escape holes without fecal stalactites implies that escape holes may have come first in the evolutionary sequence of this behavioral pattern. This idea could be tested by conducting a worldwide phylogenetic study of *Brenthia*.

There are several structures in arthropods, including in other Lepidoptera, that are reminiscent of fecal stalactites. The sand pillars constructed by some fiddler crabs help them locate their burrows rapidly and thus avoid predation (Christy 1991, 1995). In *Monoloxis* and *Brenthia*, fecal stalactites may function secondarily as decoy larvae, and they recall the "fake" larvae fabricated by early instar *Adelpha basiloides* (Bates) (Nymphalidae) (Aiello 1984). Fecal stalactites remind us of the horizontal and more rigid fecal rods produced by early instars of many Nymphalidae, either as continuations of leaf veins or as formations anchored to the leaf margin. The techniques involved in construction of fecal rods and stalactites may be similar, but their functions are quite different. Fecal rods are used as resting and molting perches by earliest instar nymphalids and are thought to provide both camouflage and safe haven from ants and other predators (Machado & Freitas 2001). Many nymphalids enhance those protections by barricading the base of the structure with loosely attached leaf bits (Muyshondt & Muyshondt 1979) or, in *Adelpha* spp., clusters of fecal pellets (Aiello 1984).

Though fecula cocoons are not common among

Lepidoptera, examples are found in several families besides those reported here for Pyralidae and Choreutidae, e.g., *Synanthedon* spp. (Sesiidae) (Barrett 1997), *Mimallo amilia* (Cramer) (Mimallonidae) (AA pers. obs. lots 1985-131, 1987-45, 1990-54, 1997-33, 2002-27). Fecula cocoons might help protect their occupants from parasitoids and predators, but their effectiveness has not been tested. Among known *Brenthia*, *Brenthia* sp. 1 is unique, so far, in using fecal pellets to construct its cocoon. All other *Brenthia* species for which we have information spin white silk cocoons: *B. coronigera* Meyrick in India (Fletcher 1920, NMNH: Rangi specimen), *B. japonica* (Arita 1971, Issiki et al. 1975), *B. pavonacella* (NMNH: Busck specimens), *B. pileae* (Arita 1971), and *Brenthia* sp. 2 in Panama (this paper). As well, white silk cocoons among webbing are found in another member of the Choreutidae, *Hemerophila albertiana* (Stoll) (AA pers. obs. lot 2001-39). It would be a challenge for a predatory or parasitoid wasp to breach one of these multi-layered silk cocoons.

Additionally, our observations indicate that though camouflaged, the larvae of *M. flavicinctalis* and *A. nactalis* may also be aposematic, exhibiting both warning coloration and unpalatability (Bowers 1993). It is known that the degree of pigmentation in lepidopteran larvae tends to correlate positively with degree of exposure to visually hunting predators (Stamp & Wilkens 1993). Exposed feeders include mimetic, camouflaged, or cryptically patterned species as well as colorful aposematic ones (Bowers 1993, Stamp & Wilkens 1993). The larvae of hidden feeders tend to be colorless, or they may appear green or brown due to their gut contents, or white due to fat body, and in species that extend from their shelters to feed, or that reside in moveable cases, the head and prothorax are pigmented and the rest of the body is not (AA pers. obs.). In contrast to conventional notions that most camouflaged pyraloid larvae are watery-looking caterpillars with pale or clear cuticles, *M. flavicinctalis* and *A. nactalis* are well-pigmented.

The larva of *A. nactalis* is strikingly colored yellow and brown, and well camouflaged within its fecula-sprinkled webbing. As well, it may be protected from chance exposure to predators by chemicals obtained from its food plant, *Cordia panamensis*, a short-lived, second growth tree that also hosts six species of metallically colored tortoise beetles: two species of *Omocerus* Chevrolat and four of *Discomorpha* Chevrolat (Chrysomelidae: Cassidinae) (Windsor et al. 1992). The larva of *M. flavicinctalis*, less well camouflaged than that of *A. nactalis*, quite likely derives chemical protection from its food plant, *Lacistema aggregatum*, a shrub or small tree that also is host to an as yet unidentified sexually dimorphic, wasp-mimicking diurnal moth (Arctiidae: Ctenuchinae) (AA pers. obs. lot 1999-8). The Flacourtiaceae belong to the Violales, a cluster of families notable for supporting an array of aposematic lepidopterans, e.g., *Heliconius* spp. (Nymphalidae) on members of the Passifloraceae (Benson et al. 1976, Trigo 2000), *Josia draconis* Druce (Notodontidae: Dioptinae) on *Turnera panamensis* Urb. (Turneraceae) (AA pers. obs. lots 1994-37, 1994-39, Miller 1996); *Siderone marthesia* (Cramer) (Nymphalidae) on *Casearia guianensis* (Aubl.) Urb. (Flacourtiaceae) (AA pers. obs. lots 1990-25, 1996-28, 2000-37); *Zunacetha annulata* Guérin (Notodontidae: Dioptinae) on *Hybanthus prunifolius* (Humb. & Bonpl.) Schulze-Menz (Violaceae) (Wolda & Foster 1978, AA pers. obs. lots 1977-25, 1979-26, 1997-11), to mention a few.

Aposematism to protect camouflaged Pyraloidea larvae against chance exposure may be a more common defense mechanism than has been reported in the literature. In addition to the two chrysaugine species discussed above, the first author has reared the larva of *Maracayia chlorisalis* Walker (Crambidae: Spilomelinae), whose clear cuticle and large, black pinacula camouflage it beneath a silk and fecula tangle on the broad, succulent leaves of its foodplant, an epiphytic cactus, *Epiphyllum phyllanthus* (L.) Haw. (Cactaceae) (lot 1978-45); and the aposematic (white, ornamented with black pinacula and yellow supraspiracular blotches) larva of *Palpita flegia* (Cramer) (Crambidae: Spilomelinae) that eats the leaves of a toxic plant, *Thevetia ahouai* (L.) A. DC. (Apocynaceae) (lot 1984-60). The adults of the latter two are white, the color most conspicuous and therefore most aposematic at night. The evolution of the ability to sequester defensive compounds as larvae and retain them into the adult stage has not been well studied (Bowers 1993).

It is doubtful that *Brenthia* larvae, being small and inconspicuous, rely on chemical protection from their host plants. If any do so, the most promising host plants, as far as plant secondary compounds are concerned, would be the Sapindaceae, which is host to *B. elongata* Heppner in the West Indies and *B. sapindella* Busck in Cuba (Heppner 1985). Another group of secondary compound candidates among known *Brenthia* host plants would be the Fabaceae, which are known to support a number of Lepidoptera aposematic as larvae and/or adults, i.e., *Ormetica sicilia* Druce (Arctiidae) on *Inga* sp. (AA pers. obs. lot 1980-44), *Utetheisa ornatrix* L. (Arctiidae) on *Crotalaria cajanifolia* Kunth (Fabaceae: Papilionoideae) (Trigo 2000), *Melanis pixe* (Boisduval) (Riodinidae) on *Albizia adinocephala*

(Donn. Sm.) Britton & Rose (AA pers. obs. lots 1988-30, 1991-5). In addition to *Brenthia* sp. 1 in Panama, the Fabaceae are hosts to at least two other *Brenthia* species: *B. albipunctata* Arita on *Spatholobus compar* Craib in Thailand (Arita 1987) and *B. pavonacella* on *Desmodium* sp. in the U.S.A. (NMNH: Busck specimens from Great Falls, Virginia, 17 and 18 July 1913; Falls Church, Virginia, 5 August 1913) as well as on *Inga vera* Willd. at Lares, Puerto Rico, where ". . . in November 1931, Mr. Francisco Sein found them abundant, feeding on the underside of the leaves. . . ." (Wolcott 1948).

In conclusion, fecal stalactites and escape holes are two mechanical constructions that may enhance larval survivorship in some species of Pyralidae and Choreutidae, and may be just part of a multiple factor defense system (Bowers 1993) that includes camouflage and aposematism, against a variety of enemies, predators or parasitoids, at different times of the night and day.

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