Natural History of *Eryphanis greeneyi* (Lepidoptera: Nymphalidae) and Its Enemies, with a Description of a New Species of Braconid Parasitoid and Notes on Its Tachinid Parasitoid

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Eryphanis Boisduval, 1870 is a Neotropical genus of medium to large butterflies encompassing nine species distributed from Costa Rica to Bolivia and reaching their peak diversity in the South American Andes (Penz 2008). So far as is known, adults are crepuscular, similar to closely related Caligo Hübner, 1819 (DeVries 1987, Freitas et al. 1997, Penz 2007). Recorded food plants are all members of the grass family (Poaceae), but the larvae have been described for only four species (Müller 1886, Dias 1979, Cubero 1985, DeVries 1987).

Eryphanis can be separated into two species groups. The zolvizora-group is comprised of three species (Eryphanis zolvizora Hewitson 1877, Eryphanis ophius Staudinger 1887, and Eryphanis greeneyi Penz & DeVries 2008) that are unified by wing coloration of the males and unique morphology of female genitalia (Penz 2008). E. greeneyi, recently described from Ecuador, has no published information on its natural history other than a mention of its bamboo (Poaceae) food plant in the species description. Although its geographic range is uncertain, it probably occurs along the east slope of the Andes from northern Ecuador to northern Peru, at elevations of 1,600–2,200 m (Penz 2008). Here, we describe the life cycle of E. greeneyi from the type locality in northeastern Ecuador and present observations on adult and larval behavior. We examine its host plant association relative to related taxa, larval coloration with respect to other taxa on the same host, and the function of larval frass throwing behavior.

Our focus on the immature stages of E. greeneyi allow us to place the species in a tritrophic context, including both the host-plant on which it feeds and its parasitoid enemies. There have been no published records of parasitism in the genus Eryphanis of which we are aware. We present data on parasitism frequency for E. greeneyi and describe a new species of braconid parasitoid that it hosts. We also describe and evaluate the taxonomic position of a tachinid parasitoid species in the genus Winthemia reared from E. greeneyi, and briefly review the biology and taxonomy of South American species in this group.

Materials and Methods

We carried out all rearing and field investigations at the Yanayacu Biological Station & Center for Creative Studies, Cosanga, Ecuador; c/o 721 Foch y Amazonas, Quito, Ecuador (e-mail: revmmoss@yahoo.com).

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habitats. The site receives ≈4 m rainfall per year with low seasonality. Landslides are common in the steep terrain surrounding YBS, most of which are dominated by *Chusquea* bamboo. Large patches of bamboo also form in flatter areas, especially along streams. For a more complete site description see Valencia (1995).

We collected eggs and larvae by visually searching potential host plants (primarily *Chusquea* spp.) along streams, roads and trails, and occasionally beating plants over a sheet. Larvae were collected throughout the year at elevations ranging from 2,000 to 2,200 m. All collections took place in a relatively small area within ≈10 km of YBS. As they were found, larvae were placed into plastic bags with a piece of their host plant and transported to the laboratory. In the laboratory, they were transferred to 1-liter glass jars for rearing and given an identification number for tracking. This laboratory, located at 2,100 m, is exposed to ambient temperatures (13–28°C) and humidity (generally 95–100% RH) but is shaded by a roof and shade cloth on the sides. In the laboratory, we added fresh food plant leaves as needed, removing frass and old host plant leaves daily. During these checks, developmental transitions and fates (e.g., mortality) were recorded. We made larval measurements the day before molting, as judged by the enlarged first thoracic caused by the expansion of the newly developing cranium. Mortality of larvae during rearing was almost 70%. This high mortality may have been due to lack of air flow in rearing jars which can result in fungal attack and increased susceptibility to disease.

If parasitoids emerged from larvae or pupae, they were killed by freezing and subsequently stored in 70% ethanol (Braconidae) or pinned and stored in a freezer (Tachinidae). These were subsequently transported to laboratory of the respective taxonomic expert (J.B.W., University of Illinois and J.O.S., Wright State University). Basic natural history information was recorded for all parasitoids, including at which stage of the host they emerged, where they pupated, how many individuals emerged, and if there were any special behaviors of immature parasitoids.

**Results and Discussion**

**Adult Behavior of *E. greeneyi***. Adult *E. greeneyi* (see Fig. 14) are rarely observed due to their largely crepuscular habits. Adults are most frequently seen from 17.45 to 1815 hours (1800 hours is sunset), although the extent to which they are nocturnally active is difficult to ascertain. No adults have ever come to black lights in our study area. On warmer mornings adults are occasionally active around daybreak as well. Males guard roughly linear territories, flying rapidly along the edges of large patches of food plant, frequently along streams or roads. They chase any moving object of comparable size including bats and the much smaller crepuscularly active nymphalid *Antirrhea adoptiva* Watkins, 1928 occurring in the area (Greeney et al. 2009a). Males can often be detected in the evening by the distinctive, sweet-musky scent produced while courting and patrolling. The smell is similar to that produced by many male *Caligo* spp. (Nymphalidae: Morphinae; H.F.G., personal observation).

We witnessed seven oviposition events, all of them occurring around dusk. In all cases but one, the female laid a single egg on the bottom of a mature food plant leaf, the single exception being a female who oviposited two eggs under the same leaf. Pausing very briefly, females hung upside down from the food plant stem and rapidly oviposited. Afterward, they flew immediately from the area without laying another egg.

**Developmental Stages of *E. greeneyi***. Egg. Egg (n = 35; ≈2.5 mm diameter; 19+ d; Fig. 1) spherical, dark orange when freshly laid, paler as development advanced, 35 longitudinal ridges, not extending all the way to the micropylar area, area between ridges slightly webbed. While searching bamboo for caterpillars, we found 19 single eggs, five clusters of two eggs, and twice found three eggs together. All eggs were found on the lower surface of mature food plant leaves.

**First Instar.** For first instars (n = 27; 9–16 mm [including caudae]), cauda, 2.5–3 mm; 21–25 d; Figs. 2 and 3), one larva took 31 d to complete the first instar, perhaps an artifact of poor food quality. Head capsule nearly round when viewed from the front with only slight epicranial crease (Fig. 2c), very finely reticulated, held slightly forward so appears slightly elongated posteriorly (Fig. 2a and b, d and e), densely covered with soft, forward curved setae (Fig. 2a–f), darker near epicranium and with very fine feathering...
at tips (Fig. 2f); ground coloration caramel brown, darkening ventrally, patterned with vertical white stripes on either side of cranial suture and laterally, lateral white stripes bordered by black stripes. Body mostly bare except for sparse, short, dark setae, roughly square in cross-section, widest at T1, tapering posteriorly (Fig. 2a and b), A10 bears a pair of long, round, smooth black caudae, each bearing two long, white, soft setae, one terminally and one projecting laterally in apical fifth of cauda; ground color reddish upon hatching, darkening to orange-brown and then pale brown as larva ages, early in instar (Fig. 2a and b) mid-dorsal, subdorsal, and spiracular dark lines run the length of the body; T1, A10, and subspiracular area whitish; by mid-instar (Figs. 4a and 5a and b) colors more subdued and browns less reddish; a dark black stripe runs spiracularly from A1 to A10; head coloration darker with central portion becoming dark olive and lateral reddish portions becoming black (Fig. 4a); head patternting fading greatly before molt (Fig. 4d). Larvae have a small, reddish eversible cervical gland which is rarely everted.

Second Instar. For the second instars (n = 20; to 25 mm [including caudae], cauda, 4.5–5 mm; 17–20 d; Figs. 4 and 5), head very different in shape from first instar (Fig. 4a and d, e and f), roughly square when viewed from the front and bearing a corona of six short conical scoli, longest epicranially; covered with short, sparse, pale setae; setae form dense, forward-projecting tufts on either side of mandibles; head including scoli finely pitted and bearing numerous small bumps (Fig. 4e and f). Immediately after molting (Fig. 4b and e) head strongly patterned, area around mid-cranial suture caramel brown, including inner portions of central scoli. Bright white stripes subtend this and extend from anterior portion of central scoli to just above forking of mid-cranial suture, white lines subtended by broad, dark red-brown stripes extending from epicranium to just above clypeus, lateral areas bright white. Immediately after molt (Fig. 4b) body color is very similar to late first instar but colors more intense; mid-dorsally A3–5 bear small, single, red-brown spots on posterior portion of each segment. Body shape similar to first instar but caudae now well developed (Fig. 4b and c), pale brown, smooth, tapering posteriorly to white tips; body and caudae mostly bare with sparse, minute pale setae; by mid-instar (Figs. 4a and 5a and b) colors more subdued and browns less reddish; a dark black stripe runs spiracularly from A1 to A10; head coloration darker with central portion becoming dark olive and lateral reddish portions becoming black (Fig. 4a); head patternting fading greatly before molt (Fig. 4d). Larvae have a small, reddish eversible cervical gland which is rarely everted.

Third Instar. For third instars (n = 26; up to 35 mm [including caudae], cauda, 9–10 mm; 19–25 d; Fig. 6),
head similar to that described for older second instar
(Fig. 6e and f), lateral broad dark-brown stripes now
paler and ending in black patches just above mid-
cranial suture fork, sides and posterior portion of dor-
sal-most cranial scoli pale orange; just after molting
(Fig. 6c) dark markings on head are mint-green;
freshly molted larvae are similar in overall appearance
and shape as late second instar but A10 slightly ex-
panded laterally and caudae proportionately longer,
slightly roughened, and bearing short, sparse, pale
setae (Fig. 6d); body noticeably glabrous but with
distinct fringe of pale setae ventrolaterally; mid-dorsal
spots on A3–5 now present as small warts; body col-
oration much cleaner than late second instar (Fig. 6a
and b); venter and prolegs dark crimson but fading
later in instar.

Fourth Instar. For fourth instars (n = 40; up to 65
mm [including caudae], cauda, 14–17 mm; 21–27 d;
Figs. 7 and 8), overall similar in shape to late third
instar (Fig. 7a and b), caudae (Fig. 8b) now noticeably
granulated and more densely covered in short setae;
spots on mid-dorsum of A3–5 now swollen into soft,
black fleshy filaments (Fig. 8c); body and head col-
oration much cleaner than late second instar (Fig. 6a
and b); venter and prolegs dark crimson but fading
later in instar.

Fifth Instar. Fifth instars (n = 47; up to 115 mm
[including caudae], cauda, ∼40 mm; 46–51 d includ-
ing prepupe; Figs. 5 and 6) are very distinct in color-
ation from previous instars (Fig. 9a); head similar in
shape to second–fourth instars but ground color now
beige to pale salmon (Fig. 10b), distinct light brown
stripes run on either side of mid-cranial suture from
top of suture fork to inner portion of dorsal-most scoli,
similar stripes laterally extend from stemmata to outer
portion of dorsal scoli, posterior margin cream colored
(note this appears to be ventral because of the way
larvae hold their heads projected forwards); head with
moderately dense, short, orange setae, densest below
and around stemmata (Fig. 10b and e); immediately
after molt head is very pale greenish cream colored
with only faint markings (Figs. 8a and 9d); body
ground color dull orange-brown, darker dorsally, lat-
erally with complex, diffuse patterning of black, or-
ange, ochre, and pale blue; body with many small
white punctuations and dorsal fleshy filaments well
developed (Fig. 9e); caudae now very well developed
(Fig. 10d), dark red-brown with strong, stiff pointed
setae giving a “Christmas tree” appearance; venter and
prolegs pale except for a black border; later in instar
larvae lose most patterning becoming generally dull

Fig. 4. Second instar of E. greeneyi at YBS, Napo Prov-
ince, 2,100 m, Ecuador. (A) Detail of anterior portion of head
of mid-instar larva. (B) Recently molted larva. (C) Detail of
caudae of early second instar. (D) Anterior view of head of
premolts larva. (E) Dorsal view of recently molted larval
head. (F) Shed head capsule of second instar. (Online figure
in color.)

Fig. 5. Second instar of E. greeneyi at YBS, Napo Prov-
ince, 2,100 m, Ecuador. (A and B) Mid-instar. (C) Late instar.
(D) Premolt. (Online figure in color.)
brown (Fig. 9b); eversible cervical gland (Figs. 10b and e and 11) well developed, bright purple-red and frequently everted when larvae are disturbed; dense tufts of short, stiff, orange-brown setae surround anus, all oriented inwards, forming an anal comb (Fig. 10f).

**Pupa.** Pupa \((n = 24; 50–58 \text{ mm}; 37–39 \text{ d}; \text{ Figs. 12 and 13})\) elongate, nearly cylindrical tapering toward cremaster; thickest around T2 tapering forward to two elongate, flattened projections arising from head (Fig. 13b); mature pupa dull sandy brown with faint, thin dark markings, mostly small flecking (Fig. 12); one dull cream-colored oval spot adorns the dorsal portion of wing pad; (cremaster, Fig. 13c) similar in coloration to rest of pupa, silk pad pale beige to white; fresh pupae (Fig. 13a) are similarly patterned but reddish, fading within a few days. Pupae are hung among dense foliage, of their bamboo food plant, often near the base of a cluster of leaf petioles where adults must emerge and expand their wings with limited mobility (Fig. 14).

**Larval Behavior of *E. greeneyi.*** First instars rest on the dorsal surface of mature host plant leaves, occasionally on the bottom and generally near the tip. They spin a silken pad in the resting area, returning there between feeding bouts. They are cryptic, resembling a small discoloration in the otherwise green leaf. Second–fourth instars rest on the dorsal surface of mature leaves as pictured for a fourth instar (Fig. 7f). In this position, they are extremely cryptic and resemble common patterns of discoloration and damage on bamboo leaves in the area (H.F.G., unpublished data). When disturbed by gently pinching or brushing them with a leaf, larvae are generally unresponsive. Fourth instars, however, will occasionally rear backward and partially evert their cervical gland. Often, they continue to thrash their head and thorax laterally for several seconds after being disturbed. When direct sunlight hits larvae they show a curious behavior, presumably a form of thermoregulation. Larvae rear backward slowly, lifting their thoracic legs off the leaf surface. If they are shaded with a leaf they slowly return to a flattened position, immediately rearing again if the shade is removed.

Fifth instars rest in large clumps of dead or dying host plant leaves where their sandy ground color and diffuse markings make them extremely well camouflaged. When pinched or touched larvae immediately rear backward and fully evert their cervical gland. Simultaneously they lift their terminal abdominal segments up and curve their caudae forward (Fig. 11). They also rapidly twitch their head and abdomen back and forth, often making audible contact between their head scoli and caudae.

**Parasitism Frequency.** Rearing of field-collected larvae of *E. greeneyi* has met with limited success. Of
45 collected third instar (or older) larvae in the field, 31 resulted in premature death of the caterpillar or pupa. We did not dissect dead caterpillars or pupae to assess likelihood of parasitism and causes of mortality are generally unknown, although microbial and/or fungal infections are a likely cause of many. This high mortality may be due to the artificial rearing conditions. Only eight of these larvae were reared to adulthood. Another six caterpillars were parasitized by Tachinidae (5) and Braconidae (1; see below). Thus, the overall parasitism frequency of those collections that yielded an adult (of any type) was 43%.

Tachinid Parasitoid Biology. On two occasions adult tachinids in the genus *Winthemia* were obtained from puparia that had emerged as larvae from *E. greeneyi* larvae. We suspect that three additional rearings that produced puparia (but no adults) also represent parasitism by this genus. These represent the only known records of tachinid parasitoids from any species in the genus *Eryphanis* that we are aware of, probably reflecting not so much an avoidance of *Eryphanis* by tachinids, but a paucity of field studies of the immatures in this genus.

The tachinids reared from *E. greeneyi* belong to the *Winthemia analis* Macquart 1846 "species complex" (Fig. 15; Reinhard 1931, Coelho et al. 1989). Originally, *W. analis* was described from one male specimen from Minas Gerais Brazil by Macquart (1846). This cursory description was later expanded upon and improved by Reinhard (1931) in his revision of the genus *Winthemia*, in which he provided an updated description based on a male from Bolivia, including a figure of the male terminalia. The male terminalia of the specimens reared from *E. greeneyi* (Fig. 16) are slightly, but noticeably, different in shape from the *W. analis* of Macquart and Reinhard, but are similar to one of the "forms" which Coelho lumped under this species (Coelho et al. 1989, see Figs. 8 and 54). Other characters also differ from Reinhard’s description (see below). Thus, our specimens probably represent a distinct species that should be split from *W. analis*. Males of the current *Winthemia* species closely resemble *W. analisella* in Thompson (1963), particularly in the position of the sex patches and shape of the cerci and surstyli (Fig. 16; see below). However, this species was not recognized in the revision of Coelho et al. (1989) and seems to be lumped with *W. analis*. Until this *W. analis* species group and the South American species of *Winthemia* as a whole are revised, which is beyond the scope of this study, we consider this taxon as an undescribed member of the *W. analis* species complex. Below, we provide some morphological and biological notes on the *W. analis* group tachinids reared in the study.

*Winthemia* sp. nr. *analis* Macquart 1846
(Figs. 15 and 16)

Male *Winthemia* sp. nr. *analis*. Males from the two rearings (*n* = 12) generally correspond to Reinhard’s
(1931) descriptions of W. analis and the closely related W. pinguis F., 1805 (not recognized by Coelho et al., 1989). Body length ranges from 7 to 10 mm. Parafrontals are golden pollinose, parafacials are moderately densely haired from lowermost frontal bristle to vibrissae, orbitals are absent and occellar bristles are present, but small. The trait of having two rows of frontal bristles, which is used to distinguish W. analis from related species (Reinhard 1931), is variable even within males reared from the same host individual: some males have a distinct secondary row and others only have fine hairs. Palpi are dark brownish fading to light yellow distally. The thoracic mesonotum is clearly marked with four longitudinal black stripes in two narrowly separated pairs. The lower calypters are opaque off-white and distinctly ringed with a darker orange coloration on their margins (Fig. 15). The abdominal tergites are black in ground color with basal pollinose bands. The sides are reddish basally and the distal 0.25–0.5 of T₅ is red as well. Median marginal bristles are absent from T₁₋₂, with one pair on T₃, and a complete row of 10–12 on T₄. Males have distinct, well defined patches of dense hairs (“sex patches”) on the ventral portion of tergite 4 only.

The Eryphanis-reared specimens differ from W. analis (s.s.) in a number of features. First, as in Thomp-
clearly divergent in rear view (Fig. 16B); the surstyli also appear longer and less robust (in rear view). With regard to (the unrecognized) *W. analisella*, our specimens have longer, thinner, and more curved postgonites, relatively less robust cerci, and perhaps slightly narrower surstyli. These differences suggest that these taxa are distinct, however, it is possible that Thompson’s *analisella* could consist of geographic variants of the species reared here.

**Female Winthemia sp. nr. analis.** Females have not been described for *W. analis*. The females of our reared *W. analis* group specimens (*n = 10*) closely match Reinhard’s (1931) description for females of *W. pinguis*, supporting a close relationship between these species as indicated by the males. In particular, females have the fifth tarsus (pretarsus) of the fore-tarsi dramatically swollen and broadened, approaching the length of the preceding three tarsal segments (as in *W. pinguis*). They also share very similar frontal widths (0.256 ± 0.009 of head width; compared with 0.29 in *W. pinguis*). However, the hind tibia bears two longer bristles on posterodorsal surface (rather than one), the abdomen lacks reddish coloration on the sides, median marginal bristles are present on T1 to T3, and the parafacials tend to have a yellowish tinge in the specimens from *E. greeneyi*.

**Winthemia Biology.** The two groups of *W. sp. nr. analis* specimens reared from *E. greeneyi* emerged from their hosts 35 and 53 d after the caterpillars were collected (in August and January, respectively). They spent 22 d and 56 d as pupae before adult emergence, respectively. This large discrepancy is probably due to...
earlier pupation of the former “clutch” that went unobserved. The number of individuals per host was 33 and eight for these two collections, and 12 for another suspected case of parasitism by this tachinid. Such large gregarious clutches are common for Winthemia species that attack large host caterpillars (Guimarães 1972).

Marcicano et al. (2009) recently reported the first known host of W. analis (s.l.) to be Brassolis sophorae L. 1758 in Brazil (Nymphalidae: Brassolini). However, this species was previously recorded as a host of W. pinguis Guimarães 1977, which is subsumed in the expansive W. analis species group. These specimens from B. sophorae could be conspecific with those reared in this study, although the geographic distance, different hosts, large number of taxa included in this species group, and low numbers of parasitoids per host (average, 1.6) suggests that the two groups are distinct. From our area, another Winthemia analis group species ("nr. analisella") is known to parasitize Antherea adoptiva (Nymphalidae: Morphini), another large caterpillar feeding on Chusquea bamboo (Greeney et al. 2009a). We only have a single specimen reared from this host, but preliminary observations suggest that it is distinct. Finally, Calvo (2004) reared an unidentified Winthemia species from the large Caligo atreus Kollar 1850 in Costa Rica that could represent yet another taxon in the W. analis species group.

Winthemia is a relatively large and taxonomically confusing genus of tachinids, widespread in all major biogeographical regions (O’Hara 2008). All species in the genus attack larval Lepidoptera, predominantly larger taxa, including Sphingidae, Saturniidae, Nymphalidae, Hesperidae, Noctuidae, and some Geometridae (Arnaud 1978, Janzen and Hallwachs 2009). The South American species were revised by Coelho et al. (1989), who recognized 14 species. The relatively low species richness in South America does not reflect an impoverished fauna inasmuch as the poor knowledge of the region and extreme taxonomic “lumping” by Coelho et al. (1989). Many, if not most of Coelho et al.’s “species” consist of multiple morphologically distinguishable taxa, and should be regarded more as species complexes than species per se.

**Braconid Parasitoid Biology.** A single male specimen of a Protopanteles Viereck braconid was reared from *E. greeneyi*. Here, we provide a description of this unique taxon.

**Protopanteles eryphanidis** Whitfield, new species (Figs. 17 and 18)

**Holotype** Male *P. eryphanidis*. Body length 2.9 mm; forewing length 3.8 mm.

**General Coloration.** Body entirely black except: maxillary and labial palps yellowish; fore and mid legs yellowish brown, darker on tarsi; hind legs with coxae black but otherwise yellowish brown with darkened femora apicodorsally and dark brown apex of tibiae and tarsi.

**Head.** Frons coarsely punctate and weakly depressed medially above clypeus, bisected by strong medial ridge extending from clypeus to near antennal bases. Flagellomeres with typical microgastrine two ranks of placodes except shorter apical ones with a single rank. Antennae as a whole slightly longer than entire body.

**Mesosoma.** Pronotum with both dorsal and ventral grooves present laterally, the ventral one deeper and more distinct. Mesoscutum and scutellum somewhat polished and very indistinctly punctate; scutoscutellar scrobe fine, more or less straight and composed of about a dozen small pits. Metanotum (Fig. 17B) strongly retracted from scutellum, without lateral setiferous lobes, anteromedially with deep medial pit. Propodeum lacking internal carinae and very weakly sculptured (sparse puncations) anteriorly, posteriorly...
with only a series of short carinulae radiating from nucha; spiracles large and round.

Legs. All legs slightly more slender than is typical for microgastrines; hind coxae long, extending to end of metasomal tergite III (Fig. 17B, left, arrow).

Wings. Stigma and major veins evenly dark brown, wing membranes very slightly infumate. Vein r slightly longer than 2RS and weakly arched, meeting 2RS at a distinct angle marked by a short stub at origin of 3RSa spectral vein. Vannal lobe of hindwing convex and evenly but not very conspicuously fringed.

Metasoma. First tergite 2.0× as long as broad, nearly parallel-sided up to 0.75 of length and then gently rounding to narrower junction with tergite II; anterior half polished and unsculptured, posterior half with sparse weak punctation (Fig. 17B, right top, arrow). Tergite II subtriangular, about as long as posteriorly broad but only 0.3 times as broad anteriorly as posteriorly.; surface convex medially but virtually unsculptured except weak ridging laterally. Laterotergites of I and II dark and polished. Remaining terga of normal unsculptured overlapping form.

Female P. eryphanidis. Not available. If/when it is discovered, it will be interesting to see whether the last tarsomere of the forelegs has a ventral excavation and opposing bristle as is typical of other Protapanteles females (Mason 1981).

Cocoon. Solitary, very pale tan/buff, coarsely spun with peculiar lacy “handles” at both ends (Fig. 18).

Host. Larvae of E. greeneyi.

Etymology. This species is named for its host genus.


Remarks. Morphologically, the new species strongly resembles the Holarctic species in general appearance (e.g., propodeal sculpturing, anterior metasomal tergites, wing venation), but it has generally longer wings and legs (especially hind coxae), a characteristic shared with some other mid-elevation Andean braconids. In addition, the cocoon is unique among the described species.

Biology. Previously described species of Protapanteles, nearly all from forested regions of the Holarctic Region, have been recorded to attack various macrolepidopteran genera (with one questionable Geometridae and never Nymphalidae (Mason 1981, Whitfield 1997, Whitfield et al. 1999). The use of Nymphalidae, along with its presence in South America, make this species record unique among the described Protapanteles. A few other undescribed species of Protapanteles have been seen in the neotropics at mid to high elevations, but none yet with host data.

Eryphanis Biology and Ecology. Eryphanis Host Associations. Most Brassolini species inhabit lowland areas in South America (Casagrande 1995), with Eryphanis, Caligo, Narope, and Opoptera being the only brassoline genera that occur at our 2,100-m altitude site. Eryphanis and Caligo, plus the Amazonian Caligopsis seleucida form a well supported monophyletic group (Penz 2007), but host plant use differs among genera. Caterpillars of C. seleucida and Eryphanis have been recorded on bamboo (Poaceae; Furtado and
Eryphanis Immature Appearance. Four species of Eryphanis have been reared, including members of both species groups. Table 1 summarizes some of their early stage characteristics. Although E. greeneyi is the only member of the zolvizora-group that has been reared, some shared similarities and differences found between this species and other Eryphanis are noteworthy. From egg to pupa, overall structural morphology is conserved, and the larval banding pattern is similar across the four species. This is not the case, however, for color. The eggs of E. greeneyi differ in color from those in the automedon-group. Furthermore, the colors of the larval body (background and stripes) also vary among species. Of particular interest are the smaller number of dorsal fleshy filaments in the fifth instar of E. greeneyi, and also the dramatic change in color from fourth to fifth instars found only in this species (see description), which likely follows the change in resting location of the larva from living leaves to stems and detrital clumps.

All species of Eryphanis with described larvae share an important natural history characteristic: their cryptic coloration from first instar to pupa conceals them on their bamboo hosts (Dias 1979, Cubero 1985, DeVries 1987). Within the community of Chusquea-feeding nymphalids at our study site, a variety strategies for cryptis are used, particularly within the species rich Pronophilini (Nymphalidae: Satyrinae). Larvae of various taxa of Pronophilini mimic stems (Greeney et al. 2009b), dead leaves (Greeney et al. 2010), green leaves, and leaves with damage spots (H.F.G., unpublished data). Among all of these, however, E. greeneyi is unique in its resemblance (from two to fourth instars) to a green leaf with damaged borders. Most other bamboo-feeding nymphalids share with E. greeneyi the dramatic change in coloration from penultimate to final instar which accompanies a shift in larval resting site (H.F.G., unpublished data).

Anal Combs and Frass Flinging in Eryphanis. Insect parasitoids and predators have been shown to use odor (or visual) cues associated with frass to locate hosts (see Weiss 2003, Weiss 2006, Stireman et al. 2006 and references therein). Frass flinging or shooting in lepidopteran larvae is hypothesized to have evolved as a mechanism to remove or disperse these potential cues (Weiss 2003). Many lepidopteran larvae possess anal combs for this purpose that are composed of a series of adjoining setae located on the larval dorsal anal lobe (epiproct) and occasionally on the ventral lobes (paraprocts) as well (Frohawk 1913, Stehr 1957, Scoble 1995). As internal hemolymph pressure increases at the posterior end of the body, the anal comb functions as a ‘latch’ that holds...
a fecal pellet inside; the release of this latch forcefully flings the fecal pellet away from the larva through the release of internal pressure (Caveney et al. 1998). Anal combs are present in a number of different families of Lepidoptera (Scoble 1995, Weiss 2003), including two genera of satyrine nymphalids (Bicyclus, Scudder 1889; Xanthothaenias, Penz et al. 2006). Within the Brassolini, however, these structures have been found only in the genus Eryphanis (C.M.P., unpublished data; larvae of 11 genera examined).

The frass-projecting ability of E. greeneyi larvae is relatively weak, compared with the great distances achieved by many Hesperiidae (H.F.G., unpublished data), but a sympatric hesperiid, Falga jeconia Evans 1955, shares this comparatively weak frass-throwing ability (Greeney and Warren 2009). Falga jeconia larvæ appear restricted to bamboo growing over flowing water, and Greeney and Warren (2009) suggested that the frass-removing properties of the water below may have relaxed selection pressures on its frass-throwing abilities. E. greeneyi may share this habitat preference, as most of our observations of adult and immature areas of linear disturbance (roads and trails), which historically has primarily occurred along streams. This may explain the relatively high levels of parasitism that we observed in field collected E. greeneyi. Thus, anthropogenic forest alteration may create habitat favorable for adult E. greeneyi but detrimental to their larvae that are ill-equipped to disperse frass away from their resting locations.

In summary, we have provided a detailed description of the immature stages of large, but little known tropical butterfly. We examined the morphology and behavior of E. greeneyi in a comparative context with respect to taxonomically and ecologically related taxa. We have also provided detailed descriptions of its parasitoids, including a new species of braconid, and we have produced a foundation for understanding the tritrophic ecological interactions that this species takes part in. Future studies of the morphology, behavior, spatial distribution, and parasitism of this and other species of Lepidoptera are likely to provide a rich source of ecological and evolutionary insight into complex community interactions.

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