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PITCHER PLANT MOTHS (EXYRA) FLY FROM PITCHERS IN RESPONSE TO SMOKE

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ABSTRACT. Pine savannas in the Southeastern United States are subject to an historical regime of periodic fire, with many and varied ecological consequences. Insectivorous plants of the genus *Sarracenia* (L.) (Sarraceniaceae) often entirely lose their above-ground leaves to these periodic fires. During the growing season, these tubular leaves, which act as pitfall traps for insects, are host to pitcher plant moths, *Exyra* (Grote) (Noctuidae), which live their entire life cycle within the plant. This study tested the effect of smoke on a small sample of *Exyra semicrocea* in pitchers, and demonstrated that they respond quickly by flight.

Additional key words: *Exyra, Sarracenia*, Fire

Pine savannas of the Southeastern United States are dominated by the large southern yellow pines, which include *Pinus palustris* (Mill.), *Pinus taeda* (L.), and *Pinus elliottii* (Engelm.). These forests do not have a dense canopy, which allows for the growth of a rich understory (Harrington et al. 2013), including in scattered suitable microenvironments pitcher plant savannas (Wells 1928, Walker & Peet 1983). Hydric pine savannas have wet, sandy soil that is nutrient poor, and contain several species of carnivorous plants, including several species of pitcher plant (Folkerts & Folkerts 1993). Such savannas and bogs, the pitcher plants they contain, and a rich associated biota are of high conservation concern because of the biological diversity of the areas and their greatly reduced modern extent (Stephens et al. 2011).

Longleaf pine forests are subject to frequent fire (Komarek 1974, Platt et al. 1991) and contain plant and animal species that are fire adapted, and which are the subject of a rich literature reviewed by Van Lear et al. (2005). Historically, fires in pine savannas of the coastal plain occurred at intervals of one to ten years (Komarek 1974, Platt et al. 1991), and the US Forest Service manages such sites with controlled burns every 3 years (USDA National Forest Service 2002). The insectivorous pitcher plants, *Sarracenia flava* (L.) and *Sarracenia leucophylla* (Raf.) are adapted to these frequent fires (Brewer 1999). The plants have subterranean rhizomes, which allow them to quickly replace their above-ground parts and avoid competition with other plants (Barker et al. 1988).

Pitcher plants have no less than 17 arthropod symbionts, given relatively little study compared to the pitcher plants themselves (Stephens et al. 2011), among which are pitcher plant moths, *Exyra* (Grote) (Noctuidae) (Stephens & Folkerts 2012). Two of the three species of *Exyra*, the pitcher plant mining moth, *E. semicrocea* (Guenée) and Riding's pitcherplant looper moth, *E. ridingsii* (Riley) are prevalent in the pitcher plant savannas of the Southeast where they inhabit the pitcher plant savannas (Stephens & Folkerts 2012). The moths live out the majority of their life inside pitcher plants (Jones 1921), only emerging at night (Stephens & Folkerts 2012). The adults lay one egg in a plant. The larvae pupate after five larval instars and the adults shelter in the plants, only flying out at night.

Given that these savannas burn frequently, and that pitcher plant moths are found in pitchers that have grown since recent fires (Ricci 2015), we would expect pitcher plant moths to be adapted to frequent fires. Prior to this study, it was unknown if the adult moths flee fires and survive, or if they fail to avoid fire and risk death. We hypothesized that the moths would leave the pitchers when fire approached, despite our experience that *Exyra* strongly resist physical efforts to force them to leave pitchers during the day. Furthermore, our experience was that when physically forced to depart pitchers, we rarely observed them to fly more than 20 meters during the daytime (McPhail and Meier pers. obs.). This distance is unlikely to be sufficient to avoid fires.

METHODS

Fire Experiment 1. On October 17, 2015, between 0700 hours and 0800 hours, at 30º 41.138'N, 88º 3.879'W within Mobile, Alabama, we placed two *Sarracenia leucophylla* pitchers in separate jars full of dry pine needles and grass. One pitcher at a time, we then set the pine needles and grass ablaze. We recorded the number of moths that left their pitcher as well as the time in which it took them to leave. No moths were killed while conducting this experiment.

Fire Experiment 2. On October 18, 2015, in the Sumatra Pine Savanna within the Apalachicola National Forest between 1300 hours and 1400 hours, we found six Pitcher Plant Mining Moths in five tubular leaves of *S. flava*. Their coordinates were 30º 2.407'N, 84º 57.684'W.

The first treatment was to observe the moths in the pitchers for two minutes to determine if they would leave the pitcher without disturbance. We recorded the number of moths that left their pitcher plants as well as the time in which it took them to leave. In the second treatment, a group member exposed the moths to two minutes of gently blowing air with a bee smoker that had not been ignited at ca. 10cm from the opening of the pitcher. We recorded the number of moths that left their pitcher plants as well as the time in which it took them to leave. In the third and final treatment for this second experiment, a group member flicked, squeezed, and shook the pitchers to provoke the moth into leaving. We recorded the number of moths that left their pitcher plants as well as the time in which it took them to leave. For the experimental trial, we exposed each of these moths to smoke from burning dry pine needles and grass within the smoker. A group member subjected each plant to smoking while holding the bee smoker 10cm away from the pitcher. It was intended that smoking of the pitcher should continue for up to two minutes if the moths remained in the pitchers. We recorded the number of moths that left their pitcher plants as well as the time which it took them to leave. Once the moths left their pitchers, we attempted to follow two of the moths to determine the distance that they would fly. No moths were killed while conducting this experiment.

Temperature of the Smoke. A bee smoker was filled with pine needles and lit. We held the smoker at 10cm from the opening into the pitcher and applied smoke to three pitchers from *S. leucophylla* in a fashion similar to that used by us in the field. We used a Fluke Hydra Series II thermocouple, set on channel 1, to read in degrees C., in the J temperature range. We took six sequential readings from each pitcher at 5 second intervals at 10 cm deep inside the pitcher, this being the minimum depth in the pitcher where moths were located. We took two readings before wafting smoke towards the pitcher, and four after the pitchers began receiving smoke.

Statistical Analysis. We used the VasserStats Online Program to perform a Chi-Square independence test comparing the frequency of departure within two minutes for each of the trials.

RESULTS

Fire Experiment 1. When we started the fire underneath two of the pitcher plants, both moths emerged. The first flew out 13 seconds after the pine needles were lit, and the other flew out 17 seconds after the needles were lit. It is interesting to note that the needles began smoking profusely a short period of time after being lit. If the time that they began to smoke is set as the reference point, then it took the first moth 4 seconds to leave the pitcher, and the second moth 7 seconds to leave the pitcher.

Fire Experiment 2. The three control trials caused no moths to leave their plants. None of the moths even moved when left alone or blown on. When the pitchers were vigorously shaken and flicked with our fingers, the moths moved around the inside of their pitchers and ultimately moved deeper into them. When smoked, every moth almost immediately left its plant (n = 6; mean = 6.5 seconds; s = 2.7). A chi-square test comparing experimental and control was highly significant ($\chi^2 = 12$, df = 2, $p = 0.0025$).

A group member followed two of the moths after they fled their pitcher plant. Both moths flew over 200 meters before entering another pitcher plant.

Influence of the smoke on temperature. Wafting smoke past the openings of *S. leucophylla* in a fashion similar to that used on the moths in the field yielded a maximum temperature change of 0.1 degrees C among all 3 pitchers tested.

DISCUSSION

We hypothesized that the moths would leave their pitchers and take flight in the presence of smoke as a means of escape before being consumed by fire. This hypothesis suggests that existing populations of pitcher plant moths can emigrate to survive fires; thus inviting comparisons to the shifting mosaics and metapopulation dynamics described by Harrison et al. (1988), Hanski et al. (1994), and Hanski et al. (1995) for butterflies. Given past personal experiences with the moths' reluctance to leave pitchers during the daytime, we were not certain that they would do so under the influence of smoke (Pers. Obs. McPhail and Meier). Fire might severely reduce a local population of pitcher plant moths if they fail to respond, and assuming that they do not employ a life cycle approach to survival (for example, pupating underground). In order to successfully employ a metapopulation strategy, *Exyra* moths must be able to successfully recolonized areas that are burned. Until recently there was no research on this subject. Ricci (2015) suggested that Riding's pitcherplant looper moths may employ a metapopulation strategy despite showing low mobility. We found in a small sample of six pitcher plant mining moth that even a few seconds exposure to smoke caused moths to leave the pitchers and fly. The results of this study support the additional hypothesis that smoke, not temperature is the stimulus that triggers the emigration of the moth from one habitat to another. Temperature differences inside the pitchers were minimal, 0.1 C, when the moths were exposed to smoke.

Despite our previous observations of daytime movements limited to 20 meters, when confronted with smoke, the moths were observed traveling much longer distances (200 meters). This ability to flee longer distances increases the opportunities for pitcher plant moths to survive fires, and relocate if necessary.

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IMMATURE STAGES AND NATURAL HISTORY OF THE NEOTROPICAL SATYRINE *PAREUPTYCHIA OCIRRHOE INTERJECTA* (NYMPHALIDAE: EUPTYCHIINA)

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ABSTRACT. The present paper describes the immature stages of the common Neotropical satyrine butterfly *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952). The solitary eggs are white and round, turning black 4 to 6 hours after oviposition. The four solitary larval instars are predominantly green and feed on grasses (Poaceae), including *Setaria* in nature and several other native and introduced species in captivity. The pupa is short and smooth and entirely green. Except for the black eggs, the immature stages are similar to those of other forest species of Euptychiina. The most remarkable and unique characteristic of *P. ocirrhoe interjecta* is the shiny black eggs, a possible synapomorphy for *Pareuptychia* not known in any other Euptychiina.

Additional key words: Atlantic Forest, *Cepheuptychia, Godartiana, Taydebis, Zischkaia*

The Euptychiina (Nymphalidae: Satyrinae) is one of the largest and most diverse butterfly subtribes, contributing a significant portion of Neotropical butterfly diversity (Peña et al. 2010, Marín et al. 2011). With over 400 recognized species (Lamas, 2004), Euptychiina butterflies occur in virtually all habitats and vegetation types from sea level to over 3500 m (DeVries 1987, Marín et al. 2011). However, despite this large species richness, immature stages have been described for a very few species and genera of Euptychiina (DeVries 1987, Murray 2001, Freitas et al. 2016). For the genus *Pareuptychia*, for example, immature stages have never been described in detail, and available information includes only textual descriptions in DeVries (1987) and pictures of larvae and pupae in Janzen and Hallwachs (2015).

Species of *Pareuptychia* are associated with forested habitats across the Neotropics (DeVries 1987), and they may be abundant. The genus is very homogeneous, and its eight described species (Nakahara et al. 2016) are very similar in wing pattern and morphology, suggesting that this is a monophyletic group (except maybe for *Pareuptychia lydia* (Cramer, 1777)). However, because of similarity in wing patterns, species limits and identities are not well established and the genus needs to be studied from both morphological and molecular perspectives (Marín et al. in prep.). In addition, knowledge about the immature stages of *Pareuptychia* could be of help in understanding the taxonomy of this group.

In this context, the present paper offers a detailed description of the immature stages of *Pareuptychia ocirrhoe interjecta* (R.F. d'Almeida, 1952) and compares them with those of other neotropical Euptychiina butterflies.

Materials and Methods

Study sites. Adults and immatures of *P. ocirrhoe interjecta* were studied in four different localities in São Paulo State, Southeastern Brazil: 1) Reserva Biológica Municipal da Serra do Japi, Jundiaí (900–1100 m; 23º13'S, 46º57'W); 2) ARIE Mata de Santa Genebra, Campinas (600–620 m; 22º49'S, 47º6'W); 3) Fazenda Santa Elisa, IAC, Campinas (630-650 m; 22º51'S, 47º5'W); 4) Parque Estadual Xixová-Japuí, São Vicente (20–200 m; 23º59'S, 46º23'W).

Sampling and rearing of immature stages. Fertile eggs were obtained from wild-captured females confined in plastic bags warmed by a 40W bulb and provided with leaves of several species of native and introduced grasses. Larvae of *P. ocirrhoe interjecta* and of the additional species mentioned in the discussion section were reared in plastic containers cleaned daily, with fresh plant material provided every two or three days (following Freitas 2007). Data were recorded on behavior and development time for all stages. Dry head capsules and pupal cases were retained in glass vials. Immature stages were fixed in Kahle-Dietrich solution (Triplehorn & Johnson 2005) when the number of specimens was sufficient. Voucher specimens of the immature stages were deposited in the Museu de Zoologia "Adão José Cardoso" (ZUEC-AVLF), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Morphology. Measurements were taken and general aspects of morphology were observed using a Leica®MZ7.5 stereomicroscope equipped with a micrometric scale. Scanning electron microscopy (SEM) was conducted using a JEOL® JSM-5800 microscope (JEOL Ltd., Japan), and samples were critical-point dried in a Bal-tec® – CPD030 (Leica Microsystems, Germany), attached with double-sided

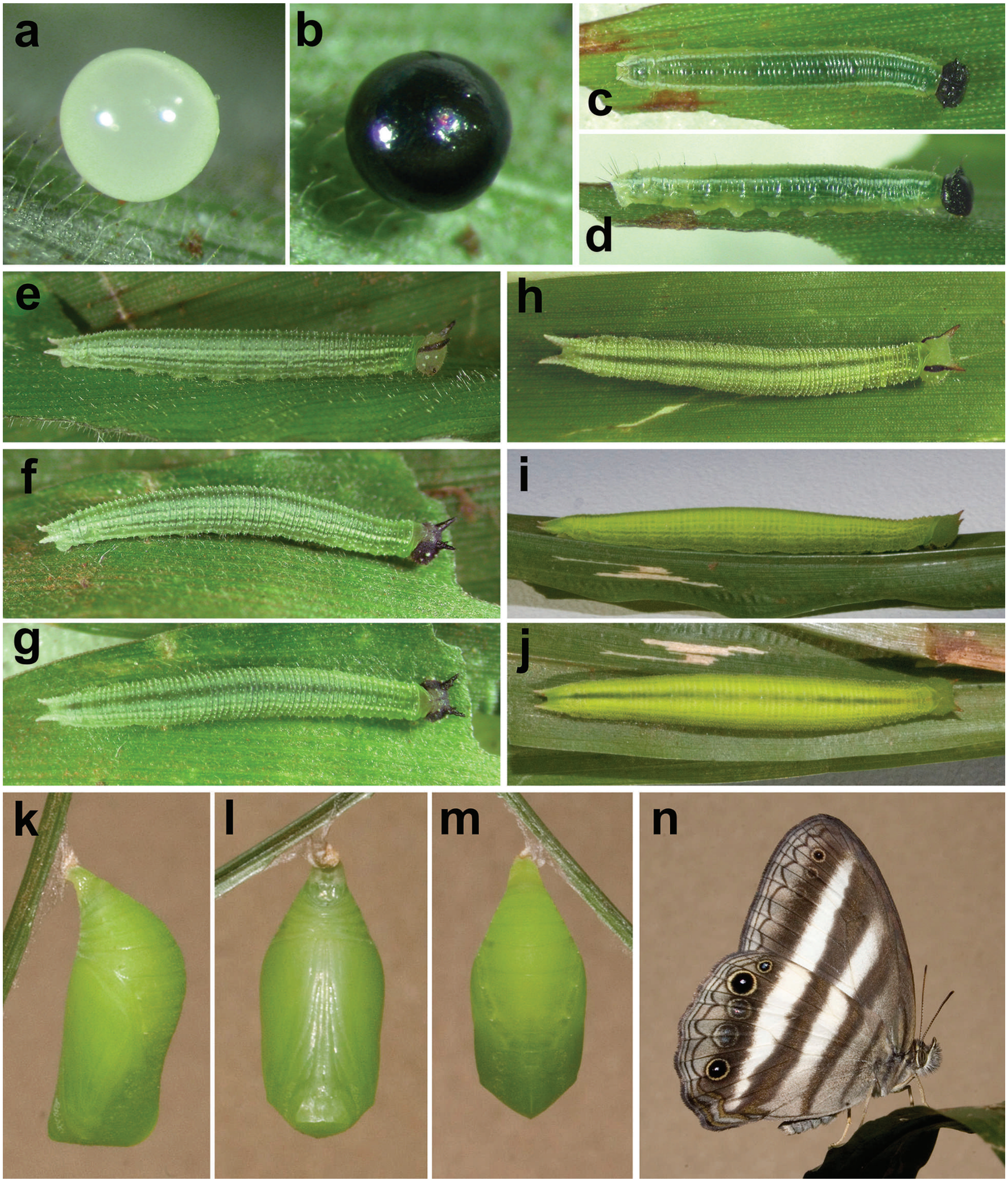

FIG. 1. Immature stages and adult of *Pareuptychia ocirrhoe interjecta*. **a, b.** egg, white and black; **c, d.** first instar, dorsal and lateral; **e.** light head capsule second instar, lateral; **f, g.** dark head capsule second instar, dorsal and lateral; **h.** third instar, dorsal; **i, j.** fourth (last) instar, lateral and dorsal; **k, l, m**. Pupa, lateral, ventral and dorsal; **n.** Adult male.

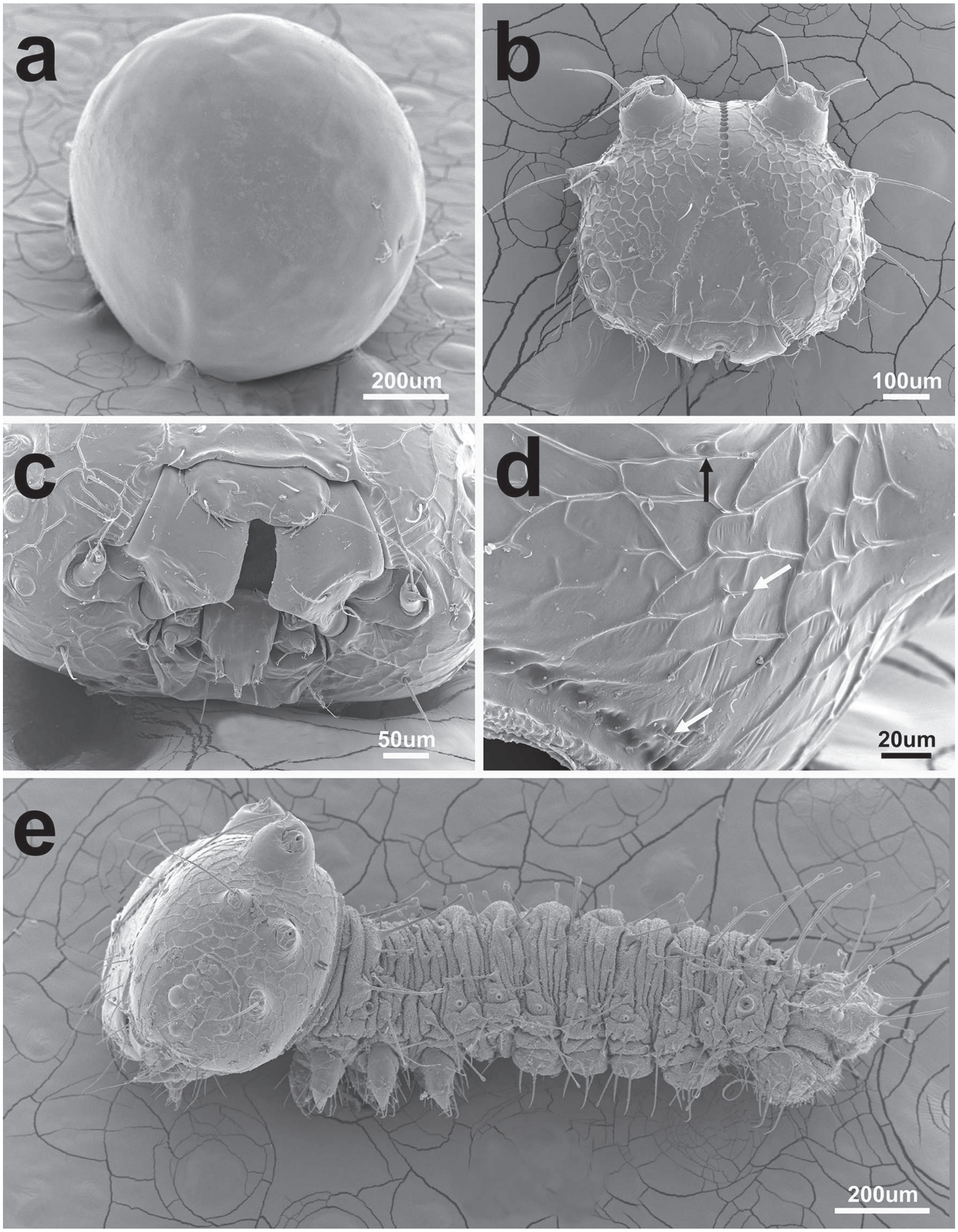

FIG. 2. Egg and first instar of *Pareuptychia ocirrhoe interjecta*. **a.** egg; **b.** Head capsule, general frontal view; **c.** Detail of frontal region; **d**. Detail of posterior region: white setae show microsetae and black seta show a pore; **e.** Early first instar, general lateral view.

tape to aluminum stubs, and coated with gold/palladium with a Bal-tec® – SCD050 sputter coater (Leica Microsystems, Germany). Egg size is presented as height and diameter, and head capsule size is the distance between the most external stemmata (as in Freitas 2007). Terminology for early stages descriptions followed García-Barros & Martín (1995) for eggs and Stehr (1987) for larvae and pupae.

RESULTS

Description of immature stages. The following descriptions and measurements are based on material reared from one female from Serra do Japi, Jundiaí, São Paulo (material reared from three other localities gave similar results).

Egg (Figs. 1a,b – 2a). White, round, turning black 4 to 6 hours after oviposition. Height and diameter 0.94 – 0.96 mm; duration 5 – 6 days (n = 8).

First instar (Figs. 1c,d – 2b-e). Head capsule width 0.64 – 0.70 mm (mean = 0.66 mm; SD = 0.026 mm; n = 5); head scoli 0.08 – 0.10 mm (mean = 0.09 mm; SD = 0.008 mm; n = 5). Head black, with enlarged chalazae, bearing a pair of short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body light green, with white longitudinal stripes, turning dark green after first meal; caudal filaments very short. Legs and prolegs light green. Setae light green from T1 to A7, black from A8 to A10, all dorsal and subdorsal clubbed at tip (Fig. 2e). Maximum length 5 mm. Duration 6 – 7 days (n = 8).

Second instar (Figs. 1e,f,g). Head capsule width 0.90 – 1.00 mm (mean = 0.94 mm; SD = 0.052 mm; n = 5); head scoli 0.40 – 0.46 mm (mean = 0.43 mm; SD = 0.022 mm; n = 5). Head green with two short dark brown scoli on vertex (Fig. 1e,g); in some individuals head is mostly dark brown (Figs. 1f,g). Body green, striped longitudinally with white; caudal filaments short. Legs and prolegs light green. Maximum length 9 mm. Duration 4 – 8 days (n = 8).

Third instar (Fig. 1h). Head capsule width 1.38 – 1.46 mm (mean = 1.45 mm; SD = 0.056 mm; n = 5); head scoli 0.60 – 0.66 mm (mean = 0.62 mm; SD = 0.024 mm; n = 5). Head green, with two diverging very short scoli on vertex; these are reddish with a posterior dark brown line extending to head capsule. Body light green with a conspicuous dark green dorsal stripe and several additional longitudinal markings; caudal filaments short. Legs and prolegs light green. Maximum length 15 mm. Duration 7 – 9 days (n = 6).

Fourth (last) instar (Figs. 1i,j). Head capsule width 2.18 – 2.20 mm (mean = 2.20 mm; SD = 0.016 mm; n = 4); head scoli 0.74 – 0.82 mm (mean = 0.78 mm; SD = 0.034 mm; n = 4). Head green, with two diverging short scoli with reddish apex on vertex. Body light green with a conspicuous dark green dorsal stripe and several fine longitudinal stripes; caudal filaments short and reddish on apex. Legs and prolegs green. Maximum length 25 mm. Duration 7 – 10 days (n = 6).

Pupa (Figs. 1k,l,m). Short and smooth; entirely green; short rounded ocular caps; cremaster light green; dorsal abdomen smooth without projections. Total length 10.0 – 10.5 mm (n = 5). Duration 9 – 14 days (n = 4).

Behavior and natural history. *P. ocirrhoe interjecta* (Fig. 1n) is common in several environments in the Atlantic Forest from sea level to 1000 m altitude. Oviposition behavior was not observed in the field, but two solitary eggs, two larvae and one pupa were collected in the field in an unidentified native species of *Setaria* (Poaceae) in a shaded narrow trail inside the forest. Eggs were laid singly in the laboratory and larvae easily accepted the same hostplant mentioned above. Larvae were solitary in all instars and did not exhibit cannibalistic behavior (several larvae of different instars were reared together in small pots). Adults were easily observed along forest edges and in clearings flying low in the understory, rarely rising above 2 m above the ground. Flight was erratic and fast and, when disturbed, butterflies performed unpredictable aerial maneuvers with alternating flashes of white and dark, which makes them difficult to capture in flight. Adults feed on fermenting fallen fruits, feces and several other decaying substances, being never observed visiting flowers. However, there are reports of adults feeding on extrafloral nectar (Barbosa 2013; AVLF pers. obs.).

DISCUSSION

The immature stages of *P. ocirrhoe interjecta* are quite morphologically simple and similar to those of several other species of Neotropical Euptychiina: larvae lack body scoli, present short head horns and caudal filaments and pupae are short and smooth. The entirely green last instar, although not rare in Euptychiina, is apparently uncommon; most known last instars of small forest Euptychiina are predominantly brown or have color tones that make them cryptic on the background of dead leaves and stems (Singer et al. 1983, DeVries 1987, Murray 2001, Kaminski & Freitas 2008, Janzen & Hallwachs 2015). Species with similar green last instars and/or pupae includes other species of *Pareuptychia* (AVLF unpublished; Janzen & Hallwachs 2015), *Cepheuptychia cephus* (Fabricius, 1775), *Taydebis peculiaris* (A. Butler, 1874), *Zischkaia pacarus* (Godart, [1824]), *Godartiana muscosa* (A. Butler, 1870) (Figure 3) and *Forsterinaria pronophila* (Freitas & Peña 2006). Although *Cepheuptychia* and *Taydebis* are genera related to *Pareuptychia* in part of the "*Pareuptychia* clade" (Peña et al. 2010), the similarity in color pattern is not related to phylogenetic relationships. For example, other forest species belonging to the "*Pareuptychia* clade" present predominantly non-green last instars, including *Chloreuptychia arnaca* (Fabricius, 1776), *Megeuptychia antonoe* (Cramer, 1775) (Janzen & Hallwachs 2015), *Splendeuptychia furina* (Hewitson, 1862) and *Splendeuptychia doxes* (Godart, [1824]) (Freitas, unpublished). The greenish last instars of *Satyrotaygetis satyrina* (H. Bates, 1865) are quite distinct from those of *Pareuptychia*, especially in the longer, strongly diverging head horns.

The most remarkable and unique characteristic of the immature stages of *P. ocirrhoe interjecta* is the shiny black eggs. This trait, present also in other species of *Pareuptychia* (DeVries 1987, AVLF unpublished), is unique among all known Euptychiina (however, color

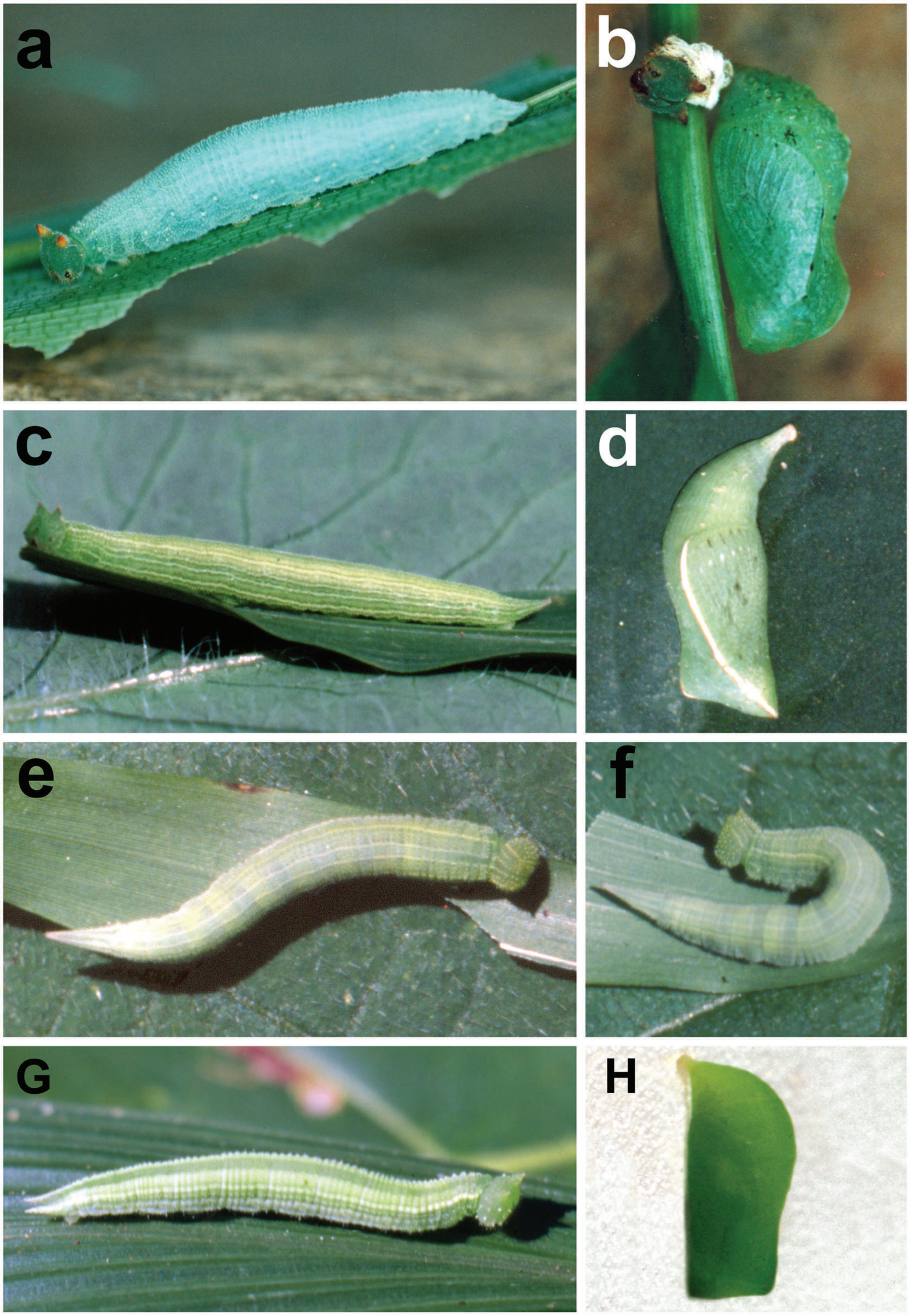

FIG. 3. Immature stages of Euptychiina (all from Brazil). **a, b.** *Cepheuptychia cephus*, fourth (last) instar and pupa (both lateral), Upper Juruá River, Marechal Thaumaturgo, Acre; **c, d.** *Taydebis peculiaris*, fourth (last) instar and pupa (both lateral), Santa Virgínia, São Luis do Paraitinga, São Paulo; **e, f.** *Zischkaia pacarus*, third instar, dorsal and lateral, Morro Grande, Cotia, São Paulo; **g, h.** *Godartiana muscosa*, fourth (last) instar and pupa (both lateral), Serra do Japi, Jundiaí, SP.

change in fertile eggs is not unique in *Pareuptychia*, and has been reported in *Calisto* Hübner, [1823] (Sourakov 1996)). Although the possible adaptive significance of this striking egg color is unknown, the similarity of these black eggs to the parasitized eggs of other species of Euptychiina is evident (Freitas et al. pers. obs.). Since it is widely known that visual cues are important for ovipositing butterflies (e.g. Rausher 1979, Williams & Gilbert 1981, Shapiro 1981, Freitas & Oliveira 1996, Sendoya et al. 2009), this opens the possibility that such cues are equally important for ovipositing females of egg parasitoids, which are known to show a low preference by black eggs (Lobdell et al. 2005). In this context, the black eggs of *Pareuptychia* could mimic parasitized eggs, thus reducing parasitoid oviposition and decreasing egg parasitism. Field and laboratory studies, however, are needed to test this hypothesis.

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