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IMMATURE STAGES OF *ARCHONIAS BRASSOLIS TEREAS* (GODART) (PIERIDAE: PIERINI), WITH NOTES ON INTERSPECIFIC INTERACTIONS BETWEEN MISTLETOE BUTTERFLIES

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ABSTRACT. The immature stages of the Neotropical mistletoe butterfly *Archonias brassolis tereas* (Godart) (Pieridae: Pierini) are described and illustrated for the first time from the Atlantic Forest of Southeast Brazil. Eggs are laid in clusters on leaves of the mistletoe *Phoradendron* sp. (Viscaceae). Larvae are gregarious and underwent five instars. Mature caterpillars present yellow aposematic color pattern; pupae are yellow with black dorsal projections. Morphology, host plant use and behavior of immature stages are similar to species in the *Catasticta* group. An additional species of mistletoe butterfly, *Brangas* sp. (Lycaenidae), with gregarious and aposematic yellow caterpillars was found in sympatry on the same leaves of the host plant. These findings suggest that both interspecific competition and larval mimicry are important traits in the ecology and evolution of mistletoe butterflies.

Additional key words: Aporiina, *Brangas*, coexistence, defensive behavior, Eumaeini, Lycaenidae, Müllerian mimicry

The Pieridae butterflies are particularly diverse in the Neotropical region, but information on their natural history and morphology of immature stages are relatively scarce or incomplete (DeVries 1987, Braby et al. 2007). Recently, contributions on the natural history of pierid species that utilize mistletoes (aerial-stem hemiparasitic plants on the order Santalales) as host plants have been richly described and illustrated (e.g., Braby & Nishida 2007, 2010, Kaminski et al. 2012, Volkmann & Núñez Bustos 2015). The New World mistletoe feeding pierids belong to two independent lineages: 1) the *Hesperocharis* group (Anthocharidini), and 2) the *Catasticta* group (Pierini), which include six genera: *Melete* Swainson, *Pereute* Herrich-Schäffer, *Leodonta* A. Butler, *Catasticta* A. Butler, *Charonias* Röber, and *Archonias* Hübner (Braby & Nishida 2010).

The genus *Archonias* is composed of a single polytypic species, *Archonias brassolis* (Fabricius), which is found from southern Mexico to northern Argentina (Lamas 2004, Braby et al. 2007). This species is found in tropical forests from sea level to 1200 m (DeVries 1987, Le Crom & Llorente-Bousquets 2004, Braby & Nishida 2011, AVLF & LAK, pers. obs.). Adults of all 12 described subspecies are involved in mimetic rings with aposematic butterflies in the genus *Parides* Hübner (Papilionidae) and *Heliconius* Kluk (Nymphalidae) (DeVries 1987).

The phylogeny of the Aporiina indicates that *Archonias* and *Charonias* are sister genera (Braby et al. 2007, Wahlberg et al. 2014), and this is precisely the only lineage for which early stages have not been described. The present work aims to provide morphological and behavioral descriptions of the immature stages of *A. brassolis tereas* (Godart). In addition, we discuss the possibility of larval mimicry and interspecific competition among mistletoe butterflies.

MATERIAL AND METHODS

In May 24, 2011, an egg cluster with 26 eggs of *Archonias brassolis tereas* was collected on a leaf of the mistletoe *Phoradendron* sp. (DC.) Naudin. (Viscaceae), which was parasitizing a *Dodonaea viscosa* Jacq. (Sapindaceae) tree, in the "Reserva Municipal Biológica da Serra do Japi" (~1,100 m a.s.l.) (23°14'S, 46°56'W). This area consists of semideciduous, mesophytic forest located in the municipalities of Jundiai and Cabreúva, in the state of São Paulo, Southeastern Brazil. The area includes nearly 28,000 ha of a mosaic of primary and, mainly, secondary forests in diverse stages of succession, in altitudes that varies from 700 m to 1,300 m a.s.l. A complete and detailed description of the area can be found in Morellato (1992).

Eggs were found in a completely grazed leaf, covered by feces of an undescribed species of *Brangas* Hübner (Lycaenidae). These eggs were collected and maintained in the laboratory. As soon as *Archonias* larvae hatched, they were separated from *Brangas* caterpillars and placed in plastic pots, where they were reared with host plant leaves offered ad libitum. Pots were cleaned daily, and data on behavior and development times were taken for all stages. Some eggs and larvae of the first and last instars were separated, fixed in Dietrich's solution and used for morphological analysis. Shed head capsules of all stages were stored for measurements. Voucher material of the immature stages and adults were deposited at Museu de Zoologia "Adão José Cardoso" (ZUEC), Universidade Estadual de Campinas (UNICAMP), Campinas, São Paulo, Brazil.

Measurements and general morphological observations were made with a Leica® EZ4 stereomicroscope equipped with a micrometric scale. Head capsule width of larvae was measured as the distance between the most external stemmata (following Kaminski et al. 2012); maximum total length for both larvae at the end of the instar and pupae corresponded to the distance from head to posterior margin of the tenth abdominal segment in dorsal view. Terminology for early stage descriptions follows Braby & Nishida (2007, 2010).

RESULTS

Description of immature stages

Egg (Fig. 1). 1.2 mm high, 0.6 mm diameter (n = 2); white, bottle-shaped, with flattened basis and apex much narrower than the middle width. Chorion with numerous longitudinal ribs and thinner weakly marked horizontal ribs. Apical rim with 5 to 7 prominent pale nodules. Micropylar area smooth. Duration ≥ 3 days (n = 5).

First instar (Fig. 2). Maximum length 2.6 mm; head capsule width 0.43–0.47 mm (n = 4). Head black, with long translucent setae. Rectangular prothoracic shield, with longer side transversal to the body, bearing three pairs of translucent setae. Body pale yellow, pinkish in the last abdominal segments. Primary setae long and translucent, the dorsal group with a fluid-droplet on its tips. Anal shield light grey. Duration 7 days (n = 5).

Second instar (Fig. 3). Maximum length 4.5 mm; head capsule width 0.70–0.71 mm (n = 3). Head and prothoracic shield black with white setae; body greenish-yellow, more vivid than first instar, meso and metathorax reddish. Numerous pale spots and white setae inserted in white paniculum through the body. Anal shield light grey. Duration 9–10 days (n = 5).

Third instar (Fig. 4). Maximum length 7.5 mm; head capsule width 1.16 mm (n = 1). Head and prothoracic shield black with white setae; body greenish-yellow, reddish in the meso and metathorax with pale spots through the body; setae inserted in white paniculum. Anal shield pale grey. Duration 5–6 days (n = 4).

Fourth instar (Fig. 5). Maximum length 14.0 mm, head capsule width 1.79–1.84 mm (n = 3). Head black with cream panicula bearing white setae; prothoracic shield black with white setae; body greenish-yellow, meso and metathorax reddish, with purer yellow in the last abdominal segments. Paler spots and white setae inserted in white paniculum through the body. Anal plate grey. Duration 7 days (n = 4).

Fifth (last) instar (Figs. 6–7). Maximum length 27.0 mm, head capsule width 2.37–2.71 mm. (n = 3). Head black with yellowish panicula bearing white setae. Prothoracic shield black with white setae. Pro and mesothorax reddish, greenish-yellow but greener in the back and yellower in the last abdominal segments. Longer white setae are projected laterally. Paler spots and white panicula bearing white setae through the body. Anal shield black. Duration 6 days (n = 3).

Pupa (Figs. 8–9). Length 26.0 mm (n = 2); bright yellow with black spots scattered through the body. Two lines of dorsolateral spots on abdomen and smaller pale spots present in all segments. Head with a long anterior projection with bifurcated tip. Prothorax and metathorax with a yellow longitudinal ridge forming a pronounced orange bump on mesothorax. A short rounded lateral protuberance is present at the base of the forewing. Abdominal segments A2–A8 with middorsal black spine-like projections, short on A2 and long on A3–A4. Abdominal segments A2–A4 with pairs of supraspiracular black spine-like projections above the wings. Cremaster bright yellow. Duration 11 days (n = 3).

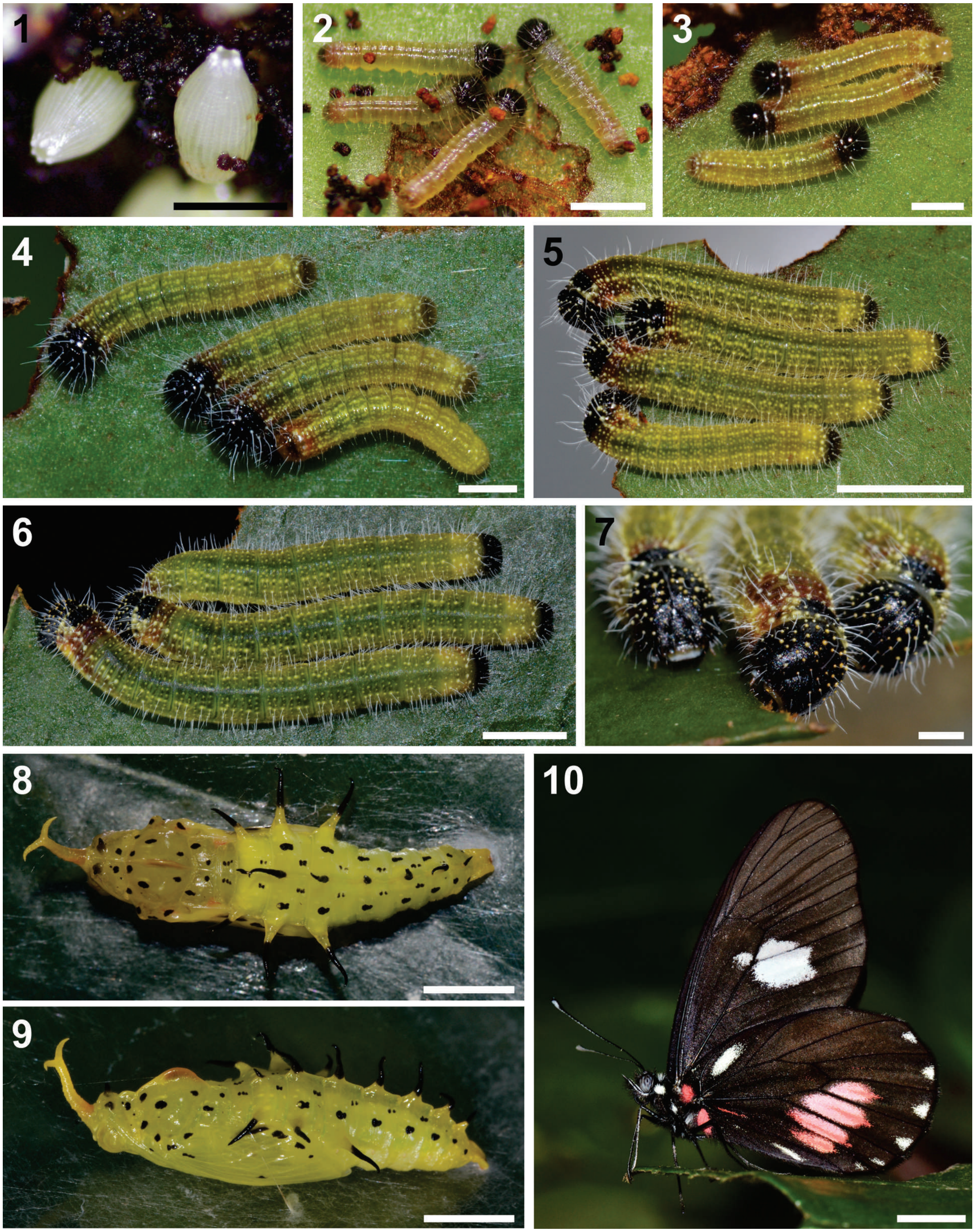
Natural history of *Archonias brassolis tereas*

Adults (Fig. 10) have been observed in several different habitats in the Atlantic Forest, including pristine and secondary forest and coastal sand forests. The territorial males are more easily spotted in forest edges and clearings where they perch and were observed chasing other conspecific males for short periods from 9:00 to 12:00. Both sexes were observed visiting flowers of several species of Asteraceae. In the study site, the only putative mimic of *A. brassolis tereas* is the swallowtail *Parides anchises nephalion* (Godart) (Papilionidae: Troidini) (Brown 1992).

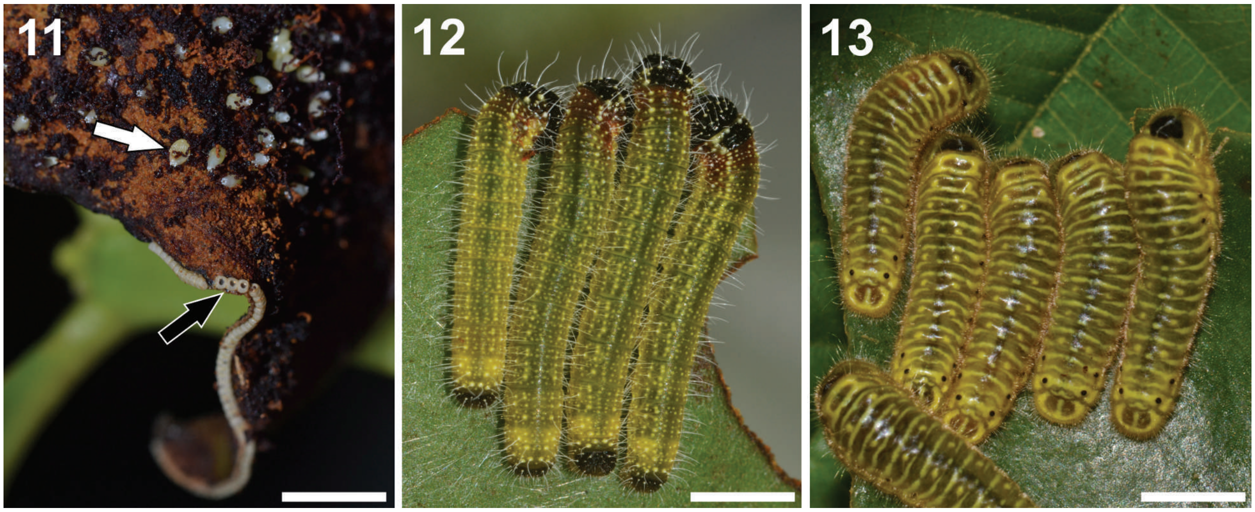
Eggs were laid in clusters with 26 eggs per cluster (n = 1 oviposition) on the upperside leaf of the food plant. The oviposition of *Archonias* shared the same leaf with empty eggs and larvae of an undescribed species of *Brangas* (Lycaenidae). These larvae had completely eaten the leaf epidermis and left the *Archonias* eggs surrounded and covered by its feces (Fig. 11). Although the effects that this could have in the *Archonias* eggs are unpredictable, food availability for caterpillars would be severely shortened since most of the mistletoe leaves would have been previously eaten by *Brangas* caterpillars and there were no additional mistletoes in the host tree. In laboratory, newly eclosed larvae devoured most of the exochorion, before proceeding to graze the leaf surface. First instar caterpillars eat by scraping the upper side of the leaf, and usually are covered by their pellets of excrements trapped in the fluid droplets present on the dorsal setae. Second instar still scrapes the leaf surface occasionally making holes at the leaf blade. From the third instar on, the whole leaf thickness is consumed at each bite. Caterpillars are gregarious since hatching, and stay most of the time leaning against each other, in parallel position. Their lateral setae are longer and usually contact setae and bodies of neighbor larvae. They all rest and eat at the same time. When molested, the caterpillar responded by regurgitating fluid from the mouth. The pupae have a conspicuous yellow color and when molested twitch with sudden jerky movements.

DISCUSSION

Both morphology and natural history of the immature stages of *Archonias brassolis tereas* are very similar to those of other species in the *Catasticta* group, especially *Catasticta* species (see Braby & Nishida 2010). Eggs have the typical bottle-like shape, with inconspicuous vertical lines, and larvae are slender and covered by



FIGS. 1–10. Life stages of *Archonias brassolis tereas* on *Phoradendron* sp., from Jundiai, São Paulo, Southeast Brazil. **1**, eggs, note that feces of *Brangas* sp. are partially covering the eggs. **2**, first instar, note the graze damage and accumulation of feces. **3**, second instar. **4**, group of third instar, the rightmost caterpillar is still at the second instar. **5**, fourth instar. **6**, fifth (last) instar. **7**, fifth instar in frontal view showing details of the heads. **8**, pupa in dorsal view. **9**, pupa in lateral view. **10**, freshly emerged adult. Scales = 0.5 mm (1–4, 7), and 0.5 cm (5–6, 8–10).



Figs. 11–13. Interspecific interaction between mistletoe butterflies on *Phoradendron* sp., from Jundiai, São Paulo, Southeast Brazil. **11**, egg clusters of *Archonias brassolis tereas* (white arrow) and *Brangas* sp. (black arrow) on the same leaf; note the feces of *Brangas* sp. partially covering the eggs. **12**, fourth instar larvae of *Archonias brassolis tereas*. **13**, last instar larvae of an undescribed *Brangas*. Scales = 0.4 cm.

short setae, inserted in panicula. The pupae are similar to those of some *Catasticta* species, such as *Catasticta ctemene* (Hewitson), *Catasticta flisa* (Herrich-Schäffer), *Catasticta hegemon* Godman & Salvin, *Catasticta sisamnus* (Fabricius), with a long anterior bifurcated projection, spine-like projections in the body, and black markings over a bright colored background. In contrast, the pupa of *Archonias* differ from *Catasticta cerberus* Godman & Salvin and *Catasticta teutila* (Doubleday), which have short projections and bird dropping aspect. Morphological and behavioral evidence from the immature stages described herein supports the close phylogenetic relationship between *Catasticta* and *Archonias* previously suggested based on molecular data (Braby et al. 2006, Wahlberg et al. 2014). The nomenclatural history and classification of *Catasticta*, however, is complex, and the genus is probably paraphyletic (see Lamas & Bollino 2004, Braby & Nishida 2010). In this way, the new data on *Archonias* immature stages can be of help in the understanding of character evolution and in the systematics of the group.

The mistletoe use has a key role in the evolution of life history attributes in Aporiina, including the colonization of new host plant families in *Eucheira* Westwood and *Neophasia* Behr (Braby & Trueman 2006). New data of *Archonias* on *Catasticta* confirm previous information indicating mistletoes as hosts (see Biezanko 1958, P. J. DeVries, pers. comm. *apud*, Braby & Nishida 2010). According to Braby & Nishida (2010), the use of mistletoes is related with the evolution of gregariousness in Aporiina, and highlights two factors: 1) selection of mistletoe host with toxic alkaloids by an aposematic ancestor; and, 2) patchy distribution of mistletoe food plant as selective force leading to the evolution of egg clustering and larval gregariousness. These same factors must have been important for the evolution of gregariousness in other mistletoe feeding species, such as species in the *Hesperocharis* group (Pieridae) and *Brangas* (Lycaenidae). Consequently, the Neotropical region present a rich community of mistletoe butterflies competing for a patchily distributed resource. In this situation, the occurrence of interspecific competition and resource partitioning among mistletoes feeding species is expected, and present results provide strong evidence in this direction. Because *Brangas* females lay large egg clusters (100–200 eggs) and larvae develop quickly feeding day and night (Kaminski et al., in prep.), *Archonias* larvae sharing the same plant would be unable to complete their cycle due to critical food shortage.

In the conceptual model proposed for the evolution of gregariousness by Braby & Nishida (2010), interspecific competition operates in the opposite direction, i.e., as a selective force limiting the clutch size and gregariousness. In addition, the competition may be important in promoting secondary host shifts events from mistletoes to the host trees parasitized by mistletoes. In Braby & Nishida (2010), there are some reports from species that co-occur on the same mistletoe clump but at least one example of a species pair that are never found together on the same mistletoe clump (*C. teutila* and *C. cerberus*). In summary, mistletoe butterflies are an excellent system to study the role of interspecific interactions in the evolution of life history attributes in herbivorous insects.

Although adults in the *Catasticta* group are frequently warning colored and involved in complex mimicry rings with other butterflies (DeVries 1987, Braby & Nishida 2010), larvae are usually inconspicuous and possibly non-warningly colored (Braby & Nishida 2010). Moreover, early instars of several species in *Catasticta* group are conspicuously bright yellow becoming inconspicuous in late instars suggesting a strong selection for crypsis (Braby & Nishida 2010). Two different syndromes have been described: 1) nocturnal feeding larvae of *Pereute* and *Leodonta* become dark brown (and cryptic when resting on tree trunks during the day), and 2) diurnal feeding larvae of several *Catasticta* become greenish (and cryptic when feeding on leaves). In the present study, a third different syndrome is reported: larvae of *Archonias* keep the conspicuous yellowish pattern in later instars and pupa. Moreover, present results suggest that *Archonias* larvae may also be involved in a mimicry ring with *Brangas* sp., with which caterpillars shown remarkable similarities on overall color pattern (Figs. 12–13). Although larval mimicry has been seldom reported in literature, recent studies suggest that this is a plausible scenario especially in species using the same host plants (Willmott et al. 2011). In this scenario, it is possible that other larval mimicry rings can be reported in mistletoe butterfly larvae, since there are several potential aposematic models such as *Brangas neora* (Hewitson) (Lycaenidae) and *Hesperocharis crocea* Bates (Pieridae) (see Braby & Nishida 2007, Janzen & Hallwachs 2016).

This study is another contribution to a better understanding of the natural history of mistletoe butterflies (see also Kaminski et al. 2012, 2014). Next steps includes rearing additional species of *Catasticta*, the largest genus of Neotropical Pieridae (immature stages are known to a small sample of the ca. 90 described species) and the discovery of the immature stages of *Charonias*, a genus that includes an endangered species in southeast Brazil (Freitas et al. 2011). Finally, the present publication would serve as motivation to Neotropical lepidopterists to search and publish more data on early stages of mistletoe butterflies.

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