Research Article

Life History of *Aricoris propitia* (Lepidoptera: Riodinidae)—A Myrmecophilous Butterfly Obligately Associated with Fire Ants

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The immature stages of *Aricoris propitia* (Stichel) are described and illustrated for the first time, using both light and scanning electron microscopy. Females oviposit in at least seven host-plant families, always in the presence of fire ants (*Solenopsis saevissima* (Smith) complex), without being attacked by them. Larvae are tended by ants during all larval and pupal stages. From the fourth instar on, larvae feed at night and rest during the day inside underground shelters constructed by ants on the host plant roots, and where pupation occurs. Several observed features, including ant-mediated oviposition, persistent ant attendance throughout all instars, and high spatiotemporal fidelity indicate that *A. propitia* is a myrmecophile obligately associated with fire ants. We propose *A. propitia* as an extraordinary model for studies on ant-butterfly evolutionary history in the Neotropics.

1. Introduction

Symbiotic associations between butterfly larvae and ants have attracted the attention of early naturalists, both in Europe and North America, since the second half of the 18th century (see references in [1]). Nonetheless, these interactions are historically poorly studied in the Neotropical region despite their richness and abundance [2, 3]. An exception in this scenario is the classic paper by Bruch [4], which describes some aspects of the life history of an Argentinean species of *Aricoris* Westwood. In addition to being the first detailed description of a myrmecophilous larva from the Riodinidae family, the aforementioned study presents the first evidence of a butterfly larva living inside ant nests in the Neotropics. This behavior has been reported for a small number of Lycaenidae clades, such as the charismatic large blue *Maculinea* Van Eecke (*Phengaris* Doherty spp.), which parasitizes ant societies in Eurasia (see [5–7]). But unlike large blue butterflies, which today are model organisms in mutualism and parasitism studies, little progress has been

achieved on the biology of *Aricoris* since the initial work by Bruch [4] (but see [8–12]).

The riodinid genus *Aricoris* contains 24 described species [13, 14] typically found in open dry areas of South America [3]. *Aricoris propitia* (Stichel) is widespread in Central and Northern Brazil ([15], C. Callaghan, pers. comm.). Since its original description in 1910, no additional information was published for this species. The purpose of this paper is to fill that gap by presenting the natural history and morphological description of immature stages of *A. propitia*, with emphasis on their obligatory association with fire ants of the *Solenopsis saevissima* (Smith) complex (Formicidae: Myrmicinae).

2. Material and Methods

2.1. Study Sites. Four sites were sampled in central and northern Brazil (Figure 1): (1) cerrado *sensu stricto* and gallery forest areas in Alto Paraíso, Goiás (13°48'S, 47°54'W) (July 2009); (2) suburban areas of the city of Assis Brasil, Acre

FIGURE 1: Overview of *Aricoris propitia* study sites in Central (a) and Northern ((b)–(d)) Brazil. (a) Cerrado *sensu stricto* area in Alto Paraíso, Goiás; (b) surroundings of Assis Brasil, Acre—note the bordering suburbs, pastures and forest; (c) sandy beach areas along the Xingu river, Porto de Moz, Pará; (d) small home garden in a neighborhood of Belém, Pará—note that within this small space the larvae were able to use three ornamental plant species (see Table 1).

(10°56'S, 69°33'W) (August–September 2006); (3) sandy beach and small-farm cultivation areas along the Xingu river, Porto de Moz, Pará (02°07'S, 52°15'W) (July 2010); (4) house garden in a neighborhood of Belém, Pará (01°25'S, 48°27'W) (several occasions between 2006 and 2009).

2.2. Sampling, Rearing, and Behavioral Observations. Available host-plants in the study sites were visually scanned for the presence of larvae and tending ants (as in [16]). Additionally, some potential host-plants with distinct signs of herbivory and visited by *S. saevissima* ants were excavated in search of larvae and pupae. Plants with immatures (eggs and larvae) were collected for identification, as well as the tending ants. We also recorded the presence of food sources that may promote ant visitation on the plants, such as extrafloral nectaries (EFNs) and/or honeydew-producing hemipterans (HPHs). The immatures of *A. propitia* used for morphological description were collected in the field and reared as follows: eggs were placed in Petri dishes and observed daily until eclosion; newly hatched larvae were reared individually in transparent 250 mL plastic pots under controlled conditions ($25 \pm 2^\circ\text{C}$; 12 h L: 12 h D). Branches

of the same host-plant on which each larva was found were offered *ad libitum*, and larvae were checked daily for food replacement and cleaning when necessary. Immatures for morphological analysis were separated, fixed in Dietrich's solution, and then preserved in 70% ethanol. Shed head capsules were collected and preserved for measuring. Voucher specimens of the immature stages were deposited at the Museu de Zoologia “Adão José Cardoso” (ZUEC), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Behavioral interactions between *A. propitia* larvae and tending ants were observed *ad libitum* [17] in the field during the day (ca 10:00–16:00 h), and sometimes at night (ca 18:00–06:00 h), for the population of Porto de Moz. Additional observations on larval ant-organs and their role in the interaction with ants were obtained from larvae reared in plastic pots with their host ants or from larvae maintained in a terrarium together with a captive colony of tending ants (from a population of Belém).

2.3. Morphology. Measurements were taken and general aspects of morphology were observed using a Leica MZ7.5 stereomicroscope equipped with a micrometric scale. Egg

TABLE 1: Summary of recorded host-plants of *Aricoris propitia*, including liquid food source types available for ants (EFNs, extrafloral nectaries; HPHs, honeydew-producing hemipterans) and localities.

Host plants	Sources of liquid food	Localities
Chrysobalanaceae		
<i>Hirtella glandulosa</i>	EFNs, HPHs	Alto Paraíso (Goiás)
Fabaceae		
<i>Senna obtusifolia</i>	EFNs	Belém (Pará)
Malpighiaceae		
<i>Byrsonima</i> sp.	HPHs	Porto de Moz (Pará)
Malvaceae		
<i>Hibiscus rosa-sinensis</i>	HPHs	Belém (Pará)
Verbenaceae		
<i>Aegiphila</i> sp.	EFNs	Assis Brasil (Acre)
Rubiaceae		
<i>Ixora coccinea</i>	HPHs	Belém (Pará)
Simaroubaceae		
<i>Simarouba</i> sp.	EFNs	Alto Paraíso (Goiás)
Turneraceae		
<i>Turnera ulmifolia</i> *	EFNs	Campinas (São Paulo)

*Lab-accepted host-plant.

size is given as height and diameter. Head capsule width of larvae was considered to be the distance between the most external stemmata; maximum total length for both larvae and pupae corresponded to the distance from head to posterior margin of the tenth abdominal segment in dorsal view (as in [18]). Measurements are given as minimum-maximum values. Scanning electron microscopy (SEM) was conducted using both JEOL JSM-5800 and Carl Zeiss LEO-1430VP microscopes, with samples prepared according to standard techniques (for details, see [19]). Terminology for early stage descriptions follows Downey and Allyn [20] for eggs, Stehr [21] for general morphology of larvae, Mosher [22] for pupae, and DeVries [23] for ant-organs.

3. Results

3.1. Natural History of *Aricoris propitia*. This butterfly is locally abundant in open areas, where it occurs close to its ant colonies. Adults can be observed flying fast near the ground, perching on the undergrowth where they become almost invisible. Males were observed defending small territories and visiting many wild flowers. Females were seen flying near host-plants infested by host ants (Figure 2(a)), which for all studied populations were ants of the *Solenopsis saevissima* complex. Oviposition occurred in the warmest period of the day, from 11 AM to 2 PM ($n = 15$ oviposition events), a period when ants are more active. Females flew in circles around a host-plant occupied by ants before starting to oviposit (prealighting phase). After landing (postalighting phase), females frequently touched the plant surface with the tip of their abdomen, particularly on ant trails, but

were never attacked by the ants. Eggs were laid singly or in small clusters of two to five eggs (Figure 2(b)). Our host-plant records indicate that the larvae of *A. propitia* are polyphagous using at least seven families of plants, including ornamental (nonnative) species cultivated in urban gardens (see Table 1 and Figure 1(d)). Also, in the laboratory, larvae accepted and developed well on leaves of *Turnera ulmifolia* L. (Turneraceae). All observed host-plants of *A. propitia* provided some source of liquid food that could be potentially used by ants, such as honeydew-producing hemipterans and/or extrafloral nectaries (see Table 1). Other potential host-plants without fire ants or visited by other ant species were also examined at some of the study sites ($n = 51$ at Assis Brasil, $n = 15$ at Alto Paraíso), but no larvae of *A. propitia* were found.

All instars are ant-tended, and even the small first instar is equipped with functional tentacular nectary organs (TNOs). From the second instar on, other ant-organs appear or become functional (Figure 3). Ants antennate the larval body intensely, but especially the anterior region where a row of papilliform setae and the openings of the anterior tentacle organs (ATOs) are located (Figure 3(a)). When everted, these organs provoke clear alterations in ant behavior, such as opening of the jaws and a marked increase in activity and aggressiveness. In the early instars (first to third) the larvae can be found during the day feeding on the host-plant leaves (Figures 2(b)–2(d)). From the fourth instar on, they rest during the day inside underground shelters constructed by ants within the host-plant roots, and that is where pupation occurs. When night falls, the larvae leave the underground shelters and climb up to feed on the host leaves (Figure 2(e)), returning to the shelters by dawn. Large quantities of mature larvae and pupae can be found inside the underground shelters, which are permanently patrolled by tending ants (Figure 2(f)).

3.2. Description of the Immature Stages. The reared immatures from the four sites were very similar and went through five instars. Developmental time is based on material from Alto Paraíso, Goiás, reared on *Turnera ulmifolia* leaves. The egg description and measurements are based on material from Assis Brasil, Acre; the larval and pupal description and measurements are based on material from Porto de Moz and Belém, Pará.

3.2.1. Egg (Figures 2(b) and 4). Duration 6–7 d ($n = 5$). Height 0.30–0.32 mm; diameter 0.54–0.58 mm ($n = 3$). Color whitish-cream when laid, changing to beige before hatching. General spherical shape, with convex upper surface and flattened bottom surface; exochorion with smooth surface and hexagonal cells in lateral view (Figure 4(a)). Slightly depressed micropylar area; annulus present, and rosette surrounded by petal-shaped cells; micropyles at center of the micropylar area (Figure 4(b)). Aeropyles in tiny protuberances in the rib intersections (Figure 4(c)).

3.2.2. First Instar (Figures 2(c) and 5(a)–5(c)). Duration 4–5 d ($n = 2$). Head capsule width 0.24–0.26 mm ($n = 3$), total length 2.2 mm. Dark brown head, prothoracic and anal

FIGURE 2: Life stages of *Aricoris propitia* tended by *Solenopsis saevissima* on *Byrsonima* sp. ((a), (d)–(f)), *Simarouba* sp. ((b), (d) and (e)), and *Hirtella glandulosa* (c). (a) Female at postlighting phase near an ant-tended treehopper aggregation (arrow); (b) eggs (white arrows) and a third instar larva (black arrow); (c) first instar tended by one worker; (d) second instar tended by ants; (e) third instar tended by ants, note that both anterior (black arrow) and tentacle nectary organs (white arrow) are everted; (f) nocturnal fifth (last) instar tended by several ants; (g) nocturnal group of larvae and treehoppers (arrow) tended by ants; (h) diurnal larval group inside a shelter in the host-plant roots.

FIGURE 3: Sequence of interactions between *Aricoris propitia* third instar larva and *Solenopsis saevissima* ants. (a) Worker antennating the row of setae on the prothoracic shield (white arrow), note the everted anterior tentacle organ (black arrow); (b) everted nectary tentacle organ (white arrow) after repeated antennation by ant on the A8 segment.

shields; yellowish orange body with beige or translucent setae (Figure 2(c)). Epicranium and frontoclypeus with several setae, pores, and two pairs of perforated cupola organs (PCOs) in the adfrontal areas (Figure 5(a)). Body with long plumose setae in the lateral areas and in the prothoracic and anal shields; the remaining dorsal and subdorsal setae are short and dendritic, and PCOs are associated with these groups of setae. The openings of the anterior tentacle organs (ATOs) are present in the metathoracic segment, but these organs are apparently not functional (Figure 5(b)). Functional tentacle nectary organs (TNOs) are present in the A8 segment (Figure 5(c)).

3.2.3. Second Instar (Figure 2(d)). Duration 5–6 d ($n = 2$). Head capsule width 0.44 mm ($n = 2$), total length 3.1 mm. Dark brown head, prothoracic and anal shields; yellowish green body with two longitudinal light brown bands (Figure 2(d)). All ant-organs present, including ATOs, TNOs, PCOs, dendritic setae, and one pair of vibratory papilla on the anterior border of the prothoracic shield. A

dorsal row of papilliform setae is also present on the posterior margin of the prothoracic shield and is maintained in the subsequent instars (Figures 3(a) and 5(d)).

3.2.4. Third Instar (Figures 2(e) and 3). Duration 6 d ($n = 2$). Head capsule width 0.72–0.84 mm ($n = 2$), total length 6.2 mm. Brown head; black prothoracic and anal shields with beige spots; green body with two longitudinal brown bands (Figure 2(e)). General morphology is similar to the second instar's, but with more numerous and enlarged setae.

3.2.5. Fourth Instar (Figures 2(g)–2(h) and 5(d)–5(e)). Duration 6 d ($n = 2$). Head capsule width 1.28–1.30 mm ($n = 4$), total length 15.2 mm. Brown head; black prothoracic and anal shields with beige and grey spots; variegated body coloring with frosted brown and beige spots (Figures 2(g) and 2(h)). General morphology is similar to preceding instar's, but with more numerous and enlarged setae (Figures 5(d) and 5(e)).

3.2.6. Fifth (Last) Instar (Figures 2(f)–2(h) and 5(f)–5(h)). Duration 6–7 d ($n = 2$). Head capsule width 1.76–1.87 mm ($n = 5$), total length 2.1 cm. Coloring is similar to fourth instar (Figures 2(f)–2(h)). Mandibles with eight teeth and six setae (Figure 5(f)). Body covered with several types of setae, including prominent setae on the lateral areas, prothoracic and anal shields; two pairs of prominent dorsal setae in the same position as primary setae on the mesothorax to A8 segments; two types of dendritic setae and several perforated cupola organs (Figures 5(g) and 5(h)). The spiracle on the A1 segment is lateroventral, whereas those on segments A2 to A8 are in a dorsal position.

3.2.7. Pupa (Figure 6). Duration 10–12 d ($n = 2$). Total length 1.29 cm, width at A1 0.33 cm. Variegated coloring with brown, beige, and dark spots (Figure 6(a)). Tegument is entirely sculptured, with irregular striations and lacking prominent tubercles (Figures 6(b)–6(e)). Prothorax bears dorsal clusters of papilliform setae (Figure 6(a)). Silk girdle crossing the A1 segment near one pair of small tubercles with several associated dendritic setae and PCOs (Figure 6(b)). Body with some small dendritic setae, and PCOs located in clusters on lateral areas close to spiracles (Figures 6(b)–6(e)); these clusters are absent on the A2 and A7 segments. The intersegmental area between the A4–A5 and A5–A6 abdominal segments features plates and files (Figure 6(f)) that may act as a stridulatory mechanism. The consolidated A9 and A10 segments constitute the ventrally flattened cremaster; with long crochets in a ventral position (Figure 6(g)).

4. Discussion

In general terms, the egg of *Aricoris propitia* resembles those described for other Nymphidiini genera in the Lemoniadiina group (such as *Juditha* Hemming, *Lemonias* Hübner, *Synargis* Hübner, and *Thisbe* Hübner), with a semispherical shape, exochorion with hexagonal cells in lateral view, aeropyles in the rib intersections, and micropylar area centered on

FIGURE 4: Scanning electron microscopy of *Aricoris propitia* egg (material from Assis Brasil, Acre). (a) Lateral view; (b) micropylar area (Mp); (c) hexagonal cells of the exochorion with aeropyles in the rib intersections (arrow).

the top surface (see [3, 24, 25]). However, it differs in that the limits of the micropylar area are slightly bounded; this pattern is shared with other *Aricoris* and *Ariconias* Hall and Harvey (L.A. Kaminski, unpublished). The first instar presents some characteristics of myrmecophilous larvae, namely, conspicuous perforated cupola organs, functional tentacle nectary organs, and short, dorsally located dendritic setae (see examples of riordinid first instar larvae in [3, 18, 26]).

Larvae of *A. propitia* present the typical pattern of Nymphidiini, with the first abdominal spiracle in a ventral position and vibratory papillae (VPs) on the prothoracic shield [27]. In addition to the sound producing organs (VPs), the mature larvae of *A. propitia* feature two other important types of riordinid ant-organs (see [3, 23, 24]): the anterior tentacle organs (ATOs) and the tentacle nectary organs (TNOs). The larvae also present another putative ant-organ: the row of papilliform setae on the prothorax, which had already been described for other *Aricoris* species [4, 8]. Tending ants frequently antennate these papilliform setae, and usually this palpation is accompanied by eversion of the ATOs. The way the ants react after ATO eversion suggests that the ATOs emit a volatile chemical similar to the ant alarm pheromone, as has been suggested for other Riordinidae [3, 23, 28]. The chemical compositions of ATO emissions by myrmecophilous butterflies are still unknown. In contrast, the chemical ecology of fire ants, including alarm pheromones and their role in interactions with other organisms, is relatively well known (e.g., [29]). Thus, the *A. propitia*/fire ants system may be helpful in answering some outstanding questions about the functioning of ant-organs in myrmecophilous butterflies.

The larvae of *A. propitia* can be considered polyphagous since they feed on at least seven families of host-plants. Polyphagy in obligate myrmecophilous butterflies, including Riordinidae, has been regarded as a consequence of ant-dependent oviposition [3, 12, 25, 30–32], and this seems to be the case for *A. propitia*. Aphytophagy, on the other hand, is quite rare in butterfly larvae [33], but it has been suggested for some species of *Aricoris* [3, 12]. It is believed that the larvae of these species are able to get food directly from ants, through regurgitations (trophallaxis) from ant workers or by preying directly on ant brood. Although *A. propitia* rest during the day inside underground shelters together with their tending ants, we do not have evidence that the larvae get some kind of food from the ants.

All known species of *Aricoris* seem to be engaged in obligatory associations with their tending ants. To date, *Aricoris domina* (Bates) has been associated with *Ectatomma* Smith [11], and seven *Aricoris* species have been associated with *Camponotus* Mayr [3, 8–12, 34]. So far, only *Aricoris hubrichi* (Stichel) and *Aricoris campestris* (Bates) have been reported to be associated with *Solenopsis* Westwood ants ([4], A.V.L. Freitas pers. comm.). Both *Aricoris* species are inserted within the derived “*epulus*-group” sensu Hall and Harvey [35]. Despite the high species richness and ecological prevalence, symbiotic interactions between butterfly larvae and *Solenopsis* are very rare ([36], L.A. Kaminski, unpublished). Apart from the association with fire ants, several natural history and morphological features of *A. propitia* are very similar to those observed for *A. hubrichi* and *A. campestris*, suggesting an evolutionary relationship among these species. As the life history of most species within the “*epulus*-group” is still unknown (see [35]), it is not possible to tell whether

FIGURE 5: Scanning electron microscopy of first ((a)–(c)), fourth ((d) and (e)), and fifth ((g) and (h)) instar of *Aricoris propitia* ((a)–(e) from Assis Brasil, Acre, and ((f)–(h)) from Belém, Pará). (a) Head in frontal view; (b) opening of the anterior tentacle organ (ATO); (c) posterior abdominal segments showing the openings of tentacle nectary organs (TNOs); (d) head and prothorax in dorsofrontal view, note the dorsal row of setae (arrow) and the vibratory papillae (VP); (e) detail of vibratory papilla, note the epicranial granulations (arrow); (f) mandible; (g) two types of dendritic setae and perforated cupola organ (PCO); (h) perforated cupola organ.

interaction with fire ants has a single origin or has arisen more than once in these lineages.

The fire ants are highly dominant organisms and considered one of the most harmful bioinvaders ever known [37]. In their native range, from southern Brazil to Suriname, they are also considered pests in disturbed areas, especially in the Amazon (e.g., [38–40]). Although *A. propitia* occurs naturally in the Amazon (the holotype is from “Amazonas”), continual deforestation over the recent decades—especially

in the “arc of deforestation” (see [41])—could be providing a recent range expansion for this butterfly. Recent studies involving several molecular markers and morphological variation have revealed that *Solenopsis saevissima* belongs to a geographically structured complex of cryptic species [40]. How populations of *A. propitia* respond to ant host structure is an interesting and yet unanswered question. A recent study [42], for example, did not find a direct influence of host ants on the population structure of the obligate myrmecophilous

FIGURE 6: Pupa of *Aricoris propitia* in lateral view (a) and details ((b)–(g)) in scanning electron microscopy ((a), from Alto Paraíso and ((b)–(g)), from Belém, Pará). (b) Laterodorsal tubercle on A1 segment with dendritic setae and perforated cupola organs; (c) dendritic setae on A1 segment; (d) spiracle on A5 segment; (e) dendritic setae; (f) detail of putative stridulatory area between A4–A5 segments; (g) detail of cremaster crochets.

butterfly *Jalmenus evagoras* (Donovan) (Lycaenidae), but showed that biogeographical and host-plant aspects have an effect on that structure. *Aricoris propitia* may be a candidate system to elucidate the effects of ant attendance on the diversification of myrmecophilous butterflies.

The system involving *Aricoris propitia* and their tending fire ants presents several features of a model system, including: (1) it is common and widely distributed; (2) it is found in easily accessible environments (open and/or altered areas); (3) it adjusts well to laboratory conditions; (4) it has a short generation time; (5) the larvae accept many host-plant species; (6) the host fire ants have economic importance and various aspects of their biology are well known. Accordingly, we expect that the basic information provided in this work will encourage further studies on this interesting butterfly-ant system.

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