

The first known riodinid ‘cuckoo’ butterfly reveals deep-time convergence and parallelism in ant social parasites

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Mutualistic interactions between butterflies and ants can evolve into complex social parasitism. ‘Cuckoo’ caterpillars, known only in the Lycaenidae, use multimodal mimetic traits to achieve social integration into ant societies. Here, we present the first known ‘cuckoo’ butterfly in the family Riodinidae. *Aricoris arenarum* remained in taxonomic limbo for > 80 years, relegated to *nomen dubium* and misidentified as *Aricoris gauchiana*. We located lost type material, designated lectotypes and documented the morphology and natural history of the immature stages. The multifaceted life cycle of *A. arenarum* can be summarized in three phases: (1) females lay eggs close to honeydew-producing hemipterans tended by specific *Camponotus* ants; (2) free-living caterpillars feed on liquids (honeydew and ant regurgitations); and (3) from the third instar onward, the caterpillars are fed and tended by ants as ‘cuckoos’ inside the ant nest. This life cycle is remarkably similar to that of the Asian lycaenid *Niphanda fusca*, despite divergence 90 Mya. Comparable eco-evolutionary pathways resulted in a suite of ecomorphological homoplasies through the ontogeny. This study shows that convergent interactions can be more important than phylogenetic proximity in shaping functional traits of social parasites.

ADDITIONAL KEYWORDS: ant-organs – convergent interactions – exploitation of mutualism – kleptoparasitism – *Lemoniadinina* – Nymphidiini – symbiosis – tactile mimicry.

INTRODUCTION

Trophobiotic interactions between caterpillars and ants, termed myrmecophily, occur widely in two families of butterflies (Lycaenidae and Riodinidae; reviewed by DeVries, 1991b; Fiedler, 1991; Pierce *et al.*, 2002). In general, these interactions are considered mutualistic and are mediated by specialized larval ant-organs that produce substrate-borne vibrations, chemical signals and nutritional rewards for ants, whereas ants can provide protection against natural enemies (e.g. Pierce & Mead, 1981; DeVries, 1991a). From the free-living ancestral strategy (commensalism or mutualism) on plants, social parasitism can evolve, when the caterpillars begin to

exploit the resources of the ant colony (Cottrell, 1984; Pierce & Young, 1986; Fiedler, 1998). An iconic example of this parasitic lifestyle is provided by the large blue butterfly, *Phengaris Doherty*, 1891 (= *Maculinea Van Eecke*, 1915), which parasitizes *Myrmica Latreille*, 1804 (Myrmicinae) ant colonies in Europe and Asia (Als *et al.*, 2004; Casacci *et al.*, 2019). Inside the ant nest, *Phengaris* caterpillars exploit ant resources either by predation on the ant brood (carnivory) or via a ‘cuckoo’ strategy, a type of kleptoparasitism in which caterpillars are fed directly by ants with regurgitations (trophallaxis) (Thomas & Wardlaw, 1992). Although rare, there are other known cases of social parasitism in Lycaenidae from Eurasia, Africa and Australia (e.g. Cottrell, 1984; Pierce, 1995; Fiedler, 1998; Heath, 2014). There is no confirmed case of social parasitism on the

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American continent (Fiedler, 2012), in the Lycaenidae or in the sister family Riodinidae, a mainly Neotropical lineage (DeVries, 1997).

In Riodinidae, a candidate group to contain social parasitic species is *Aricoris* Westwood, 1851, a Neotropical genus, previously referred to as *Hamearis* Hübner, 1816 and *Audre* Hemming, 1934 (Hall & Harvey, 2002), which contains few anecdotal reports of caterpillars found in ant nests (Bruch, 1926; Bourquin, 1953; DeVries *et al.*, 1994; DeVries, 1997). In the first detailed description of a myrmecophilous larva of Riodinidae, Bruch (1926) reports that larvae of *Aricoris signata* (Stichel, 1910) were found inside *Solenopsis* Westwood, 1840 (Myrmicinae) ant nests. Although the larvae were found together with ants, *A. signata* larvae are phytophagous and apparently do not receive a food resource from the ants, i.e. this species is not a true social parasite (Fiedler, 2012). The same type of behaviour was observed in the closely related species *Aricoris propitia* (Stichel, 1910), whose caterpillars rest during the day inside underground shelters constructed by tending ants (Kaminski & Carvalho-Filho, 2012). Other observations of *Aricoris* larvae in ant nests were made by DeVries *et al.* (1994), who recorded two species (cited as '*Audre* nr. *aurinia*' and '*undetermined* sp.') inhabiting *Camponotus* Mayr, 1861 (Formicinae) ant nests in Jujuy, northern Argentina. In contrast to the observations on *A. signata* and *A. propitia*, the caterpillars were not phytophagous and did not accept any type of solid food item in the laboratory, suggesting that the larvae might feed via ant trophallaxis (DeVries *et al.*, 1994; DeVries, 1997). Callaghan (2010) reported the observation of fresh adults of *Aricoris tutana* (Godart, 1824) emerging from an ant nest in Central Brazil and suggested that larvae might feed on ant resources. Thus, only circumstantial evidence of social parasitism in Riodinidae has existed so far (DeVries *et al.*, 1994; Gallard, 2017).

In this study, we describe the life cycle of a kleptoparasitic species of *Aricoris* from South America and thus confirm that this strategy also evolved in Riodinidae, which until now was regarded as an exclusive strategy of the family Lycaenidae (Fiedler, 2012). This study began with observations by Volkmann & Núñez-Bustos (2010), who reported *Aricoris gauchoana* (Stichel, 1910) caterpillars feeding on exudations of scale insects and suggested that caterpillars could complete their life cycle inside the ant nest. After comparison of immature and adult specimens, we conclude that the species identified as *A. gauchoana* by Volkmann & Núñez-Bustos (2010) is the same species reported by DeVries *et al.* (1994) as *Audre* nr. *aurinia* and later cited as *Audre aurinia* Hewitson, 1863 by Pierce (1995) and as *Aricoris incana* (Stichel, 1910) by Hall & Harvey (2002). Through the examination of the literature and museum

collections, we show that this kleptoparasitic species is not represented by the name *A. gauchoana*, but by the obscure name *Hamearis arenarum* H. Schneider, 1937 from Uruguay and currently relegated to anonymity as a *nomen dubium* (Hall & Harvey, 2002; Callaghan & Lamas, 2004; Siewert *et al.*, 2014a). Thus, the purposes of this article are as follows: (1) to confirm the first instance of 'cuckoo' caterpillars in Riodinidae; (2) to elucidate the status of this taxon, redescribing the species *Aricoris arenarum* (Schneider, 1937) and designating lectotypes; (3) to describe their immature morphology and natural history; and (4) to discuss convergence and parallelism between the families Lycaenidae and Riodinidae, thus contributing new perspectives on the evolution of social parasitism in butterflies.

MATERIAL AND METHODS

STUDY SITES, BEHAVIOURAL OBSERVATION AND COLLECTION

The fieldwork was conducted in areas of montane 'chaco' vegetation in Capilla del Monte (30°52'S, 64°32'W, 985 m a.s.l.), San Ignacio (30°56'S, 64°31'W, 1053 m a.s.l.) and Villa Giardino (31°3'S, 64°29'W, 1050 m a.s.l.) and high-elevation grasslands in La Cumbre (30°56'S, 64°23'W, 1400 m a.s.l.), Córdoba, Central Argentina. These populations were monitored over several years by L.V. (see Volkmann & Núñez-Bustos, 2010) and studied in detail in the summer months (January and February) of 2013–2019 by L.V. and L.A.K. The behaviour of adults and caterpillars (early instars) was observed *ad libitum* (*sensu* Altmann, 1974) in the field during the day (~10.00–17.00 h) and night (~22.00–02.00 h). Host plant branches containing early instars, honeydew-producing Hemiptera and tending ants were collected, maintained in plastic pots (~500 mL) and observed with a stereomicroscope in the laboratory. Additionally, a 'black morph' colony of *Camponotus punctulatus* Mayr, 1868 (Formicinae) from San Ignacio was collected that contained brood chambers with immature and adult ants of all castes. The ant nest was kept in the laboratory and fed weekly with honey and insects. After 2 days to stabilize the colony, we inserted two third instar *A. arenarum* caterpillars, which were monitored until the end of their development. These observations were complemented with data obtained by P.J.D. in April 1992 in Volcán (23°59'S, 65°27'W, 1800 m a.s.l.), Jujuy, Argentina; and by L.A.K. and L.V. in January 2020 in Castillos (33°49'S, 57°40'W, 90 m a.s.l.), Soriano, Uruguay. Plants with immatures, in addition to tending ants, were collected for identification. Immatures for morphological analysis were fixed in Dietrich's solution and preserved in 70% ethanol. Shed head capsules were collected and preserved for measurement. Vouchers

of tending ants, hemipterans and immature stages were deposited at the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil.

MORPHOLOGY

Morphological examination and measurements were made using a stereomicroscope (Nikon AZ100M). To study the genitalia, dissections were made according to the standard practice of soaking the abdomens in 10% KOH overnight or heating in a bain-marie for 5–10 min and storing the pelts and genitalia in glycerol. Wings for the study of venation and appendages were detached, soaked briefly in bleach, then washed in alcohol and mounted on slides. Egg size is given as height and diameter. Larval head capsule width was measured as the distance between the most external stemmata, and the maximum length for both larvae and pupae correspond to the distance from the head to the posterior margin of the abdominal segment in dorsal view. Measurements are given as a range. Colour patterns of immature stages were recorded using a digital camera *in vivo*, and a stereomicroscope was used for eggs and early instars. Scanning electron microscopy (SEM) was conducted using a JEOL JSM-6060 microscope, with samples prepared according to standard techniques (for details, see Kaminski *et al.*, 2012). The terminology of the genitalia follows Klots (1970) and that of the venation follows Miller (1970). The taxonomic status of the names is based on the study by Callaghan & Lamas (2004). We follow Downey & Allyn (1980) for egg morphology, Stehr (1987) for the general morphology of larvae and pupae, and Cottrell (1984) and DeVries (1988) for ant-organs.

The studied material belongs to the following collections: CAM, Coleção Alfred Moser, São Leopoldo, Rio Grande do Sul, Brazil; CENB, Collection Ezequiel Núñez-Bustos, Buenos Aires, Argentina; CJC, Curtis Callaghan Collection, Bogotá, Colombia; CLK, Coleção Lucas Kaminski, Porto Alegre, Rio Grande do Sul, Brazil; DZRS, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; DZUP, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; FCE, Collection the Facultad de Ciencias, Universidad de la República (UDELAR), Montevideo, Uruguay; IML, Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Boston, MA, USA; MfN, Museum für Naturkunde, Berlin, Germany; MLP, Museo de La Plata, La Plata, Argentina; MNHNPA, Museu Nacional de Historia Natural, Asunción, Paraguay; MNRJ, Museu Nacional da Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; NHMUK, Natural History

Museum, London, UK; OM, Coleção Olaf Hermann Hendrik Mielke, Curitiba, Paraná, Brazil; SFN, Senckenberg Research Institute and Natural History Museum Frankfurt, Frankfurt am Main, Germany; ZfB, Zentrum für Biodokumentation, Schiffweiler, Saarland, Germany. Abbreviations used throughout the text are as follows: DFW, dorsal forewing; DHW, dorsal hindwing; FW, forewing; HW, hindwing; PCO, perforated cupola organ; TNO, tentacle nectary organ; VFW, ventral forewing; VHW, ventral hindwing.

EVOLUTIONARY COMPARISON WITH SOCIAL PARASITISM IN LYCAENIDAE

The life cycle of *A. arenarum* was compared with that known for lycaenids and classified according to the system proposed by Fiedler (1998). Based on this classification, we decided to compare the ecological and morphological traits of *A. arenarum* in detail with those of *Niphanda fusca* (Bremer & Grey, 1853) (Lycaenidae: Polyommatainae), a social parasite with a similar life cycle. To demonstrate the evolutionary relationship between *A. arenarum* and *N. fusca*, the age of divergence and estimated origins of myrmecophily, we used the dated phylogenomic hypothesis proposed by Espeland *et al.* (2018). The systematic position of *A. arenarum* was deduced from morphological and molecular evidence (Hall & Harvey, 2002; Seraphim *et al.*, 2018). The life cycle of *N. fusca* has been inferred based on the documentary ‘Relationships in Nature’ (MBC TV, Republic of Korea, available at: <https://www.youtube.com/watch?v=Qc8LDIIpnTA>), photographs posted in the ‘Ant Room’ blog (available at: <http://blog.livedoor.jp/antroom/>) and the rich literature for this well-studied model species (e.g. Nagayama, 1950; Hojo *et al.*, 2009, 2014). Owing to the taxonomic sampling of the phylogeny of Espeland *et al.* (2018), which collapses many important lineages of social parasitic and non-parasitic lycaenids and subsamples relevant riodinid lineages, we prefer not to carry out a formal character reconstruction analysis. This can be done with the addition of new life-history data and a more comprehensive phylogeny, ideally covering most of the diversity in the subtribe Lemonyadina and in the genus *Aricoris* in particular. Thus, as a first approach to identify convergence and parallelism in traits and interactions we used a simple comparative natural history method from a phylogenetic perspective (Bittleston *et al.*, 2016).

RESULTS

SYSTEMATICS

History of classification

The subspecies *Hamearis aurinia gauchiana* Stichel, 1910 was described based on two female syntypes

from Uruguay (Stichel, 1910). One female labelled as Type from the Staudinger collection is at the MfN (Fig. 1A). A male specimen was also found in the same collection without a type or locality label, but with a number (3557) and an identity label in Stichel's handwriting indicating 'gauchoana Stichel'. However, this male represents a different species, lacking the prominent submarginal rows of spots on both wings and with a nearly uniform grey ground colour on the VHW. Comparison of the female type specimen with Stichel's description confirms this as a syntype of *H. a. gauchoana*. However, in all the literature since then, including widely used South American field guides, the name *gauchoana* has been associated erroneously with the male phenotype and not the female (e.g. Hayward, 1973; Biezanko *et al.*, 1978; Canals, 2000, 2003; Hall & Harvey, 2002; Núñez-Bustos, 2010; Volkmann & Núñez-Bustos, 2010; Siewert *et al.*, 2014b). Adults illustrated by D'Abbrera (1994) under the name 'gauchoana' are *A. incana*. The name 'gauchoana' was always treated as a subspecies of *Aricoris aurinia* and never separated formally as a species until the study by Hall & Harvey (2002).

In 1937, H. Schneider described two riordinid species from Uruguay: *Hamearis arenarum* and *Hamearis montana* (as 'montaña' [sic]). Neither was illustrated, nor were the type depositories indicated. Schneider's material is located at two German Institutions: the SFN and the ZfB. Among the specimens at the SFN were a male and female with labels in Schneider's distinctive handwriting indicating the type locality of *H. montana* as Aiguá, [Maldonado department], Uruguay. These specimens are on loan and are at present in the Smithsonian Museum, Washington, DC, USA (examined and cited by Hall & Harvey, 2002). Photographs of those specimens are available at the Butterflies of America website (Warren *et al.*, 2016) and fit Schneider's description, suggesting that these are indeed syntypes of that species (Hall & Harvey, 2002). Additional syntype specimens in the ZfB are: two males, one from Aiguá and the other labelled 'Uruguay'; and three females, two from the Sierra de la Animas, Maldonado, Uruguay and another labelled 'Uruguay' (Fig. 1B). Comparison of Stichel's female syntype of *H. a. gauchoana* with Schneider's female syntype of *H. montana* indicates that they refer to the same species (Fig. 1A–C); thus *H. montana* Schneider, in addition to its junior subjective synonyms, *Hamearis erycina* Schweizer & Kay, 1941 and *Audre drucei nordensis* Callaghan, 2001, become junior subjective synonyms of *H. a. gauchoana*.

In addition, one male (Fig. 1D) and one female (Fig. 1E) were located at ZfB with labels in Schneider's handwriting with the name '*Hamearis arenarum* Schneider, neue [new]'. Both specimens are from La

Barra, 29 November 1936. Both fit the description of *H. arenarum*. The specimens referred to in the description are one male and several females from Rincón de la Bolsa, San José, Uruguay, currently known as Ciudad del Plata. La Barra was located in the same vicinity. Both localities are found near the south coast of Uruguay in the Montevideo area, and thus, the specimens can be considered as belonging to the same population. From Schneider's detailed description, it is clear that *H. arenarum* refers to the male (no. 3557) at the MfN, which Stichel labelled as *H. gauchoana*. For instance, Schneider refers to the VHW as being 'uniform light grey with a row of small black dots' (our translation) (Figs 1D, E, 2A). Thus, *arenarum* is the valid name for what has been referred to in the literature as *gauchoana*.

The resulting synonymies for these two species are as follows:

Aricoris gauchoana (Stichel, 1910)
= *montana* (Schneider, 1937), syn. nov. (*Hamearis*)
= *erycina* (Schweizer & Kay, 1941), syn. nov. (*Hamearis*)
= *drucei nordensis* (Callaghan, 2001) syn. nov. (*Audre*)

Aricoris arenarum (Schneider, 1937), (*Hamearis*)
= *gauchoana* Auctorum non Stichel, 1910

ARICORIS ARENARUM (SCHNEIDER, 1937)

Hamearis arenarum Schneider, 1937: *Entomologische Rundschau* 55(12): 137–138.

Type locality

La Barra, Uruguay. A male lectotype (ZfB), here designated, has the following labels: /Atencion! selten Hamearis arenarum Schneider [female symbol] Neue Art / La Barra 29.xi.36 / LECTOTYPE *Hamearis arenarum* Schneider, 1937 Callaghan & Kaminski det. 2020/. The characteristic lectotype label will be sent to the curator of the collection.

Proposed common names

Brown patchwork (Canals, 2003), cuckoo metalmark (English); colage parda (Canals, 2003), hormiguera ocrácea (Volkmann & Núñez-Bustos, 2010), hormiguera chopí (Spanish); formigueira chupim (Portuguese); panambi chopi (Guarani).

Diagnosis

Despite historical confusion, *A. arenarum* and *A. gauchoana* are easily differentiated by the wing colour pattern (Fig. 1). However, some difficulty might exist in distinguishing *A. arenarum* from other



Figure 1. Adult types of *Aricoris* described from Uruguay. A, *Hamearis gauchoana*, holotype female in dorsal view (left), ventral view (centre) and labels (right). B, *Hamearis montana*, lectotype male in dorsal view (left), ventral view (centre) and labels (right). C, *H. montana*, female paralectotype in dorsal view (left), ventral view (centre) and labels (right). D, *Hamearis arenarum*, lectotype male in dorsal view (left), ventral view (centre) and labels (right). E, *H. arenarum*, female paralectotype in dorsal view (left), ventral view (centre) and labels (right). Scale bar: 1 cm.

Aricoris species, such as *Aricoris aurinia* and *Aricoris indistincta* (Lathy, 1932), which also have a nearly solid grey tone ventrally on the hindwing and the general orange colour pattern dorsally. However, *A. arenarum*

can be identified externally by the median band of spots on the VHW, in which, when visible, the spot in cell M_3 is displaced distally, aligned to that in cell M_2 . Internally, *A. arenarum* male genitalia (Fig. 2B–D)

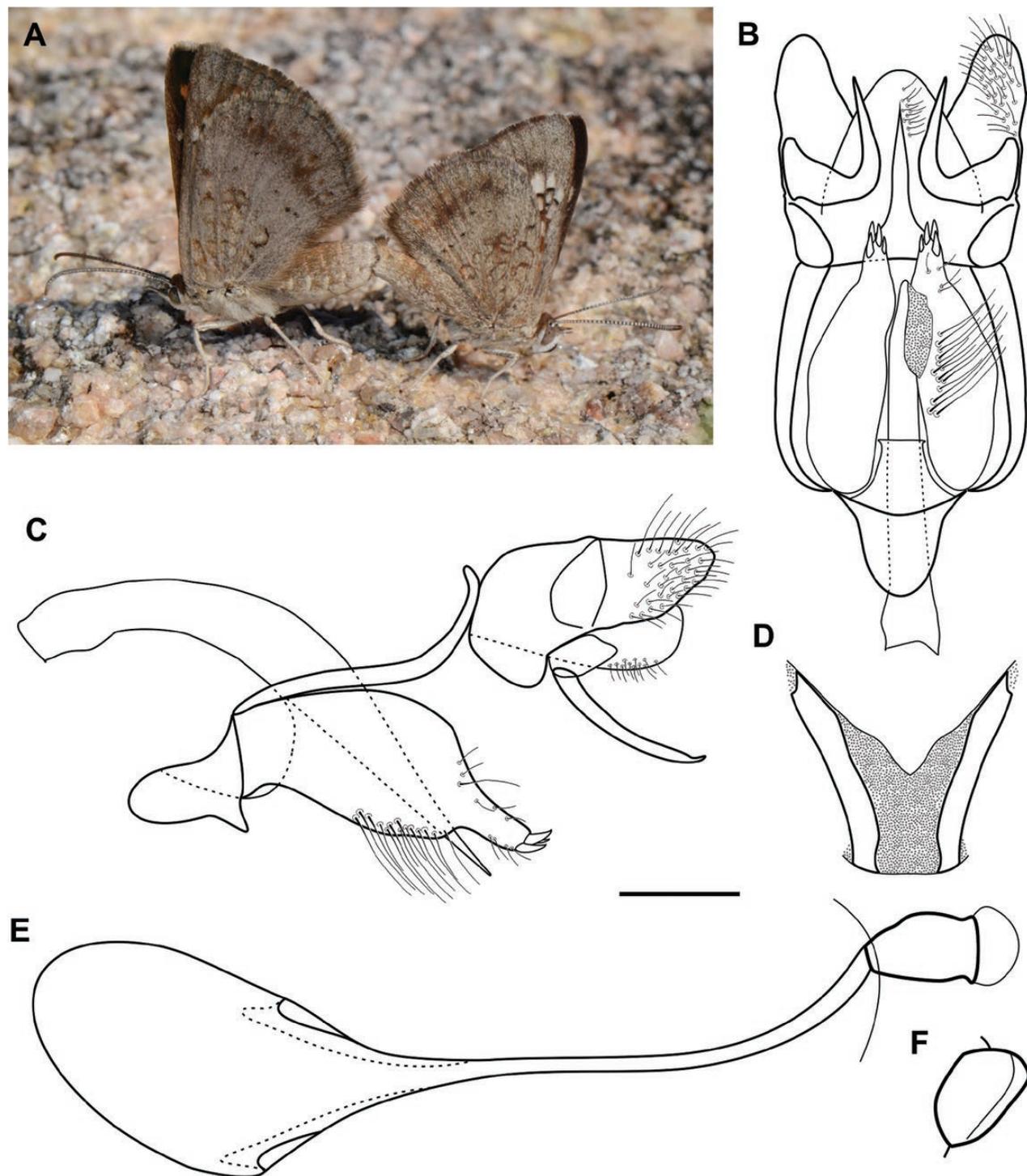


Figure 2. Adults of *Aricoris arenarum*. (A) In copula in Castillos, Uruguay, showing the female (left) and male (right); note cryptic coloration on the ground. (B–F) Male (B–D) and female (E, F) genitalia of *A. arenarum*. B, lateral view. C, ventral view. D, eighth sternite in ventral view. E, ventral view. F, papilla analis. Scale bar: 0.5 mm.

can be distinguished based on the presence of an indentation in the valvae ventral edge, below the tip, and because the two prongs of the eighth abdominal

sternite do not extend beyond the pleural membrane, characters present also in the ‘*chilensis*’, ‘*constantius*’ and ‘*colchis*’ groups (*sensu* Hall & Harvey, 2002).

Redescription of adult morphology: male (Fig. 1D)

Average forewing length 16.6 mm, range 18–20 mm ($N = 6$).

Wing shape and venation: FW with four radial veins; R_1 and R_2 branch before the discal cell. HW with humeral vein long, curved, and 2A reaching the anal margin before the midpoint. FW costa slightly indented before a pointed apex; distal margin to tornus curved convex to origin; inner margin slightly indented. HW costa straight to Sc, then curved to a rounded apex at M_1 , then curved abruptly to anal angle; the distal margin slightly indented between Cu_2 and 2A; inner margin slightly concave to base.

Dorsal surface: Ground colour of discal area in wings orange; limbal area black; base orange, variably infused with black scaling. FW costa with grey-brown scaling; discal cell with three large, irregular black spots, with two similar spots below in cell Cu_2 ; distad an irregular post-discal band of white spots from cells R_2 to 2A, edged basad in black and variably infused with orange scaling; the second middle spot offset distally, the next two in cells M_2 and M_3 together, those in cells Cu_2 and 2A offset basally, all bordered basad by black separating them from orange discal area; distally a submarginal row of prominent rounded yellow-orange spots; distad of this a marginal row of small, indistinct orange/yellow spots; fringe black with variable grey. HW costa with variable black; basal area ground colour dark brown with an irregular central yellow-orange band; post-discal area yellow-orange enclosing an irregular postmedian band of small black spots, with those in cells M_2 and M_3 offset distad; limbal area orange containing a submarginal row of black spots, one in each cell except Cu_2 where there are two, encircled with yellow-orange scaling; margin black, fringe variably grey-brown.

Ventral surface: Ground colour of both wings variable grey-brown. FW discal area with yellow-orange scaling and three large orange spots outlined variably in black and separated with white scaling; cell Sc with three faint grey spots; cell Cu_2 with two large black spots separated with white; post-discal row of rounded white spots bordered basally with black scaling, and distally with black scaling from cell M_2 to Cu_2 ; submarginal row of faint black spots surrounded by lighter scaling, grey with some yellow-orange distad, margin grey; fringe light grey-brown. HW discal area with dorsal figures faintly outlined in dark grey; postmedian irregular row of small dark spots, margin black, fringe grey-brown.

Head: Frons light brown; upper surface white. Labial palpi 3.1 mm long; first two segments white, third

black and curved. Proboscis light brown; swollen at base. Antennal length 60% of forewing length.

Body: Thorax and abdomen dark-brown dorsally; collar light brown. Ventral surface and appendages white. Forelegs truncated, with tibia and unimerous tarsus slender and nearly same length; femur shortened. Midlegs and hindlegs grey-brown, with long, black spurs with scattered spines on inner margin of tarsal segments. Abdomen black-brown dorsally, white ventrally.

Genitalia (Fig. 2B–D; N = 5): Uncus widely separated in ventral view. Socci high, triangular. Tegumen deeply notched between leaves, basally rounded. Falces pointed, turned inward. Vinculum curved from tegumen to just before saccus, wide, supporting extension of eighth sternite segment caudad. Valvae long, pointed, indented ventrally before tip; rounded tips with three or four socketed teeth; dorsally nearly flat. Aedeagus curved, with long, pointed tip. Eighth sternite segment (rami) narrow, curved outward, not joined at base or extending beyond the plural membrane.

Redescription of adult morphology: female (Fig. 1E)

Female (Fig. 1E): Forewing length 16.8 mm, range 18–21 mm ($N = 5$). The female differs from the male as follows.

Wing shape: FW distal margin slightly more rounded than male, with more rounded apex, costa straight; otherwise the same.

Dorsal surface: Lighter ground colour and generally greater width of the median band, in which the yellow-orange spots are larger and joined.

Ventral surface: Lighter than male; ground colour of both wings grey. FW row of white spots wider than dorsal and continuous. On HW, markings less prominent.

Head: Smaller than the male. Proboscis is narrow and light brown.

Body: Same colour as male. Forelegs more elongated than in males; mid- and hindlegs have fewer spines and no black spurs.

Genitalia (Fig. 2E, F): Signae long, narrow, parallel, symmetrical, with short points. Ductus bursae long, narrow, connected directly to ostium bursae. Ostium bursae funnel shaped; constricted at bottom, where

thin ductus seminalis emerges. Lamella antivaginalis lightly sclerotized, flat and slightly notched, with variable pieces of sclerotized material attached. Papillae anales rounded.

Variation

This species shows considerable variation in the extent of the infusion of yellow-orange scaling in dorsal view, especially in the width and colour of the post-discal spots, being orange or completely white in some specimens examined. There is no significant and consistent geographical variation noted among these forms between populations.

Immature-stage morphology (Figs 3–8)

The descriptions and measurements of the immature stage are based on material from both Villa Giardino (Cordoba) and Volcán (Jujuy), Argentina. Developmental times were not recorded and should be variable according to the locality and time of year, because the first generation that emerges in the spring should enter larval diapause during the winter.

Egg (Fig. 3): Height 0.58–0.60 mm; diameter 0.76–0.78 mm ($N = 10$). Colour whitish cream when laid, changing to pale green before hatching. General semispherical shape, with convex upper surface and flattened bottom surface; exochorion with smooth surface and covered by hexagonal cells (Fig. 3A). Several irregular tiny aeropyle openings on the ribs (Fig. 3B). Micropylar area slightly depressed, with five micropyles at the centre (Fig. 3C).

First instar (Figs 4A–E, 6C–E, 8D): Head capsule width 0.29–0.36 mm ($N = 10$); maximum body length 2.7 mm. Black head; dark grey prothoracic shield and greyish anal shield; orange-reddish body, with a

longitudinal whitish band dorsally and translucent setae. Epicranium and frontoclypeus with several primary setae, pores, and two pairs of PCOs in the adfrontal areas. Three pairs of thoracic legs of similar length (Fig. 4A). Body covered by microtrichiae, with short dendritic setae in the lateral areas (Fig. 4B); long setae (~500 μm) directed forwards on prothoracic shield and backwards on anal shield; the remaining dorsal and subdorsal setae are short and dendritic, and tiny PCOs (~10 μm) are associated with these groups of setae (Fig. 4C). Functional TNOs are present in the A8 abdominal segment (Fig. 4D). Proleg with uniordinal crochets in uniserial lateroseries, interrupted near centre by conspicuous fleshy pad (Fig. 4E).

Second instar (Fig. 4F–J): Head capsule width 0.47–0.50 mm ($N = 5$); maximum body length 3.2 mm. General colour pattern similar to first instar, but with more intense orange-reddish tones in the body. Epicranium and frontoclypeus with additional dendritic setae, pores and PCOs (Fig. 4G). Thoracic legs of similar length (Fig. 4F). Body covered by microtrichiae and setae, including scattered dendritic setae and PCOs dorsally (Fig. 4I), row of mid-sized setae laterally and posteriorly, and dorsal pairs of long, clubbed setae on prothorax shield and A1–A7 abdominal segments; these long setae are absent in meso- and metathoracic segments (Fig. 4F, H). Functional TNOs are present in the A8 abdominal segment, delimited by two sclerotized and elevated plates (Fig. 4J).

Third instar (Fig. 8E): Head capsule width 0.79–0.80 mm ($N = 2$); maximum body length 4.4 mm. Head, prothoracic shield, TNO plates and anal shield black; body orange-reddish, with longitudinal whitish bands dorsally. Thoracic legs of similar length; one pair of vibratory papillae arising on margin of prothoracic shield. In general, the morphology is similar to that of

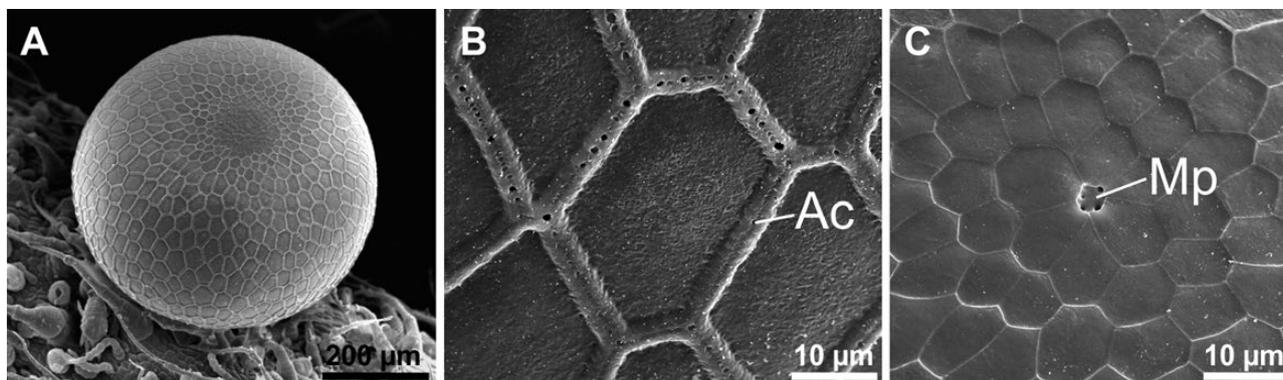


Figure 3. Scanning electron micrographs of *Aricoris arenarum* egg. A, lateral view. B, hexagonal cells of the exochorion with aeropyles (Ac) in the rib intersections. C, micropylar area (Mp).

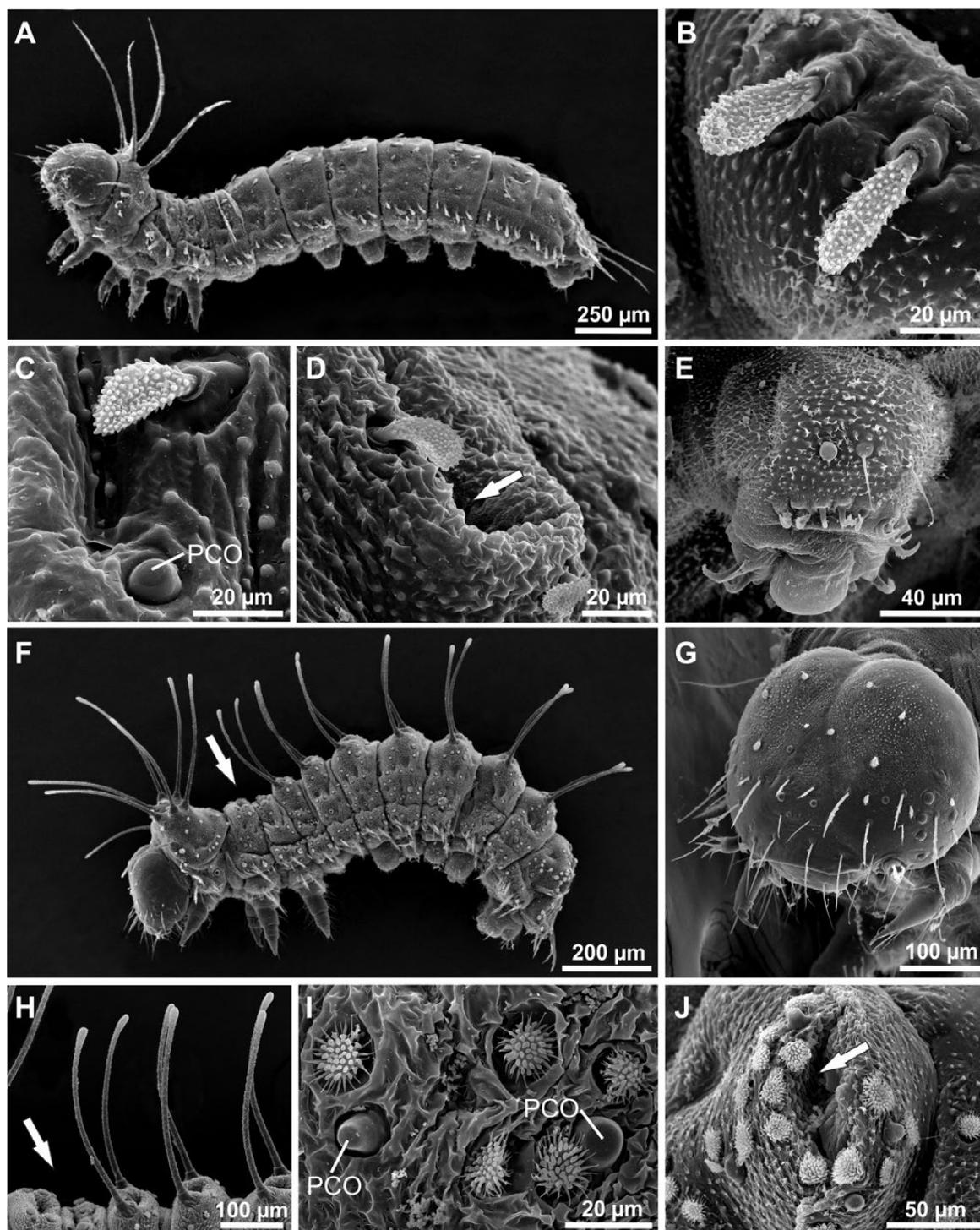


Figure 4. Scanning electron micrographs of the first (A–E) and second (F–J) instars of *Aricoris arenarum*. A, lateral view. B, lateral setae on mesothorax. C, dorsal seta and PCO on mesothorax. D, opening of TNO (arrow). E, proleg of segment A4 in lateroventral view. F, lateral view; note reduce setae on metathorax (arrow). G, head in laterofrontal view. H, dorsal setae in lateral view; note reduced setae on metathorax (arrow). I, dendritic setae and PCOs on mesothorax. J, opening of TNO (arrow).

the second instar, including short dorsal setae on the meso- and metathoracic segments (Fig. 8E), but with more numerous, longer and thicker setae.

Fourth instar (Fig. 6G): Head capsule width 0.87–0.90 mm ($N = 2$); maximum body length 8.7 mm. Head, prothoracic shield, TNO plates, anal shield and pinnacles of dorsal setae black with small white points that correspond to microscopic setae. Body plum reddish; long setae on prothoracic shield, lateral and dorsal abdominal areas whitish beige; vibratory papillae orange. Pairs of long dorsal setae arising on meso- and metathoracic segments.

Fifth (last) instar (Figs 5A–H, 6F, 8F): Head capsule width 1.6–1.8 mm ($N = 2$); maximum body length 21 mm. Head black; prothoracic shield, TNO plates and anal shield dark grey with small white points that correspond to microscopic setae. Body pale pink, covered by small black dots that correspond to microscopic setae; long setae on prothoracic shield and dorsal abdominal areas whitish beige; vibratory papillae orange; lateral setae on body white. Head surface smooth (Fig. 5A, B), with small spiniform elevations in cephalodorsal area (Fig. 5E); PCO distribution scattered, and two types of setae (Fig. 5A, B): filiform setae directed forwards, ventro-frontally associated with mouthparts, and short dendritic setae dorso-frontally. Prothoracic shield with a pair of forward-directed vibratory papillae at anterior margin (Fig. 5D). Body covered by microtrichiae and setae, including dendritic setae and PCOs dorsally (Fig. 5F–H), row of mid-sized setae laterally and posteriorly, and dorsal pairs of long, clubbed setae on prothorax shield, meso- and metathoracic segments and abdominal segments A1–A7 (Fig. 5A, C). Functional TNOs are present in abdominal segment A8, flanked by two sclerotized and elevated plates (Fig. 5A, G). Spiracle (Fig. 5H) on segment A1 is lateroventral, whereas those on segments A2–A8 are in a subdorsal position.

Pupa (Figs 5I–L, 6G): Total length 13.8 mm; width at segment A1 3.2 mm ($N = 2$). Body brown, with some beige areas dorsally. Tegument corrugated, with irregular striations and lacking prominent tubercles (Figs 5I, 6G); wing case and ventral surface smooth. Prothorax bears dorsal clusters of short papilliform setae. Silk girdle crossing abdominal segment A1. Body with some small dendritic setae, and PCOs located in clusters on lateral areas close to spiracles (Fig. 5J, K); these clusters are absent on segments A2 and A7. Scars of TNOs, apparently non-functional, are present dorsally on A8. The consolidated segments A9 and A10 constitute the ventrally flattened cremaster; with short crochets in a ventral position (Fig. 5L).

Distribution (Fig. 7)

The known populations present a disjunct distribution associated with relictual open areas in many parts congruent with the Peripampasic Orogenic Arc (Ferretti *et al.*, 2012). The distribution of *A. arenarum* is Argentina (from province of Jujuy to La Pampa and Buenos Aires; Klimaitis *et al.*, 2018), southern Paraguay, Uruguay and southern Brazil (states of Rio Grande do Sul and Santa Catarina). A single old specimen from south-east Brazil (Rio Batalha, state of São Paulo) was lost in the MNRJ fire in September 2018.

Material examined

Argentina: No locality, one ♂, no. 54/364, MNRJ-Ent5-14312, ex Coll. E. May, one ♂, no. 54/365 (lost material) (MNRJ). Buenos Aires: Sierra de la Ventana, December 1996, one ♀ (CJC), 24 November 2003, one ♀ (CENB), Tandil, December 1957, three ♂, March 1958, one ♂, Coleccion Hano (IML), February 1959, one ♂, MC76790, December 1959, two ♂, MC76793-94, Collection Biezanko (MCZ). Córdoba: Capilla del Monte (30°52'S, 64°32'W, 985 m a.s.l.), 28 January 2015, one ♂, one ♀, 26 November 2015, one ♂, L. A. Kaminski leg. (CLK); Córdoba, 16 November 2005, one ♀ (CJC); La Cumbre (30°56'S, 64°23'W, 1400 m a.s.l.), 27 January 2015, one ♂, DNA-voucher LAK370, L. A. Kaminski leg. (CLK). Mina Clavero, 1600 m, 29 January 2003, one ♂, A. Moser leg. (CAM). San Ignacio (30°56'S, 64°31'W, 1053 m a.s.l.), 16 February 2014, two ♂, DNA-voucher LAK261, LAK262., L. A. Kaminski leg. (CLK). Villa Carlos Paz, 750 m, 28 January 2003, one ♀, A. Moser leg. (CAM). Jujuy: Morro de Alizar, 9 January 1977, two ♂, two ♀, C. Callaghan leg. (CJC). Rio Lozano, 30 September 1976, one ♂, one ♀, C. Callaghan leg. (CJC). Volcán, Rio del Medio, 1952 m, 21 January 1992, one ♂ (CJC), 28 November 1974, one ♂, one ♀, A. Willink & Stange leg. (IML). La Pampa: El Carancho (37°26'S, 65°2'W, 320 m a.s.l.), 19 December 2018, two ♂, one ♀, DNA-voucher LAK609, L. A. Kaminski leg. (CLK). Misiones: Posadas (as 'Pasadas' [sic]), December 1922, Joicey Bequest Brits. Mus. 1934-120, NHMUK 013673434. Rio Negro: December 1956, one ♀ (MLP). Santa Fé: Villa Ana, February 1924, three ♂, one ♀; October 1924, one ♂; November 1924, one ♂, one ♀; January 1925, one ♂, one ♀; February 1925, one ♀; March 1925, one ♂, two ♀; September 1925, three ♂, five ♀; 10–31 October 1926, one ♂; January 1926, one ♂; February 1926, one ♂, two ♀; March 1926, one ♀, K. J. Hayward leg. (IML); 1–18 February 1946, one ♀, K. J. Hayward & A. Willink leg. (IML).

Brazil: Rio Grande do Sul: Caçapava do Sul, Guaritas (30°49'S, 53°30'W, 250 m a.s.l.), 20 January 2020, one ♂, L. A. Kaminski leg. (CLK). Don Pedrito,

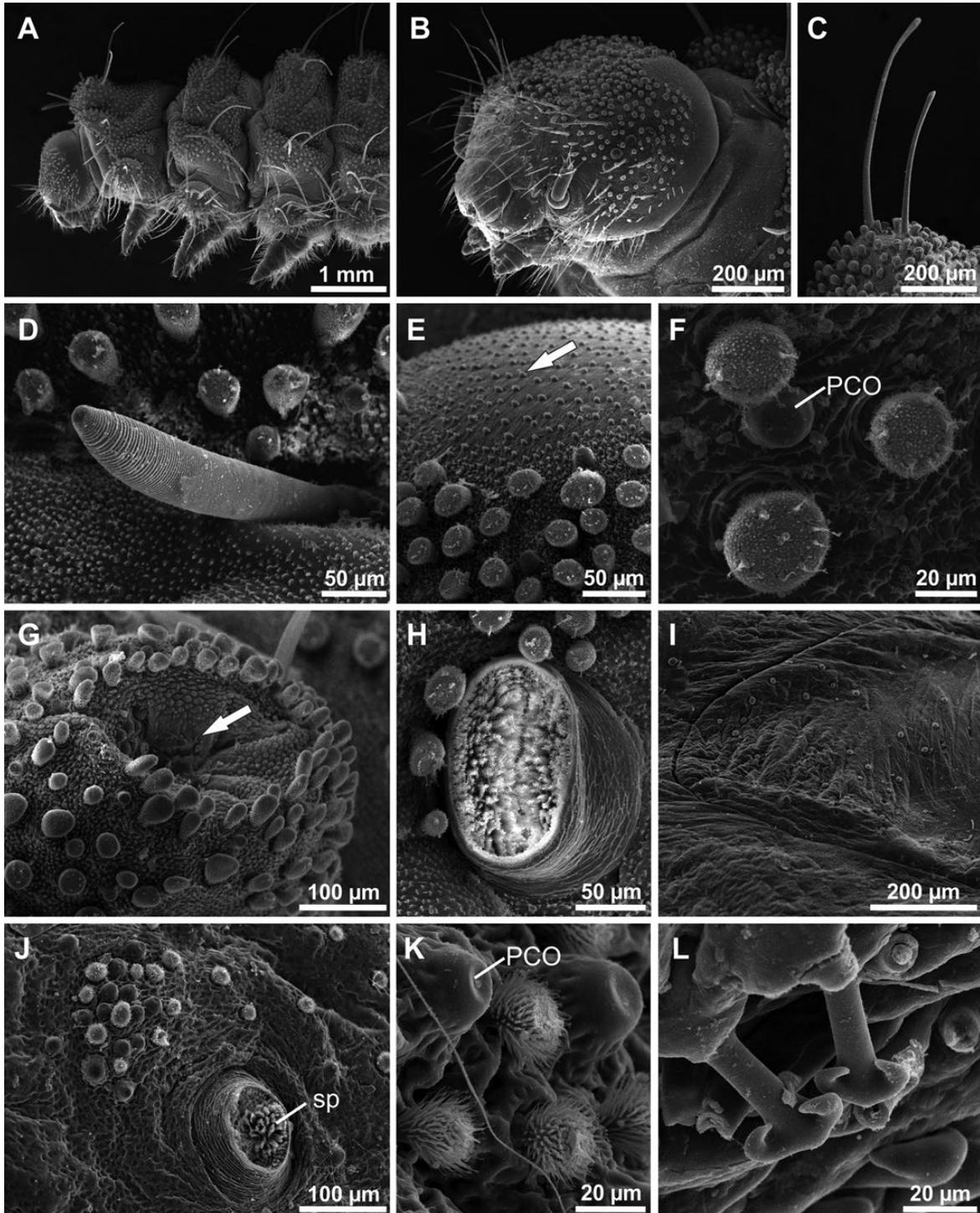


Figure 5. Scanning electron micrographs of the last instar (A–H) and pupa (I–L) of *Aricoris arenarum*. A, head and thorax in lateral view. B, head in laterofrontal view. C, long dorsal setae on mesothorax. D, vibratory papillae. E, detail of spiniform elevations (arrow) on cephalodorsal area. F, dendritic setae and PCOs on segment A2. G, opening of TNO (arrow). H, prothoracic spiracle. I, dorsal view of metathorax. J, cluster of dendritic setae and PCOs above spiracle (sp) on segment A5. K, detail of dendritic setae and PCOs. L, detail of cremaster crochets.



Figure 6. Life cycle of *Aricoris arenarum* tended by 'black morphs' of *Camponotus punctulatus* ants on *Geoffroea decorticans* (Fabaceae), showing both free-living and social parasitic phases. A, female at post-landing phase. B, eggs close to ant-tended treehoppers (dashed ellipse). C, eggs (white arrows) and first instar caterpillars (black arrows) close to scale insets, both tended by ant workers. D, first instar caterpillar (black arrow) close to ant-tended treehoppers. E, sequence of worker drinking honeydew from treehopper (top panel, white arrow) and first instar requesting trophallaxis from ant (bottom panel, white arrow); note the typical larval posture and long prothoracic setae. F, last instar caterpillar tended by ants inside brood chamber. G, penultimate instar (black arrow indicates the everted larval TNO) and pupa inside the ant nest (white arrow). Scale bars: 5 mm in A, B, C, D, F, G; 2 mm in E.

20–21 November 2012, two ♂, two ♀ Romanowski *et al.* leg. (DZRS). Encruzilhada do Sul, 400–500 m, 2–3 December 2000, one ♂, A. Moser leg. (CAM). Estação Ecológica do Taim, 13 January 1999, two ♂; 4–7 March 2013, one ♀, A. Moser leg. (CAM); 7 March

2013, two ♀, CLDZ 9252–9253; 25–26 November 2013, five ♂, three ♀, CLDZ 9247–9251, 9254–9256, H. P. Romanowski *et al.* leg. (DZRS); 7 March 2013, one ♂, DNA-voucher LAK228, V. Pedrotti & A. Moser leg. (CAM). Jaguari, 16 January 2001, one ♂,

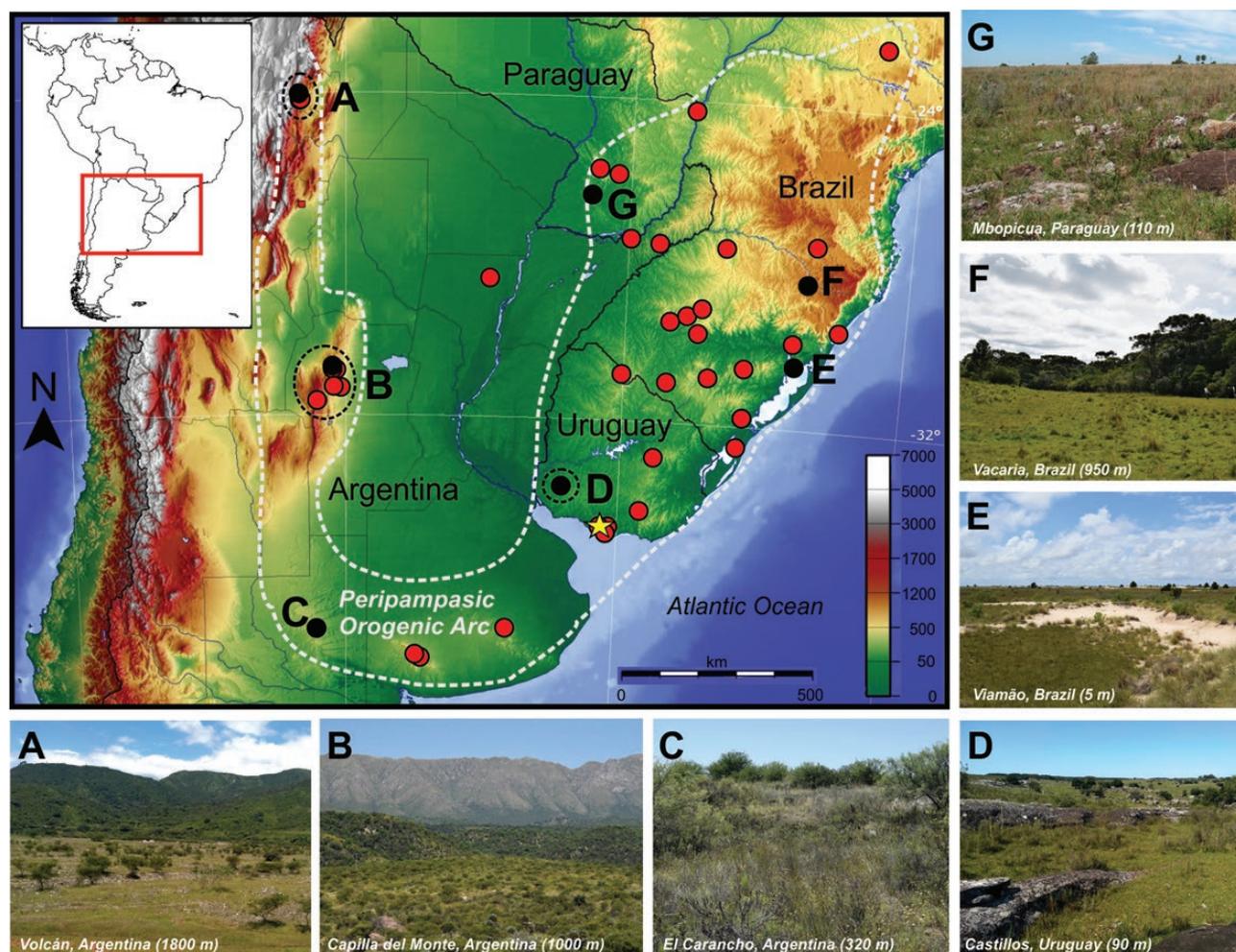


Figure 7. Map of South America (top left) and detail of topographic map of Río de la Plata basin (red rectangle) showing the geographical distribution of *Aricoris arenarum* (red circles), type locality in Uruguay (yellow star) and overview of studied vegetation habitats (black circles). A, mountain Chaco in Volcán, Jujuy, Argentina. B, mountain Chaco in Capilla del Monte, Córdoba, Argentina. C, dry Espinal in El Carancho, La Pampa, Argentina. D, Pampean grassland in Castillos, Uruguay. E, coastal sand grasslands in Parque Estadual de Itapuã, Viamão, Rio Grande do Sul (RS), Brazil. F, grassland–Atlantic forest mosaic in Vacaria, RS, Brazil. G, natural grasslands in Mbopicua, Paraguari, Paraguay. Dashed white line delimits the Peripampasic Orogenic Arc (modified from Ferretti *et al.*, 2012), and black dashed line indicates the life cycle study sites (A, B, D, respectively).

A. Moser leg. (CAM). Jari, 23 November 2011, one ♂, CLDZ-8021 (DZRS). Pelotas, 30 November 1956, one ♂, C. Biezanko leg. DZ 38.500; 25 November 1957, one ♂, J. L. Mantovani leg., DZ 38.350 (DZUP). Pinhal, April 1971, one ♂, C. A. Trois leg. (DZRS). Santa Maria, 2–8 November 1972, three ♀, DZ 38.680, DZ 38.300, DZ 38.630 (DZUP). São Leopoldo, 8 January 1994, four ♂, one ♀; 15 January 1994, one ♂, A. Moser leg. (CAM). Vacaria, Bela Vista, one ♂ (DZUP). Viamão, Parque Estadual de Itapuã (30°23'S, 51°17'W, 5 m a.s.l.), 20 January 2002, one ♀; February 2002, one ♂, E. C. Teixeira leg. (DZRS). Torres, Praia Paraiso, 13–17 March 2012, one ♂, one ♀, A. Moser leg. (CAM). Tupanciretã, 16 March 2012,

one ♀, CLDZ 8022, B. O. Azambuja leg. (DZRS). São Paulo: Rio Batalha, one ♀, no. 54/368 (lost material) (MNRJ). Santa Catarina: Curitibanos, 7 March 1983, one ♂, one ♀ H. Miers leg. OM67315, OM67637 (OM).

Paraguay: No locality, one ♂, Crowley bequest 1901–18 (NHMUK). Guairá: Villarica, 20 March 1930, three ♂, two ♀ (MLP); 20 February 1950, one ♂, one ♀, Colección Breyer (IML). Paraguari: Mbopicua (26°20'S, 57°8'W, 110 m a.s.l.), 9 March 2014, one ♂, DNA-voucher LAK133, L. A. Kaminski leg. (MNHNPA), Sapucaí, 10 December 1902, one ♀; 30 March 1903, one ♂; 1 November 1903, one ♂; 17 November 1904, one ♂; 23 December 1904, one ♂; 19 November 1904,

one ♂, W. Foster leg., Rothschild Bequest B. M. 1939-1 (NHMUK).

Uruguay: Canelones: Castillos (33°49'S, 57°40'W, 90 m a.s.l.), 23 January 2020, one ♂, three ♀, L. A. Kaminski leg. (CLK). Las Piedras, 12 September 1976, one ♀, A. Carmenes leg. (FCE-LP). Lavalleja: Minas, Cerro Arequita (34°17'S, 55°16'W, 155 m a.s.l.), 23 January 2020, one ♂, L. A. Kaminski leg. (CLK). Maldonado: La Barra, 29 November 1936, one ♂, one ♀, H. Schneider leg. (ZFB). Montevideo: Montevideo, 13 November 1926, one ♀, Col. De S. Dobree, (NHMUK). Treinta y Tres: Santa Clara, 17 February 1960, one ♂, MC76792, L. Zolessi leg., Collection Biezanko (MCZ).

Behaviour and natural history

Populations of *A. arenarum* are found located at particular sites. Females have a slow and passive flight, a feature first noted by Schneider (1937). During the late afternoon (13.00–18.00 h), males can be observed lekking in small territories in the same places. The physiognomy of the vegetation of these sites ranges from mountain Chaco habitats (Fig. 7A, B), with sparse shrubs and an abundance of 'espinillo' *Vachellia caven* (Molina) Seigler & Ebinger and 'chañar' *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart (Fabaceae), to dry Espinal (Fig. 7C) and Pampean grasslands, from coastal sand dunes (type locality) to highlands in the Atlantic Forest domain (Fig. 7D–G) (for details of vegetation types see Cabido *et al.*, 2018; Oyarzabal *et al.*, 2018).

These sites are always occupied by large polydomic colonies of 'black morphs' of *C. punctulatus*. This dominant ant nest in the ground is active both during the day and at night and monopolizes the liquid food sources on plants, such as extrafloral nectaries and honeydew-producing hemipterans. For taxonomic details of this polytopic ant species and discussion about red and black morphs see Kusnezov (1952).

The females of *A. arenarum* spend the hottest hours of the day in searching for ant trails and laying eggs on the vegetation (Figs 6A, B, 8C), always near hemipteran aggregations tended by *C. punctulatus* (Fig. 6C–E). We found caterpillars associated with four scale insect (Coccoidea) morphotypes and one treehopper (Membracidae) species. Some plants could contain dozens of eggs, many of which proved infertile. Oviposition was observed several times ($N = 12$ in Argentina, $N = 2$ in Uruguay). Substrates for oviposition include different host plant families, primarily grass species (Poaceae) in Pampean grasslands and scrub species in mountain chaco, such as *Geoffroea decorticans* and *Galactia marginalis* Benth. (Fabaceae), the invasive *Pastinaca sativa* L. (Apiaceae), *Schinus fasciculata* (Griseb.)

I.M. Johnst. (Anacardiaceae), *Baccharis ulicina* Hook. & Arn. (Asteraceae) and *Gnaphalium* sp. (Asteraceae). Although females can lay their eggs remarkably close to ant–hemipteran associations, the ants are often aggressive and try to prevent oviposition.

First and second instar larvae live together with ant–hemipteran associations (Fig. 6C–E); while the ants tend the hemipterans, the caterpillars await the release of honeydew, stealing the drops before the ants can feed. In the laboratory, a first instar larva was observed cannibalizing a conspecific egg. Plants infested by scale insects and treehoppers that are heavily tended by ants can harbour many caterpillars (15–20). These caterpillars can also request honeydew from hemipterans through rapid head movements; this behaviour was observed when the ants were absent in the field and laboratory. Caterpillars can also receive food resource via trophallaxis directly from ants; for this, they raise the anterior portion of the body and touch the ant mouthparts with their long, forward-directed prothoracic setae (Fig. 6E).

From the third instar on, the caterpillars change the free-living behaviour on plants to a social parasitic lifestyle within the ant nest. The details of how this transition takes place are still unknown. We never found mature larvae (from the third instar on) on the plants, only first and second instars. During the excavation of the base of a plant previously occupied by larvae, we found a third instar caterpillar buried ~20 cm below the ground, apparently following the ant trails. In Córdoba, we excavated several ant nests in search of caterpillars, but we did not find any. In Jujuy, mature caterpillars were found inside brood chambers of *C. punctulatus* [cited as *Camponotus distinguendus* (Spinola, 1851) by DeVries *et al.*, 1994; DeVries, 1997] immediately underneath the stones in a rocky field; probably, they were warming up on a cold day together with the ant brood.

In the laboratory, caterpillars from both Córdoba (first to third instars) and Jujuy (last instar) populations were offered plant material (grass and/or chañar) with honeydew-producing hemipterans, and both living and macerated ant brood, but the caterpillars did not feed on them. Third instar larvae placed inside the experimental ant nest completed their development without the availability of food plant items and/or honeydew-producing hemipterans. During the parasitic phase, the caterpillars remained in the ant brood chambers and received trophallaxis from the worker ants (Figs 6F, G, 8F). There were no agonistic interactions between larvae and ants. Workers occasionally antennated the caterpillars, especially on segment 8A near the TNOs. In response, the larvae everted the TNOs, but without providing visible secretions. Pupation took place inside the ant nests (Fig. 6G).

DISCUSSION

Ant colonies are homeostatic fortresses with complex communication and recognition systems (Hughes *et al.*, 2008). Many organisms can circumvent these security systems and live as social symbionts within the ant nest (Hölldobler & Wilson, 1990). Multiple transitions from pre-adapted free-living ancestors to social parasitism have been documented in myrmecophilous beetles, illustrating the predictability of this evolutionary process (Maruyama & Parker, 2017). In butterflies, social parasitism appeared a few times in Lycaenidae through different evolutionary routes (Cottrell, 1984; Pierce, 1995; Osborn & Jaffé, 1997; Fiedler, 1998). Riodinidae, the sister family that diverged ~90 Mya (Espeland *et al.*, 2018; Fig. 8A), shares pre-adaptive traits (e.g. PCOs) and developed ant-organs analogous to those of Lycaenidae that also enable myrmecophily (DeVries, 1991b). The discovery of social parasitism in Riodinidae offers the opportunity for a deeper analysis of the different evolutionary routes that lead to social parasitism in butterflies. In a comparative framework, Fiedler (1998) proposed three types of lycaenid–ant parasitism: (1) the Miletinae type, derived from a hemipteran-predator ancestor; (2) the Aphnaeini type, derive from an ancestor with obligate myrmecophily; and (3) the *Maculinea* type, derived from a facultative myrmecophilous ancestor. In addition, Fiedler (1998) pointed out that social parasitism occurs predominantly in highly seasonal habitats and suggested that this phenomenon started with caterpillars seeking shelter in ant nests.

The case of *A. arenarum* fits the Aphnaeini type, because most known *Aricoris* species are phytophagous and establish obligate trophobiotic interactions with their tending ants (Kaminski & Carvalho-Filho, 2012; Volkmann & Kaminski, 2015). Thus, the evolution of social parasitism within *Aricoris* must be much younger than the estimated age for the split between *Ariconias* and *Aricoris* (~11 Mya; Seraphim *et al.*, 2018; Chazot *et al.*, 2019). These butterflies have diversified widely in the open and/or dry seasonal areas of South America (Caatinga, Cerrado, Chaco and Pampa), and the use of underground shelter during the day is a behaviour likely to be associated with their success in extreme environments. Thus, in addition to escaping daytime predation, the caterpillars can escape from the typical high temperatures of these environments. During the cold or dry winter months, the *Aricoris* caterpillars usually go into diapause within these underground shelters (DeVries, 1997; Volkmann & Kaminski, 2015). Both behaviours agree with the idea of the importance of abiotic factors (seasonality) and use of ant shelters for the evolution of social parasitism. In contrast, the key to the evolution of social parasitism in *A. arenarum* seems to be the kleptoparasitic

exploitation of ant–hemipteran mutualistic systems through tactile mimicry.

The detailed comparison with *N. fusca*, an Asian Lycaenidae with a remarkably similar life cycle, supports this hypothesis. Both species occur in a subtropical to temperate climate and are associated with a dominant *Camponotus* species. The *A. arenarum* and *N. fusca* females oviposit only in the presence of ant–hemipteran associations. Throughout the ontogeny, the morphology of the caterpillars is extremely similar, generally through convergent evolution, although some traits seem to represent cases of parallelism (Fig. 8; Table 1). In the first instar, the long, forward-directed setae are present on the thorax and are used to request hemipteran honeydew (Fig. 8D, H). The comparative analysis of chaetotaxy indicates parallelism for the setae on the prothorax, with homologous setae performing the same function, whereas the dorsal mesothoracic setae are elongated only in *Niphanda*, indicating convergence. In the second instar, long setae occur dorsally along the body, except for the metathorax, which presents short setae (Fig. 8E, I). This reduction of the metathoracic setae facilitates the movement of the anterior portion of the body, which is essential for reaching the mouth of the ant during trophallaxis. In ants, trophallaxis is induced by a simple tactile communication mechanism (the touch of the labium by antennae or legs), and different lineages of kleptoparasites use different structures to request ant regurgitations through tactile mimicry (Hölldobler & Wilson, 1990). In addition to the food resource, it has recently been shown that trophallaxis might also transfer social information (Hayashi *et al.*, 2017). Thus, ant regurgitations might contain the access key to the ant nest, a hypothesis that needs to be tested.

In *N. fusca*, adoption is mediated by tentacle organs (TOs) in the third instar (Nagayama, 1950; Hojo *et al.*, 2014), but we still do not know whether active adoption by tending ants occurs in *A. arenarum*. The TNOs of *A. arenarum* have lost the main riodinid function of producing nutritional rewards and appear to play a direct role in chemical communication with ants. These organs are homologous in position with Lycaenidae TOs, which are also used exclusively for chemical communication (Henning, 1983; Axén *et al.*, 1996; but see Gnatzy *et al.*, 2017). At the same time, the anterior tentacle organs (ATOs), which are present in *Aricoris* and related genera in Lemonyadina, with a functional role in chemical communication (Ross, 1966; DeVries, 1988), have been lost in *A. arenarum*. Thus, a functional reorganization of these ant-organs, unique among the Riodinidae, has resulted in a body plan and functioning remarkably similar to that of Lycaenidae, i.e. tentacle organs only in the eighth

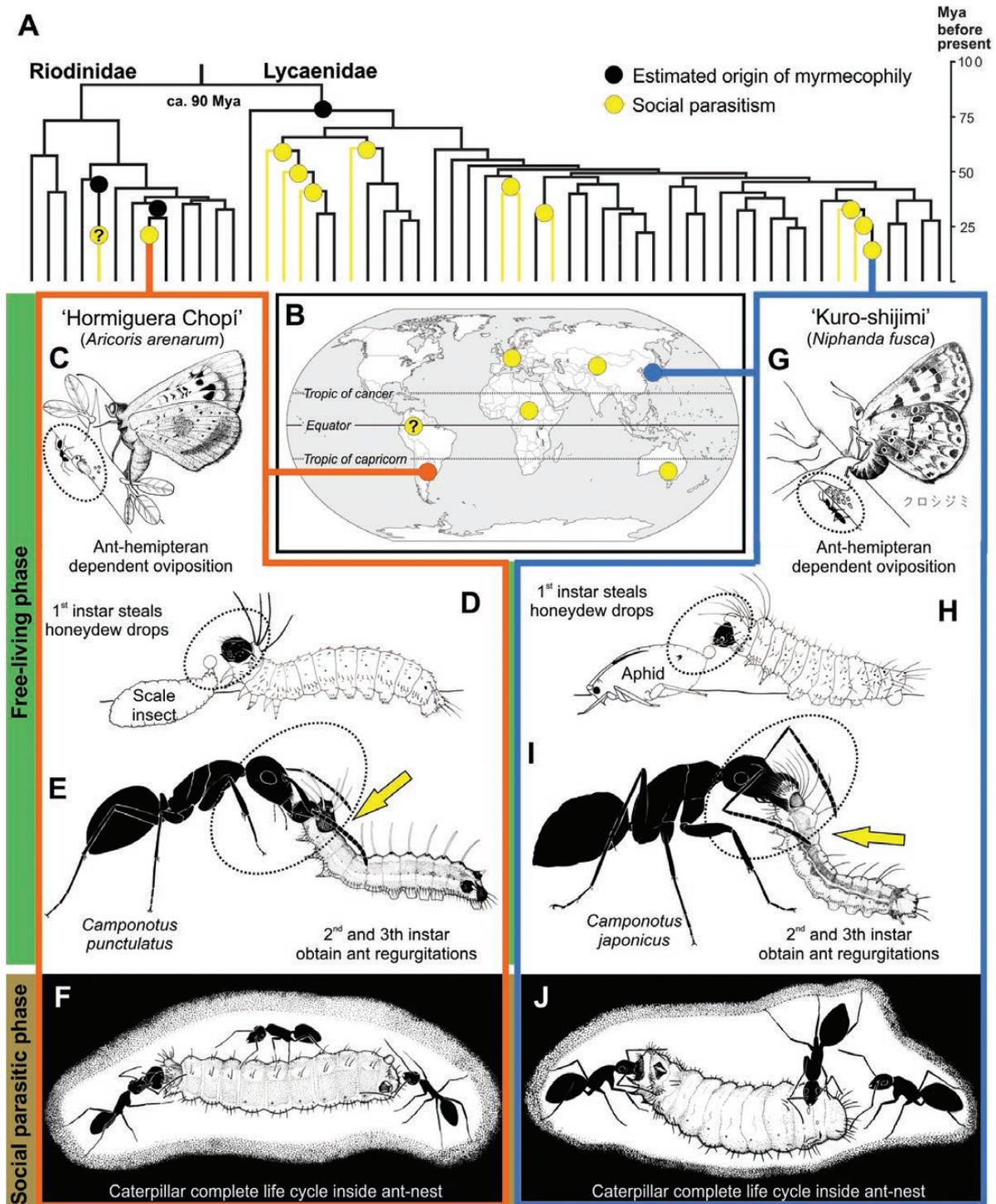


Figure 8. Comparative phylogenetic position, geographical distribution and life cycles of two ‘cuckoo’ butterflies: ‘Hormiguera Chopi’ *Aricoris arenarum* (orange lines) and ‘Kuro-shijimi’ *Niphanda fusca* (blue lines), respectively. A, phylogeny of Riodinidae and Lycaenidae based on the study by [Espeland et al. \(2018\)](#), showing estimated dated origins of myrmecophily (black dots), social parasitic lineages (yellow dots) according to [Fiedler \(2012\)](#) and an unconfirmed case (yellow dot with question mark). Orange, *A. arenarum*; blue, *N. fusca*. B, world map indicating continental records of social parasitism in butterflies. C–F, *A. arenarum* life cycle sequence, illustrating: C, female oviposition close to ant–hemipteran

Table 1. Homoplastic ecomorphological traits shared between *Aricoris arenarum* (Riodinidae) and *Niphanda fusca* (Lycaenidae) (for details, see Fig. 8 and Discussion)

Ecomorphological trait	Potential type of homoplasy	Hypothetical adaptive significance
Ant–hemipteran-dependent oviposition	Convergence	Increases the likelihood of interaction
Loss of plant specificity and oviposition on Poaceae	Convergence	Exploitation of new ant–plant–hemipteran systems
Feed on liquids (hemipteran honeydew and ant regurgitations)	Convergence	Reduction of symbiotic cost by not feeding directly on plant tissue, hemipterans or ants
Social parasitism	Convergence	Stable and enemy-free environment (ant nest) during cold months and nutritional benefits
Pinkish last instar caterpillars	Convergence	Lack of plant pigments and/or no selection for visual crypsis
Long thoracic setae directed forwards	Parallelism and convergence	Tactile communication with hemipterans and ants
Reduction of dorsal setae on metathorax	Parallelism	Improved mobility of the anterior portion, facilitating ant trophallaxis
Tentacle organs on eighth abdominal segment	Convergence and parallelism	Chemical communication with tending ants

abdominal segment and apparently used for chemical communication. The functional plasticity of ant-organs seems to be a recurring phenomenon in riodinids (Kaminski, 2008; Nielsen & Kaminski, 2018). We do not yet know the role of circular hydrocarbons in chemical mimicry in *A. arenarum*, but this is a key process in *N. fusca* and other social parasitic caterpillars (Akino *et al.*, 1999; Hojo *et al.*, 2009). Although the acoustic context has not yet been explored in *Niphanda* and *Aricoris*, all species of the latter genus that have been studied present structures potentially used for acoustic communication (vibratory papillae; Fig. 5D–E), as observed in other social parasitic systems (DeVries *et al.*, 1993; Barbero *et al.*, 2009).

Although parasitic caterpillars show spectacular cases of convergence, they can also be markedly different depending on the ecological context. Some parasitic caterpillars are defended by a thick cuticle and modified setae that prevent ant attacks and allow them to enter the ant nests forcefully (e.g. Dupont *et al.*, 2016), in which case the caterpillar–ant interaction is basically antagonistic (Miletinae type). The *Maculinea*

type involves an herbivorous phase and neotenic-looking caterpillars that use multimodal sensorial mimicry to live in ant nests (Casacci *et al.*, 2019). The Aphnaeini type can include different multifaceted strategies and, possibly, this type should be split into several biological groups (see discussion by Cottrell, 1984; Osborn & Jaffé, 1997; Boyle *et al.*, 2015). Overall, this categorization reflects different basic eco-evolutionary pathways that resulted in a suite of ecomorphological homoplasies shared within the members of each type. The extraordinary similarity between *A. arenarum* and *N. fusca* shows that the exploitation of symbiotic systems involving plants, hemipterans and ants in a similar ecological context can result in similar morphological and behavioural solutions, even in deeply diverged lineages, illustrating the importance of convergent multispecies interactions in evolution (Bittleston *et al.*, 2016).

CONCLUDING REMARKS

The life cycle of *A. arenarum* is described, which represents the first ‘cuckoo’ caterpillar in Riodinidae.

association (dashed ellipse); D, first instar feeding on hemipteran honeydew (dashed ellipse); E, third instar with reduced setae on metathorax (yellow arrow) feeding on ant regurgitation (dashed ellipse); F, last instar inside ant nest. G–J, *N. fusca* life cycle sequence, depicting: G, sequence of female oviposition (dashed ellipse); H, first instar feeding on hemipteran honeydew (dashed ellipse); I, third instar with reduced setae on metathorax (yellow arrow) feeding on ant regurgitation (dashed ellipse); J, last instar inside ant nest.

Ecomorphological traits are compared with those of parasitic Lycaenidae, in particular with those of the Asian *N. fusca*. Despite divergence ~90 Mya, multiple traits show remarkable homoplasy between these two species, either through convergence or through parallelism. This discovery provides new insights into the evolution of social parasitism in butterflies and shows that ecological determinants (e.g. the parasitic strategy and host ant system) are more important than phylogenetic proximity in shaping the morphological and behavioural traits of social parasites. The tortuous taxonomic history of *A. arenarum*, spending > 80 years in limbo, exemplifies the current state of knowledge about the diversity of this family of butterflies. There are shortfalls at all levels, from alpha taxonomy, which generates taxonomic impediments, to basic natural history information (DeVries, 1997). Although much recent effort has been made to address the taxonomy and evolution of these butterflies (e.g. Dolibaina *et al.*, 2013; Espeland *et al.*, 2015, 2018; Hall, 2018; Seraphim *et al.*, 2018), many gaps still exist, and cryptic diversity is poorly explored. New findings of caterpillars within ant nests, such as *Alesa rothschildi* (Seitz) in the Amazon canopy (see Gallard, 2017) and unpublished anecdotal observations by the authors suggest that social parasitism in riordinids might have arisen independently in all Nymphidiini subtribes and, possibly, also in Eurybiini (Fig. 8A). As exemplified by the present study, each discovery in Riordinidae might reveal new strategies and possibilities of convergence with Lycaenidae. This diversity is severely threatened by anthropic activity, and the description of vanishing yet-unknown life cycles and evolutionary pathways is urgent, even more so for their protection.

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