



SOCIEDADE BRASILEIRA
DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution

www.rbentomologia.com



Systematics, Morphology and Biogeography

A new species of *Actinote* Hübner (Nymphalidae: Heliconiinae: Acraeini) from southeast Brazil



André Victor Lucci Freitas^{a,*}, Ronaldo Bastos Francini^b, Márlon Paluch^c, Eduardo Proença Barbosa^a

^a Universidade Estadual de Campinas, Instituto de Biologia, Departamento de Biologia Animal, Campinas, SP, Brazil

^b Universidade Católica de Santos, Santos, SP, Brazil

^c Universidade Federal do Recôncavo da Bahia, Centro de Ciências Agrárias, Ambientais e Biológicas, Cruz das Almas, BA, Brazil

ARTICLE INFO

Article history:

Received 24 October 2017

Accepted 26 January 2018

Available online 9 February 2018

Associate Editor: Livia Pinheiro

Keywords:

Atlantic Forest

Araucaria Forest

Actinote alalia

Species redescription

Immature stages

ABSTRACT

The present paper describes a new species of *Actinote* (Nymphalidae, Heliconiinae, Acraeini) from southeastern Brazil, and describes the morphology of the adults and immature stages of this species. *Actinote mantiqueira* sp. nov. occurs in the Serra da Mantiqueira and Serra do Mar in the Atlantic Forest. Adults from this population are very similar to other species of the “orangish red mimicry complex”, including *Actinote alalia* (C. Felder & R. Felder, 1860), its sister species, restricted to the mountains of southern Brazil. *Actinote mantiqueira* sp. nov. and *A. alalia* are distinguishable by wing pattern, male genitalia and larval morphology, and have strongly allopatric distributions. A redescription of *Actinote alalia* is also provided.

© 2018 Sociedade Brasileira de Entomologia. Published by Elsevier Editora Ltda. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

The genus *Actinote* Hübner, [1819] (*sensu* Lamas, 2004, see also Silva-Brandão et al., 2008) is composed of 35 described species, occurring in the Neotropical region from southern Mexico (Guerrero, Veracruz, Oaxaca and Chiapas) to northern Argentina in the border provinces of La Rioja, Córdoba and Buenos Aires (Lamas, 2004; Paluch, 2006; Paluch et al., 2006; Neild, 2008; Willmott et al., 2009, 2017). The genus reaches its greatest species richness in the montane areas of southeastern Brazil (Brown, 1992; Lamas, 2004; Paluch, 2006; Silva-Brandão et al., 2008; Neild, 2008; Willmott et al., 2009). Larvae of all known species feed on host plants within the family Asteraceae and are highly gregarious in all instars (Francini, 1989, 1992; Freitas et al., 2010 and references therein). With some notable exceptions (e.g. *Actinote zikani* R.F. d’Almeida, 1951, see Francini et al., 2005, 2011), adults of *Actinote* are associated with forest edges, clearings and other open environments where their host plants grow (Francini, 1989; Francini and Freitas, 2010; Freitas et al., 2009a,b, 2010).

Species of *Actinote* are cyanogenic in all life stages and rarely preyed upon by natural enemies, which include visually oriented vertebrates (Brown and Francini, 1990), and adults are usually

involved in Müllerian and Batesian mimicry complexes with several species of butterflies and moths (Brown, 1992). In part because of this mimicry, *Actinote* butterflies are notoriously difficult to tell apart (e.g., D’Almeida, 1925, 1935; Francini, 1989, 1992; Penz and Francini, 1996), and species identification can be challenging, often resulting in misidentification (especially for females) and mixed series frequently identified as a single species (Francini, 1989; Paluch, 2006). Conversely, larvae of most species are usually quite distinct, even among very similar species, and can be very helpful for species identification, especially within the “orange-yellow mimicry complex” (Francini, 1989; Francini et al., 2004). Molecular data, however, has proven to be ineffective in discriminating among species in some clades, such as in the *Actinote pellenea* clade (formed by *A. pellenea* Hübner, [1821], *Actinote carycina* Jordan, 1913 and *Actinote pyrria* Fabricius, 1775) (Silva-Brandão et al., 2008; Silva-Brandão et al., *in prep.*).

The species in the “orangish red mimicry complex” (Francini, 1989) are classic example of these problems in identification. All species within the group are very similar (most of them, in fact, share a common ancestor, see Silva-Brandão et al., 2008), characterized by a dark orange and brown dorsal striped pattern, with a ventral pattern that is somewhat variable among species and therefore useful for identification. Four southeast Brazilian species have been described within the group, from 1860 to 1913, including *Actinote alalia* (C. Felder & R. Felder, 1860).

In the original description of *Acraea alalia*, Felder & Felder (1860) provided just a brief description of male wing pattern; the numbers

* Corresponding author.

E-mail: baku@unicamp.br (A.V.L. Freitas).

of individuals used for the description and the exact type locality were not provided, with just the country of origin, Brazil, being mentioned. Lamas (1997) designated a male (without the head) as the Lectotype of *A. alalia*, and proposed that the type locality was southeastern Brazil. In the same year, Penz and Francini (1996) described three new species based on material previously misidentified as *A. alalia*, solving most of the problems related to this complex of cryptic species. Finally, in a recent unpublished thesis about the genus *Actinote*, Paluch (2006) redescribed *A. alalia* in detail, including host plant, voltinism and its geographical distribution.

Detailed morphological study of all southeastern Brazil populations of *A. alalia* have revealed that this species, as presently conceived, comprises two distinct taxa, distinguishable by wing pattern, male genitalia and larval morphology, and with clearly allopatric distributions (a molecular study of the “orangish red mimicry complex” is currently being prepared). In the present paper, a new species of *Actinote*, previously identified as *A. alalia*, is described based on morphology of adults and immature stages. Due to several incongruences in the original description (not acknowledged by Paluch, 2006), we also present a redescription of *Actinote alalia*.

Material and methods

Drawings and measurements of wings, legs and palpi were made using a Leica® MZ7.5 stereomicroscope equipped with a micrometric scale and a drawing tube. Photographs of the male and female genitalia and some measurements were taken using a Zeiss® Discovery V20 Stereomicroscope. Dissections were made using standard techniques, where legs, palpi, and abdomens were soaked in hot 10% KOH solution for 10 min before dissection, and dissected parts were stored in glycerol. To study the venation, wings were diaphonized by soaking them in alcohol and NaClO solution (bleach) and mounted in slides. Taxonomic nomenclature follows Lamas (2004), modified after Wahlberg et al. (2009). Male and female genitalia terminology follows Klots (1970). Nomenclature of venation used herein follows Wootton (1979) modified from Comstock and Needham (1898–99). Specimens of *Actinote* were examined in 14 public and private collections (see below) (no specimens of *A. alalia* or of the new species were found in the MNHN and USNM). The Lamas collection of Neotropical butterfly type specimen photographs at the MUSM (also available online in Warren et al., 2017), representing most currently relevant names and recognized species of *Actinote* (Lamas, 2004), was examined.

The acronyms for visited collections are: NHMUK, The Natural History Museum, London, England; CGCM, Coleção Carlos Guilherme Costa Mielke, Curitiba, Paraná, Brazil; CLDZ, Coleção de Lepidoptera, 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; IOC, Instituto Oswaldo Cruz, Rio de Janeiro, RJ, Brazil; MC, Coleção Moser, São Leopoldo, Rio Grande do Sul, Brazil; MECB, Museu Entomológico Ceslau Biezanko, Departamento de Fitossanidade, Universidade Federal de Pelotas, Pelotas, Rio Grande do Sul, Brazil; MNHN, Muséum National d’Histoire Naturelle, Paris, France; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; OM, Coleção Olaf Mielke, Curitiba, Paraná, Brazil; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; ZUEC, Museu de Zoologia da Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil; ZUEC-AVLF, André V. L. Freitas Collection, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Results

Actinote mantiqueira Freitas, Francini, Paluch & Barbosa, **sp. nov.**
Actinote alalia; Ebert, 1969:35; Lewis, 1973:43, fig. 1; Lewis, 1975:43, fig. 1; Penz & Francini, 1996:313, fig. 4a,b,c, 317; Francini & Penz, 2006: figs. 8, 9, Plate 12; Silva-Brandão et al., 2008:519, 528, figs. 3, 4, 5; Freitas et al., 2009b:88; Freitas et al., 2010:100, 103.
Actinote alalia alalia; Eltringham & Jordan, 1913:10.
Actinote undescribed species; Freitas et al., 2010:103.

Diagnosis

The wing color and pattern are typical of the “orangish red mimicry complex” (Francini, 1989), with dark brown stripes on an orangish red background on the dorsal wing surfaces (Fig. 9), but the new species can be distinguished from all other previously described species in this complex by several morphological characters (see Francini and Penz, 2006). The males of *Actinote mantiqueira* sp. nov. can be distinguished from those of *Actinote alalia* by the usually broader transverse dark brown bands on the dorsal forewing (Fig. 2A and E). On the dorsal forewing, *A. mantiqueira* sp. nov. can be distinguished from *A. alalia* by the presence of a usually continuous dark band in the internal margin (this is mostly orange in *A. alalia*). On the ventral hindwing, *A. mantiqueira* sp. nov. can be distinguished from *A. alalia* by the faintly marked, orange v-shaped transverse band (this band is conspicuously marked in *A. alalia*), by the absence of a complete dark bar crossing the middle of the discal cell (this dark bar is present in *A. alalia*, delimiting a basal orange area), and by the absence of a distinct patch of orange scales in the humeral angle, basally to the humeral vein (this region is covered by cream scales in *A. mantiqueira* sp. nov.) (Fig. 2B and F). Females are very similar in both species (Fig. 2C and G), and hardly discernible; the most consistent character is the presence of a distinct patch of orange scales in the humeral angle, basally to the humeral vein, in *A. alalia* (cream in *A. mantiqueira* sp. nov.) (Fig. 2D and H). The male genitalia of both species are very similar, and the main difference is the profile of the saccus, which is more triangular and pointed in *A. mantiqueira* sp. nov., and bumped and abruptly enlarging near the base in *A. alalia* (Fig. 3D and L).



Fig. 1. Holotype male (A) and allotype female (B) of *Actinote mantiqueira* sp. nov. (left = dorsal; right = ventral). Scale bar = 10 mm.

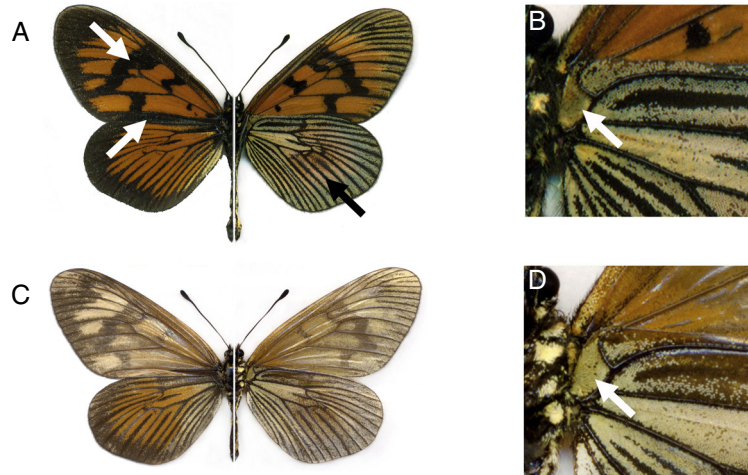
Actinote mantiqueira*Actinote alalia*

Fig. 2. Comparative plate showing the main differences in wing pattern between *Actinote mantiqueira* sp. nov. and *Actinote alalia*. (A) Male paratype of *A. mantiqueira* sp. nov. (dorsal left, ventral right); (B) detail of humeral region in male VHW; (C) female paratype of *A. mantiqueira* sp. nov. (dorsal left, ventral right); (D) detail of humeral region in female VHW; (E) male of *A. alalia* (dorsal left, ventral right); (F) detail of humeral region in male VHW; (G) female of *A. alalia* (dorsal left, ventral right); (H) detail of humeral region in female VHW.

Description

Male (Figs. 1A, 2A,B, 4A–D, 9A): Antenna black, 11–12 mm in length ($n = 11$), extending to mid-costa, with 42 antennomeres, 9 of which form a well-defined club. Palpus length about 2.0 times head height. Male palpus shown in Fig. 4B. Forewing narrow and elongated, length 25–28 mm (mean = 26.8 mm, SD = 1.08 mm, $n = 11$); hindwing rounded, about two-thirds length of forewing, length 18–21 mm (mean = 19.7 mm, SD = 0.90 mm, $n = 11$). Male wing venation as shown in Fig. 4A. Male foreleg (Fig. 4C) with a single tarsomere. Male midleg as shown in Fig. 4D. Body dark brown, abdomen ventrally covered by cream scales. Forewing dorsal background dark orange with dark brown veins and stripes as follows: a broad dark brown margin, broad in apex and narrowing toward tornus; entire space from anal margin to 2A dark brown; three additional broad dark brown transverse stripes, first extending from costa to CuA₂, two thirds from base, second v-shaped crossing discal cell in mid portion, and third crossing space CuA₂–2A halfway from base. Many individuals present a dark cubital spot adjacent to discal cell near wing base. Hindwing dorsal background dark

orange with broad dark brown margin; all veins dark brown, and narrow dark brown stripes extending in inter-venal spaces; some individuals can present transverse patches of dark scales crossing proximally spaces M₁–M₂, M₂–M₃, M₃–CuA₁ and CuA₁–CuA₂, in some cases almost forming a v-shaped transverse band. Ventral forewing with a pattern very similar to dorsal pattern, but lacking broad dark brown margin; ventral hindwing more homogeneously cream, with dark brown veins and stripes in inter-venal spaces.

Male genitalia (Fig. 3A–G): Valvae elongated and curved, length about four times width of median portion; broader at base; apex rounded with a conspicuous curl toward middle line of body. In dorsal view, basal portion of uncus wide, abruptly narrowing, ending in a point. Tegumen long and broad, trapezoidal with a slight constriction at middle. Gnathos absent. In ventral view, saccus shaped as an isosceles triangle, about half length of genital capsule. Aedeagus about half length of genital capsule, ending in a sharp point, in lateral view straight. Juxta broad, about same width of base of one valva (in ventral view), tear-shaped (with an anterior pointed process); length equal to width.

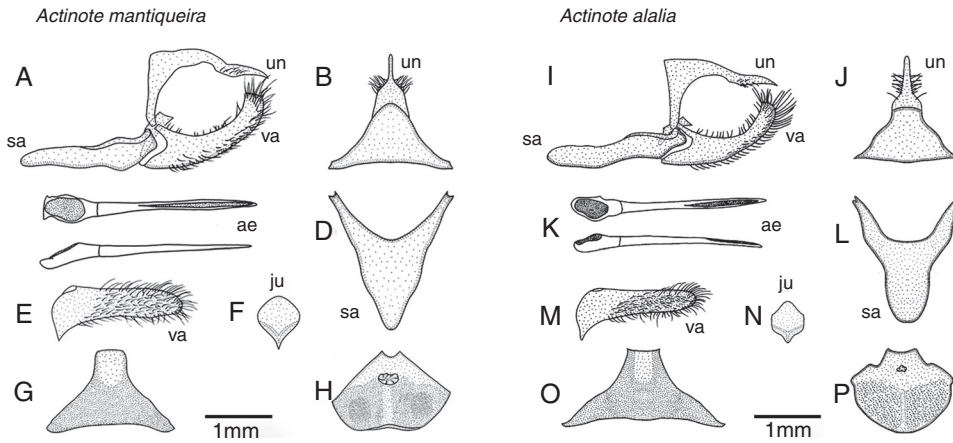


Fig. 3. Male and female genital characters of *Actinote mantiqueira* sp. nov. (A–H) and *Actinote alalia* (I–P). *A. mantiqueira* sp. nov.: (A) lateral view of male genitalia; (B) uncus in dorsal view; (C) aedeagus dorsal (above) and lateral (below); (D) saccus, ventral view; (E) valva, ventral view; (F) juxta; G. 8th sternite; (H) female sterigma. *A. alalia*: (I) lateral view of male genitalia; (J) uncus in dorsal view; (K) aedeagus dorsal (above) and lateral (below); (L) saccus, ventral view; (M) valva, ventral view; (N) juxta; (O) 8th sternite; (P) female sterigma. ae, aedeagus; ju, juxta; sa, saccus; un, uncus; va, valva.

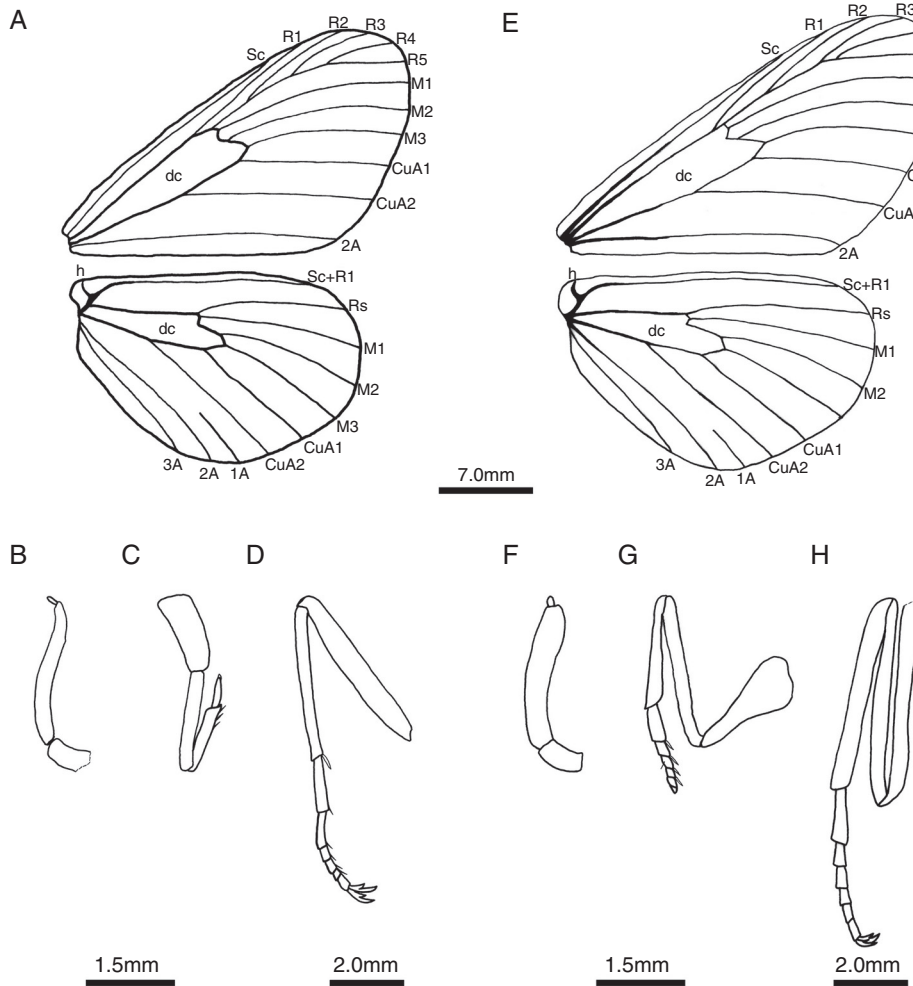


Fig. 4. Morphological characters of males (A–D) and females (E–H) of *Actinote mantiqueira* sp. nov. (A) Wing venation; (B) Palpus; (C) Foreleg; (D) Midleg; (E) Wing venation; (F) Palpus; (G) Foreleg; (H) Midleg.

Female (Figs. 1B, 2C,D, 4E–H, 8B): Antenna black, 12 mm in length ($n=3$), extending to mid-costa, with 41 antennomeres, 10 in club. Female palpus as shown in Fig. 4F. Forewing narrow and elongated, length 29–31 mm (mean = 29.3 mm, SD = 1.53 mm, $n=3$). Hindwing rounded, not translucent, length 20–22 mm

(mean = 20.7 mm, SD = 1.15 mm, $n=3$). Female wing venation is shown in Fig. 4E. Color pattern of female wings similar to that of males but paler. Foreleg with six segments on tarsus, with third segment bearing one short setae (Fig. 4G). Female midleg as shown in Fig. 4H.

Female genitalia (Fig. 3H): Corpus bursae rounded, signa absent. Ductus bursae not sclerotized, same length as corpus bursae; sterigma trapezoidal.

Taxonomy and variation

As has been reported for most species of *Actinote*, *A. mantiqueira* sp. nov. also presents intraspecific variation, especially in female color pattern (males are more uniform). Minor variation has also been reported in wing venation and genitalia. The most variable characters are the extent of the humeral vein, which can reach or not the wing edge, and the shape of the saccus apex, which can vary from pointed to almost rounded. The populations from Serra da Bocaina (São Paulo State) are slightly different on the ventral hindwing, with the orange v-shaped transverse band more conspicuously marked.

Holotype (Fig. 1A). Male from Pindamonhangaba, São Paulo, Brazil (22°46'3.62"S 45°31'27.08"W). Deposited in the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC), Unicamp, Campinas, São Paulo, Brazil. Labels on the holotype (five labels separated by transverse bars): /HOLOTYPUS/Mirante do Pico do Itapeva, Pindamonhangaba, São Paulo: Brazil 28.XII.2016, 2000 m, 22°46'3.62"S 45°31'27.08"W, L. M. Magaldi, leg./Holotypus—*Actinote mantiqueira* Freitas, Francini, Paluch & Barbosa det. 2017/DNA voucher – BLU 936/ZUEC LEP 10004/.

Allotype (Fig. 1B). Same data as Holotype. Deposited in the Museu de Zoologia da Universidade Estadual de Campinas (ZUEC), Unicamp, Campinas, São Paulo, Brazil. Labels on the allotype (five labels separated by transverse bars): /ALLOTYPUS/Mirante do Pico do Itapeva, Pindamonhangaba, São Paulo: Brazil 28.XII.2016, 2000 m, 22°46'3.62"S 45°31'27.08"W, L. M. Magaldi, leg./Allotypus—*Actinote mantiqueira* Freitas, Francini, Paluch & Barbosa det. 2017/DNA voucher – BLU 939/ZUEC LEP 10005/.

Paratypes (All from Brazil). *Minas Gerais*: Itamonte, Caminho para Agulhas Negras, Parque Nacional do Itatiaia, 1800 m, 1 male, 4.XII.1991, A. V. L. Freitas leg. (ZUEC-AVLF). *São Paulo*: Piquete, Estrada para São Francisco dos Campos do Jordão, 1800 m, 1 male, 5.XII.2004, R.B.Francini leg. (R. B. Francini col. #22); Campos do Jordão, Alto da Boa Vista, 1800 m, 1 male, 6.XII.2007 (DNA voucher AC 110), A. V. L. Freitas leg.; Pindamonhangaba, Pico do Itapeva, 1800 m, 1 female, 31.XII.2005, A. V. L. Freitas leg.; 6 males (DNA vouchers AC111, AC112, AC113, AC114, AC115, AC116), 6.XII.2007, A. V. L. Freitas leg. (ZUEC-AVLF); Mirante do Pico do Itapeva, 2000 m, 3 males, 28.XII.2016, 22°46'3.62"S 45°31'27.08"W, L. M. Magaldi, leg. (DNA vouchers BLU 937, BLU 938, BLU 940) (ZUEC LEP 10006, ZUEC LEP 10007, ZUEC LEP 10008) (ZUEC); Santo Antônio do Pinhal, Estrada para o Pico Agudo, 1220 m, 20.XI.2013, 22°51'1"S 45°39'42"W, T.S.Souza leg. (ZUEC LEP 10003) (ZUEC).

Additional studied material (all from Brazil). *DZUP – Minas Gerais*: Camanducaia, Monte Verde, 1650 m, 3 males and 6 females, 22.XII.1968, 1 male, 23.XII.1968, 4 males, 27.XII.1968, H. Ebert leg. DZ 3769, DZ 3772, DZ 3771, DZ 5848, DZ 5865, DZ 6041, DZ 5961, DZ 5937, DZ 5896, DZ 3773, DZ 3774, DZ 3474, DZ 7869, DZ 3770; Santos Dumont, Rio Novo, 850 m, 1 male, 13.XI.1953, H. Ebert leg. DZ 5849; Barbacena, Serra da Mantiqueira, 1100 m, 1 female, 4.XII.1952, H. Ebert leg. DZ 7091; Poços de Caldas, 1250 m, 1 male, 10.XII.1966, 2 males, 11.XII.1966, 1 male, 15.XII.1966, 3 males, 17.XII.1966, H. Ebert leg. DZ 3776, DZ 3786, DZ 3785, DZ 3787, DZ 3767, DZ 3788, DZ 2977; Delfim Moreira, 15 Km SE, 1500–1700 m, 2 females, 22–23.I.2004, Mielke & Casagrande leg. DZ 9290, DZ 9250. *Rio de Janeiro*: P. N. Itatiaia, 1600 m, 2 females, 12.I.1973, Mielke leg. DZ 5969, DZ 5857; Imbariê, 25 m, 1 female, 29.VII.1964, H. Ebert leg. DZ 5928; Itatiaia, Oeste, 1400 m, 2 males, 22.XII.1957, H. Ebert leg. DZ 3782, DZ 3110; Teresópolis, 1000 m, 1 female, 5.I.1973, Mielke leg. DZ 7997. *São Paulo*: Campos do Jordão, 1700 m, 1 female, 30.I.1966, H. Ebert leg. DZ 5945,

Campos do Jordão, Toriba, 2 males, 12.XI.1922, 1 male, 16.XII.1952, D Almeida & L.Travassos Filho leg. DZ 3781, DZ 3762, DZ 2974; Bananal, Bocaina, 2 males and 2 females, 2.I.1937, Travassos leg. DZ 3780, DZ 3779, DZ 5913, DZ 5904. *IOC – Minas Gerais*: Passa Quatro, Fazenda dos Campos, 1600 m, 1 female, 2.XII.1915, 1 female, 5.XII.1915, J.F. Zikán leg. I.O.C. no 25195, No. 25196. *Rio de Janeiro*: Itatiaia, Campo Belo, 2 females, 10.XII.1919, 1 female, 12.II.1920, km12, 1 female, 20.I.1925, J.F. Zikán leg. I.O.C. No. 25193, No. 25177, No. 25198, No. 25217, 1 female, 30.XI.1920, 1 female, 29.XII.1920, M. Zikán leg. I.O.C. No. 25176, No. 25178. *São Paulo*: Bananal, 3 males and 3 females, 8.I.1937, L. Travassos Filho leg. Coll. Travassos. MNRJ – *Rio de Janeiro*: Nova Friburgo, 1 female, III.1934, Col. J. Oiticica Filho. *São Paulo*: Campos do Jordão, 3 females, 29.I.1933, Travassos & J. Oiticica Filho, Col. J. Oiticica Filho; Bananal, Bocaina, 3 females, I.1937, A. Costa leg. Col. Dr. A. Costa No. 4376, No. 4377, No. 4365. *ZUEC-AVLF – Minas Gerais*: Andradas, Pico do Gavião, 1600 m, 1 male, 12.XII.2017, 22°1'1"S 46°37'37"W, A.V.L. Freitas, L.M. Magaldi, J.Y.O. Carreira & A. Tacioli leg.; Poços de Caldas, Serra do Cristo, 1560 m, 2 males, 15.XII.2017, L. M. Magaldi & A. Tacioli leg. *São Paulo*: Silveiras, ponte sobre o Rio do Higino, Serra da Bocaina, 2 males (DNA vouchers AC176, AC180) and 2 females (DNA vouchers AC174, AC179), 17.I.2009, K. L. Silva-Brandão leg.; Serra da Bocaina, 1450 m, 2 males, 19.XII.2017, 22°47'54"S 44°42'48"W, L.M. Magaldi, A. Tacioli & A.H.B. Rosa leg.

Immature stages

Egg (Figs. 5A,B, 8C). Light yellow when first laid, changing gradually to pinkish red after 24 h; barrel-shaped with 13–16 vertical ribs and several (~14–17) weakly marked horizontal ribs; mean height 0.683 mm (range 0.67–0.71 mm, $n=3$), mean diameter 0.412 mm (range 0.37–0.44 mm, $n=9$). Aeropyles localized only near base of egg, in two irregular rows (not every vertical rib bears an aeropyle).

First instar (Figs. 6 and 7A). Head brown, smooth, without scoli, mean width 0.33 mm (range 0.29–0.36 mm, $n=3$); body pale cream, without scoli and with long pale setae arising from pinacula; legs pale brown, prolegs pale, anal plate pale brown. Prothoracic plate pale and difficult to observe under stereomicroscope. T1 presents only 2 subventral setae, similar to *Actinote alalia*. Head chaetotaxy and body chaetotaxy are presented in Figs. 6 and 7A, respectively. Maximum reported length 3.0 mm.

Last instar (Figs. 7B and 8D). Head dark brown, smooth with thin pale setae and without scoli, spines or chazae, mean width 3.14 mm (range 3.01–3.24 mm, SD=0.073 mm, $n=4$); body dark brown dorsally, pale cream laterally and ventrally, covered with medium sized dark brown scoli bearing brown setae from T1 to A1 and from A7 to A10, and white setae from A2 to A6; legs black, prolegs pale cream; anal plate dark brown. Maximum length: 40 mm ($n=4$). Scoli distribution as in Fig. 7B. Prepupa changes color, becoming pale cream with a more homogeneous coloration.

Pupa (Fig. 8E). General profile elongated, ground color pale yellow cream with dark brown markings in wing cases and abdomen; abdominal segments mobile, with a series of five pairs of subdorsal black spines from segments A2 to A6. Total length 20–21 mm ($n=2$).

Adult and immature behavior, host plants and natural history. Larvae of *A. mantiqueira* sp. nov. have been recorded using *Eupatorium intermedium* and *Eupatorium* sp. (a species very similar to *E. intermedium*) (Asteraceae) (Fig. 8A) as host plants (Penz and Francini, 1996; RBF and AVLF pers. obs.). Females were observed ovipositing from 12:00 to 02:00 PM on the underside of mature leaves of their host plants (Fig. 8B). Ovipositions are large (Fig. 8C), varying from 409 to 453 eggs ($n=4$). Newly hatched larvae first consumed the chorion, and after 3–5 h began to feed on leaf tissue. First instars fed on the underside leaf tissue by scraping the leaf surface, while later instars were observed consuming the entire leaf. In first

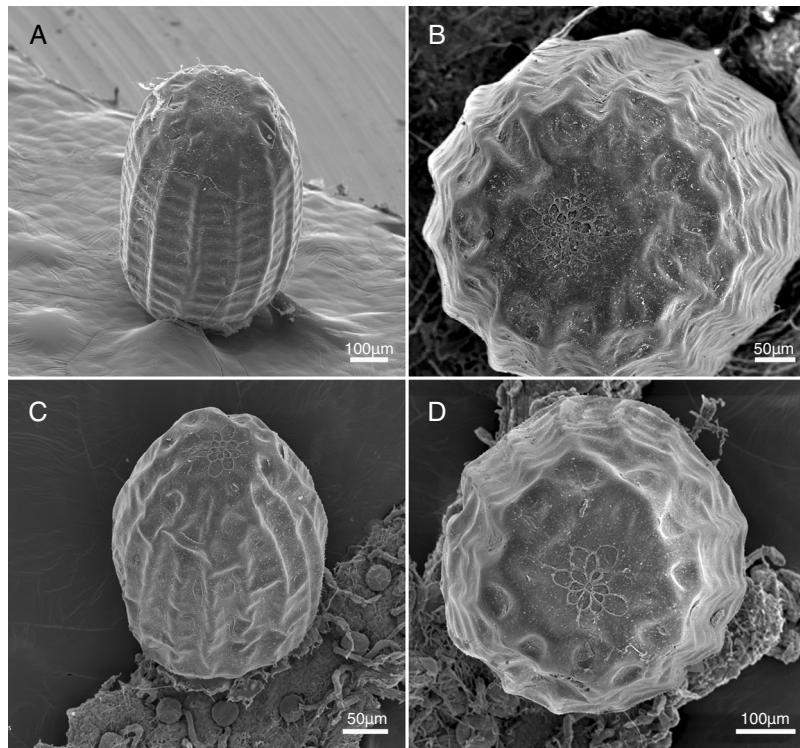


Fig. 5. Eggs of *Actinote mantiqueira* sp. nov. (A – lateral view, B – dorsal view) and *Actinote alalia* (C – lateral view, D – dorsal view) in scanning electron microscopy.

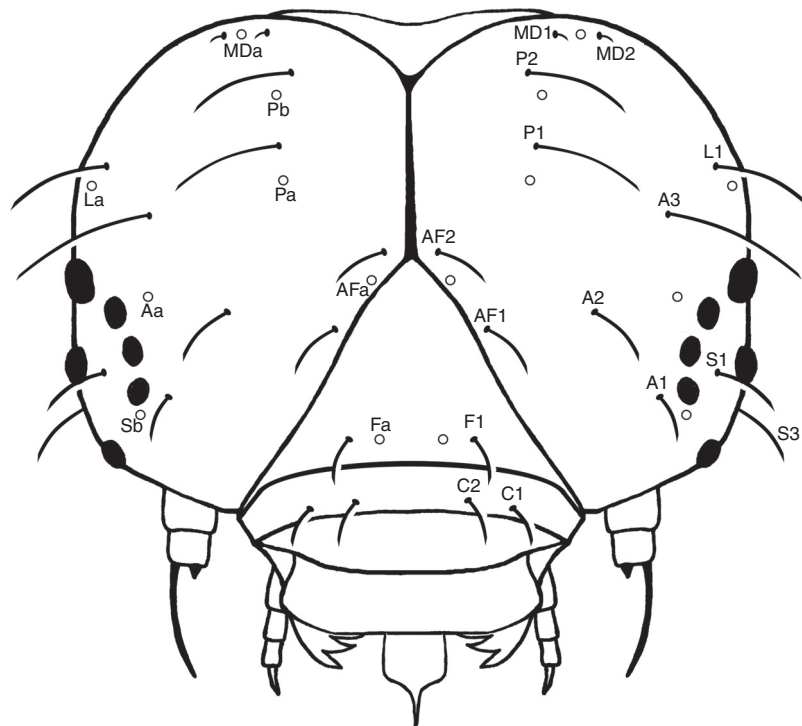


Fig. 6. Chaetotaxy of first instar head capsule of *Actinote mantiqueira* sp. nov. (setae nomenclature on the right side and pore nomenclature on the left side).

instars, frass pellets were glued onto the leaf by silk, not falling to the ground. Larvae were consistently gregarious in all instars, and all activities, such as feeding, resting, or moving between leaves, occurred simultaneously.

Adults were only observed on sunny days, quickly disappearing when weather conditions became cloudy. Males began to fly around 10:00 AM, usually flying 2–5 m high. Females were seldom

observed, and territorial behavior, courtship behavior or copulation were not perceived. All known populations of *A. mantiqueira* sp. nov. were recorded in well-preserved subtropical wet montane forest above 1000 m altitude, where the climate approaches temperate conditions, including cold winters with frequent frosts and temperature frequently falling below 0 °C. Males were observed feeding on flowers of *Croton urucurana* Baill. (Euphorbiaceae),

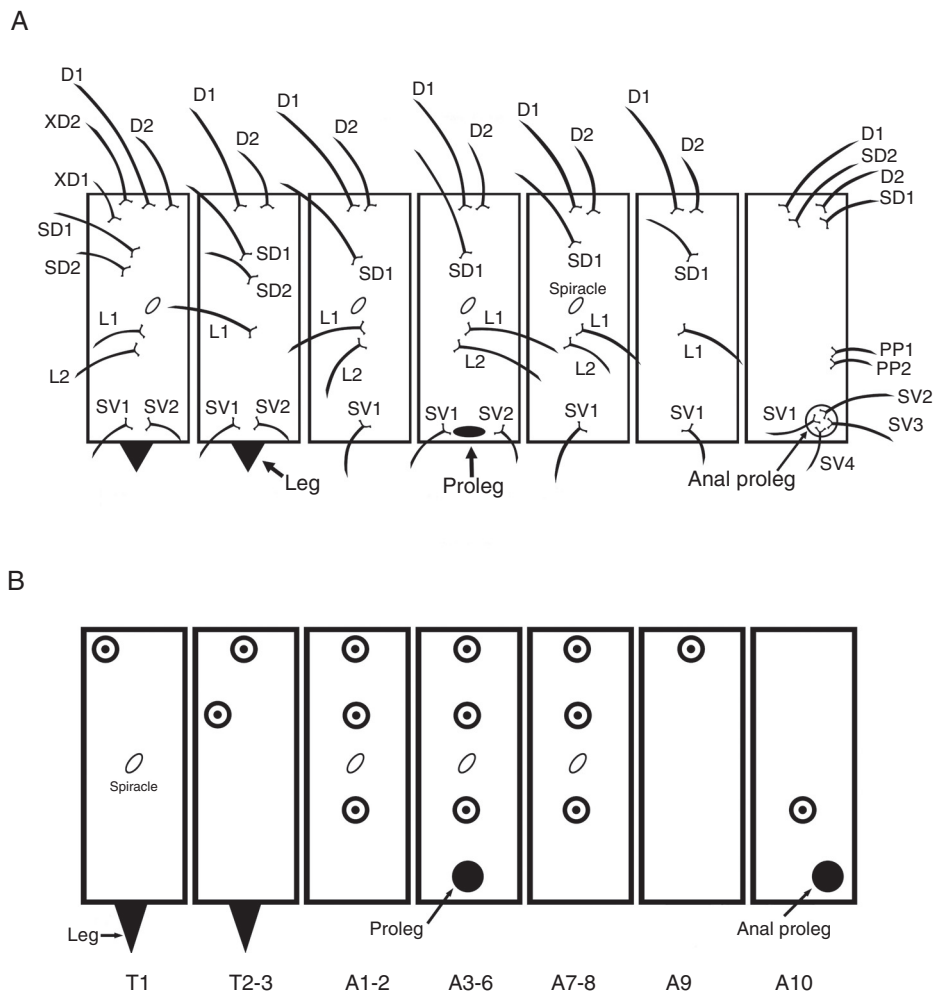


Fig. 7. Larval body diagrams of *Actinote mantiqueira* sp. nov. (A) First instar body chaetotaxy; (B) last instar scoli distribution.

Chromolaena punctulata (D.C.) R. King & H. Robins (Asteraceae) and on several other species of forest edge plants. Adults are univoltine in all known populations, with only one flight period during the warmer months, from late November to early February. Adults of *A. mantiqueira* sp. nov. are sexually dimorphic, with males having a deep orange coloration (Figs. 1A, 2A,B, 9A), and females being much more translucent and sometimes having the subapical spot on the forewing light cream (Figs. 1B, 2C,D). In most studied sites individuals were never abundant, with usually 5–30 individuals observed in a typical day of field work (4–5 h of observation), most of which were males. This species is part of the “orangish red mimicry complex” of *Actinote* (sensu Francini, 1989) (Fig. 9), and is sympatric with five other *Actinote* co-mimics, namely *Actinote bonita* Penz, 1996 (Fig. 9B), *Actinote conspicua* Jordan, 1913 (Fig. 9C), *Actinote quadra* (Schaus, 1902) (Fig. 9D), *Actinote dalmeidai* Francini, 1996 (Fig. 9E), and *Actinote surima* (Schaus, 1902) (Fig. 9F) and one pierid co-mimic, *Dismorphia melia* (Godart, [1824]) (Pieridae: Dismorphiinae) (see Dias et al., 2016).

Habitat. In all known localities, the species is associated with well-preserved montane ombrophilic forest, usually at altitudes above 1000 m. Males and females are easily observed in forest edges and in areas of contact between forest and high altitude natural grasslands (Fig. 10A and B).

Geographic distribution. The species is known from the Serra da Mantiqueira region, from the Serra da Bocaina and Serra dos Órgãos, at altitudes from 1000 to 2000 m (Fig. 11).

Etymology. Mantiqueira is a word in native Tupi language meaning “rain drops” (from *amana* = rain and *tykyra* = drop) and is the name of a large mountain range in SE Brazil (Serra da Mantiqueira), where most of the known populations of *A. mantiqueira* sp. nov. occur.

Redescription of *Actinote alalia* (C. Felder & R. Felder, 1860)

Acraea alalia C. Felder & R. Felder, 1860:105. Brazil (NHMUK); Kirby, 1871:136; Müller, 1877:219; Lamas, [1997]:31 (includes LECTOTYPE designation: male [southeastern] Brazil).

Acraea eulalia [sic]; Müller, 1878:296; R. Llano & M. Llano, 1973:70.

Actinote alalia; Mabilde, 1896:64; D’Almeida, 1935:71, 93; Lewis, 1973:227; Lewis, 1975:227; D’Abrera, 1987:445; Ackery, 1988:136; Mielke, 1994:769; Lamas, 1997:31; Penz & Francini, 1996:309; Paluch et al., 2003:573; Lamas, 2004:263; Paluch et al., 2005:416; D’Abrera, 2006:247; Iserhard et al., 2010:313, 318, 319; Dolibaina et al., 2011:351.

Actinote alalia alalia; Eltringham & Jordan, 1913:10; Jordan, 1913:374; Jordan & Eltringham, 1916:19.

Acraea (Actinote) alalia; Pierre, 1987:22.

Actinote sp1.; Silva-Brandão et al., 2008:519, 528, figs. 3,4,5.

Description

Male (Figs. 2E, F, 9G): Antenna black, 11–12 mm in length ($n=5$) extending to mid-costa, with 41 segments, 11 of which

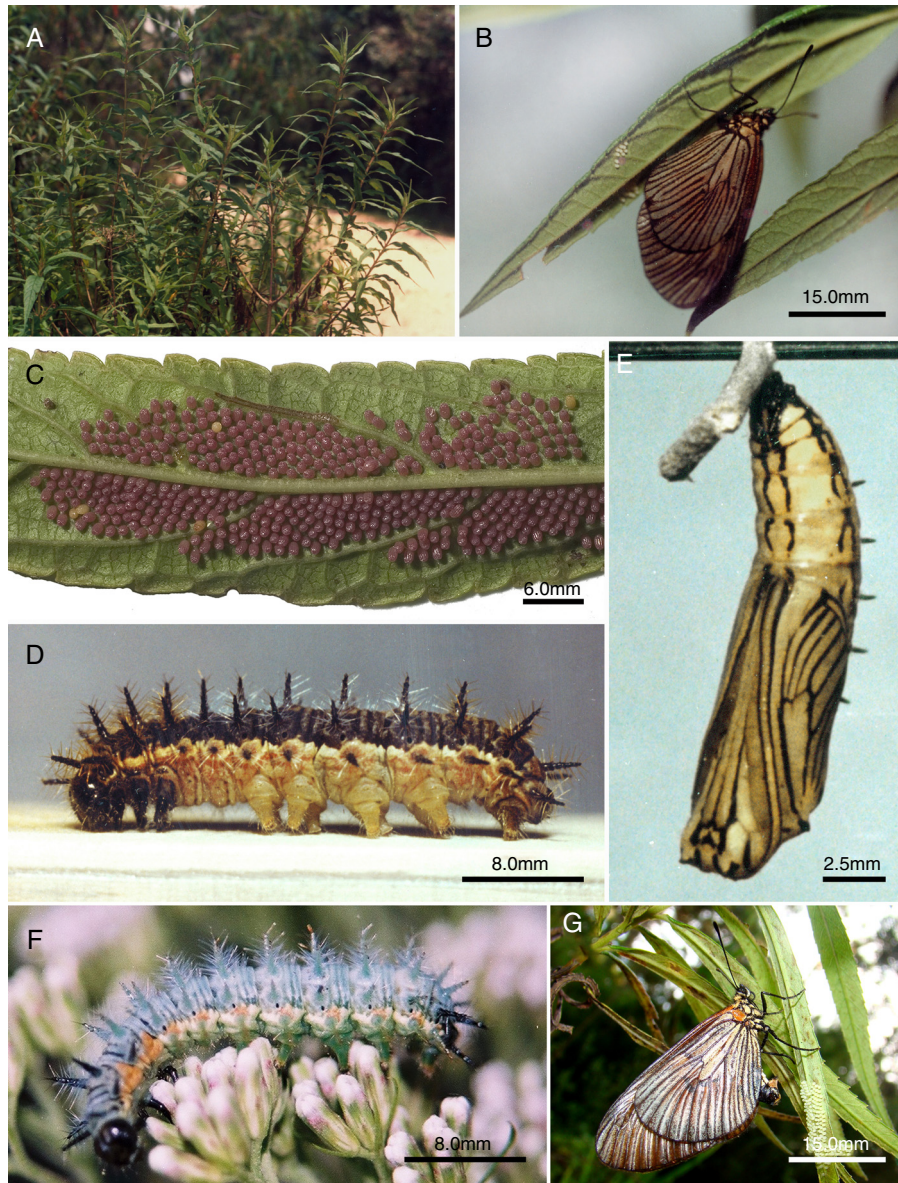


Fig. 8. Natural history of *A. mantiqueira* sp. nov. (A–E) and *Actinote alalia* (F–G). (A) Shrub of *Eupatorium intermedium*, host plant of *A. mantiqueira*; (B) Female of *A. mantiqueira* sp. nov. ovipositing; (C) close view of an oviposition of *A. mantiqueira* sp. nov.; (D) Last instar of *A. mantiqueira* sp. nov. (lateral view); (E) Pupa of *A. mantiqueira* sp. nov. (latero-ventral view); (F) Last instar of *A. alalia* (lateral view); (G) Female of *A. alalia* ovipositing (photo by Lucas A. Kaminski).

form a well-defined club. Forewing narrow and elongated, length 25–28 mm (mean = 26.8 mm, SD = 1.09 mm, $n = 5$); hindwing rounded, length 18–21 mm (mean = 19.8 mm, SD = 1.09 mm, $n = 5$). Body dark brown, abdomen ventrally covered by cream scales. Forewing background dark orange with dark brown veins and stripes as follows: a broad dark brown margin, broad in apex and narrowing toward tornus; space from anal margin to 2A dark brown in final third only; four additional narrow dark brown transverse stripes, first extending from costa to CuA_2 , two thirds from base, second crossing end of discal cell from R sector to M_3 , third v-shaped crossing discal cell in mid portion, and fourth v-shaped crossing space CuA_2 -2A half from base. Hindwing background dark orange with broad dark brown margin; all veins dark brown, and narrow dark brown stripes extending in inter-venal spaces. Transverse patches of dark scales crossing proximally spaces M_1 - M_2 , M_2 - M_3 , M_3 - CuA_1 and CuA_1 - CuA_2 . Ventral forewing with a pattern very similar to dorsal pattern, but lacking broad dark brown margin; ventral hindwing background cream, with a well-marked dark

brown v-shaped band from $Sc+R_1$ to 3A, with an adjacent well defined broad v-shaped orange band. Discal cell usually crossed by an oblique dark brown stripe, defining an orange basal half and a cream distal half region.

Male genitalia (Fig. 3I–O): Valvae elongate and curved, length about four times width of median portion; broader at base; apex rounded with a conspicuous curl toward middle line of body. In dorsal view, basal portion of uncus wide, abruptly narrowing, ending in a point. Tegumen long and broad, trapeze-shaped with a slight constriction at middle. Gnathos absent. In ventral view, saccus with an abrupt slight narrowing near base, then projecting as a broad lobe with rounded end; about half length of genital capsule. Aedeagus about half length of genital capsule, ending in a sharp point, in lateral view slightly curved downwards. Juxta broad, about same width of base of one valva (in ventral view), diamond-shaped with an anterior short pointed process; length equal to width.

Female (Figs. 2G, H, 8G). Antenna black, 13 mm in length ($n = 2$), extending to mid-costa, with 41 segments, 11 of which form a

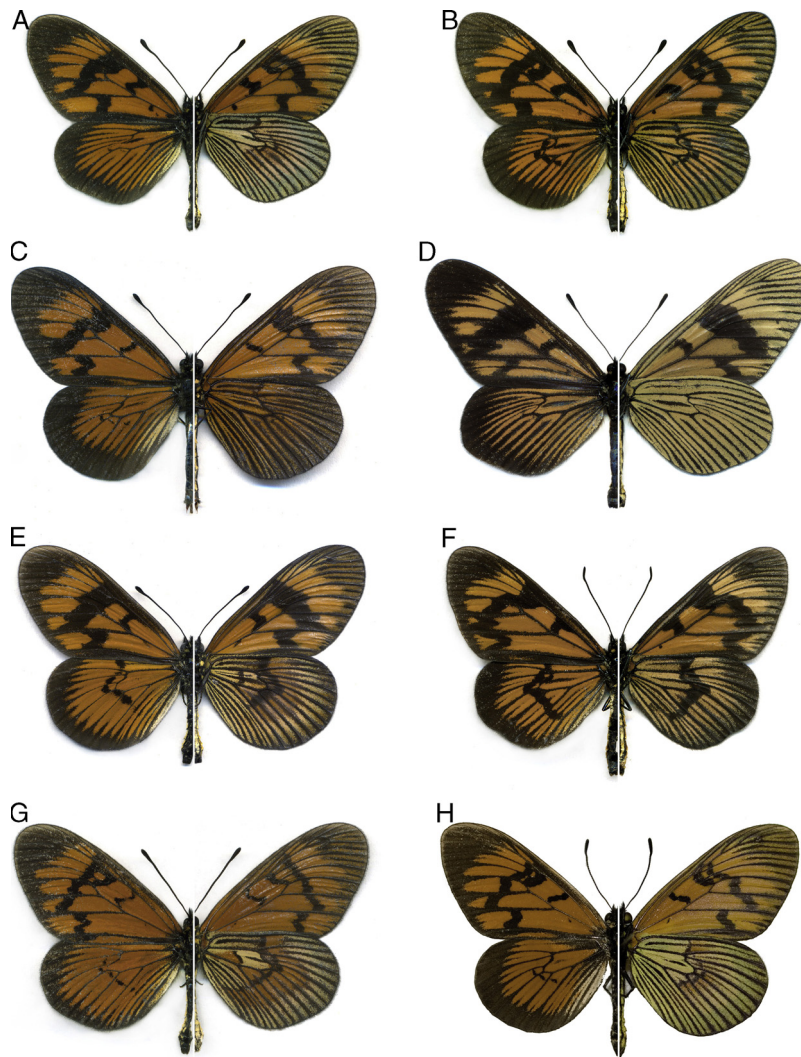


Fig. 9. Comparative plate showing all known Brazilian species of *Actinote* belonging to the “orangish red mimicry complex”, dorsal left and ventral right (males only). (A) *Actinote mantiqueira* sp. nov. (paratype), (B) *Actinote bonita*, (C) *Actinote conspicua*, (D) *Actinote quadra*, (E) *Actinote dalmeidai*, (F) *Actinote surima*, (G) *Actinote alalia*, (H) *Actinote catarina*.

well-defined club. Forewing narrow and elongated, length 31–33 mm ($n=2$). Hindwing rounded, not translucent, length 23 mm ($n=2$). Color pattern of female wings similar to that of males but paler.

Female genitalia (Fig. 3P): Corpus bursae rounded, signa absent. Ductus bursae not sclerotized, same length as corpus bursae; sterigma rounded.

Taxonomy and variation

Actinote alalia was described by C. Felder & R. Felder (1860) based on an unstated number of specimens without a specified locality in Brazil. A male syntype deposited in the NHMUK (figured in Warren et al., 2017), was examined by Gerardo Lamas and designated as the lectotype by him (Lamas [1997]). Based on the provenance of most of the Felder’s material, Lamas ([1997]) suggested that this specimen should have come from southeastern Brazil. Indeed, the wing pattern of the above lectotype corresponds to *Actinote alalia* populations from southern Brazil in terms of the following visible characters: (1) the narrow transverse dark brown bands on the dorsal forewing; (2) a mostly orange band in the internal margin of the dorsal forewing; (3) a conspicuous orange v-shaped band transversally crossing the ventral hindwing, and (4) a complete

dark bar crossing the middle of the discal cell and delimiting a basal orange area (see Fig. 2). Based on these observations and the data presented in this paper, the type locality of *A. alalia* should be changed to “southern Brazil”. As has been reported for most species of *Actinote*, *A. alalia* also presents intraspecific variation, especially in the female color pattern (males are much more uniform). As for *A. mantiqueira* sp. nov., minor variation has also been reported in wing venation and genitalia. The most variable characters are the extent of the humeral vein, which can reach or not the wing edge, and the shape of saccus apex, that can vary from pointed to almost rounded.

Examined material (all from Brazil). DZUP – Paraná: Curitiba, 900 m, 1 male and 2 females, 28.II.1969, Mielke leg. DZ 3153, DZ 5864, DZ 5905, 1 female, 13.XII.1968, Mielke leg. DZ 3119; Palmas, 1100 m, 7 males and 1 female, 6.II.1976, Mielke & Buzzi leg. DZ 3136, DZ 3161 DZ 3133, DZ 3132, DZ 3121, DZ 3129, DZ 3160, DZ 5929, 2 males, I.1930, Stawiarski leg. DZ 3765, DZ 3784; Prudentópolis, 1200 m, 10 males and 1 female, 2.II.1976, Mielke & Buzzi leg. DZ 3106, DZ 3128, DZ 3157, DZ 3137, DZ 3116, DZ 3120, DZ 3108, DZ 3148, DZ 3134, DZ 3138, DZ 5872; Castro, 1000 m, 1 male and 2 females, 25.I.1971, Mielke leg. DZ 3147, DZ 6017, DZ 6001; Guarapuava, 1200 m, 2 males and 1 female, 18.II.1978, Mielke & Miers leg. DZ 3152, DZ 3122, DZ 5888; Porto União, 1 male and

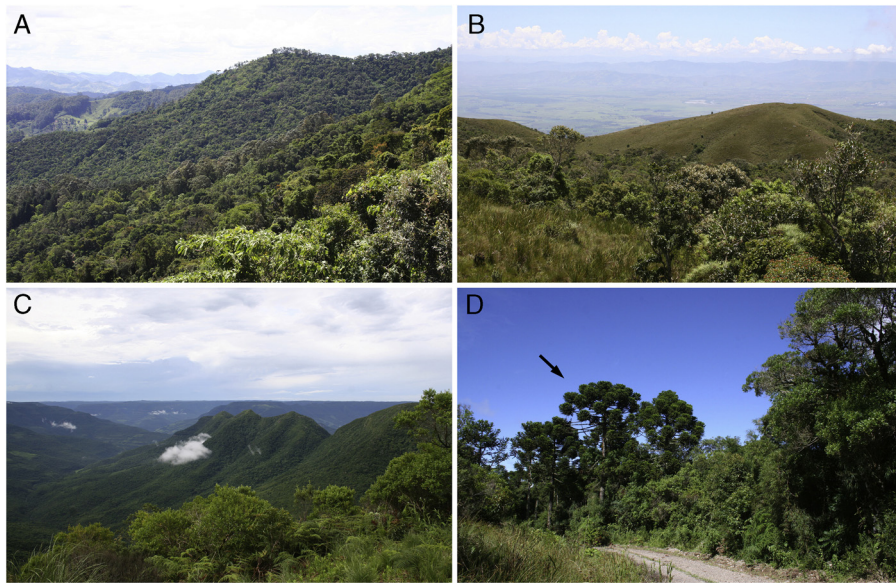


Fig. 10. (A and B) Habitat of *Actinote mantiqueira* sp. nov.; (C and D) Habitat of *Actinote alalia*. (A) General view of the montane forests in Campos do Jordão, São Paulo State (1400–1600 m a.s.l.); (B) region of contact between grassland and high altitude forest, Pico do Itapeva, Pindamonhangaba, São Paulo State (1800 m a.s.l.); (C) general view of the montane forests in São Francisco de Paula, Rio Grande do Sul State (900–1100 m a.s.l.); (D) close view of the montane forest in São Francisco de Paula, Rio Grande do Sul State (900 m a.s.l.); the characteristic *Araucaria* trees are visible near the trail (black arrow).

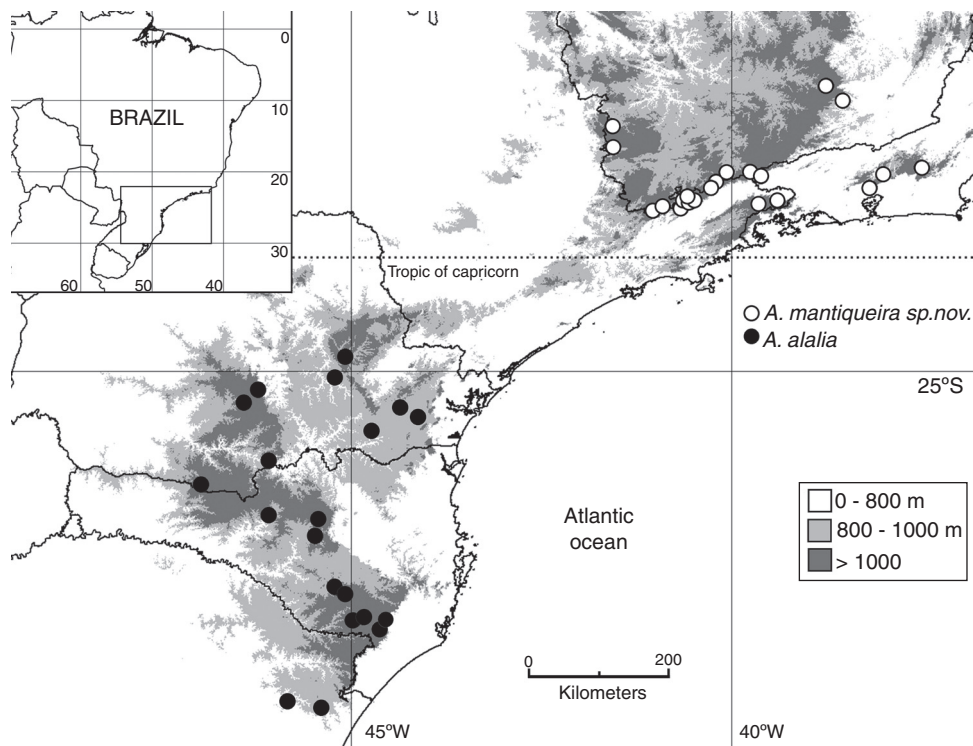


Fig. 11. Recorded distribution of *Actinote mantiqueira* sp. nov. (open circles) and *Actinote alalia* (solid circles) in Brazil. Locality data include records compiled from Paluch (2006), museum data (see text) and recent sightings (AVLF, unpublished data).

1 female, Stawiarski leg. DZ 3775, DZ 6071; São José dos Pinhais, Colônia Muricy, 1 male, 14.XII.2001, Paluch leg. DZ 4758; Lapa, 1 male, no data, H. Ebert leg. DZ 3768; Ponta Grossa, 1 female, IV.1956, Coll. F. Justus, DZ 8014. *Santa Catarina*: Rio das Antas, 4 males and 2 females, I.1953, Camargo leg. DZ 3764, DZ 3763, DZ 3778, DZ 3777, DZ 5912, DZ 6009; Santa Cecília, 1000 m, 1 male, 22.II.1973, Mielke leg. DZ 3105; Ponte Alto do Norte, 1000 m, 1 male, 12.II.1973, Mielke & Sakakibara leg. DZ 3783; São Joaquim, 1250 m, 1 female, 24.II.1973, Mielke leg. DZ 5897, São Joaquim,

Mantiqueira, 8 females, 26.II.1973, Mielke leg. DZ 5936, DZ 5881, DZ 5873, DZ 5993, DZ 5921, DZ 5977, DZ 6025, DZ 5985, São Joaquim, Planalto de Lages, 1300 m, 1 female, 2–4.II.1973, H. & H. D. Ebert leg. DZ 5953; Lages, Painei, 1000 m, 1 female, 24.II.1983, Mielke & Casagrande leg. DZ 5856, 1 female, 23.II.1973, Mielke leg. DZ 6033, Lages, Parque Pedras Brancas, 920 m, 2 females, 13.II.1973, Mielke & Sakakibara leg. DZ 5920, DZ 6066. *Rio Grande do Sul*: Serra Geral, Canela, 800 m, 1 male, 22.I.1973, H & H. D. Ebert, H. DZ 3766. ZUEC – *Santa Catarina*: Bom Jardim da Serra, 1 male and 1 female,

1360 m, 11.I.2011, L.A.Kaminski leg. ZUEC-AVLF – Rio Grande do Sul: São Francisco de Paula, Floresta Nacional do Pinho, 4 males (DNA vouchers AC117, AC118, AC119, AC120), 31.XII.2007, L.A.Kaminski leg.; 1 male, 1.I.2009, L.A.Kaminski; 1 female (DNA voucher AC210), 7.XII.2009, L.A.Kaminski leg. MZSP – Paraná: Lapa, 2 males, 1 female, XI.1940, B. Pohl leg. Santa Catarina: Rio das Antas, 1 female, I.1953, Camargo leg.

Immature stages

Egg (Fig. 5C and D). Light yellow when first laid, changing gradually to pinkish red during the first 24 h; barrel-shaped with 13–15 vertical ribs and several (~12) weakly marked horizontal ribs; mean height 0.72 mm (range 0.71–0.73 mm, $n=3$), mean diameter 0.42 mm (range 0.24–0.52 mm, $n=3$). Aeropyles localized only near base of egg, in two irregular rows (not every vertical rib bears an aeropyle).

First instar. Head light brown, smooth, without scoli; body pale cream, without scoli and with long pale setae arising from pinacula; legs pale brown, prolegs pale, anal plate pale brown. Prothoracic plate pale and difficult to observe under stereomicroscope. T1 presents only 2 subventral setae, the same condition as in *Actinote mantiqueira* sp. nov.

Last instar (Fig. 8F). Head dark brown, smooth with thin pale setae and without scoli, spines or chalazae; body bluish dorsally, green ventrally, with a conspicuous lateral band, this is orange in thoracic segments and cream in abdominal segments. Covered with medium sized scoli bearing bluish setae; scoli are dark in T1-T2 and A9-A10 and bluish in T3 through A8; legs black, prolegs green; anal plate dark brown.

Pupa. General profile elongated, ground color pale yellow with dark brown markings in wing cases and abdomen; abdominal segments mobile, with a series of five pairs of subdorsal black spines from segments A2 to A6.

Adult and immature behavior, host plants and natural history. Oviposition of *A. alalia* was recorded on *Grazielia serrata* (Spreng.) R. M. King & H. Rob (Asteraceae). Females were observed ovipositing at the end of the afternoon, approximately 05:00 PM. (L. A. Kaminski, pers. comm.) on the underside of mature leaves of their host plants (Fig. 8G). Ovipositions are large, varying from 411 to 442 eggs ($n=2$). Newly hatched larvae first consumed the chorion, and after 3–5 h began to feed on leaf tissue. First instars fed on the underside leaf tissue by scraping the leaf surface, while later instars were observed consuming the entire leaf. In the first instar, frass pellets were glued onto the leaf by silk, not falling to the ground. First instars were gregarious and all activities, such as feeding, resting, or moving between leaves, occurred simultaneously.

As reported for *A. mantiqueira* sp. nov., adults of *A. alalia* were only observed on sunny days, quickly disappearing when weather conditions became cloudy. Males began to fly around 10:00 AM, usually flying 3–5 m high. Females were seldom observed, and territorial behavior courtship behavior or copulation were not perceived. All known populations of *A. alalia* were recorded in preserved subtropical wet montane forest above 800 m altitude, where the climate approaches temperate conditions, including cold winters with frequent frosts and temperature frequently falling below 0°C. Males were observed feeding on flowers of several species of forest edge plants. Adults are univoltine in all known populations, with only one flight period during the warmer months, from December to February. Adults of *A. alalia* are sexually dimorphic, with males having a deep orange coloration (Figs. 2E, F, 9G), and females being much more translucent (Fig. 2G and H). In most study sites individuals were never abundant, with usually 2–6 individuals observed in a typical day of field work (4–5 h of observation), most of which were males. This species is part of the “orangish red mimicry complex” of *Actinote* (*sensu* Francini, 1989) (Fig. 9),

and is sympatric with three other *Actinote* co-mimics, namely, *Actinote dalmeidai* (Fig. 9E), *Actinote surima* (Fig. 9F) and *Actinote catarina* Penz, 1996 (Fig. 9H) and one pierid co-mimic, *Dismorphia melia* (Godart, [1824]) (Pieridae: Dismorphiinae) (see Dias et al., 2016).

Habitat. In all known localities, the species is associated with preserved montane mixed forest (also known as Araucaria Forest due to the presence of Paraná pine *Araucaria angustifolia*), usually in altitudes above 800 m. Males and females are observed in forest edges and in areas of contact between forest and high altitude natural grasslands (Fig. 10C and D).

Geographic distribution. The species is known from the mountains of southern Brazil in the States of Paraná, Santa Catarina and Rio Grande do Sul, at altitudes from 800 to 1400 m (Fig. 11).

Discussion

Due to the strong similarities in wing pattern, high intraspecific variation and low differentiation in female color pattern, some species of *Actinote* are difficult to tell apart (D’Almeida, 1935; Francini, 1989; Paluch, 2006), and several complexes of cryptic species have been recognized within the genus, as is the case of the “orangish red mimicry complex” (Penz and Francini, 1996). Consequently, several new species have been recognized and described in recent years throughout the Neotropics (Penz and Francini, 1996; Francini et al., 2004; Paluch et al., 2006; Neild, 2008; Willmott et al., 2009, 2017). Remarkably, while some of these new species are rare and localized, and known from no more than 10 individuals (e.g. *Actinote eberti* Francini, Freitas & Penz, 2004), some have proven to be common and widespread, such as *Actinote pratensis* Francini, Freitas & Penz, 2004. This last species has been observed in several additional localities since its description, and was found breeding in a backyard at Campinas State University (Freitas, pers. obs.). Conversely, while adults can be hard to distinguish, caterpillars are sufficiently distinct to permit positive identifications to the species-level, as early noticed by D’Almeida (1935) and afterwards by Francini (1989).

In the present case, both adults and immature stages of *A. mantiqueira* sp. nov. are distinct enough to support the description of this new species, also allowing easy differentiation from *A. alalia*. In addition, *A. mantiqueira* sp. nov. is common and abundant in montane forests above 1200 m in southeastern Brazil, facilitating the acquisition of sufficient information to confidently determine its taxonomic status as a new species distinct from *A. alalia*.

Based on a previous molecular study, *A. mantiqueira* sp. nov. and *A. alalia* are sister species with a low level of molecular distinction (Silva-Brandão et al., 2008), and preliminary analysis suggest that these two species diverged in Late Pleistocene (Silva-Brandão and Freitas unpublished; L. M. Magaldi PhD, *in prep.*). Climatic changes in the Pleistocene are considered important to explain the geographic distribution and diversification of the Neotropical fauna and flora (Vuilleumier, 1971; Simpson, 1979; Whitmore and Prance, 1987), and similar examples of closely related species of Late Pleistocene origin that are endemic to distinct Brazilian mountain ranges are known for birds (Mata et al., 2009; Freitas et al., 2012), frogs (Leite et al., 2008), mammals (Gonçalves et al., 2007), and other butterflies (AVLF, *in prep.*). However, additional studies are needed to investigate further this issue.

In summary, the present study is a good example of how increasing knowledge of immature stages and natural history can help better understanding biodiversity, and in the present case, this information has helped in the recognition of a new, undescribed species of locally common butterfly.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

We thank Cristiano A. Iserhard, Lucas A. Kaminski, Junia Y. O. Carreira, Luiza M. Magaldi, Karina L. Silva-Brandão, Thadeu S. Souza, André Tacioli and Augusto H. B. Rosa for providing fresh specimens and/or helping in field work. Tamara M. C. Aguiar for helping spreading the specimens (including part of the type series). Carla Penz read and criticized an early version of the manuscript and Lucas Kaminski and Keith Willmott carefully read the last version of the manuscript. Fábio Raposo do Amaral helped with discussions about biogeography and paleoclimate. EPB thanks FAPESP for a PhD fellowship (2012/03750-8) and a post-doc fellowship (2016/15873-8). MP thanks Dr. Gerdt Guenther Hatschbach (*in memoriam*) and Osmar dos Santos Ribas (Museu Botânico Municipal, Curitiba – PR) by the identification of the host plant of *Actinote alalia*, and to Dr. Jorge Manuel Saraiva Bizarro by the great incentive and help in field work in Paraná. RBF thanks to Universidade Católica de Santos for logistic support. AVLF acknowledges support from FAPESP (Biota-Fapesp Grants 2011/50225-3, 2013/50297-0) and from the Brazilian Research Council – CNPq (Grants 302585/2011-7 and 303834/2015-3). This publication is part of the “RedeLep – Rede Nacional de Pesquisa e Conservação de Lepidópteros” – SISBIOTA-Brasil/CNPq (563332/2010-7).

References

- Ackery, P.R., 1988. Host plants and classification: a review of nymphalid butterflies. *Biol. J. Linnean Soc.* 33 (2), 95–203.
- Brown Jr., K.S., Francini, R.B., 1990. Evolutionary strategies of chemical defense in aposematic butterflies: cyanogenesis in Asteraceae-feeding American Acraeinae. *Chemoecology* 1 (2), 52–56.
- Brown Jr., K.S., 1992. In: Morellato, L.P.C.O. (Ed.), *Borboletas da Serra do Japi: diversidade, habitats recursos alimentares e variação temporal. História natural da Serra do Japi*. Unicamp, Fapesp, Campinas, SP, pp. 142–187.
- Comstock, J.H., Needham, J.G., 1898–99. The wings of insects. *Am. Nat.* 32 (374), 81–89.
- D’Abrera, B.L., 1987. *Butterflies of the Neotropical Region. Part III. Brassolidae, Acraeidae & Nymphalidae (partim)*. Victoria, Black Rock, Hill House, pp. viii + 385–525.
- D’Abrera, B.L., 2006. *World Butterflies*. Hill House Publications, Melbourne, 272 pp.
- D’Almeida, R.F., 1925. Quelques rectifications sur les *Actinote* de la partie orientale de l’Amérique du Sud (Lép. Rhopalocères). *Ann. Soc. Entomol. Fr.* 94 (3), 333–354.
- D’Almeida, R.F., 1935. Les *Actinote* de la partie orientale de l’Amérique du Sud. *Ann. Acad. Bras. Ciênc.* 7 (1), 69–88 (31 March), (2): 89–112 + 13 plates (30 June).
- Dias, F.M.S., Leviski, G.L., Casagrande, M.M., Mielke, O.H.H., 2016. *Dismorphia melia* (Godart, [1824]) (Pieridae: Dismorphiinae): external morphology of the last instar and pupa, with notes on its taxonomy, variation and distribution. *J. Lepid. Soc.* 70 (1), 61–71.
- Dolibaina, D.R., Mielke, O.H.H., Casagrande, M.M., 2011. Borboletas (Papilionoidea e Hesperioidea) de Guarapuava e arredores, Paraná, Brasil: um inventário com base em 63 anos de registros. *Biota Neotrop.* 11 (1), 341–354.
- Eltringham, H., Jordan, H.E.K., 1913. Nymphalidae: Subfam. Acraeinae. *Lepidopterorum Catalogus* 11, 1–65.
- Ebert, H., 1969. On the frequency of butterflies in eastern Brazil, with a list of the butterfly fauna of Poços de Caldas, Minas Gerais. *J. Lepid. Soc.* 23 (Suppl. 3), 1–48.
- Felder, C., Felder, R., 1860. Lepidopterologische Fragmente. *Wiener entomologische Monatschrift* 4 (4), 97–112.
- Francini, R.B., (Ms thesis) 1989. *Biologia e ecologia das borboletas Actinote (Lepidoptera: Nymphalidae, Acraeinae) do sudeste do Brasil*. Universidade Estadual de Campinas, Campinas.
- Francini, R.B., (Ph.D. thesis) 1992. *Ecologia das taxocenoses de Actinote (Lepidoptera: Nymphalidae) em Asteraceae (Angiosperma, Magnoliatae) no sudeste do Brasil: subsídios para conservação*. Unicamp, Campinas.
- Francini, R.B., Freitas, A.V.L., Penz, C.M., 2004. Two new species of *Actinote* (Lepidoptera Nymphalidae) from Southeastern Brazil. *Zootaxa* 719, 1–10.
- Francini, R.B., Penz, C.M., 2006. An illustrated key to male *Actinote* from Southeastern Brazil (Lepidoptera, Nymphalidae). *Biota Neotrop.* 6 (1), <http://www.biotaentotropica.org.br/v6n1/pt/abstract?identification-key+bn00606012006>.
- Francini, R.B., Freitas, A.V.L., Brown Jr., K.S., 2005. Rediscovery of *Actinote zikani* (D’Almeida) (Nymphalidae, Heliconiinae, Acraeini): natural history, population biology and conservation of an endangered butterfly in SE Brazil. *J. Lepid. Soc.* 59 (3), 134–142.
- Francini, R.B., Freitas, A.V.L., 2010. Aggregated oviposition in *Actinote pellenea pelle-nea* Hübner (Lepidoptera: Nymphalidae). *J. Res. Lepid.* 42, 74–78.
- Francini, R.B., Barbosa, E.P., Freitas, A.V.L., 2011. Immature stages of *Actinote zikani* (Nymphalidae: Heliconiinae), a critically endangered butterfly from southeastern Brazil. *Trop. Lepid. Res.* 21 (1), 20–26.
- Freitas, A.V.L., Kaminski, L.A., Matos, R.G., Silva-Brandão, K.L., 2009a. Immature stages of the Andean butterfly *Actinote rufina* (Nymphalidae: Heliconiinae: Acraeini). *Trop. Lepid. Res.* 19, 18–21.
- Freitas, A.V.L., Francini, R.B., Souza, T.S., 2009b. Immature stages and natural history of the threatened butterfly *Actinote quadra* (Nymphalidae: Heliconiinae: Acraeini). *Trop. Lepid. Res.* 19, 83–88.
- Freitas, A.V.L., Barbosa, E.P., Francini, R.B., 2010. Immature stages of the butterfly *Actinote conspiciua* (Nymphalidae: Heliconiinae: Acraeini). *Trop. Lepid. Res.* 20, 100–104.
- Freitas, G.H.S., Chaves, A.V., Costa, L.M., Santos, F.R., Rodrigues, M., 2012. A new species of *Cincludes* from the Espinhaço Range, southeastern Brazil: insights into the biogeographical history of the South American highlands. *Ibis* 154, 738–755.
- Gonçalves, P.R., Myers, P., Vilela, J.F., Oliveira, J.A., 2007. Systematics of Species of the Genus *Akodon* (Rodentia: Sigmodontinae) in Southeastern Brazil and Implications for the Biogeography of the Campos de Altitude. *Miscellaneous Publications (University of Michigan, Museum of Zoology)*, No. 197, pp. 1–24.
- Hübner, J., 1819. *Verzeichniss bekannter Schmettlinge [sic]*. Augsburg, J. Hübner 2/8, 17–176.
- Iserhard, C.A., de Quadros, M.T., Romanowski, H.P., Mendonça Jr., M.deS., 2010. Borboletas (Lepidoptera: Papilionoidea e Hesperioidea) ocorrentes em diferentes ambientes na Floresta Ombrófila Mista e nos Campos de Cima da Serra do Rio Grande do Sul, Brasil. *Biota Neotrop.* 10 (1), 309–320.
- Jordan, H.E.K., 1913. I. Unterfamilie: Acraeinae. In: Seitz, A. (Ed.), *Die Gross-Schmetterlinge der Erde*, vol. 5. Alfred Kernen, Stuttgart, pp. 358–374, pls. 81–83.
- Jordan, H.E.K., Eltringham, H., 1916. Nymphalidae, subfam. Acraeinae. *Genera Insectorum* 169, 1–81, 2 pls.
- Kirby, W.F., 1871. *A Synonymic Catalogue of Diurnal Lepidoptera*. John Van Voorst, London, vii + 690 pp.
- Klots, A.B., 1970. Lepidoptera. In: Tuxen, S.L. (Ed.), *Taxonomist’s Glossary of Genitalia in Insects*. Munksgaard, Copenhagen, pp. 115–130.
- Lamas, G., 1997. Lista comentada de los nombres propuestos para los Acraeini neotropicales, y su material-tipo (Lepidoptera: Nymphalidae, Heliconiinae). *Rev. Peru. Entomol.* 39, 29–48 (“December 1996” [18 February 1997]).
- Lamas, G., 2004. Checklist: Part 4A. Hesperioidea-Papilionoidea. In: Heppner, J.B. (Ed.), *Atlas of Neotropical Lepidoptera*, vol. 5A. Association for Tropical Lepidoptera/Scientific Publishers, Gainesville, xxxvi + 439 pp.
- Leite, F.S.F., Juncá, F.A., Eterovick, P.C., 2008. Status do conhecimento, endemismo e conservação de anfíbios anuros da Serra do Espinhaço, Brasil. *Megadiversidade* 4, 158–176.
- Lewis, H.L., 1973. *Butterflies of the World*. Follett, Chicago, xvi + 312 pp.
- Lewis, H.L., 1975. *Las Mariposas del Mundo*. Ed. Omega, Barcelona, 228 pp.
- Llano, R.J., Llano, M.S., 1973. Observaciones sobre *Actinote mamita* Burmeister 1878 (Lep. Fam. Acraeidae). *Acta Zool. Lilloana* 29, 67–76.
- Mabilde, A.P., 1896. Borboletas do Estado do Rio Grande do Sul. Guia prática para os principiantes colecionadores de insectos contendo a descrição fiel de perto de 1000 borboletas com 280 figuras lithographadas em tamanho, formas e dezenhos conforme o natural. Estudo sobre a vida de insectos do Rio Grande do Sul e sobre a caça, classificação e a conservação de uma collecção mais ou menos regular. *Typographia Gundlach & Schuldt, Pôrto Alegre*, 240 pp., 24 pls.
- Mata, H., Fontana, C.S., Maurício, G.N., Bornschein, M.R., de Vasconcelos, M.F., Bonatto, S.L., 2009. Molecular phylogeny and biogeography of the eastern Tapaculos (Aves: Rhinocryptidae: Scytalopus, Eleoscytalopus): cryptic diversification in Brazilian Atlantic Forest. *Mol. Phylogenet. Evol.* 53, 450–462.
- Mielke, C.G.C., 1994. Papilionoidea e Hesperioidea (Lepidoptera) de Curitiba e seus arredores, Paraná, Brasil, com notas taxonômicas sobre Hesperioidea. *Rev. Bras. Zool.* 11 (4), 759–776.
- Müller, F., 1877. Beobachtungen an brasilianischen Schmetterlingen. III. *Kosmos (Leipzig)* 2 (9), 218–224.
- Müller, F., 1878. Pflanzengattungen, an denen mir bekannte Tagfalter-Raupen leben. *Stettiner entomologische Zeitung* 39 (7/9), 296.
- Neild, A.F.E., 2008. *The Butterflies of Venezuela Part 2: Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae)*. Meridian Publications, Greenwich, London, 272 pp.
- Paluch, M., (Ph.D. thesis) 2006. *Revisão das espécies de Actinote Hübner [1819] (Lepidoptera, Nymphalidae, Heliconiinae, Acraeini)*. Universidade Federal do Paraná, Curitiba.
- Paluch, M., Casagrande, M.M., Mielke, O.H.H., 2005. Comportamento de agregação noturna dos machos de *Actinote surima surima* (Schaus) (Lepidoptera, Heliconiinae, Acraeini). *Rev. Bras. Zool.* 22 (2), 410–418.
- Paluch, M., Casagrande, M.M., Mielke, O.H.H., 2006. Três espécies e duas subespécies novas de *Actinote* Hübner (Nymphalidae, Heliconiinae, Acraeini). *Rev. Bras. Zool.* 23 (3), 764–778.
- Paluch, M., Casagrande, M.M., Mielke, O.H.H., 2003. Tampão genital de *Actinote* Hübner, como caráter taxonômico (Lepidoptera, Nymphalidae, Acraeinae). *Rev. Bras. Entomol.* 47 (4), 573–580.
- Penz, C.M., Francini, R.B., 1996. New species of *Actinote* Hübner (Nymphalidae: Acraeinae) from Southeastern Brazil. *J. Lepid. Soc.* 50 (4), 309–320.
- Pierre, J., 1987. *Systématique cladistique chez les Acraea* (Lepidoptera, Nymphalidae). *Ann. Soc. Entomol. Fr. (N.S.)* 23 (1), 11–27.
- Silva-Brandão, K.L., Wahlberg, N., Francini, R.B., Azeredo-Espin, A.M.L., Brown Jr., K.S., Paluch, M., Lees, D.C., Freitas, A.V.L., 2008. Phylogenetic relationships of

- butterflies of the tribe Acraeini (Lepidoptera, Nymphalidae, Heliconiinae) and the evolution of host plant use. *Mol. Phylogenet. Evol.* 46, 515–531.
- Simpson, B.B., 1979. Quaternary biogeography of the high montane regions of South America. In: Duellman, W.E. (Ed.), *The South American Herpetofauna: Its Origin, Evolution, and Dispersal*. University of Kansas, Lawrence, KS, pp. 157–188, x + 485 pp.
- Vuilleumier, B.S., 1971. Pleistocene changes in the fauna and flora of South America. *Science* 173, 771–780.
- Warren, A.D., Davis, K.J., Stangeland, E.M., Pelham, J.P., Willmott, K.R., Grishin, N.V., 2017. Illustrated Lists of American Butterflies (North and South America) 10–XII–2017, <http://butterfliesofamerica.com/L/Neotropical.htm>.
- Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L., Brower, A.V.Z., 2009. Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary. *Proc. R. Soc. Lond. B* 276, 4295–4302.
- Whitmore, T.C., Prance, G.T. (Eds.), 1987. *Biogeography and Quaternary History in Tropical America*. Oxford University Press, New York, Oxford, x + 214 pp.
- Willmott, K.R., Freitas, A.V.L., Hall, J.P.W., Silva-Brandão, K.L., Paluch, M., 2009. A new species of *Actinote* Hübner from the Eastern Andes of Ecuador (Lepidoptera: Nymphalidae: Heliconiinae). *Proc. Entomol. Soc. Wash.* 111, 47–56.
- Willmott, K.R., Lamas, G., Hall, J.P.W., 2017. Notes on the taxonomy of *Actinote intensa* Jordan (Lepidoptera: Nymphalidae: Heliconiinae) and the description of a new sibling species from eastern Ecuador. *Trop. Lepid. Res.* 27 (1), 6–15.
- Wootton, R.J., 1979. Function, homology and terminology in insect wings. *Syst. Entomol.* 4, 81–93.