

Nomenclature, variation, and the biological species concept in *Lamasina* (Lycaenidae: Theclinae: Eumaeini)

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ABSTRACT. The correct generic name for the species that belong to *Eucharia* Boisduval, 1870, a homonym, is either *Annamaria* D'Abbrera & Bálint, 2001, which has been considered to be unavailable, or *Lamasina* Robbins, 2002, a replacement name for *Eucharia*. A recent re-interpretation of the original description of *Annamaria* was incorrect, and *Annamaria* is confirmed as being unavailable under Article 13.1 of the Code. A proposed neotype for *Papilio ganimedes* Cramer, 1775 is invalidated, and a possible syntype is illustrated. Results of an analysis of variation in the *Lamasina ganimedes* complex are distinctly different from those previously published and provide insufficient evidence to support the hypothesis that *L. lathyi* (Bálint, 2005) is distinct under a biological species concept. *Lamasina lathyi* is a synonym of *L. ganimedes* **syn. nov.** Statistical evidence overwhelmingly falsifies the published hypothesis that the *L. rhapsodia* (Johnson, 1991) (14 males) and *L. columbia* (Bálint, 2005) (8 females) species complexes are distinct rather than males and females of the same complex. *Lamasina columbia* is endemic to western Colombia. The hypothesis that *L. rhapsodia* (Bálint, 2005) from Bolivia is a distinct species is not better supported than the hypotheses that the one known specimen of *L. rhapsodia* is a geographical variant or an aberrant specimen. *Lamasina rhapsodia* is a synonym of *L. rhapsodia* **syn. nov.** Superficial similarity in ventral wing patterns in genera *Paiwarria* Kaye, 1904 and *Lamasina* is noted. A nomenclatural checklist for *Lamasina* is presented. **KEY WORDS.** *Annamaria*, availability of names; *columbia*; *ganimedes*; invalid neotype.

RESUMO. Nomenclatura, variação e o conceito biológico de espécie em *Lamasina* (Lycaenidae: Theclinae: Eumaeini). O nome genérico correto para as espécies de *Eucharia* Boisduval, 1870, um homônimo, é *Annamaria* D'Abbrera & Bálint, 2001, que tem sido considerado não válido, ou *Lamasina* Robbins, 2002, um nome substituído para *Eucharia*. Uma reinterpretação recente da descrição original de *Annamaria* é considerada incorreta, confirmando a não disponibilidade do nome com base no Artigo 13.1 do Código. O neótipo de *Papilio ganimedes* Cramer, 1775 é invalidado e um possível síntipo é ilustrado. Os resultados da análise de variação do complexo *Lamasina ganimedes* diferem significativamente daqueles publicados anteriormente, fornecendo poucas evidências para sustentar a hipótese que *L. lathyi* (Bálint, 2005) é uma espécie distinta sob o conceito biológico de espécie. *Lamasina lathyi* é um sinônimo de *L. ganimedes* **syn. nov.** A evidência estatística falseia categoricamente a hipótese publicada que os complexos de espécies *L. rhapsodia* (Johnson, 1991) (14 machos) e *L. columbia* (Bálint, 2005) (8 fêmeas) são diferentes e não machos e fêmeas do mesmo complexo. *Lamasina columbia* é endêmica do oeste da Colômbia. A hipótese de *L. rhapsodia* (Bálint, 2005), da Bolívia, ser uma espécie válida não está tão bem suportada quanto as hipóteses que consideram o único exemplar conhecido da espécie como uma variante geográfica ou um indivíduo aberrante. *Lamasina rhapsodia* é um sinônimo de *L. rhapsodia* **syn. nov.** Foi observada uma semelhança superficial entre os gêneros *Paiwarria* Kaye, 1904 e *Lamasina* referente aos padrões das asas em vista ventral. É apresentada uma checklist para *Lamasina*.

PALAVRAS-CHAVE. *Annamaria*; *columbia*; disponibilidade de nomes; *ganimedes*; invalidação de neótipo.

BOISDUVAL (1870) described genus *Eucharia* (Lycaenidae: Theclinae) for three hairstreak butterflies with brilliant green undersides (*ganymedes*, *imperialis*, *regalis*). KIRBY (1871) selected *Papilio ganimedes* Cramer, 1775 as the type species (*ganymedes* had been a subsequent misspelling, ROBBINS & LAMAS 2002), but

SCUDDER (1875) noted that *Eucharia* Boisduval was a junior homonym of *Eucharia* Hübner, [1820] and *Eucharia* Koch, 1835. Although *Eucharia* Boisduval was consistently cited over the ensuing century (COMSTOCK & HUNTINGTON 1959-1964, HEMMING 1967, ELIOT 1973), D'ABRERA & BÁLINT (2001) did not mention it

when they transferred *P. ganimedes* to their newly proposed name, *Annamaria*. ROBBINS (2002) proposed *Lamasina* as a replacement name for *Eucharia* Boisduval, placed four species in *Lamasina*, and explained why *Annamaria* D'Abbrera & Bálint was unavailable under Article 13.1 of the International Code of Zoological Nomenclature (1999, ICZN hereafter). BÁLINT (2005) disagreed with this taxonomic treatment, presented a new species level taxonomic arrangement based on characters of the wings and androconia, and recognized the name *Annamaria* as nomenclaturally valid.

The purpose of this paper is to provide evidence that modifies BÁLINT's (2005) nomenclatural and taxonomic conclusions. Specifically, we show that Bálint has proposed nomenclatural changes in *Lamasina* that do not meet the requirements of the ICZN (1999). We analyze variation in the *Lamasina ganimedes* species group and show that it is inconsistent with Bálint's species level taxonomy. We present new data on Bálint's *L. rhapsissima* (all males) and *L. columbia* (Bálint, 2005) (all females) species groups that falsify Bálint's conclusion that they are separate species groups. Finally, we show that there is yet insufficient evidence on geographical variation to definitively determine biological species in *Lamasina*, but suggest a provisional classification that better fits current evidence.

MATERIAL AND METHODS

Wing characters and androconia were examined in 32 males and 28 females of *Lamasina* (data listed in Appendix I). This sample included: 1) 21 males and 25 females; 2) the types or presumed types of *Thecla draudti* Lathy, 1926; *Thecla godmani* Goodson, 1945; *Papilio ganimedes* Cramer, 1775; *Thecla nobilis* Herrich-Schäffer, [1853]; *Thecla bimaculata* Möschler, 1877; and *Thecla mirabilis* Lathy, 1930; all of which we have examined in person and photographed; and 3) photographs of 6 males and 2 females in various publications (listed in Appendix I), including the types of *Annamaria columbia* and *A. rhapsodia* Bálint, 2005. Because BÁLINT (2005) differentiated species solely on the basis of wing pattern, wing venation, and androconia, photographs are sufficient to code most characters. BÁLINT (2005) illustrated some types of *Lamasina* species, and we illustrate the remaining ones (Figs 1-3). The collections from which we examined specimens and their acronyms are: (AME) Florida Museum of Natural History (formerly Allyn Museum of Entomology), University of Florida, Gainesville, FL, USA; (AMNH) American Museum of Natural History, New York, NY, USA; (BMNH) Natural History Museum, London, UK; (CMNH) Carnegie Museum of Natural History, Pittsburgh, PA, USA; (GWB) George W. Busby Collection, Bedford, NH, USA; (JHKW) Jason Hall & Keith Willmott Collection, Smithsonian Institution, Washington, DC, USA; (MLM) Michael L. McInnis Collection, Floyds Knobs, Indiana, USA; (MNHN) Muséum National d'Histoire Naturelle, Paris, France; (MUSM) Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; (RCB) Robert C. Busby Collection, Andover, MA, USA; (RMNH) Nationaal

Natuurhistorische Museum ("Naturalis") [formerly Rijksmuseum van Natuurlijke Historie], Leiden, Netherlands; (SMNS) Staatliches Museum für Naturkunde, Stuttgart, Germany; (USNM) National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; (ZMHB) Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Morphological characters were prepared and scored using standard entomological techniques (ROBBINS 1991), including genitalic dissections and wing slides to score venation characters. Wing vein terminology follows COMSTOCK (1918) except when citing characters verbatim from D'ABRERA and BÁLINT (2001). The length of the forewing discal cell was measured from digitized images of wing slides from the base of the forewing to the origin of vein M_2 . Similarly, forewing length was measured from the base of the forewing to the apex. The presence of ventral forewing "black" androconia was assessed using a binocular microscope. The width of the black portion of the ventral hindwing postmedian line was measured at vein M_2 using a stereomicroscope ocular grid for specimens and using a vernier caliper for photographs. We scored the relative widths of black lines on the ventral forewing using BÁLINT's (2005) criterion (conspicuously wider, equal to, or narrower), but had difficulty scoring a number of specimens. Examples of the different character states are illustrated.

In the analysis of variation section, the Neotropics are partitioned into biogeographical areas modified slightly from BROWN (1982). The Trans-Andean Region is Mexico to western Ecuador and northwestern Peru, including the Río Magdalena valley of Colombia. The Guiana Region is bounded on the west by a line from the delta of the Río Orinoco (Venezuela) to Manaus (Brazil) and includes the area to the east of this line and to the north of the Amazon River. The Upper Amazon Region consists of those areas west of Manaus (both north and south of the Amazon River) to the eastern slope of the Andes. Species distributions are mapped.

The biological species concept of MAYR (1963) is used except that we do not recognize subspecies for the reasons listed in WILSON & BROWN (1953).

Likelihoods are calculated according to standard statistical techniques (EDWARDS 1972).

A summary of the proposed provisional classification is presented in a format similar to that of the previous checklist for the Eumaeini (ROBBINS 2004b).

RESULTS

Nomenclature

Annamaria D'Abbrera & Bálint, 2001

The original description of *Annamaria* D'Abbrera & Bálint read "In NEOTROPICAL VII:1107 treated as *Evenus draudti*. Likewise by other workers. However is distinguished from *Evenus* by shorter cell of f.w. (1/3rd of costal length), and extension of Vein 1 of h.w. into a lobed tail at tornus. Compound androconial patch on ♂ f.w. consisting of single circle within cell & quadri-



Figures 1-3. Dorsal surface, ventral surface, and labels of three male *Lamasina* types: (1) the possible holotype of *L. ganimedes* in RMNH; (2) a male syntype of *L. bimaculata* in ZMHB; (3) the male holotype of *L. godmani* in BMNH, the arrow points to blue scales that occur in males of the *Lamasina ganimedes* complex, but not females.

furcate patch immediately outside discocellulars. Further, androconial patches on post discal & submarginal tornal areas of f.w. respectively."

ROBBINS (2002) noted that *Annamaria*, D'Abbrera & Bálint, 2001 is unavailable under Article 13.1.1 (ICZN 1999) because the description did not provide "a description or definition that states in words characters that are purported to differentiate the taxon". Rather, the words of the original description differentiate *Evenus draudti* from *Evenus* Hübner. In short, the description reads "In NEOTROPICAL VII:1107 [the type species was] treated as *Evenus draudti*. Likewise [it was so treated] by other workers. However, [it] is distinguished from *Evenus* by shorter cell of f.w. (1/3rd of costal length), and extension of Vein 1 of h.w. into a lobed tail at tornus. [It has a] compound androconial patch on ♂ f.w. consisting of single circle within cell & quadrifurcate patch immediately outside discocellulars. Further, androconial patches on post discal & submarginal tornal areas of f.w. respectively."

BÁLINT (2005) responded that *Annamaria* was valid for four reasons. First, he claimed that Robbins "had a subjective intention" in proposing *Lamasina* as a replacement for *Annamaria*. Irrespective of its validity, we question whether such a statement belongs in a scientific journal.

Second, Bálint stated that *Eucharia* Boisduval was a *nomen oblitum* with a reference to Article 23.9.2 (ICZN 1999). However, designation of a *nomen oblitum* requires two conditions, one of which is that the junior synonym or homonym – the *nomen protectum* – had to be used in at least 25 works by at least 10 authors in the preceding 50 years and encompassing a span of not less than 10 years. Presumably Bálint considered *Annamaria* to be the *nomen protectum*, but it had been used only by D'ABBRERA & BÁLINT (2001). We do not understand this argument.

Third, BÁLINT (2005) argued that *Salazaria* D'Abbrera & Bálint, 2001 was described in a manner analogous to *Annamaria*. Since *Salazaria* was accepted as nomenclaturally valid (ROBBINS

2004b), *Annamaria* is nomenclaturally valid also. This argument is incorrect because the description of *Annamaria* explicitly differentiates *Evenus draudti* from *Evenus* while the description of *Salazaria* does not explicitly differentiate *Thecla sala* Hewitson – the type species – from *Johnsonita* Salazar & Constantino. On the other hand, the description of *Salazaria* implicitly differentiates *Thecla sala* and *Thecla salaeides* Draudt – and not *Salazaria* – from *Johnsonita*. Because the nomenclatural validity of *Salazaria* depends upon interpretation and could generate instability, an application to the International Commission on Zoological Nomenclature is being submitted to stabilize the nomenclature of eumaeine generic names proposed in D'ABRERA & BÁLINT (2001).

Fourth, BÁLINT stated without evidence that the original description of *Annamaria* fulfills the requirements of Article 13.1.1 (ICZN 1999). As noted, the words differentiate only the type species. However, the characters in the original description also differentiate only the type species. In fact, with the possible exception of *Salazaria*, the characters in all their original descriptions characterize only the type species. This finding supports the idea that D'ABRERA & BÁLINT purported to differentiate the type species; it is inconsistent with BÁLINT's contention that they purported to differentiate the genus.

In summary, ICZN (1999) Article 13.1 is clear that a new taxon must be "accompanied by a description or definition that states in words characters that are purported to differentiate the taxon". The words in the original description of *Annamaria* D'Abbrera & Bálint differentiate the type species; they do not differentiate the genus. The characters in the original description distinguish the type species; they do not distinguish the genus. There is no evidence that the authors purported to differentiate *Annamaria*. The name *Annamaria* D'Abbrera & Bálint is nomenclaturally unavailable, and we use *Lamasina* hereafter.

Papilio ganimedes Cramer, 1775

BÁLINT (2005) designated a neotype for *Papilio ganimedes*. According to Article 75.3.4 (ICZN 1999), a validly proposed neotype requires "the author's reasons for believing the name-bearing type specimen(s) (i.e. holotype, or lectotype, or all syntypes, or prior neotype) to be lost or destroyed, and the steps that had been taken to trace it or them; ...". In this case, Bálint provided no evidence that he had taken steps to trace a possible syntype. He provided no evidence that syntypes were not extant, only that he believed them to be lost. Therefore, the neotype designation is invalid.

We illustrate a male in RMNH that someone has labeled as a possible holotype of *Papilio ganimedes* (Fig. 1). It is often difficult to trace old types (LAMAS 2007), and we cannot be sure whether or not this specimen is actually a type. However, the wing pattern is reasonably similar to Cramer's figure (illustrated in BÁLINT 2005), it is "set" in the same manner as the original Cramer figure, several of Cramer's types have been found in

RMNH (DE JONG 2005, CHAINEY 2005), and the potential type is the same species as Bálint's invalid neotype. Identification of the name *Papilio ganimedes* has posed no problems since LATHY (1926) corrected the taxonomy of DRAUDT (1919-1920), negating the need for a neotype designation.

Taxonomy

Lamasina Robbins, 2002

D'ABRERA and BÁLINT (2001) distinguished *Lamasina* (under the name *Annamaria*) by a short forewing discal cell (1/3rd of costal length) and by extension of hindwing vein 1 (= vein 2A) into a lobed tail at the tornus. The first distinguishing trait is problematic. BÁLINT (2005) later reported a forewing discal cell less than 1/4th the length of the costa (1/6th in males), not 1/3rd as originally reported. Further, he measured forewing length to the terminus of vein R₅. We presume that Bálint meant vein R₃ because the lack of veins R₄ and R₅ is a synapomorphy for the Eumaeini (ELIOT 1973). In wing slides of *L. draudti*, the proposed type species of *Annamaria*, the length of the discal cell is 35% of the length of the costa in the male and 41% in the female (Figs 4-5). The second distinguishing trait is inaccurate for two reasons. First, *L. rhapsissima* lacks a lobed tail at the tornus. Second, when a lobed tail at the tornus is present, as in *L. draudti*, hindwing vein 1 (= vein 2A) does not extend into it (Figs 4-5). In summary, the original description of *Annamaria* was morphologically incorrect irrespective of its nomenclatural status.

BÁLINT (2005) differentiated *Lamasina* by a short male forewing discal cell, the form of the androconia on the dorsal forewing, and a lobed "tail" at the hindwing tornus. The first two characters are not unique within the Eumaeini, as BÁLINT (2005) noted. The third is restricted to one species complex within the genus. The closest relatives of *Lamasina* were not identified. There was no phylogenetic analysis or argument suggesting that any of these characters was a synapomorphy. BÁLINT (2005) noted that the combination of characters is unique.

Analysis of variation the *Lamasina ganimedes* complex

We characterize the *L. ganimedes* complex by an elongate lobe at the tornus (BÁLINT 2005) that is unique within the Eumaeini. Besides the presumed type of *L. ganimedes*, we illustrate the types of *L. godmani* and *L. bimaculata* (Fig. 1); the types of *L. nobilis*, *L. draudti*, and *L. lathyi* were already illustrated (BÁLINT 2005). ROBBINS (2004b) recognized *L. draudti* (= *L. godmani*) and *L. ganimedes* (= *L. nobilis* and *L. bimaculata*) in a checklist, but BÁLINT (2005) partitioned this complex into three species (*L. draudti*, *L. ganimedes*, *L. lathyi*) with non-overlapping ranges based on five characters of the wings and androconia. We assess variation of these characters and map their distributions according to our systematic conclusions (Fig. 20).

Bálint character 1. Dorsal forewing with (*L. draudti*) or without (*L. ganimedes*, *L. lathyi*) scent patches in cells M₁-M₂ and M₂-M₃. Every male in the *L. ganimedes* complex that we examined (18 males) has dorsal forewing scent patches distal of the disco-cellular veins, including in cells M₁-M₂ and



Figures 4-5. Venation of *L. draudti*: (4) male (Río Carare, Colombia); (5) female (Colombia).

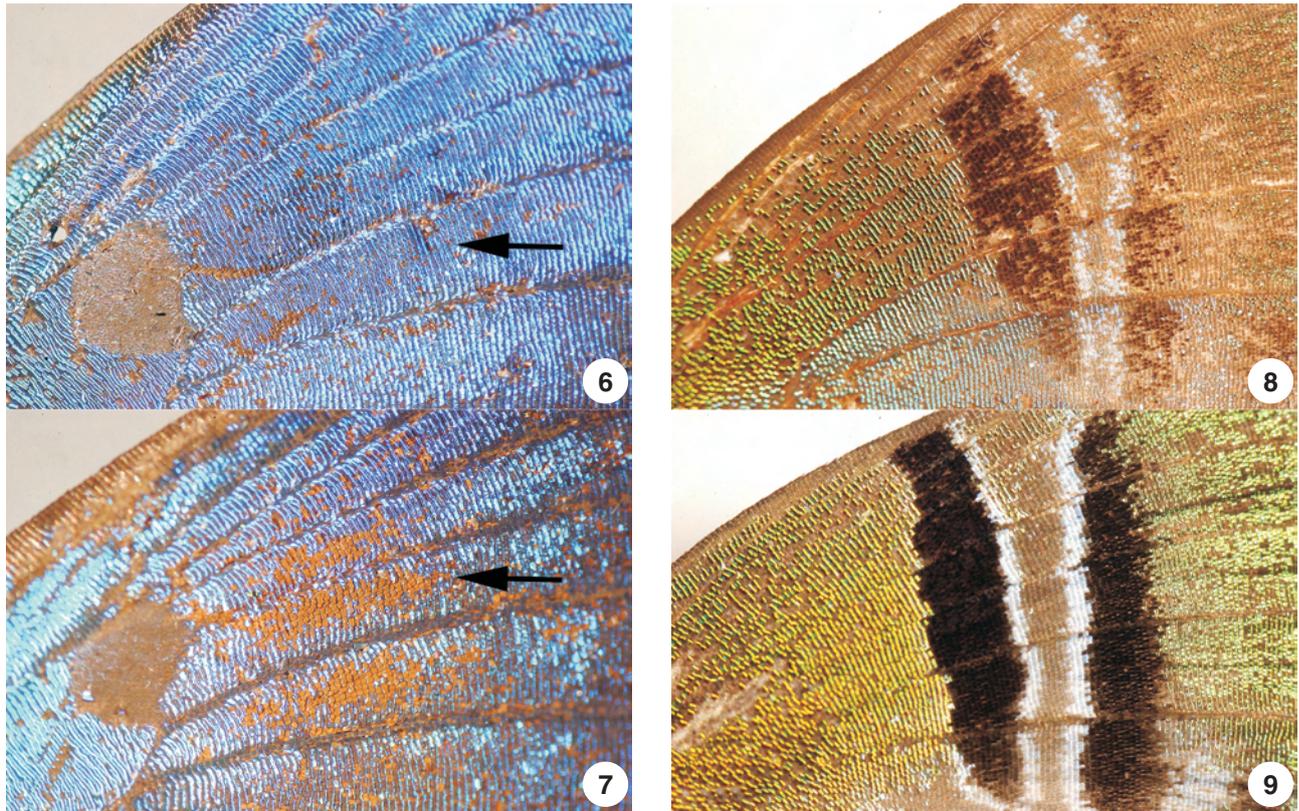
M_2 - M_3 (Figs 6-7). In the Guiana and Upper Amazon Regions, these androconia are mostly covered with blue wing scales (7 males). In the Trans-Andean Region, these androconia are only partially covered with blue scales (11 males), but the extent to which they are covered is variable. This sample includes the Guatemalan holotype of *Thecla godmani* (Fig. 3), which had been reported to lack these androconia (GOODSON 1945).

Bálint character 2. Ventral forewing with distal black band conspicuously wider than (*L. draudti*), equal to (*L. lathyi*), or narrower than (*L. ganimedes*) the more basal black line. In the Trans-Andean Region, the distal black line may be conspicuously narrower than (16 specimens) or about equal in width to (5 specimens) the basal line (Figs 8-9). In the Guiana Region, the distal line may be conspicuously wider than (3 specimens, Figs 1 and 2), about equal to (1 specimen), or narrower than (1 specimen) the width of the basal line. For example, the male of *L. ganimedes* that BÁLINT (2005) illustrated (his fig. 13) has the lines about equal, and the two females that he illustrated (his figs 15 and 17) have the distal line wider. In the Upper Amazon Region, both lines may be about the same width (11 specimens) or narrower (1 specimen) than the basal line.

Bálint character 3. Ventral hindwing postmedian red

band bordered basally with a conspicuous black line (*L. draudti*) or with a faint or no black line (*L. ganimedes* and *L. lathyi*). The “red band” ranges in color from red (Fig. 3) to dark maroon to black (Fig. 1), and measurements in the latter case may be somewhat inaccurate. All 21 specimens from the Trans-Andean Region have a conspicuous black distal edge to the postmedian line at vein M_2 , ranging from 1.05 to 1.79 mm wide (Figs 10 and 11). The distal black edge of the postmedian line is less conspicuous at vein M_2 in the Guiana and Upper Amazon Regions, ranging from 0 to 0.85 mm wide (Figs 10 and 11).

Bálint character 4. Ventral forewing with (*L. ganimedes*) or without (*L. draudti* and *L. lathyi*) a basal black scent patch along the cubital vein. All 18 males that we examined have “black” androconia (under a microscope, the scale color may be tan, gray, or black) near the base of the cubital vein. The androconia are intermixed with regular wing scales, but it is difficult to score the extent of the androconia because the base of the ventral forewing in “set” specimens is covered by the hindwing. In the Guiana Region, the possible type of *L. ganimedes* (Fig. 1) is representative of males with few regular wing scales mixed with androconia at the base of the cubital vein, but the type of *Thecla bimaculata* is representative of males



Figures 6-9. (6-7) Dorsal forewing androconia in cells M_1 - M_2 and M_2 - M_3 (arrows): (6) the darker blue area is androconia covered with blue scales (*L. ganimedes*, Rio Negro, Meta, Colombia); (7) patches of blue scales covering the androconia are lacking (*L. draudti*, Guapiles, Costa Rica); (8-9) ventral forewing black bands in female *L. draudti*: (8) distal band narrower than basal one (Alluriquin, Pichincha, Ecuador); (9) distal band width about the same as the basal band (10 Km E Santo Domingo, Pichincha Ecuador).

in which the androconia are mixed with regular wing scales so that the scent patch is less conspicuous (Fig. 2). In the Trans-Andean and Upper Amazon Regions, the number of androconia is also variable, some being similar to the type of *T. bimaculata* (Fig. 3), and others having fewer androconia mixed with regular wing scales (Figs 12 and 13).

Bálint character 5. Dorsal forewing deep (*L. ganimedes*) or light azure (*L. draudti*, *L. lathyi*) color. The hue of iridescent colors varies with angle of view and with lighting conditions (natural, artificial, wavelength, etc). We cannot accurately score this character based on our images of the *L. ganimedes* complex and can neither confirm nor falsify it.

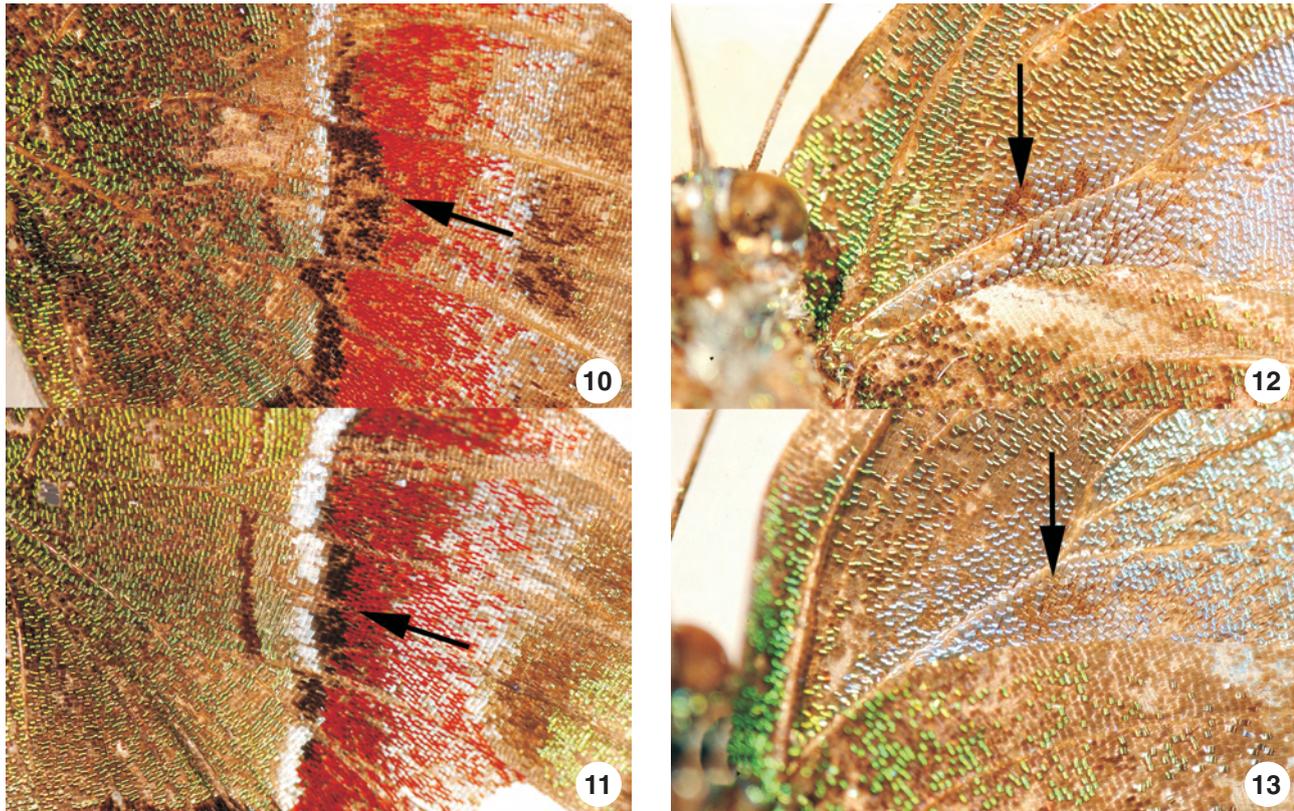
Lamasina rhapsissima complex

We examined 14 individuals in the *L. rhapsissima* species group as characterized by Bálint (males of *L. rhapsissima* and *L. columbia* in Appendix I). They occur in Andean montane forest between 800 and 1700 m, and have the same arrangement of hindwing tails as males of the *L. ganimedes* complex, a forewing discal cell about 35% of the length of the forewing costa as

in males of the *L. ganimedes* complex, and male genitalia almost indistinguishable from those of the *L. ganimedes* complex (Figs 14 and 15). All 14 individuals are males, and no females have been reported.

We examined eight individuals in the *L. columbia* species group as characterized by Bálint (females of *L. rhapsissima* and *L. columbia* in Appendix I). They occur in Andean montane forest between 600 and 1300 m, and have the same arrangement of hindwing tails as females of the *L. ganimedes* complex, a forewing discal cell about 40% of the length of the forewing costa as in females of the *L. ganimedes* complex, and female genitalia indistinguishable from those of the *L. ganimedes* complex (Figs 16 and 17). All eight individuals are females, and no males are known. The distribution of the *L. columbia* species group is essentially the same as that of the *L. rhapsissima* species group. Females of the *L. columbia* species group were collected at the same two Ecuadorian localities as males of the *L. rhapsissima* species group (Appendix I), so these species groups are sympatric.

There are two hypotheses, and we ask which one is more likely. The first hypothesis, which was proposed by BÁLINT



Figures 10-13. (10-11) Ventral hindwing black postmedian line in males at vein M_2 (arrow): (10) distal band > 1 mm in *L. draudti* (Bugaba, Panama); (11) distal band < 1 mm in *L. ganimedes* (Rio Negro, Meta, Colombia); (12-13) ventral forewing "black" androconia interspersed among regular wing scales (arrows): (12) *L. draudti* (Bugaba, Panama); (13) *L. ganimedes* (25 Km Puyo-Napo Rd, Pastaza, Ecuador).

(2005), is that there are two species complexes, one known from 14 males and one known from 8 females. The alternate hypothesis is that there is one species complex with 14 males and 8 females. Let (p) be the probability of sampling a male and (1-p) the probability of sampling a female. The likelihood that there are two species complexes, one known from 14 males and one known from 8 females, is $(p)^{14}x(1-p)^8$. The likelihood of the alternate hypothesis is $((22!)/((14!)x(8!)))x(p)^{14}x(1-p)^8$. The alternate hypothesis is 319,770 times more likely than Bálint's hypothesis (EDWARDS 1972 for methods). In lieu of any evidence to the contrary, we combine these two species complexes as the *L. rhapsissima* complex.

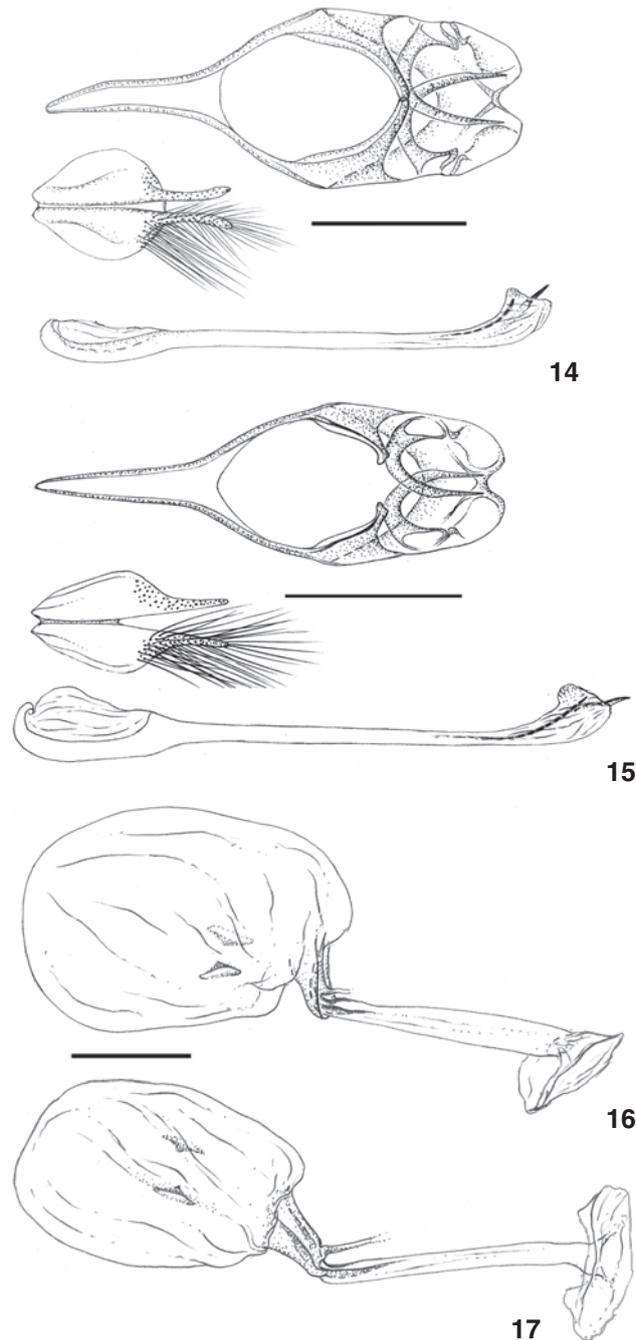
Assessing variation in the *L. rhapsissima* complex is difficult because of the paucity of specimens. As with the *L. ganimedes* complex, males have androconia on the dorsal forewing and hindwing (the hindwing androconia were not noted in BÁLINT [2005] although evident in his fig. 18) that are partially covered with blue wing scales (as well as ventral forewing androconia intermixed with regular wing scales along the cubital vein). The extent of the blue scales covering the androconia varies geographically within the *L. rhapsissima* complex,

as it does in the *L. ganimedes* complex. The wing shape of individuals from western Colombia, however, is less "wide" than those from the eastern slope of the Andes (Figs 18 and 19). Further, females from western Colombia, including the mislabeled type of *L. columbia* ("Bogota"), lack the green scales that are prominent at the base of the ventral wings of specimens from the eastern slope of the Andes (Figs 18 and 19). We map the distributions of these phenotypes according to our systematic conclusions (Fig. 21).

BÁLINT (2005) differentiated *L. rhapsodia* from *L. rhapsissima* by darker blue dorsally, a slightly different ventral hindwing pattern, and slightly different dorsal forewing androconia. This species was described from one Bolivian male, so it is not possible to assess the significance of this variation.

DISCUSSION

Males in the *L. ganimedes* complex have ventral forewing blue scales (Fig. 3) that do not occur in females, a homoplastic sexual dimorphism that occurs only in the *Eumaeus*, *Brangas*, *Atlides*, and *Micandra* Sections of the Eumaeini (ROBBINS 2004a). ROBBINS (2004a,b) presented no phylogenetic evidence concern-



Figures 14-17. (14-15) Male genitalic capsule in ventral aspect (posterior to the right) with valvae separated and penis in lateral aspect: (14) *L. draudti* ("Bogota", Colombia), (15) *L. rhapsissima* (Abitagua, Pastaza, Ecuador); (16-17) female genitalia bursa copulatrix in lateral aspect, posterior to the right: (16) *L. draudti* ("Bogota", Colombia); (17) *L. rhapsissima* (La Salud, Chanchamayo, Peru). There are semi-membranous "plates" at the posterior end of the ductus bursae that are difficult to illustrate. Scale 1mm.

ing the relations of *Lamasina* other than that it belongs to one of these Sections. He placed *Lamasina* next to *Evenus* because both genera share some wing pattern characteristics, but *Lamasina* is not otherwise demonstrably related to any other genus, a view first expressed by GODMAN & SALVIN (1887). BÁLINT'S (2005: 119) statement that "ROBBINS (2004) suggested *Evenus* ... as sister group [of *Lamasina*]" has no basis in fact.

Assessing the monophyly of *Lamasina* is complicated by not knowing its closest relatives. However, male and female genitalia are exceedingly similar between the *L. draudti* and *L. rhapsissima* species groups (Figs 14-17), and are different from all other eumaeines (Robbins unpubl.). On this provisional basis, ROBBINS (2004b) recognized *Lamasina* as a monophyletic genus. BÁLINT (2005) did not support his recognition of *Lamasina* with a phylogenetic argument, perhaps because he considers the concept of monophyly to be a threat to taxonomy (BÁLINT 2006). Indeed, the three androconial and wing pattern distinguishing characters proposed by BÁLINT (2005) either occur in other eumaeine genera or do not occur in all *Lamasina* species. However, when the closest relatives of *Lamasina* are determined, it is possible that one or more of these characters may be recognized as synapomorphies.

There is insufficient data in the *L. ganimedes* complex to partition it confidently into species under a biological species concept. Wing pattern and androconial characters are highly variable, as we have documented. It is not known if the "phenotypes" recognized by BÁLINT (2005) are allopatric, parapatric, or sympatric. And if they are sympatric, we do not know if the proposed distinguishing characters gradually intergrade, abruptly intergrade in a narrow geographical band, or do not intergrade. The variation that we document, however, is inconsistent with that reported by BÁLINT (2005) and does not support his taxonomic conclusions. For this reason, we propose a provisional classification that is better supported by evidence.

In the *L. ganimedes* complex, Trans-Andean Region males have fewer blue scales covering the dorsal forewing androconia (a modification of Bálint Character 1, Figs 6 and 7). Similarly, both sexes from the Trans-Andean Region have a thicker black postmedian line on the ventral hindwing (greater than 1 mm wide at vein M_2) than those from the Guiana and Upper Amazon Region (less than 1 mm wide at vein M_2) (Bálint Character 3, Figs 10 and 11). We have no evidence to falsify the hypothesis that the Trans-Andean Region specimens represent a distinct species, but admittedly data from the critical geographical area where these phenotypes meet (if they do) are yet lacking. Further, the name *L. draudti*, which applies to these Trans-Andean specimens, has not previously been treated as a synonym, so far as we are aware. The type of *Thecla godmani* from Guatemala could represent a distinct species, but with only one individual, it would be premature to remove this name from synonymy with *L. draudti*.

The Upper Amazon phenotype of *L. ganimedes*, which BÁLINT (2005) named *L. lathyi*, represents either a geographical form of

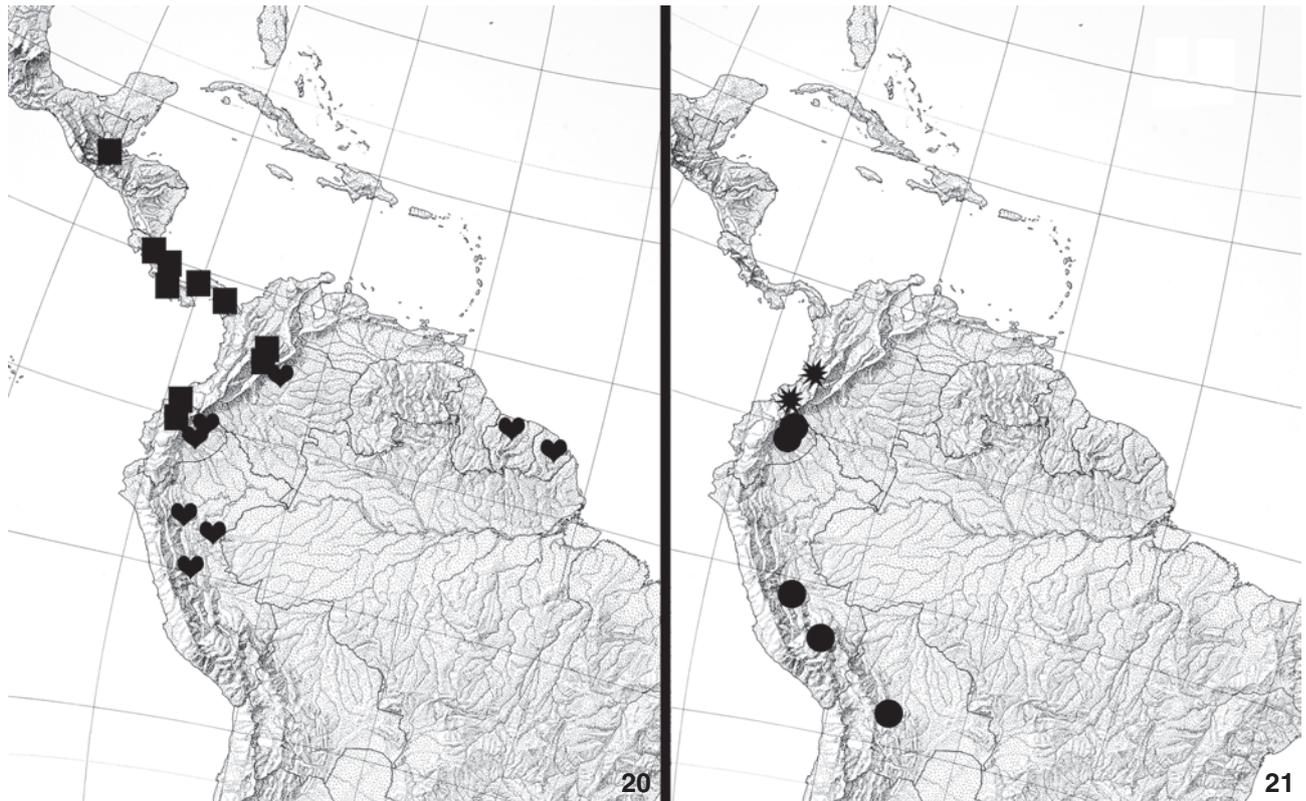


Figures 18-19. *Lamasina rhapsissima* complex: (18) *L. columbia* male (Calima Dam, Valle, Colombia) and female (Calima, Valle, Colombia); (19) *L. rhapsissima* male (eastern Ecuador, the holotype in MNHN) and female (La Salud, Chanchamayo, Peru), arrow points to green scales at the base of the ventral wings.

L. ganimedes or a distinct biological species. None of the evidence proposed by BÁLINT (2005) or that we have documented supports the latter hypothesis better than the former hypothesis. Relative widths of the ventral forewing black lines (Bálint Character 2, Figs 8 and 9) are very difficult to score in some individuals and are variable in all geographical regions, contrary to BÁLINT's (2005) results. The extent of the ventral forewing androconia is more pronounced on average in males from the Guiana Region than the Upper Amazon (Bálint Character 4, Figs 1-3 and 12-13), but is not distinguishing. For example, the mixture of androconia and regular wing scales in the male type of *Thecla bimaculata* (Fig. 2) from the Guiana Region is similar to that of males in other regions (Figs 3 and 12-13). Finally, males from the Guiana Region are darker blue than those from the Upper Amazon (Bálint Character 5), but females cannot be distinguished. We do not know if the blue color of males intergrades where these phenotypes meet, but distinguishing species on this basis is somewhat analogous to partitioning human beings into species based on skin color variation in males. In sum, there is no convincing evidence that the available name *L. lathyi* represents a distinct biological species, for which reason we synonymize it with *L. ganimedes* *syn. nov.*

Classification in the *L. rhapsissima* complex is more tenuous. The green scales at the base of the ventral wings of female *L. rhapsissima* are lacking in females from western Colombia (Figs 18-19). Both males and females from western Colombia—consistently and with little variation—have a different wing shape (less wide) than those from the eastern Andes (Figs 18-19). There are also other evident differences (Figs 18-19), such as a wider border on the dorsal forewing of males, that provide substantive evidence for reproductive isolation. We recognize the western Colombian phenotype, to which the name *L. columbia* applies, as a distinct species. The single male from Bolivia (*L. rhapsodia*) may represent a developmental aberration, a clinal geographical form, or a distinct species. BÁLINT (2005) provided no evidence under a biological species concept that better supports the hypothesis that the Bolivian specimen represents a distinct species. For this reason, *L. rhapsodia* is a synonym of *L. rhapsissima* *syn. nov.*

The combination of the all-male *L. rhapsissima* and the all-female *L. columbia* species groups is intriguing for its potential evolutionary significance. The *L. ganimedes* complex has traditionally been grouped with the unrelated *Paiwarria telemus*



Figures 20-21. Distribution maps for *Lamasina*: (20) *L. draudti* (squares), *L. ganimedes* (hearts); (21) *L. columbia* (stars), *L. rhapsissima* (circles). The “hearts” in French Guiana and Surinam represent the country, not specific localities within these countries.

(Cramer, 1775) and *P. antinous* (C. Felder & R. Felder) because they have superficially similar ventral wing patterns (i.e., DRAUDT 1919-1920). Two other species of *Paiwarria* Kaye, 1904, *P. episcopalis* (Fassl) and *P. chuchuvia* Hall & Willmott, however, have males with brilliantly iridescent green undersides and thick black bands while the females have gray undersides with long straight white lines (HALL & WILLMOTT 2005). This sexual dimorphism in ventral wing pattern mirrors the sexual dimorphism in the *L. rhapsissima* complex. Unfortunately, these species are so rarely seen in the field that it would be difficult to study this intriguing result.

ROBBINS (2004b) tentatively placed *Denivia saphonota* Constantino, Salazar & Johnson in *Lamasina* even though he knew this species only from the original description and illustration. This species was recorded only from females from western Colombia, it had a forewing discal cell length about 40% of the length of the costa—like females of the *L. ganimedes* complex—and a male of *Lamasina* was known from western Colombia (Fig. 18) that at the time did not have an associated female. These reasons were the basis for its placement, but the subsequent discovery of a female *Lamasina* from western Colombia (Fig. 18) falsifies the original justification of the generic placement in *Lamasina*.

BÁLINT (2005) transferred *D. saphonota* to *Brevianta* Johnson, Kruse & Kroenlein. He did not note that this species has the same forewing discal cell as females of *Lamasina*. Rather, he based this action on phenotypic wing similarity and a “membranous large and wide female genital ductus bursae.” It is hard to understand this action because the ductus bursae of *Brevianta* is sclerotized, not membranous. BÁLINT’s (2005) transfer may be correct (we have not had the opportunity to dissect a specimen), but the placement of *D. saphonota* remains dubious until accurate character evidence is published.

The following provisional classification summarizes our analysis of variation:

Lamasina Robbins, 2002, nom. nov.

Eucharia Boisduval, 1870, preocc. (Hübner, [1820])

Annamaria D’Abrera & Bálint, 2001, unavail. (ICZN 1999, Art. 13.1)

draudti (Lathy, 1926) (*Thecla*) – “Central America”; Colombia

godmani (Goodson, 1945) (*Thecla*) – Guatemala

ganimedes (Cramer, 1775) (*Papilio*) – “West Indies”

ganymedes (Fabricius, 1776) (*Papilio*), missp. – “West Indies”

nobilis (Herrich-Schäffer, [1853]) (*Thecla*) – Surinam

bimaculata (Möschler, 1877) (*Thecla*) – Surinam

lathyi (Bálint, 2005) (*Annamaria*), **Syn. nov.** – Peru
columbia (Bálint, 2005) (*Annamaria*) – Colombia
raptissima (K. Johnson, 1991) (*Thecla*), repl. name – Ecuador
mirabilis (Lathy, 1930) (*Thecla*) – Ecuador
 preocc. (not Erschoff, 1874)
mirabilissima (D'Abbrera, 1995) (*Evenus*), repl. name – Ecuador
rhapsodia (Bálint, 2005) (*Annamaria*), **Syn. nov.** – Bolivia

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Appendix I. Specimens Examined. Those localities in quotation marks are undoubtedly incorrect. The species names are those recognized in this paper. The biogeographic regions are described in the text. The distributions are mapped except for those in quotation marks (Fig. 10).

- Lamasina draudti* (Lathy). [Trans-Andean Region] **Guatemala**: 1 male Chisoy Valley [holotype *Thecla godmani* Goodson] (BMNH). **Costa Rica**: 1 male Guápiles (USNM), 1 male Carrillo (USNM), 1 female Heredia, La Selva (USNM). **Panama**: 1 male Bugaba (USNM), 1 male Cerro Campana (USNM), 1 female Cana (USNM), 1 female Altos de Pacora (USNM). **W. Colombia**: (including Magdalena Valley). 1 male “Bogota” (USNM), 1 male and 1 female Río Carare (USNM), 1 male “Bogota” [lectotype of *Thecla draudti* Lathy] (MNHN), 1 male Muzo (illustrated in BÁLINT 2005), 1 female no further data (USNM), 1 female “Bogota” (USNM), 1 male and 1 female (AMNH). **W. Ecuador**: 1 male km 5 Lita-Alto Tambo (JHKW), 1 female Alluriquín (USNM), 1 female 12 km E Sto Domingo (USNM), 1 female Río Mira (JHKW). **Mislabeled**: 1 female Santa Catarina [Brazil] (USNM).
- Lamasina ganimedes* (Cramer). [Upper Amazon Region] **E. Colombia**: 2 males Meta, Río Negro (USNM), 1 female Villavicencio (USNM). **E. Ecuador**: 1 male KM 25 Puyo-Napo Rd (USNM), 1 male and 1 female Sucumbíos, Cerro Lumbaqui Norte (JHKW), 1 female Sucumbíos, 0.5 km SW Lumbaqui (USNM). **Peru**: 1 female Tingo María (USNM), 2 females Tingo María (MUSM), 1 female alto Río Contaya (MUSM), 1 female Tarapoto-Yurimaguas (MUSM). [Guiana Region] **French Guiana**: 1 female (illustrated in BÁLINT 2005). **Surinam**: 1 male no further data [possible syntype *Papilio ganimedes* Cramer] (RMNH), 1 female no further data [lectotype *Thecla nobilis* Herrich-Schäffer] (SMNS), 1 male no further data [holotype *Thecla bimaculata* Möschler], (ZMHB). **Guyana**: 1 male Junantins (illustrated in BÁLINT 2005, this locality is a mystery to us, but could possibly refer to Tonantins in Amazonas, Brazil.).
- Lamasina columbia* (Bálint). **Colombia**: 1 male Valle, Calima Dam, 800m (USNM); 1 female Valle, Calima, 1200m (AME); 1 male Nariño, La Planada, 1700m (illustrated in SALAZAR 1993); 1 female “Santa Fé de Bogotá” [holotype *Annamaria columbia*] (illustrated in BÁLINT 2005).
- Lamasina rhaptissima* (Johnson). **Ecuador**: 1 male Rio Pastazza [sic] [holotype *Thecla mirabilis* Lathy] (MNHN); 1 male Pastaza, Abitagua, 1300m (AMNH); 3 males and 2 females Pastaza, 25 KM N Puyo, 1000m (GWB, MLM); 1 male Pastaza, 32 KM S Puyo, 1000m (GWB); 2 males and 1 female Tungurahua, Río Topo, 1300m (RCB); 1 female Sucumbíos, Cerro Lumbaqui Norte, 900-1000m (RCB); 1 female Napo, Rio Pimpilala (SW of Talag), 600-900m.[RCB]. **Peru**: 1 male “Iquitos” (MUSM); 1 male Cuzco, Marcapata, Caradoc, 4000 ft (listed in D’ABRERA 1995 and BÁLINT 2005 from Ecuador); 1 male Junín, Chanchamayo (illustrated in BÁLINT 2005); 1 female Junín, Chanchamayo, La Salud, 1300m (CMNH). **Bolivia**: 1 male Potosí, Río Limatambo, ~1600 m [holotype *Annamaria rhapsodia*] (illustrated in BÁLINT 2005).

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