

# Phylogeny, taxonomy, and sympatry of *Timaeta* (Lycaenidae: Theclinae: Eumaeini): an Andean montane forest endemic

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Taxonomy of the Andean lycaenid hairstreak genus *Timaeta* Johnson et al. and its fifteen sexually dimorphic species is detailed for the first time. Species accounts summarize nomenclature, distribution, habitat, behavior, and distinguishing traits, as well as noting why each species is considered distinct under a biological or phylogenetic species concept and how males and females were associated.

An identification key for males and a nomenclatural checklist are included.

Nomenclatural actions include the description of *Timaeta christina* Robbins & Busby sp. n., *Timaeta matthewi* Busby & Robbins sp. n., *Timaeta walteri* Busby & Robbins sp. n., *Timaeta roberti* Busby & Robbins sp. n., *Timaeta cospata* Robbins & Busby sp. n., *Timaeta pilosa* Robbins & Busby sp. n., *Timaeta gabriela* Busby & Robbins sp. n., and *Timaeta romero* Robbins & Busby sp. n.. *Timaeta neblina* (Salazar & K. Johnson, 1997) is a new synonym of *Timaeta eronos* (H.H. Druce, 1890). A phylogenetic analysis is based on 17 coded morphological characters and yields two most parsimonious 30-step trees. Successive weighting does not change tree topology. The node chosen to delimit *Timaeta* is the one that had the highest jackknife support and was most stable with past usage. Generic names *Trochusinus* K. Johnson, Salazar & Vélez, 1997 and *Jagiello* Bálint & Wojtusiak, 2000 are confirmed as synonyms of *Timaeta* K. Johnson, Kruse & Kroenlein, 1997. Recent revisions of primarily Andean butterfly genera have had a significant proportion of previously unnamed species, and *Timaeta* fits this pattern with eight of 15 species previously undescribed. Most sister lineages within *Timaeta* are sympatric, and more than half the species occur between 1500m and 2000m in eastern Ecuador. This pattern of sympatry is similar to that of primarily lowland eumaeine genera, but contrasts with repeated reports of elevational allopatry/parapatry in Andean butterflies and birds.

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## Introduction

The primarily Neotropical Eumaeini (Lycaenidae: Theclinae) have diversified extensively in montane habitats, especially in contrast to the primarily Neotropical and similarly diverse Riodinidae (Robbins 2004a). Among the Eumaeini, about 95% of the 150 species in the *Micandra* Section are montane

(Robbins 2004b). And half of the 12 genera of the *Micandra* Section are endemic to Andean habitats between 700 and 4,500m elevation. This paper is a revision of *Timaeta*, one of the Andean endemics, and is the first phylogenetic analysis of a primarily montane lycaenid genus in the Eumaeini.

The Andean lepidopteran fauna is remarkably rich,

but because it has been chronically undersampled, many previously undescribed butterfly and moth species are only now being discovered (Willmott et al. 2001, Brehm et al. 2005, Peña & Lamas 2005). The Andean butterfly fauna has been repeatedly noted to consist of elevationally allopatric/parapatric species (Adams 1985, Pycrz & Wojtusiak 2002, Hall 2005, Bollino & Costa 2007), and a similar pattern has also been reported in Andean birds (Remsen & Cardiff 1990, Bates & Zink 1994). Alternately, most species in another Andean butterfly genus were sympatric with their sister lineages (Willmott et al. 2001), as also occurs in primarily lowland Neotropical lycaenid genera (Robbins 1991, 2005, Robbins & Duarte 2005, Robbins & Busby In Press). The number of phylogenetic analyses of Andean lepidopteran genera is yet too few to determine the prevalence of elevational parapatry/allopatry among sister lineages and is unexplored in the Eumaeini.

The goals of this paper are taxonomic and biogeographic. The taxonomic goal is to present evidence for the monophyly of *Timaeta* and for a classification of its 15 sexually dimorphic species that is slightly modified from that in Robbins (2004b). Specifically, we characterize *Timaeta* and its included species, describe eight new species, explain why we consider each to be distinct under a biological or phylogenetic species concept, note the evidence that we used to associate males and females, and infer phylogenetic relations among *Timaeta* species. The biogeographic goal is to summarize information on diversification and sympatry among *Timaeta* species using the inferred phylogeny and distributional data. We specifically ask whether a pattern of sympatry or elevational allopatry/parapatry predominate among sister lineages in *Timaeta*.

### Taxonomic history

*Timaeta* belongs to the Eumaeini because it has ten forewing veins, "greyhound shaped" male genitalia lacking a juxta, hairy eyes, and a male foretarsus that is fused, stubby tipped, and used for walking (Eliot 1973). *Timaeta* was placed provisionally in the *Micandra* Section of the Eumaeini (Robbins 2004b) because it has female genitalia with fan-shaped signa (they occur also in the *Hypostrymon* and *Lamprospilus* Sections), blue scales on the ventral forewing of males (they occur also in the *Eumaeus*, *Brangas*, and *Atlides* Sections), and several male forewing venation characters (Schatz & Röber 1885-1892, Clench 1971) that are not yet well-documented. Regardless of whether this placement is correct, *Temecla* Robbins and *Phothecla* Robbins appear to be the closest relatives of *Timaeta* on the basis of characters listed in Robbins and Duarte (2004). In preliminary

analyses of DNA sequences from 163 Eumaeini, including two *Timaeta* and one *Temecla* species, *Temecla* + *Timaeta* is monophyletic (Quental et al. in prep.).

The generic nomenclature of *Timaeta* and its proposed synonyms, *Trochusinus* K. Johnson, Salazar & Vélez and *Jagiello* Bálint & Wojtusiak (Robbins 2004b), has been unstable because diagnostic characters in the original descriptions were inaccurate. For example, "caecum comprising one fourth or less of aedeagus" was proposed as a diagnostic character of male *Timaeta* (Johnson et al. 1997a:24), but no eumaeine species has been reported to have a caecum length greater than one fourth of the aedeagus. Lack of androconia was noted as a diagnostic character of male *Trochusinus* (Johnson et al. 1997b:4), but two species that they placed in *Trochusinus* (*eronos* H.H. Druce and *balzabamba* Goodson) have conspicuous androconia along the posterior edge of dorsal hindwing vein Cu<sub>2</sub> (Draudt 1919-1920, D'Abbrera 1995, Figs. 19, 29, 65). *Jagiello* (*J. molinopampa* Bálint & Wojtusiak was the only included species) was described "... also on the grounds of differences in genital morphology" (Bálint & Wojtusiak 2000:183), but these differences were not detailed, and the genitalia are very similar to those of *T. timaeus* (Figs. 36, 38, 51-52).

The species level taxonomy of *Timaeta* has also been unresolved. Wing pattern sexual dimorphism makes associating males and females difficult. For example, Draudt (1919-1920) did not correctly associate the sexes of any species known at the time, D'Abbrera (1995) correctly associated the sexes of one species, and Bálint & Wojtusiak (2000) did not correctly identify the female of *T. molinopampa*. Most species are rare in collections, making it difficult to assess variation. Finally, the inaccurate original generic characterizations of *Timaeta* and its synonyms have caused confusion, with some *Timaeta* species being transferred from or to genera that do not belong to the *Micandra* Section (Robbins 2004b, detailed below).

Extensive field work in Ecuadorian and Peruvian montane forest in the past decade has more than quadrupled the number of *Timaeta* specimens available for study, provided new data on distribution and variation, and allowed many male and female phenotypes to be associated for the first time. This new information makes a revision of *Timaeta* feasible.

### Materials and methods

The generic and species level taxonomy is based on an analysis of morphological variation among 171 male and 34 female pinned specimens of *Timaeta*

from various museum and private collections, as noted below. Each species account includes notes on nomenclature and history, morphological variation, how the sexes are associated (females of three species are yet unknown or unrecognized), geographical distribution, elevation, and male "territorial" behavior. The evidence supporting the hypothesis that each available name represents a distinct species under a biological and/or phylogenetic species concept is discussed. Distribution of each species is mapped. In a few cases, the distributions of "unrelated" *Timaeta* species are combined on a single map for the purpose minimizing the number of maps needed. Months are abbreviated by their first three letters. Brackets are used for information not explicitly noted on holotype labels and for descriptions of the labels. All paratype labels are light blue.

The taxonomy in this paper is largely based on morphology of the males, as has been suggested for genera in which it is difficult to associate males and females (Robbins 2004a). Males of *Timaeta* in collections outnumber females by about 5 to 1. Males have androconial characters that females lack. Holotypes of eight of the ten previously available names (two are synonyms) in *Timaeta* species are males.

Genitalic terms follow those in Klots (1970), as modified for the Eumaeini in Robbins (1991). Wing vein terminology follows Comstock (1918). Androconial terminology follows Robbins (1991). All other morphological terms follow Snodgrass (1935).

Acronyms for the collections from which data were gathered are as follows:

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
DZUP	Universidade Federal do Paraná, Paraná, Curitiba, Brazil
FROM	Francisco Romero Collection, Maracay, Venezuela
JHKW	Jason Hall and Keith Willmott Collection, Smithsonian Institution, Washington, DC, USA
MCCV	Mauro Costa Collection, Caracas, Venezuela
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador
MNHN	Muséum National d'Histoire Naturelle, Paris, France

MIZA	Museo del Instituto de Zoología Agrícola, Maracay, Venezuela
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú
RCB	Robert C. Busby Collection, Andover, MA, USA
SMF	Forschungsinstitut und Naturmuseum Senckenberg Frankfurt, Frankfurt-am-Main, Germany
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
UNCC	Museo de Historia Natural, Universidad Nacional de Caldas, Manizales, Colombia
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZSM	Zoologische Staatssammlung, München [= Munich], Germany

A summary of the new classification is presented in the format of the previous checklist for the Eumaeini (Robbins 2004b). A key is presented to facilitate identification of males. Characters for identifying females are included in the species accounts, but the identification of some females is still uncertain.

## Taxonomy

### *Timaeta* K. Johnson, Kruse & Kroenlein

*Timaeta* K. Johnson, Kruse & Kroenlein, 1997: 23 n. gen., type species: *Pseudolycaena timaeus* C. Felder & R. Felder, 1865 (by original designation).

*Trochusinus* K. Johnson, Salazar & Vélez, 1997: 4 n. gen., type species: *Thecla trochus* H.H. Druce, 1907 (by original designation). Robbins, 2004b: 120 (syn. n.).

*Jagiello* Bálint & Wojtusiak, 2000: 184 n. gen., type species: *Jagiello molinopampa* 2000 (by original designation). Robbins, 2004b: 120 (syn. n.).

**Diagnosis.** The synapomorphies that characterize *Timaeta* in the phylogenetic results ("unambiguous changes only", Fig. 74) are (1) posterior edge of labides in lateral aspect dorso-ventrally flat (character 5), (2) male ventral hindwing cubital spot brown (character 11, "reversed" in *T. trochus* and *T. walteri*), and (3) male hindwing tails absent (character 12). Two sexual dimorphisms in *Timaeta* are conspicuous even though their occurrences are homoplastic. First, males lack an orange-red ventral hindwing cubital spot and females have it. Second, males lack hindwing tails while the females possess them. The first dimorphism occurs in no other eumaeine genus

of which we are aware, but males of two *Timaeta* species have the orange cubital spot, which is a reversal according to the phylogenetic results (Fig. 74). The second dimorphism also occurs in *Micandra platyptera* and some species of *Erora*, and is homoplastic within *Timaeta* because females of *T. molinopampa* and *T. werneri* lack tails.

**Head.** The antennal stalk has 14-18 white ringed segments, and the club is incrassate with the ventral nudum confined to club, which may be dark yellow or orange. The amount of white scaling along the length of the stalk is variable, with more white scales in *T. molinopampa*. The frons is typical of the Eumaeini with ventrally oriented gray-brown flat scales intermixed with rather robust, but thin dark gray or black scales protruding outwards that give a "hairy" appearance. The number of protruding scales is greatest in *T. molinopampa* and least in *T. aepea*, which is consistent with the observation that the number of these scales increases with elevation. Five species have blue scales along the lateral edges of the frons in males, as noted in the phylogenetic characters. Otherwise, the head is not sexually dimorphic except that length of the third segment of the labial palps is generally a bit longer in females.

**Forewing length.** Varies from about 9 to 18 mm.

**Wing shape, venation, and pattern** (Figs. 1-35). Males of most species have rounded wings, epitomized by the wings of *T. aepea* (Fig. 17), but the hindwings of *T. christina* are elongate (Figs. 3-4). A hindwing anal lobe is absent or vestigial except in *T. christina* and *T. molinopampa*. The "loss" of hindwing vein  $M_2$  in both sexes is an excellent generic character in those 12 *Timaeta* species in which it occurs (see phylogenetic results). The ventral forewing postmedian line, which is often obscured in males, extends from the costal margin to the inner margin, unlike some co-occurring eumaeine genera, such as *Lathecla* Robbins.

**Androconia** (Figs. 63-65). Males of *T. timaeus* and *T. christina* have androconia in the anterior portion of the dorsal hindwing and at the base of the ventral forewing, a combination of scent patches that is widespread in the Eumaeini. Five species have a "comb" of piliform black setae along the posterior edge of dorsal hindwing vein  $Cu_2$  with additional androconia at the base of these scales (Fig. 65). This structure is otherwise unreported in the Eumaeini.

**Genitalia** (Figs. 36-62). Male genitalia are typical of the *Micandra* Section (see characters in Robbins & Duarte 2004), including absence of brush organs (sensu Eliot 1973). The peculiar rounded tips of the valvae (Figs. 36-40, character 1) is reported within the Eumaeini only in some *Timaeta* and *Temecla*, but

its "loss" within *Timaeta* appears to be homoplastic (Fig. 74). The female genitalia are not especially distinctive except for their "fan-shaped" signa, again typical of many *Micandra* Section genera. Shape of the posterior end of the ductus bursae and its lamellae is the primary differentiating structure among *Timaeta* female genitalia, but we yet lack sufficient information on intraspecific variation to determine the extent to which females can be identified by these structures.

**Distribution and seasonality.** *Timaeta* is restricted to the Andes from northern Venezuela to Bolivia at elevations from 750 to 3200m. Although the vast majority of specimens reported in this paper were collected between August and December, this pattern may well be an artifact of the months when collectors were most often in the field.

## Checklist

*Timaeta* K. Johnson, Kruse & Kroenlein, 1997

Syn. *Trochusinus* K. Johnson, Salazar & Vélez, 1997

Syn. *Jagiello* Bálint & Wojtusiak, 2000

*timaeus* (C. Felder & R. Felder, 1865)

(*Pseudolycaena*) . . . . . Colombia

Syn. *circinata* (Hewitson, 1874) (*Thecla*)

. . . . . Bolivia

Syn. *lecromi* (K. Johnson, Eisele & . . .

MacPherson, 1993) (*Androcona*) . . . . .

. . . . . Colombia

*christina* Robbins & Busby, sp. n. . . . . Peru

*molinopampa* (Bálint & Wojtusiak, 2000)

(*Jagiello*) . . . . . Peru

*werneri* (Salazar, Vélez, Cardona & K. John-

son, 1997) (*Trochusinus*) . . . . . Colombia

*matthewi* Busby & Robbins, sp. n. . . . . Ecuador

*walteri* Busby & Robbins, sp. n. . . . . Ecuador

*trochus* (H.H. Druce, 1907) (*Thecla*) . . . . . Colombia

*roberti* Busby & Robbins, sp. n. . . . . Ecuador

*aepea* (Hewitson, 1874) (*Thecla*) . . . . . Ecuador

*cospata* Robbins & Busby, sp. n. . . . . Peru

*eronos* (H.H. Druce, 1890) (*Thecla*) . . . . . Colombia

Syn. *neblina* (Salazar & K. Johnson, 1997)

(*Micandra*), syn. n. . . . . Colombia

*pilosa* Robbins & Busby, sp. n. . . . . Ecuador

*gabriela* Busby & Robbins, sp. n. . . . . Ecuador

*romero* Robbins & Busby, sp. n. . . . . Venezuela

*balzabamba* (Goodson, 1945) (*Thecla*) . . . . .

. . . . . Venezuela; Ecuador

**Wing pattern key for male *Timaeta***

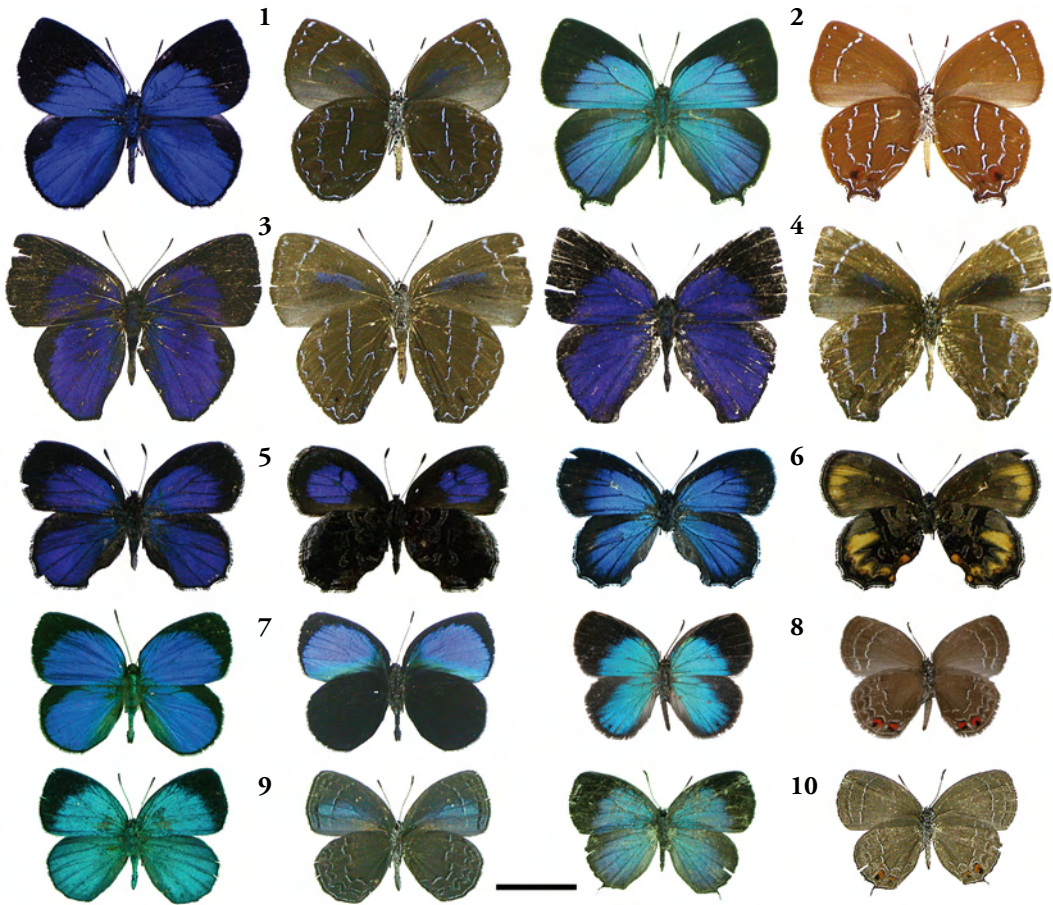
1. With a conspicuous hindwing anal lobe (e.g., Fig. 4) ..... 2
  - Without a hindwing anal lobe (e.g., Fig. 1) ... 3
2. A scent patch in the middle of the dorsal hindwing and at the base of the ventral forewing, hindwing outer margin smooth (Fig. 3) ..... *T. christina*
  - No androconia, hindwing outer margin scalloped (Fig. 5) ..... *T. molinopampa*
3. Scent patch in the anterior half of the dorsal hindwing and at the base of the ventral forewing (Fig. 1) ..... *T. timaeus*
  - Hair-like androconia along posterior edge of dorsal hindwing vein  $Cu_2$  (e.g., Fig. 21) ..... 4
    - No evident androconia (e.g., Fig. 11) ..... 7
4. Without blue scales on the ventral forewing (although when viewed with a microscope, there may be a few scattered blue scales, Fig. 27) ..... *T. romero*
  - With green-blue scales in the posterior distal part of the ventral forewing and the discal cell almost entirely dark brown (Fig. 23) ... .. *T. gabriela*
  - With blue scales covering a large part of the ventral forewing, including the distal part of the discal cell (e.g. Fig 19) ..... 5
5. With blue scales in the distal part of the ventral forewing extending anterior of the blue in the discal cell, with dark scales at the end of the discal cell, and with lightly marked marginal and postmedian lines on the ventral hindwing (Fig. 19) ..... *T. eronos*
  - With a uniform patch of brilliant blue scales covering the median portion of the ventral forewing, including the distal part of the discal cell (e.g. Fig. 21) ..... 6
6. With a broad, well defined black marginal border on the dorsal forewing from the costal to the inner margin and with a dark marginal border on the ventral forewing extending from the apex to the inner margin (Fig. 21) ..... *T. pilosa*
  - With a somewhat diffuse marginal border on the dorsal forewing and with a dark marginal border on the ventral forewing that extends from the apex to vein  $Cu_2$  (e.g. Fig. 29) ... .. *T. balzabamba*
7. Hindwing anal angle not smoothly rounded, with a small black tuft of scales on the ventral surface (e.g., Fig. 15) ..... 8
  - Hindwing anal angle rounded, without a small black tuft of scales on the ventral surface (e.g., Fig. 17) ..... 10
8. An orange/red cubital spot on the ventral hindwing (e.g., Fig. 11) ..... 9
  - Without an orange/red cubital spot on the ventral hindwing (Fig. 15) ..... *T. roberti*
9. Dorsal surface a rich blue. Ventral forewing with a light dusting of blue scales in the posterior distal part of the wing (Fig. 11) ..... *T. walteri*
  - Dorsal surface green or green-blue. Ventral forewing with green-blue scales concentrated in the posterior 2/3 of the wing (Fig. 13) ... .. *T. trochus*
10. Dorsal wing color green-blue (e.g., Fig. 9) ... 11
  - Dorsal wing color blue (e.g., Fig. 7) ..... 12
11. Dorsal forewing with “crisp” marginal border. Green-blue scales restricted to the posterior and distal part of the ventral forewing. Postmedian lines on both the ventral forewing and hindwing present (Fig. 9) . *T. matthewi*
  - Dorsal forewing with “diffuse” marginal border. A light “dusting” of green-blue scales in the middle of the ventral forewing. No postmedian line visible on the ventral hindwing (Fig. 17) ..... *T. aepea*
12. Dorsal forewing mostly bright blue with a well defined black border (Fig. 7) .... *T. werneri*
  - Dorsal forewing with blue restricted to the area posterior of vein  $Cu_1$  (Fig. 30) ... *T. cospata*

***Timaeta timaeus* (C. Felder & R. Felder)**

Figs 1-2, 31, 36, 51, 63, 66

*Pseudolycaena timaeus* C. Felder & R. Felder 1865: 248.*Thecla timaeus* Hewitson 1867:80. D'Abrera 1995: 1133.*Timaeta timaeus* Johnson et al. 1997a: 24 comb. n., ♀ lectotype in BMNH examined, see type locality discussion below.*Thecla circinata* Hewitson, 1874:19. Johnson et al. 1997a: 24, ♂ lectotype in BMNH, Bolivia. D'Abrera 1995: 1133, syn. n.*Timaeta circinata* Robbins 2004b: 120 lectotype examined.*Androcona lecromi* K. Johnson, Eisele & MacPherson 1993:8. Le Crom & Johnson 1997: pl. XVIII, holotype ♂ in UNCC illustrated.*Timaeta lecromi* Robbins 2004b: 120 syn. n., comb. n.

**Diagnosis and recognition as a distinct species.** *Timaeta timaeus* forms a clade with *T. christina* and *T. molinopampa*, supported by three synapomorphies (Fig. 74). Superficially, this lineage can be distinguished from other *Timaeta* by the presence of hindwing vein  $M_2$  in both sexes. *Timaeta timaeus* is sympatric with *T. christina* (known only from males), but occurs at a lower elevation than *T. molinopampa*. Males are differentiated from both by lack of a hindwing anal lobe. The lesser extent of the dorsal hindwing scent patch also consistently



**Figs 1-10.** *Timaeta* adults (dorsal surface on left, ventral surface on right). 1, *T. timaeus* male (Ecuador, Zamora-Chinchipe); 2, *T. timaeus* female (Ecuador, Morona-Santiago); 3, *T. christina* male holotype (Peru, Amazonas), anal lobes bent downwards so they are barely visible, see following figure; 4, *T. christina* male (Ecuador, Tungurahua), dorsal hindwing androconia barely visible, but see figure 63; 5, *T. molinopampa* male (Ecuador, Loja); 6, *T. molinopampa* female (Ecuador, Loja); 7, *T. weneri* male (Ecuador, Esmeraldas); 8, *T. weneri* female (Ecuador, Pichincha); 9, *T. matthewi* male holotype (Ecuador, Morona-Santiago); 10, *T. matthewi* female (Ecuador, Morona-Santiago). Scale 1 cm.

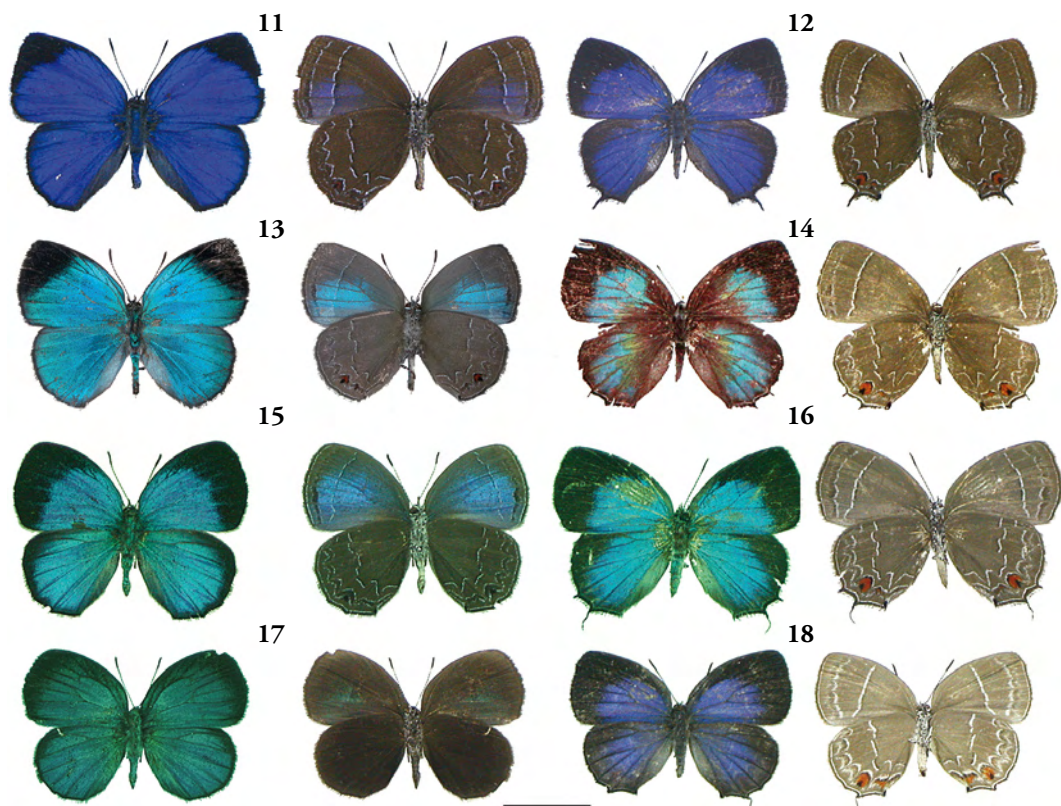
differentiates males from those of *T. christina* (detailed in next species account). Many elements of the ventral wing pattern differentiate both sexes of *T. timaeus* from those of *T. molinopampa* (Figs. 5-6). There is no evident elevational variation in these differentiating wing pattern characters.

**Description of male.** Mean forewing length=16.25 mm, SD=0.979, N=10. Wing pattern (Fig. 1), wing venation (Fig. 31), genitalia (Fig. 36), and androconia (Fig. 63) illustrated.

**Description of female.** Mean forewing length=16.70 mm, SD=1.567, N=10. Wing pattern (Fig. 2) and genitalia (Fig. 51) illustrated.

**Variation.** Female underside ground color varies from reddish brown to dark maroon-brown, but it is unclear if this variation is seasonal. It does not seem to be correlated with elevation.

**Reasons for associating males and females.** Draudt (1919-1920:756) noted that the ventral wing pattern of *T. circinata* "is marked exactly like *timaeus*", but placed them in different species groups. D'Abbrera (1995) treated *Thecla circinata* as the male of *T. timaeus*. Johnson et al. (1997a) suggested that *T. timaeus* and *T. circinata* were likely to be sexes of the same species. Our sample indicates that *T. timaeus* and *T. circinata* occur in the same



**Figs 11-18.** *Timaeta* adults (dorsal surface on left, ventral surface on right). 11, *T. walteri* male holotype (Ecuador, Pichincha); 12, *T. walteri* female (Ecuador, Pichincha); 13, *T. trochus* male (Ecuador, Zamora-Chinchipe); 14, *T. trochus* female (Ecuador, Zamora-Chinchipe), base of dorsal wings "stained"; 15, *T. roberti* male holotype (Ecuador, Morona-Santiago); 16, *T. roberti* female (Ecuador, Morona-Santiago); 17, *T. aepea* male (Ecuador, Morona-Santiago); 18, *T. aepea* female (Ecuador, Morona-Santiago). Scale 1 cm.

habitats, and no other male-female association has been proposed. It is possible that our study series of *T. timaeus* includes females of *T. christina*. However, there is no indication that variable characters, such as size, shade of blue on the dorsal wings, and extent of dorsal blue color, are bimodal. Further, males of *T. christina* have not been recorded from Colombia, the type locality of *T. timaeus*.

**Habitat and elevation.** Montane forest between 1500 and 2200m elevation.

**Male behavior.** Three males set up mating territories in a clearing at the edge of the Rio Mackay, Tungurahua, Ecuador (1°23.9'S, 78°17.0.94'W), 1700m at 1452, 1452, and 1522 hours about 3m above the ground on 6 Sep 1999 (vouchers in USNM).

**Distribution** (Fig. 66). Occurs from Venezuela to Bolivia. In Colombia and Ecuador, it is found on both the eastern and western slopes of the Andes.

**Type locality.** Although Felder and Felder (1865)

described *Pseudolycaena timaeus* from Bogotá, Nova Granada, Johnson et al. (1997a) designated a Felder Collection lectotype from Venezuela with a "Rothschild Bequest B.M. 1919-1, B.M. Type No Rh. 579" label. The lectotype matches the original figure of *P. timaeus* very well, but photographs of this specimen from the 1970s show that it lacks a Venezuela locality label and that the Rothschild Bequest number is 1939-1, not 1919-1. Indeed, it would be an invalid lectotype if it had a Venezuela locality label. Despite the incorrect information in Johnson et al. (1997a), the original figure is definitive, and identification poses no problems.

Material examined. 37 males (3 genitalic dissections), 18 females (2 genitalic dissections), the female lectotype of *T. timaeus*, the male lectotype of *T. circinata*, photographs of the male holotype of *T. lecromi*, and photographs of two Venezuelan males (MCCV).

*Timaeta christina* Robbins & Busby, sp. n.

Figs 3-4, 37, 64, 67

**Type material.** Holotype ♂ Peru, AM, Mendoza, Quebrada Yanahuayco, 1600-1800m, 06[°]24[']S/77[°]26[']W, viii [Aug 19]98, [leg.] B. Calderón. Deposited MUSM (Fig. 3). [One white label, a red holotype label.]

**Paratypes** (9♂). Ecuador: 1♂ Tungurahua, Rio Machay, 1900m, 1 Dec 1997, leg. J.P.W. Hall & K.R. Willmott (Fig. 4, JHKW); 1♂ Tungurahua, km. 14 Limón-Gualaceo Rd., 1950m, 30 Sep 1997, leg. J.P.W. Hall & K.R. Willmott (JHKW); 2♂ Zamora-Chinchipe, San Francisco, casa de Arcoiris, km. 23 Loja-Zamora Road, 2100m, 3°59.30'S 79°5.58'W, 25 Nov 2003, leg. K.R. Willmott (JHKW); 1♂ Zamora-Chinchipe, aqueduct above Rio San Francisco, Loja-Zamora Road, 2000m, 4 Feb 2002, leg. K.R. Willmott (JHKW); 1♂ Zamora-Chinchipe, km. 24 Loja-Zamora Road, nr. Sabanilla, Qbda. San Ramon, 1700m, 3°58.16'S 79°03.75'W, 27, 29 Oct 1997, leg. K. R. Willmott (MECN); 1♂, Zamora-Chinchipe, Romerillos, 1600m, Nov 1999, leg. I. Aldas & R.C. Busby (RCB); Peru: 2♂ Amazonas, Abra Pardo Miguel, 2200m, 05°42'S 77°48'W, 18 Nov 1996 (USNM), 19 Nov 1996 (MUSM).

**Diagnosis and recognition as a distinct species.** *Timaeta christina* forms a clade with *T. timaeus* and *T. molinopampa* (Fig. 74). Males of *T. christina* have an elongate hindwing with an anal lobe (Figs. 3, 4) while males of *T. timaeus* have a rounded hindwing without an anal lobe (Fig. 1). The ventral wing pattern of male *T. christina* is easily distinguished from that of male *T. molinopampa* (Figs. 3-5). Females of *T. christina* are unknown or unrecognized, as noted already. *Timaeta christina* is sympatric with *T. timaeus*, but occurs at lower elevations than *T. molinopampa*. There is no evident elevational variation in those wing pattern characters that differentiate it, but the number of known specimens of *T. christina* is yet small.

**Description of Male.** Mean forewing length 17.13 mm, SD=0.876, N=8. Wing pattern (Figs. 3-4), genitalia (Fig. 37), and androconia (Fig. 64) illustrated. The male genitalia are indistinguishable from those of *T. timaeus*. The scent patch on the dorsal hindwing covers a larger area than that of *T. timaeus*. Specifically, wing cell Cu<sub>1</sub>-Cu<sub>2</sub> always has androconia whereas in *T. timaeus* they are absent or restricted to the basal part (Figs. 63-64). Because these androconia are mixed with regular wing scales, the androconial patch in *T. christina* is not as readily apparent as that in *T. timaeus*.

**Description of Female.** Unknown or unrecognized.

**Etymology.** This beautiful species is named for

Christine Lamas Weinberg, daughter of Gerardo Lamas. Lamas first recognized this species as distinct. The name is a non-latinized noun in apposition and is indeclinable.

**Type locality.** Mendoza (Amazonas State), where lepidopterist Benigno Calderón lives, is located in wet montane forest on the eastern slopes of the Andes.

**Habitat and elevation.** Montane forest between 1600 and 2200m elevation.

**Male behavior.** According to J. Hall and K. Willmott, males perch on vegetation on the side of streams, much like males of *T. timaeus*. In some cases, males of *T. christina* perch up to 10m above the ground.

**Distribution** (Fig. 67). Eastern slope of the Andes in Ecuador and northeastern Peru.

Material examined. The type series of 10 males (3 genitalic dissections).

*Timaeta molinopampa* (Bálint & Wojtusiak)

Figs 5-6, 32, 38, 52, 68

*Jagiello molinopampa* Bálint & Wojtusiak 2000: 187 Holotype ♂ Peru, Amazonas, Molinopampa in MUSM.

*Timaeta molinopampa* Robbins 2004a: 120 comb. n.

**Diagnosis and recognition as a distinct species.** *Timaeta molinopampa* forms a clade with *T. christina* and *T. timaeus* (Fig. 74), but occurs at higher elevations. It is differentiated most easily by its unique wing pattern (Figs. 5, 6), which does not seem to vary with elevation.

**Description of Male.** Mean forewing length=13.65 mm, SD=1.101, N=20. Wing pattern (Fig. 5), wing venation (Fig. 32), and genitalia (Fig. 38) illustrated. No evident androconia.

**Description of Female.** Mean forewing length=14.50 mm, SD=0.707, N=2. Wing pattern (Fig. 6) and genitalia (Fig. 52) illustrated.

**Reasons for associating males and females.** The underside wing patterns of the male and female are arguably more similar to each other than to those of any other eumaeine species. They are the only *Timaeta* with scalloped hindwing margins (Figs. 5, 6). Both sexes occur in the same habitat. Both male and female genitalia are exceedingly similar to those of *T. timaeus*. Bálint and Wojtusiak (2000) proposed a different female for this species, but its underside wing pattern is considerably different from that of the male. The illustration of the female genitalia in Bálint and Wojtusiak (2000) is not sufficiently detailed to determine its generic placement.

**Habitat and elevation.** Montane vegetation (bushes and occasional short trees) between 2500 and 3200m elevation.

**Distribution** (Fig. 68). Eastern slope of the Andes in



southeastern Ecuador and northeastern Peru.

**Material examined.** 33 males (2 genitalic dissections), 2 females (1 genitalic dissection), and a photograph of the male holotype and a figure of its genitalia.

*Timaeta wernerii* (Salazar, Vélez, Cardona & K. Johnson)

Figs 7-8, 33, 39, 53, 69

*Trochusinus wernerii* Salazar, Vélez, Cardona, & K. Johnson, 1997: 9 Holotype ♂ Colombia, Chocó, San José del Palmar in UNCC.

*Timaeta wernerii* Robbins 2004a: 120. comb. n.

**Diagnosis and recognition as a distinct species.** Both sexes of *T. wernerii* can be readily differentiated by wing pattern (Figs. 7, 8). The female lacks tails (shared only with *T. molinapampa*) and has two orange-red ventral hindwing cubital spots with black “pupils”. The large blue patch on the ventral hindwing of males with the immaculate black hindwing differentiates the male. Also, the shape of the rounded valva tips with a straight medial margin (Fig. 39) is otherwise unrecorded in the Eumacini. And among the 12 species lacking hindwing vein  $M_2$ , *T. wernerii* is the only species with the male genitalia dorsal cornutus more than half the length of the ventral one.

**Description of Male.** Mean forewing length=13.05 mm, SD=0.071, N=2. Wing pattern (Fig. 7), wing venation (Fig. 33) and genitalia (Fig. 39) illustrated. No evident androconia.

**Description of Female.** Mean forewing length=12.15 mm, SD=0.495, N=2. Wing pattern (Fig. 8) and genitalia (Fig. 53) illustrated.

**Reasons for associating males and females.** The tailless females of *T. wernerii* are distinctive, as noted in the description above. They are sympatric with males of *T. wernerii*, *T. balzabamba*, and *T. trochus*, but have a different ventral postmedian line than males of *T. trochus* or *T. balzabamba* (a vestigial postmedian line is present in some males).

**Habitat and elevation.** Wet montane forest from 800 to 1700m elevation.

**Distribution** (Fig. 69). Western slope of the Colombian and Ecuadorian Andes.

**Material examined.** 2 males (1 genitalic dissection), 2 females (1 genitalic dissection), a photograph of the male holotype and the “stylized” illustration of its genitalia in the original description.

*Timaeta matthewii* Busby & Robbins, sp. n.

Figs 9-10, 40, 54, 69

**Type material.** Holotype ♂ Ecuador, Morona-Santiago, 1 km E. Rio Abanico, 1600m, 2°15.4'S,

78°11.7'W, 02 October 2001, Robert C. Busby, leg. Deposited USNM (Fig. 9). [One white label, a red holotype label.]

**Paratypes** (4♂). **Colombia:** 1♂ Central Cordillera, Cañon del Tolima, 1700m, Coll. Fassel (SMF). **Ecuador:** 1♂ Morona-Santiago, 14 km. W. of Macas, Rio Abanico, 1600m, 22 Sep 1999, leg. Robert C. Busby (RCB); 1♂ Morona-Santiago, 14 km. W. of Macas, Rio Abanico, 1600m, 16 Sep 1999, leg. Robert C. Busby (RCB); 1♂ Sucumbíos, 2 km El Reventador-Lumbaqui Rd, 1° 01.5'S 77° 30.6'W, 1500m, 29 Dec 2005, leg. Robert C. Busby (MECN).

**Diagnosis and recognition as a distinct species.**

*Timaeta matthewii* is a phylogenetically distinct species (Figs. 74, 75). Among those 12 species lacking hindwing vein  $M_2$ , it shares valva tips that are rounded only with *T. wernerii* (Figs. 39-50), but can be differentiated from this species by its wing pattern (Figs. 7-10) and by the medial edge of the valva tips being curved (Fig. 40).

**Description of Male.** Mean forewing length=12.50 mm, SD=1.225, N=5. Wing pattern (Fig. 9) and genitalia (Fig. 40) illustrated. No evident androconia.

**Description of Female.** Mean forewing length=11.60 mm, SD=0.849, N=2. Wing pattern (Fig. 10) and genitalia (Fig. 54) illustrated.

**Etymology.** This handsome species is named for Matthew W. Busby. He is the son of Robert C. Busby, who first realized that this species is distinct from *T. roberti*, a species with a similar wing pattern. The name is a noun in apposition and is indeclinable and non-latinized.

**Type locality.** The Rio Abanico locality is about 14 km west of Macas (map distance) and is heavily forested.

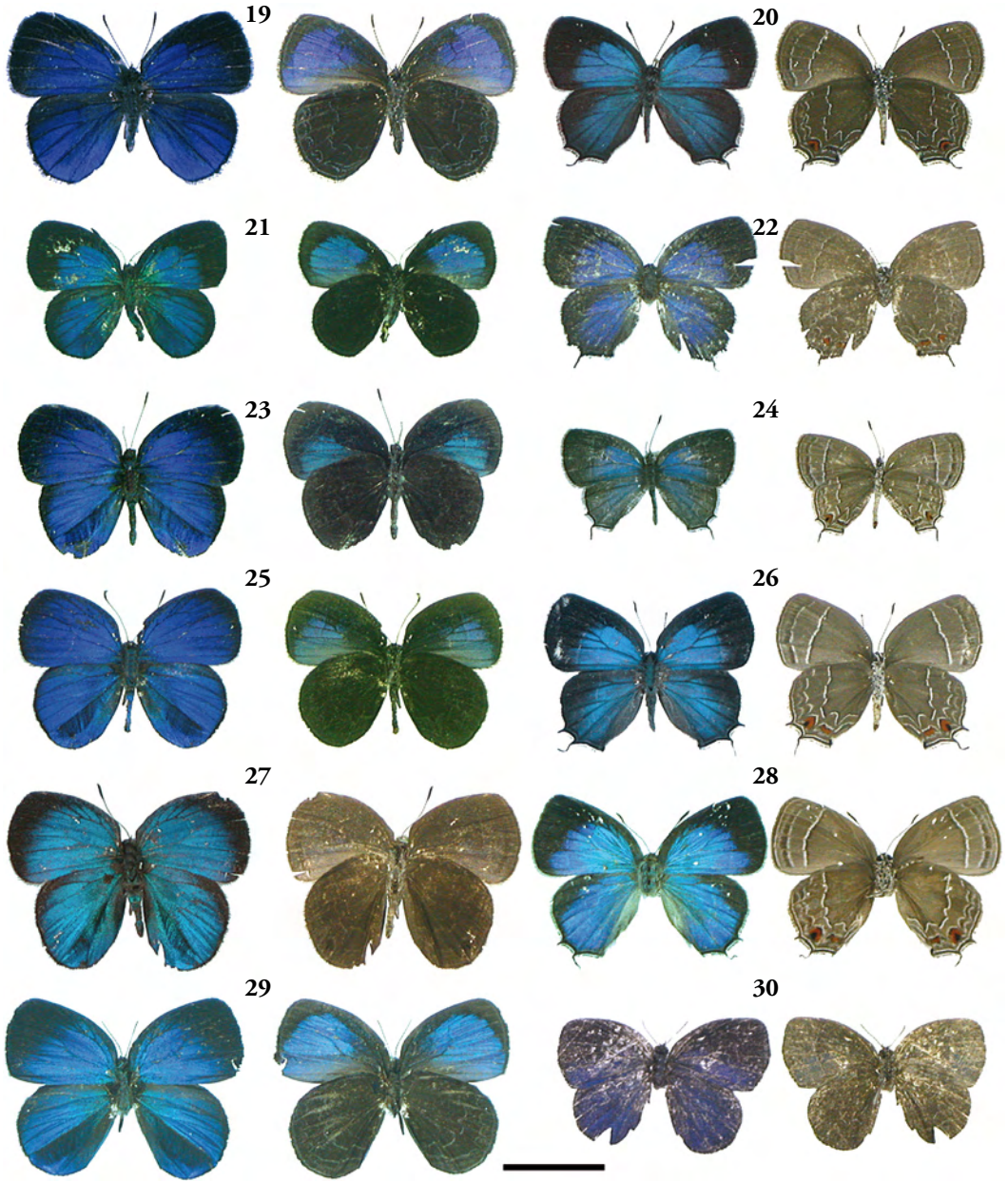
**Other Specimens Examined.** The type series is restricted to males. Ecuador: 1♀ Morona-Santiago, Nueve de Octubre, 2°12.2'S 78°13.1'W, 1800m, 2 Oct 2000, Robert C. Busby, leg. (RCB); 1♀ Zamora-Chinchipec, Zamora (ridge W of town), 1450m, 20 May 2000, leg. Robert C. Busby (USNM).

**Reasons for associating males and females.** One female of *T. matthewii* was found at the same area as males. Both sexes have the same postmedian line on the ventral wings—most notably the forewing postmedian line at the coastal margin is strongly curved.

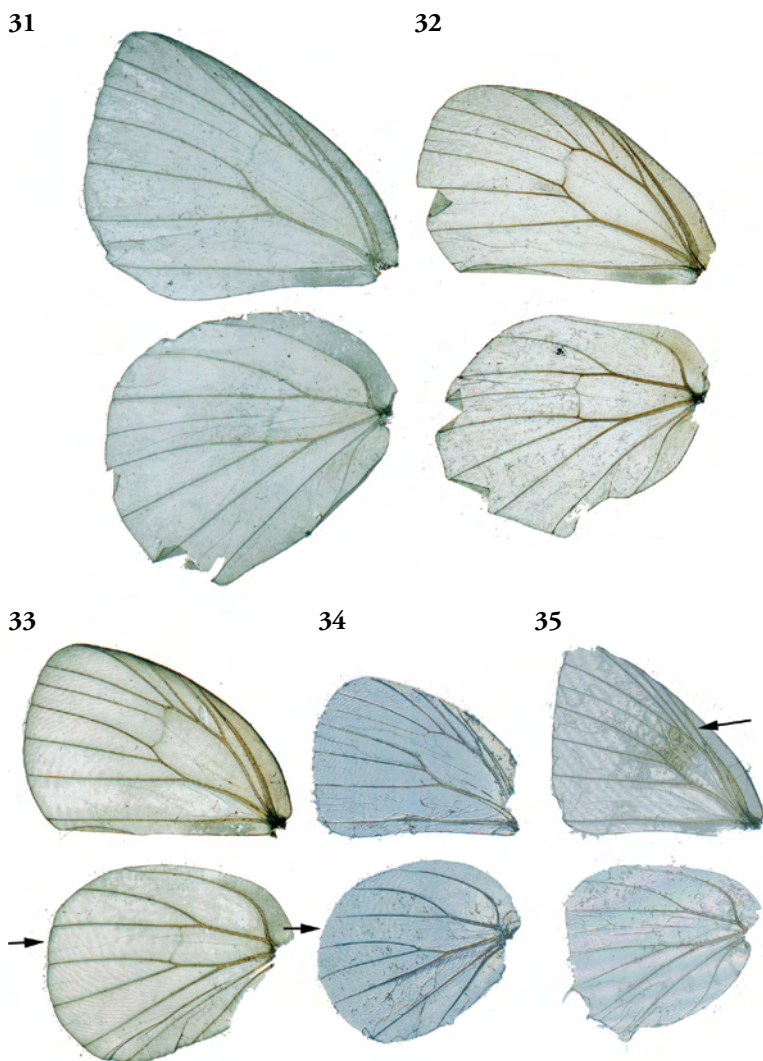
**Distribution** (Fig. 69). Central Colombia to eastern Ecuador.

**Habitat and elevation.** Montane forest at elevations between 1450 and 1800m.

**Male behavior.** Ecuadorian males set up mating territories in the early afternoon around 1330 hours on steep hillsides within the forest perching at a height



**Figs 19-30.** *Timaeta* adults (dorsal surface on left, ventral surface on right). 19, *T. eronos* male (Ecuador, Napo); 20, *T. eronos* female (Ecuador, Morona-Santiago); 21, *T. pilosa* male holotype (Ecuador, Morona-Santiago); 22, *T. pilosa* female (Peru, Junin); 23, *T. gabriela* male, in copula (Ecuador, Sucumbios); 24, *T. gabriela* female, in copula (Ecuador, Sucumbios); 25, *T. gabriela* male holotype (Ecuador, Morona-Santiago); 26, *T. gabriela* female, (Ecuador, Pastaza); 27, *T. romero* male holotype (Venezuela, Aragua); 28, *T. romero* female (Venezuela, Aragua); 29, *T. balzabamba* male (Colombia, Meta?); 30, *T. cospata* male holotype (Peru, Cusco). Scale 1 cm.



**Figs 31-35.** Wing venation (forewing on top). 31, *T. timaeus* male (Ecuador, Tungurahua); 32, *T. molinopampa* male (Ecuador, Loja); 33, *T. weneri* male (Ecuador, Pichincha)—arrow points to missing hindwing vein  $M_2$ ; 34, *T. pilosa* male (Peru, Junín)—arrow points to missing hindwing vein  $M_2$ , androconia along the posterior edge of hindwing vein  $Cu_2$  not visible, see figure 65; 35, *Temecla tema* male (Peru, Madre de Dios)—arrow points to anastomosis of veins  $Sc$  and  $R_1$ , as noted in Robbins & Duarte (2004).

of 6-8m above the ground on the sunny edge of tree-fall gaps.

**Material examined.** 5 males (3 genitalic dissections) and 2 females (1 genitalic dissection).

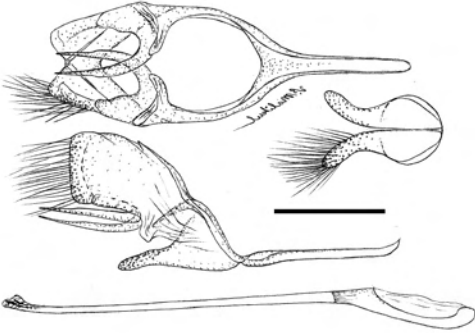
**Remarks.** The wing pattern of male *T. matthewi* is similar to that of *T. roberti*, but is smaller and lacks the black scales at the anal angle of the ventral hindwing (see below).

#### *Timaeta trochus* species group

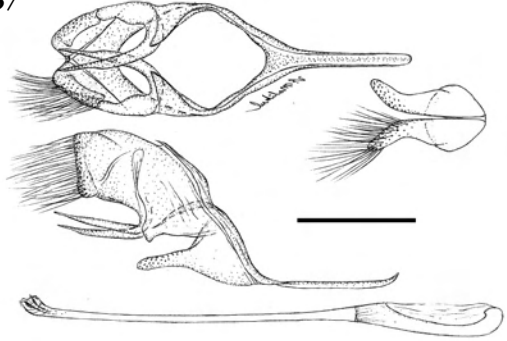
The *T. trochus* species group (*T. trochus*, *T. walteri*, *T. roberti*) is distinguished by a small tuft of black scales at the anal angle of the ventral hindwing of males (a few individuals of *T. timaeus* have a similar patch of scales) and a posteriorly pointing process

(>1.5 mm) lacking setae on the male genitalia valva (Fig. 75). The species in this group have indistinguishable male genitalia (Figs. 41-43). The lamella postvaginalis (female genitalia) differs in shape slightly among the three species (Figs. 55-57), but we do not have enough information on variation to know if these differences are distinguishing. Indeed, we are somewhat uncertain whether we have correctly distinguished females of *T. trochus*. Males of *T. trochus* and *T. walteri* have an orange ventral hindwing cubital spot (except in worn individuals), which occurs in no other *Timaeta* species. All three species occur at different elevations in western Ecuador, but our sample sizes of *T. trochus* and *T. roberti* are small, and *T. walteri* is known from one locality.

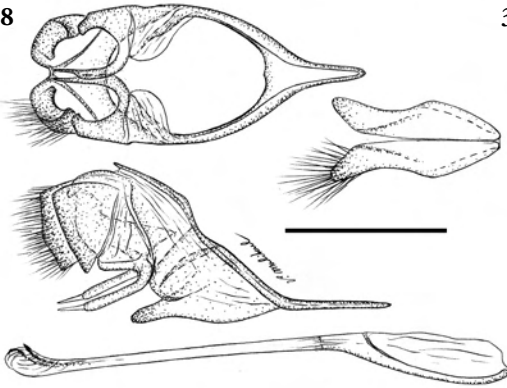
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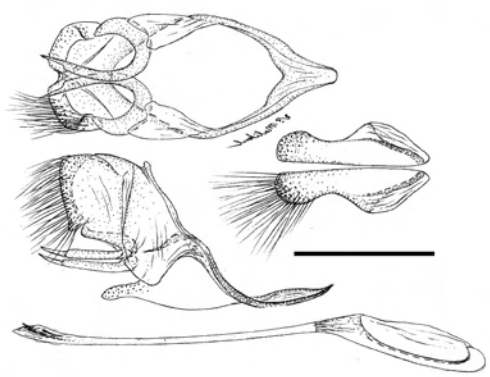
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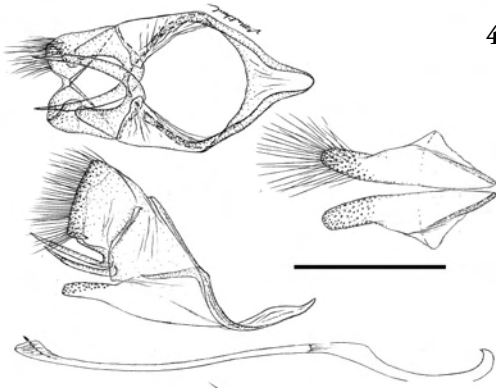
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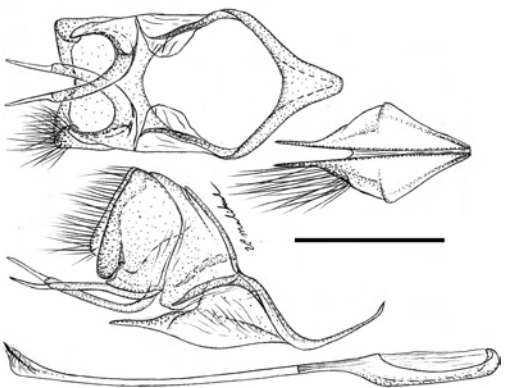
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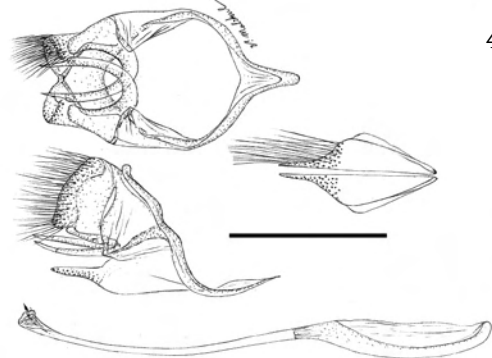
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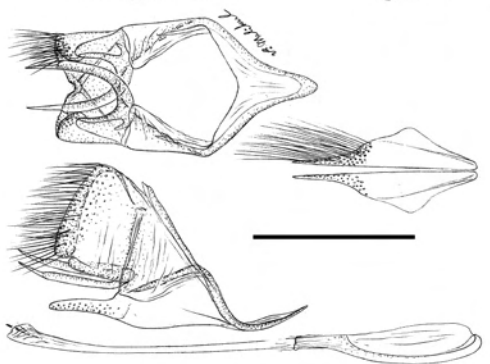
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42



43



***Timaeta walteri* Busby & Robbins, sp. n.**

Figs 11-12, 41, 55, 70

**Type material.** Holotype ♂ Ecuador, Pichincha Province, 30 km. W. of Aloag, 2200m, 19-20.x[Oct]. 1991, leg. Robert C. Busby. Deposited USNM (Fig. 11). [One white label, a red holotype label.]

Paratypes. (5♂ & 5♀). Ecuador, Pichincha, 30 km. W. of Aloag, 2200m, leg. R.C. Busby: 2♂ 19-20 Oct 1991 (RCB, USNM), 1♂ 24 Oct 1992 (RCB), 2♂ 15 Oct 1992 (RCB), 1♀ 10 Oct 1996 (Fig. 12, USNM), 1♀ 24 Oct 1992 (RCB), 1♀ 31 Oct 1992 (RCB), 1♀ 13-15 Oct 1988 (labeled 72 km. E. of Santo Domingo, but it is the same locality, RCB); 1♀ 26 km. W. of Aloag, 2400m, 28 Oct 1994, leg. Robert C. Busby (RCB).

**Diagnosis and recognition as a distinct species.**

*Timaetus walteri* is the phylogenetic sister of *T. trochus* (Figs. 74, 75), but size, dorsal color, and shape of the forewing dorsal border consistently differentiate males. The dorsal color of male *T. walteri* is a rich blue white that of male *T. trochus* is green or greenish-blue throughout its range (Figs. 11, 13). *Timaetus walteri* occurs at higher elevations than *T. trochus* in western Ecuador (albeit, the data are insufficient to conclude much). Because wing pattern and genitalic structures in *T. trochus* do not vary with elevation (from 760-2500m elevation), it appears unlikely that *T. walteri* is an ecotypic variant of *T. trochus*.

**Description of Male.** Mean forewing length=13.63 mm, SD=1.013, N=6. Wing pattern (Fig. 11) and genitalia (Fig. 41) illustrated. No evident androconia.

**Description of Female.** Mean forewing length=13.10 mm, SD=0.742, N=5. Wing pattern (Fig. 12) and genitalia (Fig. 55) illustrated.

**Etymology.** This handsome species is named in honor of Walter C. Price Jr. for his support of the research of Robert C. Busby in Ecuador. This support led to many new discoveries reported in this paper, including the recognition of *T. walteri* as a distinct species. The name is a noun in apposition and is indeclinable and non-latinized.

**Type locality.** The road from Aloag to Santo Domingo descends through a large valley from highlands above 3000m to the lowlands. It is a major thoroughfare in which the native vegetation is gradually replaced by agriculture.

**Reasons for associating males and females.** The ventral postmedian lines are the same in both sexes. A series of males and females were both collected at

the type locality, and no other *Timaeta* species have been found in this area.

**Habitat and elevation.** Montane forest on the western side of the Ecuadorian Andes between 2200 and 2400m elevation.

**Male behavior.** Males set up mating territories on a group of small trees (4-5 meters in height) at the bottom of a steep streambed between 1200 and 1230 hours. Females were found at several locations less than 1 km distant along the Aloag/Santo Domingo Road, mostly landing on low vegetation at the edge of the mountain slope.

**Distribution** (Fig. 70). Western Ecuador.

**Material examined.** The type series of 6 males (1 genitalic dissection) and 5 females (1 genitalic dissection).

***Timaeta trochus* (H.H. Druce)**

Figs 13-14, 42, 56, 70

*Thecla trochus* H.H. Druce, 1907: 573 Colombia, Muzo, Rio Minero, 2500 feet in BMNH, holotype ♂ illustrated. D'Abbrera 1995: 1134 holotype ♂ illustrated.

*Trochusinus trochus* K. Johnson et al. 1997b: 7 comb. n.

*Timaeta trochus* Robbins 2004a: 120. comb. n., holotype examined.

**Diagnosis and recognition as a distinct species.** *Timaetus trochus* is the phylogenetic sister of *T. walteri* (Fig. 74, 75), but differs as noted in the previous species account

**Description of Male.** Mean forewing length=12.06 mm, SD=0.702, N=5. Wing pattern (Fig. 13) and genitalia (Fig. 42) illustrated. D'Abbrera (1995) suggested that there might be a "discocellular androconial patch" on the dorsal forewing, but we find no evident androconia.

**Variation.** Males are green above (Fig. 13), but a male from Rio Aguacatal (Colombia) has more of a blue tint, being intermediate between the dorsal colors in figures 11 and 13.

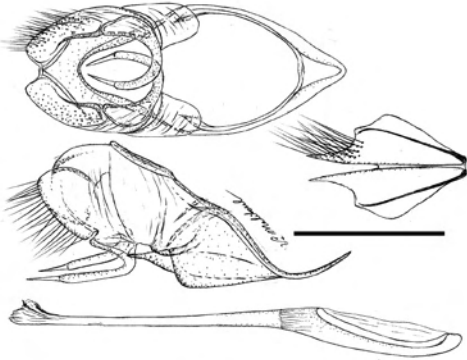
**Description of Female.** Mean forewing length=13.10 mm, SD=0.566, N=2. Wing pattern (Fig. 14) and genitalia (Fig. 56) illustrated.

**Reasons for associating males and females.** Both sexes have the same ventral postmedian line and have been found in the same valley in Zamora-Chinchipec Province, Ecuador, albeit at different elevations.

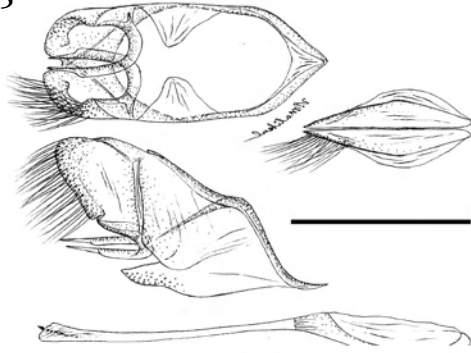
**Habitat and elevation.** 760-2500m in a variety of

**Figs 36-43.** Male genitalia. 36, *T. timaeus* (Ecuador, Tungurahua); 37, *T. christina* (Ecuador, Zamora-Chinchipec); 38, *T. molinopampa* (Ecuador, Loja); 39, *T. wernerii* (Ecuador, Pichincha); 40, *T. matthewii* (Ecuador, Morona-Santiago); 41, *T. walteri* (Ecuador, Pichincha); 42, *T. trochus* (Colombia, Cundinamarca); 43, *T. roberti* (Ecuador, Morona-Santiago). Scale 1 mm.

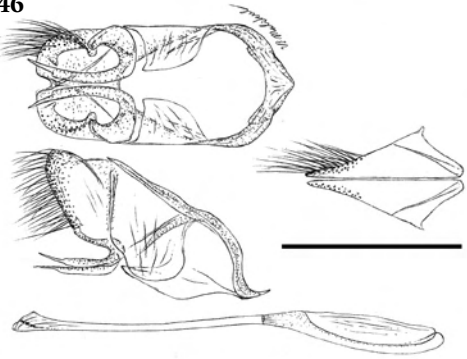
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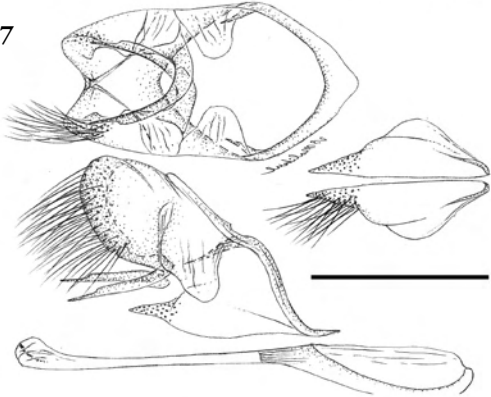
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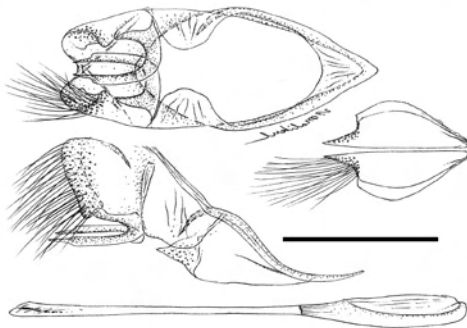
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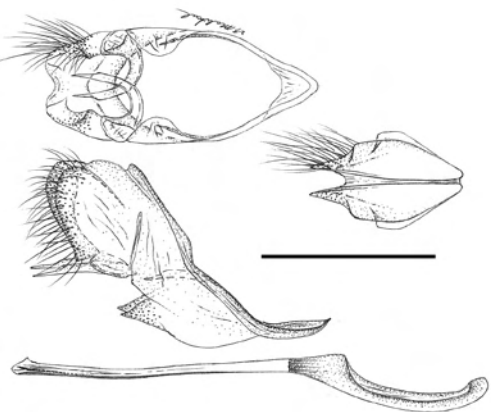
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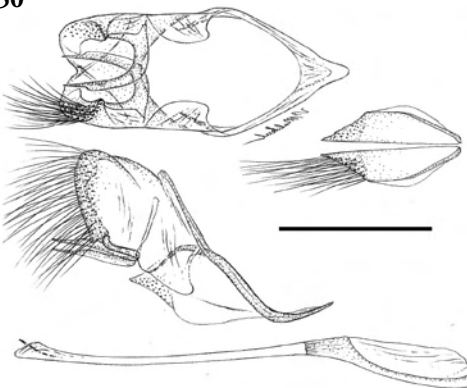
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**Figs 44-50.** Male genitalia. 44, *T. aepea* (Ecuador, Morona-Santiago); 45, *T. cospata* (Peru, Cusco); 46, *T. eronos* (Colombia, Tolima); 47, *T. pilosa* (Ecuador, Morona-Santiago); 48, *T. gabriela* (Ecuador, Morona-Santiago); 49, *T. romero* (Venezuela, Aragua); 50, *T. balzabamba* (Ecuador, Cotopaxi). Scale 1 mm.

montane habitats. The only two specimens from the western slope of the Ecuadorian Andes are from 800–900m.

**Distribution** (Fig. 70). Both slopes of the Andes in Colombia and Ecuador, as well as the interior mountains of Colombia.

**Remarks.** *Timaeta trochus* has the widest elevational range of any species in the genus. A male from Pacho, Colombia (SMF) was illustrated in Draudt (1919–1920) as *Thecla trochus*. Material examined. 6 males (3 genitalic dissections), 2 females (2 genitalic dissections), and the male holotype in BMNH—its genitalia were stylistically rendered in Johnson et al. (1997b).

*Timaeta roberti* Busby & Robbins, sp. n.

Figs 15–16, 43, 57, 71

**Type material.** Holotype ♂ Ecuador, Morona-Santiago, Nueve de Octubre, 2°12.2'S 78°13.1'W, 1800m, 22 September 2000, Robert C. Busby, leg. Deposited USNM (Fig. 15). [One white label, a red holotype label.]

**Paratypes** (8♂ & 1♀). Ecuador, Morona-Santiago Province: 1♂ & 1♀ Rio Abanico, 1600m, 2°15.0'S 78°12.1'W, 11 Sep 2000 (Fig. 16), 23 Sep 2000, Robert C. Busby, leg. (USNM, RCB); 5♂ Nueve de Octubre, 2°12.2'S 78°13.1'W, 1800m, 29 Sep 2001, 2 Oct 2000, 3 Oct 2000, 3 Oct 2000, 15 Sep 2006, leg. Robert C. Busby (USNM, MECN, RCB); 2♂ 18 km Macas-9 de Octubre Road, (Rio Abanico), 2°15.3'S, 78°12.2'W, 1600m, 2 Oct 2004, I. Aldas, R.C. Busby, leg. (USNM), 11 Jan 2006, D.H. Ahrénholz, R.C. Busby, leg. (RCB). Napo Province: 1♂ Tena, ca. 450m, Aug 1956, coll. J. Förster (ZSM). Because Tena is in the lowlands in close proximity to higher elevations via the roads to Baeza and to Baños, we presume that this specimen was actually collected in the mountains. No *Timaeta* is otherwise known from the immediate vicinity of Tena.

**Diagnosis and recognition as a distinct species.** Superficially, the color and wing pattern of *T. roberti* is most similar to that of *T. matthewi* (Figs. 9–10, 15–16), but *T. roberti* forms a clade with *T. trochus* and *T. walteri* (Figs. 74, 75). Despite geographical variation in male dorsal color and shape of the dorsal forewing border in *T. roberti* (detailed below), these two characters plus the lack of a ventral hindwing orange cubital spot in the male definitively distinguish *T. roberti* from *T. trochus* and *T. walteri* (Figs. 11, 13, 15). Although its geographical range overlaps that of *T. trochus* and *T. walteri*, *T. roberti* has not been found at exactly the same locality as either and appears to be restricted to 1500–1800m elevation.

**Description of Male.** Mean forewing length=13.73 mm, SD=1.603, N=11. Wing pattern (Fig. 15) and genitalia (Fig. 43) illustrated. No evident androcoxia.

**Variation.** Male dorsal color varies from green in eastern Peru and Ecuador to green-blue in western Ecuador. Width of the male dorsal forewing border in figure 15 is typical of specimens from eastern Ecuador, but the border in the one male from Peru is about half the width. In western Ecuador, width of the border varies between these extremes.

**Description of Female.** Mean forewing length=13.6 mm, N=1. Wing pattern (Fig. 16) and genitalia (Fig. 57) illustrated.

**Etymology.** This handsome species is named for Robert C. Busby Jr., son of Robert C. Busby, who first recognized that this species is distinct from *T. matthewi*. The name is a noun in apposition and is indeclinable and non-latinized.

**Type locality.** About 17 km west of Macas (map distance), the Nueve de Octubre locality in 2000 was a ridge with disturbed vegetation in an otherwise heavily forested area. The vegetation has suffered further degradation since then.

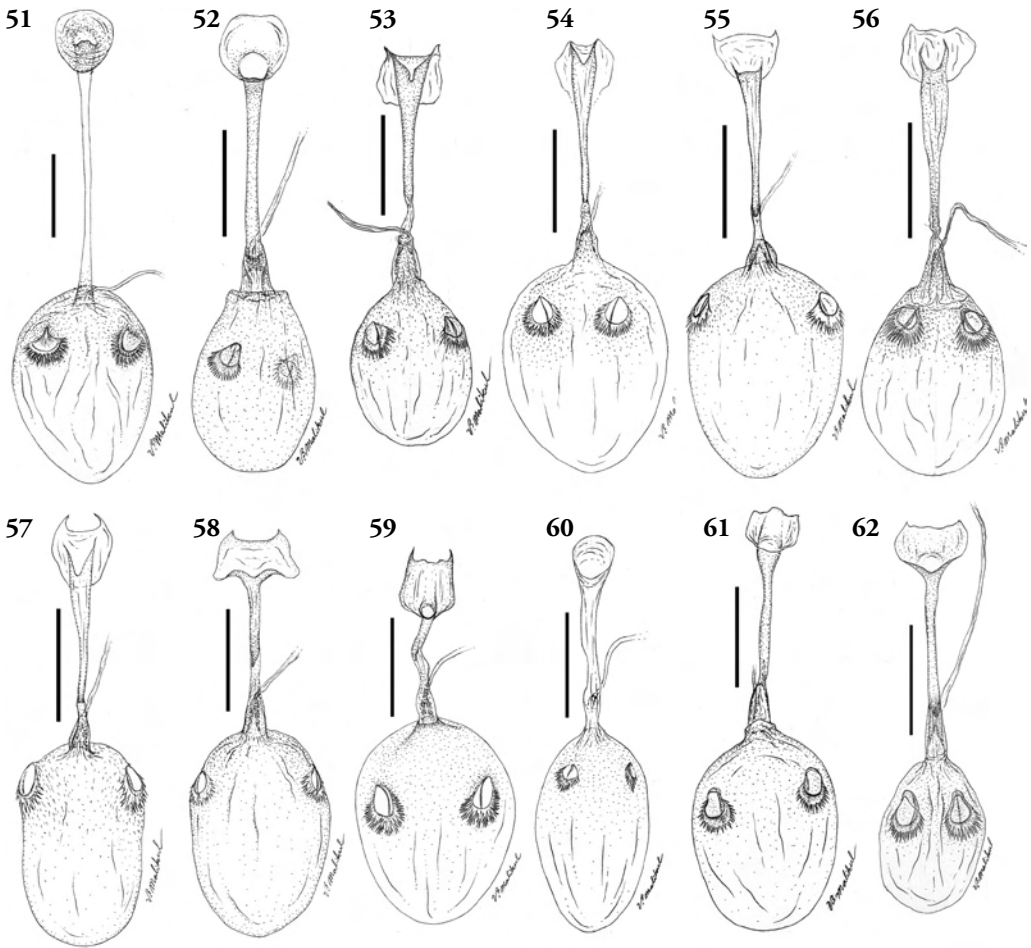
**Other Specimens Examined.** Because of geographical variation in male wing pattern, we restrict the type series to specimens from eastern Ecuador. Ecuador, Pichincha Province: 1♂ Maquipucuna, nr. Nanegalito, 1550m, 28 Nov 1992, leg. R. A. Raguso, 1130 hours, perched 10' up, dappled light (USNM); 1♂ Maquipucuna, nr. Nanegalito, 1700m, 2 Dec 1992, leg. R. A. Raguso, 1100 hours, 20' perch, light gap (USNM); 2♂ Palmito Pamba, km. 5 rd. Nanegal-G. Moreno, 1500–1700m, 15 Oct 1996, leg. J.P.W. Hall & K. R. Willmott (JHKW), 25 May 2007, R. Aldas, R.C. Busby, leg. (RCB). 1♂ Peru, AM, Quebrada Yanahuayco, 1800m, 06°24'S 77°26'W, Dec 2004, leg. B. Calderón (MUSM).

**Reasons for associating males and females.** The ventral postmedian lines of males and females are nearly identical. The female was collected on a ridge frequented by males.

**Distribution** (Fig. 71). Western and eastern Ecuador and northeast Peru.

**Habitat and elevation.** Montane forest at elevations between 1500 and 1800m. Unlike *T. trochus*, there is little variation in the elevation at which this species occurs, despite being known from three disparate localities.

**Male behavior.** Males in eastern Ecuador set up mating territories on vegetation 3–4 meters above the ground along ridge tops. While most frequently encountered between the hours of 1200 and 1300 hours, an occasional male has been seen as late as 1530 hours. Males in western Ecuador set up mating



**Figs 51-62.** Female genitalia. 51, *T. timaeus* (Colombia, Cundinamarca); 52, *T. molinopampa* (Ecuador, Loja); 53, *T. werneri* (Ecuador, Pichincha); 54, *T. matthewi* (Ecuador, Morona-Santiago); 55, *T. walteri* (Ecuador, Pichincha); 56, *T. trochus* (Ecuador, Loja); 57, *T. roberti* (Ecuador, Morona-Santiago); 58, *T. aepea* (Ecuador, Morona-Santiago); 59, *T. eronos* (Ecuador, Napo); 60, *T. pilosa* (Peru, Junin); 61, *T. gabriela* (Peru, Junin); 62, *T. romero* (Venezuela, Aragua). Scale 1 mm.

territories on hilltops, treefall gaps, forest edges, and along trails between 1100 and 1430 hours (under the names *Thecla balzabamba* and *T. eronos*, Raguso & Gloster 1996, vouchers in USNM).

**Material examined.** 16 males (4 genitalic dissections) and 1 female (1 genitalic dissection).

### *Timaeta aepea* (Hewitson)

Figs 17-18, 44, 58, 71

*Thecla aepea* Hewitson 1874: 165 ♀ from Ecuador in BMNH.

*Timaeta aepea* Robbins 2004b: 120 ♀ syntype examined, comb. n.

**Diagnosis and recognition as a distinct species.** *Timaeta aepea* is phylogenetically distinct (Figs. 74, 75) and occurs at lower elevations than any other *Timaeta* species on the eastern slope of the Andes. Male forewings and hindwings of *T. aepea* are rounded with no distinguishable apex on either wing and no discernable elongation at the hindwing anal angle, as is the case in some *Timaeta* species such as *T. molinopampa* and *T. christina*. The dorsal wing color is usually a more intense green color than that of any other *Timaeta*. The ventral forewing has a small scattering of green scales in contrast to the much more brightly marked ventral forewings of most other *Timaeta* species.



**Description of Male.** Mean forewing length 12.27 mm, SD=1.053, N=13. Wing pattern (Fig. 17) and genitalia (Fig. 44) illustrated. No evident androconia.

**Variation.** Some males have remnant portions of a postmedian line on both the forewing and hindwing. While most males are green dorsally, occasional ones have a blue tint.

**Description of Female.** Mean forewing length 12.50 mm, SD=0.707, N=2. Wing pattern (Fig. 18) and genitalia (Fig. 58) illustrated.

**Nomenclature.** This species was described from at least one Ecuadorian female in Hewitson's collection from Buckley. There is an old female lacking an abdomen in the Hewitson collection from Ecuador (BMNH) that has been labeled "B.M. type No. Rh. 885" with "*Thecla aepea* Hew." handwritten on a round, red-circular type label. This specimen matches the original figure, and our identification of this species is based on the wing pattern of this specimen.

**Reasons for associating males and females.** Three males and two females were collected within three meters of each other at Mendez (Morona-Santiago, Ecuador) (see male behavior notes below). These are the only male and female *Timaeta* specimens known from the eastern Andes below 1100m elevation.

**Distribution** (Fig. 71). Eastern Ecuador and Peru.

**Habitat and elevation.** This species occurs in areas with relatively intact forest remnants and also in more disturbed landscapes with small patches of remnant forest surrounded by cultivated land, predominantly cow pastures. With recorded elevations between 900 and 1100m, *Timaeta aepea* occurs consistently at lower elevation than any other *Timaeta* in the eastern Andes (*T. trochus* is unrecorded below 1250m in the eastern Andes and there is one old, dubious record of *T. gabriela* at 750m).

**Male behavior.** Males set up mating territories at different times at different localities. In Puyo (Pastaza), males consistently perched on a single plant about two meters high between 0900 and 1000 hours (observations made over a decade). In Mendez (Morona-Santiago), males of *T. aepea* were observed on two different hilltops about 500m apart. On one hill, the males perched on tall grass at the top edge of a cow pasture between 1130 and 1230 hours. Two females were collected in an adjacent hedgerow, but no courtship was observed. On the second hill, males perched on an isolated bush about two meters high between the forest and a cow pasture between 1030 and 1330 hours.

**Remarks.** D'Abrera (1995) illustrated a male and female of *T. aepea* from Peru. The male is actually a female *Timaeta* of uncertain identity. The female appears to be correctly identified. This is the first

time that a male has been associated with the female syntype.

**Material examined.** 14 males (3 genitalic dissections), 2 females (1 genitalic dissection), and a female syntype in BMNH.

### *Timaeta cospata* Robbins & Busby, sp. n.

Figs 30, 45, 72

**Type material.** Holotype ♂ Peru: Cusco, Qda. Morro Leguia, 13°08'S 71°33'W, 30 Aug 1989, 1950-2150m, Leg. R. Robbins. Deposited MUSM (Fig. 30). [One white label, a green dissection label, a red holotype label.]

**Paratypes.** None.

**Diagnosis and recognition as a distinct species.** We recognize *T. cospata* as a distinct species with reluctance because it is known from only one male that is in poor condition. Although we cannot assess variation within this species, it is phylogenetically distinct (Figs 74, 75). It forms a clade with *T. aepea* and the *T. eronos* complex (5 species). The latter complex shares two synapomorphies (characters 14 & 15) that *T. cospata* does not possess (Figs 74, 75). The wing pattern and male genitalia of *T. cospata* and *T. aepea* have many differences (Figs. 17, 30, 44, 45), and these species occur, so far as is known, at widely disjunct elevations. The male of *T. cospata* is immediately distinguishable by the wide black border on the anterior half of the dorsal forewing.

**Description of Male.** Mean forewing length 11.1 mm, N=1. Wing pattern (Fig. 30) and genitalia (Fig. 45) illustrated. No evident androconia.

**Description of Female.** Unknown or not recognized.

**Etiymology.** This name is arbitrary, non-latinized, and indeclinable. It is intended to draw an association with the Cosnipata Valley where the type was collected.

**Type locality.** The road from Paucotambo (3600m) to Atalaya (500m) steeply descends the heavily forested Cosnipata Valley. The holotype was collected in a light rain along the side of the road.

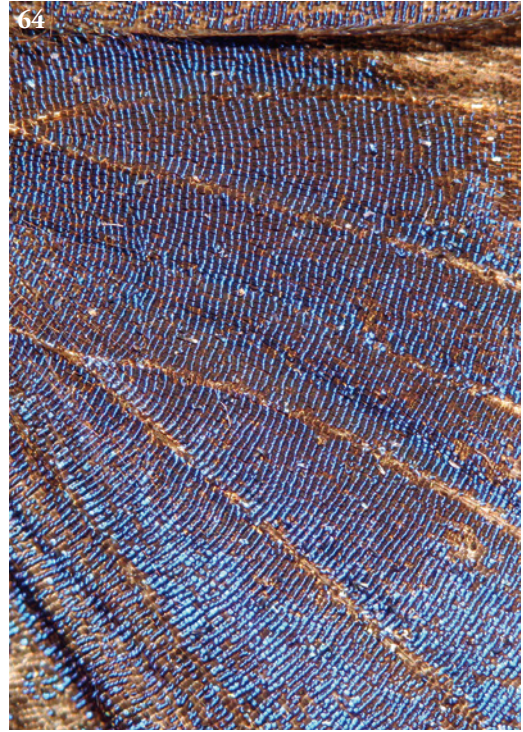
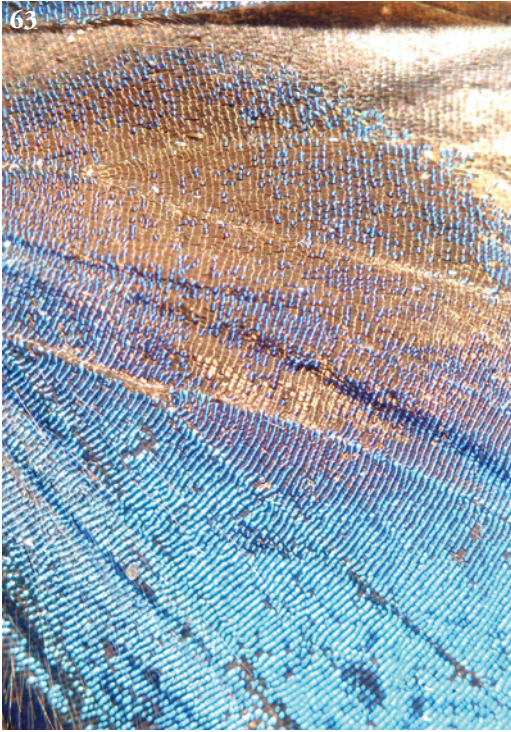
**Distribution** (Fig. 72). The type locality.

**Habitat and Elevation.** Wet montane forest at 1950-2150m.

**Material examined.** The holotype male and its genitalia.

### *Timaeta eronos* species group

The *T. eronos* species group (*T. eronos*, *T. pilosa*, *T. romero*, *T. balzabamba*, and *T. gabriela*) is characterized by a unique 'comb'-like scent patch along the posterior edge of dorsal hindwing vein Cu<sub>2</sub> and by blue scales at the lateral edge of the frons (characters



**Figs 63-64.** Dorsal hindwing androconia in *Timaeta*. 63, *T. timaeus* (Ecuador, Tunghurua); 64, *T. christina* (Ecuador, Tunghurua), arrow points to androconia distal of the discal cell.

14 & 15). Shape of the male and female genitalia, however, are quite variable among these species and do not characterize the group.

### *Timaeta eronos* (H.H. Druce)

Figs 19-20, 46, 59, 72

*Thecla eronos* H.H. Druce 1890: 151 ♂ Interior of Colombia in BMNH. D'Abreu 1995: 1134 holotype ♂ illustrated.

*Trochusinus eronos* K. Johnson et al. 1997b: 7 comb. n.

*Timaeta eronos* Robbins 2004b: 120 holotype ♂ examined, comb. n.

*Micandra neblina* Salazar & K. Johnson 1997: 6 Holotype ♀ from Manizales, Colombia in UNCC, but see below.

*Timaetus neblina* Robbins 2004b: 120. syn. n. of *T. aepea*. Herein syn. n. of *T. eronos*.

**Diagnosis and recognition as a distinct species.** The genitalia and wing pattern of *Timaeta eronos* are distinct from the other four species in the *T. eronos* complex (Figs. 19-29, 46-50, 59-62). Shape of the male genitalia saccus (characters 3 & 4) supports a sister group relationship with *T. pilosa* (Figs. 74), with which it is sympatric.

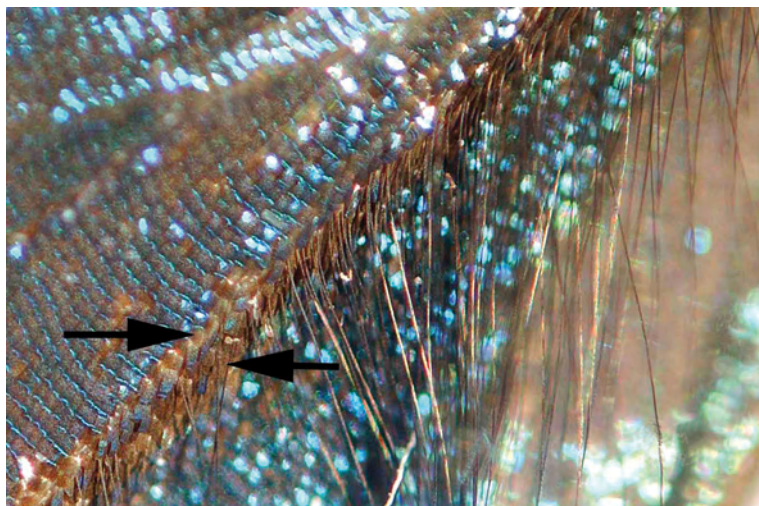
**Description of Male.** Mean forewing length 12.86 mm, SD=0.627, N=7. Wing pattern (Fig. 19) and genitalia (Fig. 46) illustrated. Androconia are typical of the *T. eronos* group.

**Description of Female.** Mean forewing length 11.88 mm, SD=0.650, N=4. Wing pattern (Fig. 20) and genitalia (Fig. 59) illustrated.

**Nomenclature.** Johnson et al. (1997b) described *Micandra neblina* from a single Colombian female, but did not illustrate its genitalia or provide verbal character evidence to support their statement that the holotype is a female. However, they illustrated the holotype (deposited in UNCC), and their figure legend lists the holotype as a male. The verbal description is consistent with the illustrated male, and the putative type in UNCC is the illustrated male, but its current locality label lists the date of collection as 26 May 1984, not August 1980, as stated in the original description.

**Reasons for associating males and females.** Both sexes have a similar postmedian line on the ventral hindwing. Both co-occur at Rio Abanico, Macas, Morona-Santiago Province, Ecuador.

**Distribution** (Fig. 72). Eastern Ecuador, central Colombia, and western Colombia.



**Fig. 65.** Dorsal hindwing androconia in *T. pilosa* (Ecuador, Morona-Santiago), arrow at left points to vein  $Cu_2$ , arrow on right points to “flat” androconia at base of the piliform androconia.

**Habitat & Elevation.** Montane forest from 1600 to 2100m.

**Male behavior.** Males perch in the afternoon 3-5m above the ground.

**Material examined.** 7 males (3 genitalic dissections), 4 females (2 genitalic dissections), the male holotype of *Thecla eronos* in BMNH (also illustrated in D’Abrera 1995)—its genitalia were stylistically rendered in Johnson et al. (1997b)—and a photograph of the labeled holotype of *Micandra neblina* in UNCC.

*Timaeta pilosa* Robbins & Busby, sp. n.

Figs 21-22, 34, 47, 60, 65, 72

**Type material.** Holotype ♂ Ecuador: Morona-Santiago, Nueve de Octubre, 2°13’S, 78°13’W, 1800m, 10.[Sep]ix.1999, [Leg.] Robbins, Busby, Estevez, Aldas. Territorial Behavior: 1322. Deposited USNM (Fig. 21). [Two white labels, a red holotype label.]

**Paratypes** (15♂ & 2 ♀). Ecuador: 3♂ Same data as holotype, but territorial times different as noted under male behavior (USNM); 4♂ Same locality as holotype, 11, 19, 20, 22 Sep 1999, leg. Robert C. Busby (MECN, RCB); 1♂ Morona-Santiago, 14 km. W. of Macas, Rio Abanico, 1600m, 16 Sep 1999, leg. Robert C. Busby (RCB); 1♀ Napo, 10km El Chaco-El Reventador Rd, 0°16.5’S 77°45.6’W, 1800-1900m, 3 Jan 2007, Robert C. Busby, leg. (RCB). Peru, Junin: 1-3 km S Mina Pichita, 11°05’S 75°25’W, 2000-2100m, 2 Oct 1996, leg. G. Lamas (1♀, Fig. 22, MUSM), 12 Nov 2003, leg. J.J. Ramirez (2♂, MUSM), 8 Sep 2002, leg. C. Peña (2♂, MUSM), 16-17 Oct 1989, leg. Mielke & Casagrande (1♂, DZUP); 2♂ Quebrada Siete Jeringas,

11°12’S 75°24’W, 1700m, 25, 29 (Fig. 65) Aug 2003, leg. C. Peña (MUSM).

**Diagnosis and recognition as a distinct species.**

*Timaeta pilosa* belongs to the *T. eronos* group and is sympatric with its sister species, *T. eronos*, without any indication of intergradation. The male wing pattern superficially resembles that of *T. balzabamba* (Figs. 21, 29), but its forewing border is broader and its genitalia are distinct (Figs. 47, 50). It is the smallest *Timaeta* species.

**Description of Male.** Mean forewing length 10.81 mm, SD=0.574, N=16. Wing pattern (Fig. 21), wing venation (Fig. 34), genitalia (Fig. 47), and androconia (Fig. 65) illustrated. Androconia are typical of the *T. eronos* group.

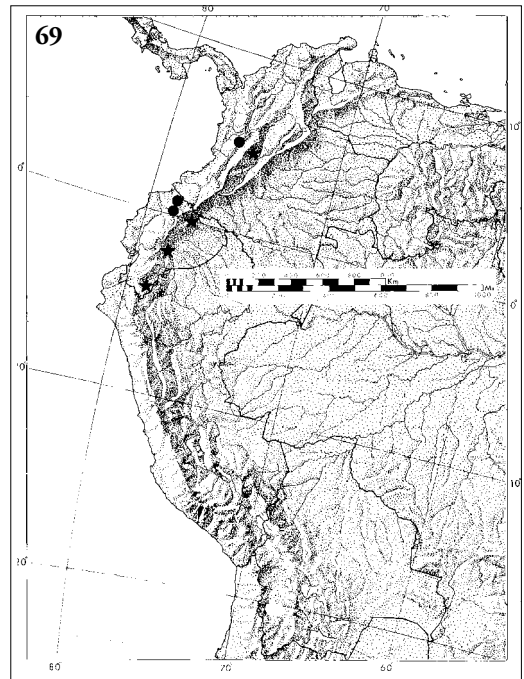
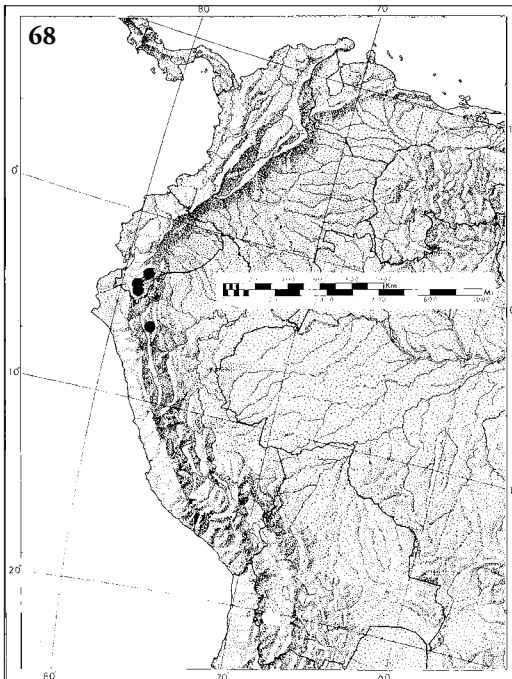
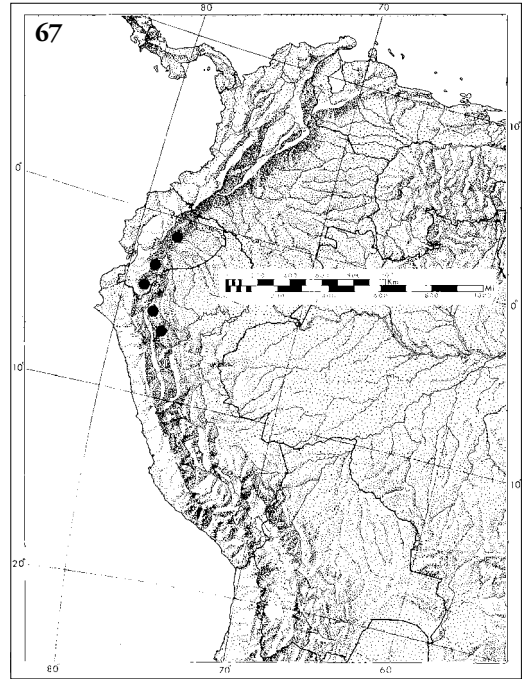
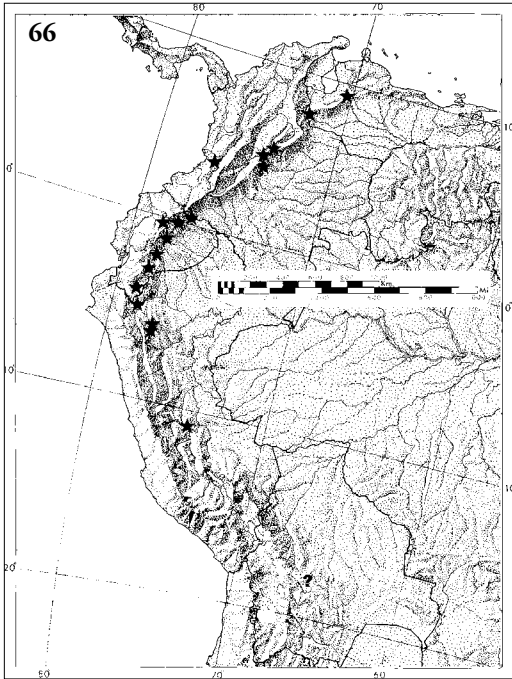
**Variation.** Extent of the blue on the male ventral forewing is constant in Ecuador, but is more restricted on average in specimens from Peru.

**Description of Female.** Mean forewing length 10.70 mm, SD=0.990, N=2. Wing pattern (Fig. 22) and genitalia (Fig. 60) illustrated.

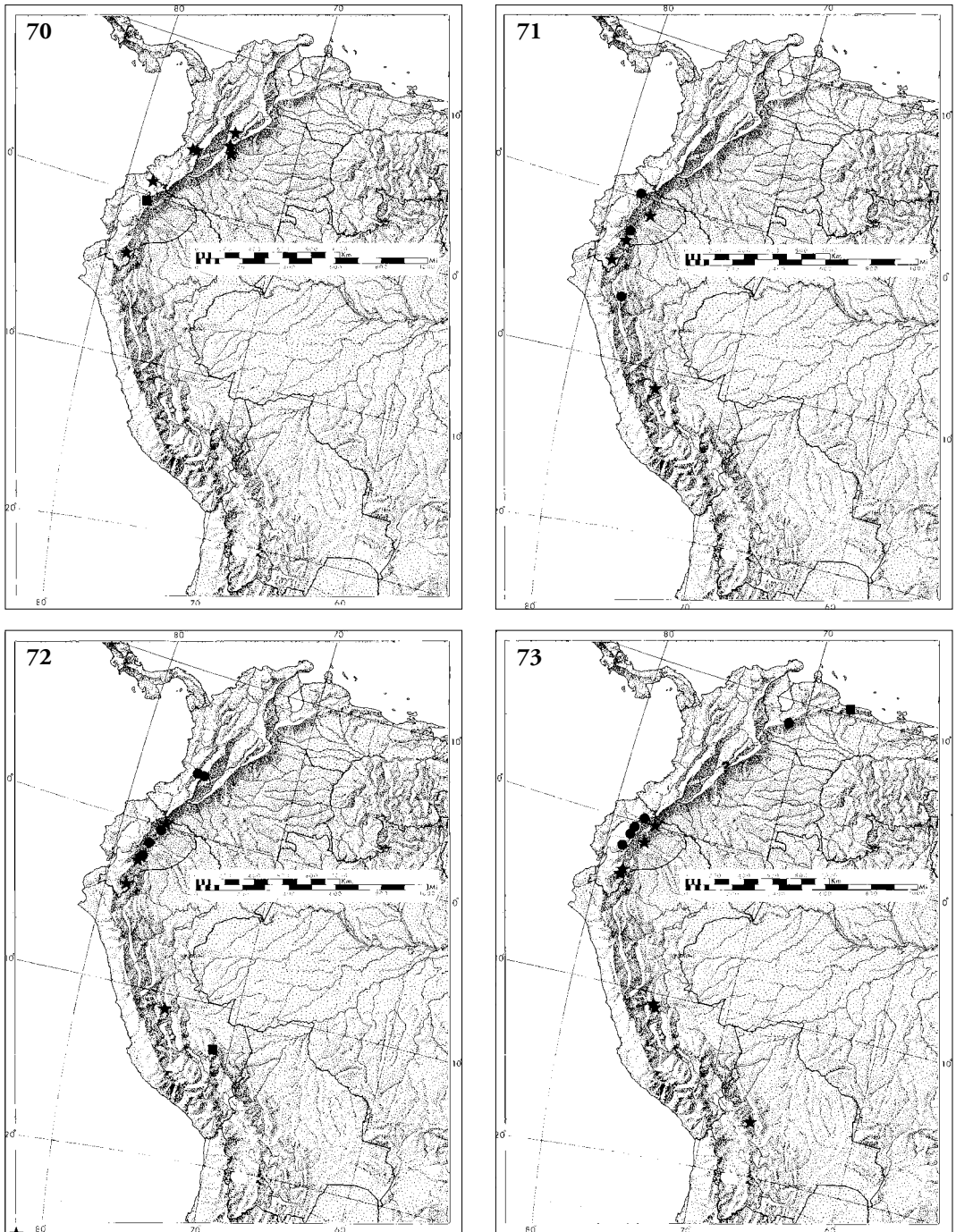
**Etymology.** The name of this species is intended to be associated with the “hair-like” scales on the inner margin of the forewing and as well as the “hair-like” dorsal hindwing androconia just posterior of vein  $Cu_2$ . The name is a feminine noun in apposition and is indeclinable and non-latinized.

**Type locality.** About 17 km west of Macas (map distance), the Nueve de Octubre locality in 1999 was a ridge with disturbed vegetation in an otherwise heavily forested area, but the vegetation has suffered further degradation since then.

**Reasons for associating males and females.** Both sexes were collected at Mina Pichita in Peru. Two males



**Figs 66-69.** Distributions. 66, *T. timaeus*, the exact locality in Bolivia (?) is uncertain; 67, *T. christina*; 68, *T. molinopampa*; 69, *T. werneri* (circles) and *T. matthewi* (stars).



**Figs 70-73.** Distributions. 70, *T. trochus* (stars) and *T. walteri* (square); 71, *T. roberti* (circles) and *T. aepea* (stars); 72, *T. eronos* (circles), *T. pilosa* (stars), and *T. cospata* (square); 73, *T. romero* (square), *T. balzabamba* (circles), the exact locality in Colombia (?) is uncertain, *T. gabriela* (stars)—the Bolivian record is based on a female.

have a vestigial postmedian line on the ventral hindwing that is the same shape as that of the female.

**Habitat and elevation.** Montane forest between 1600 and 2100m elevation.

**Male behavior.** Males at Nueve de Octubre (Morona-Santiago) set up mating territories in the early afternoon along a sunny ridge on low vegetation along a trail edge at about 2m above the ground. Specific records for 10 Sep 1999 are 1322, 1326, 1328, and 1423 hours (vouchers in USNM).

**Distribution** (Fig. 72). Eastern Ecuador and Peru.

**Material examined.** The 16 males (2 genitalic dissections) and 2 females (1 genitalic dissection) in the type series.

*Timaeta gabriela* Busby & Robbins, sp. n.

Figs 23-26, 48, 61, 73

**Type material.** Holotype ♂ Ecuador: Morona[-] Santiago, 14 km Limon-Gualaquiza Road, 3°02.1'S 78°28.2'W, 1500m, 30 September 2006 Robert C. Busby, leg. Deposited USNM (Fig. 25). [One white label, one red holotype label.]

**Paratypes** (11 ♂ & 5 ♀). Ecuador: 1 ♂ & 1 ♀ (in copula, Figs. 23, 24) Sucumbíos, 2 km El Reventador-Lumbacqui Road, 0°01.5'S 77°30.6'W, 1500m, 01 Jan 2006, leg. Robert C. Busby (RCB); 1 ♀ Pastaza, 37km Puyo-Arajuno Road, 1°21.1S 77°42.7'W, 1100m, 9 Sep 2000, leg. Robert C. Busby (RCB); 1 ♂ Morona-Santiago, Chiquinda, 1600m, Nov 1999 leg. I. Aldas, R.C. Busby (USNM); 1 ♀ Morona-Santiago, Río Abanico, km 20 Macas-9 de Oct., 1600m, 1 Nov 1996, leg. J.P.W. Hall & K.R. Willmott (JHKW); 3 ♂ the type locality, 22 Sep 2006 (RCB); 2 ♂ same data as holotype (RCB). Peru, Junin: Quebrada Siete Jeringas, 11°12'S 75°24'W, 1700m, 25 Aug 2003 (1 ♂ & 1 ♀, MUSM), 27 Aug 2003 (1 ♂, MUSM), 8 Nov 2003 (1 ♂, MUSM), leg. C. Peña; 1 ♂ La Merced. Bolivia: 1 ♀ Rio Songo, 750m, Coll. Fassl (SMF).

**Diagnosis and recognition as a distinct species.** The wing pattern and male genitalia of *T. gabriela* is distinct from the other members of the *T. eronos* species group (Figs. 19-29, 46-50). It is sympatric with *T. eronos* and *T. pilosa*, and we know of no evidence to suggest that it might be a geographical variant of *T. balzabamba* or *T. romero*. Males are distinguished by a green-blue ventral forewing patch, but with the discal cell dark (Figs. 23, 25). Females are distinguished by the shape of the ventral hindwing postmedian line (Figs. 24, 26).

**Description of Male.** Mean forewing length 11.11 mm, SD=0.469, N=12. Wing pattern (Figs. 23, 25) and

genitalia (Fig. 48) illustrated. Androconia are typical of the *T. eronos* group. Variation. Dorsal color varies from blue (Figs. 23, 25) to green-blue. The basal edge of the dorsal forewing border is somewhat diffuse. In "worn" specimens the border appears to be broader than in "fresh" individuals, perhaps due to the loss of blue scales. Forewing vein  $M_2$  in *T. gabriela* may arise from the discal cell, from the origin of vein  $M_1$ , or from the "middle" of vein  $M_1$  (stalked).

**Description of Female.** Mean forewing length 10.67 mm, SD=0.988, N=5. Wing pattern (Figs. 24, 26) and genitalia (Fig. 61) illustrated.

**Reasons for associating males and females.** A pair was collected *in copula* (Figs. 23, 24). While the ventral hindwing of this male is mostly black, some males have a remnant postmedian line that is the same shape as the line on the female. Further, the shape of this postmedian line differentiates females of *T. gabriela* from those of *T. eronos* and *T. pilosa*.

**Etymology.** This beautiful species is named for Gabriela Aldas, daughter of Ismael Aldas, who collected the first Ecuadorian specimen of this species. The name is a feminine noun in apposition and is indeclinable and non-latinized.

**Type locality.** A long ridge with patches of remnant forest.

**Distribution** (Fig. 73). Eastern slope of the Andes from Ecuador to Bolivia.

**Habitat and elevation.** Montane forest between 1100 and 1700m elevation in disturbed areas where small tracts of remnant cloud forest remain. The Bolivian female was collected at 750m, which is inconsistent with the remainder of the type series. Although *T. gabriela* is sympatric with *T. eronos* and *T. pilosa*, as noted, a majority of the specimens of *T. gabriela* were recorded at lower elevations.

**Behavior.** Males set up mating territories in treetops 6-8m above the ground between 1300 and 1500 hours. The pair *in copula* was collected at about 1330 hours.

**Material examined.** 12 males (2 genitalic dissections) and 5 females (2 genitalic dissections).

Remarks. The Bolivian female has an identification label (*mimula*), but the name *Thecla mimula* Draudt belongs to *Lathecla* (Robbins 2004b, Lamas & Robbins in prep.).

*Timaeta romero* Robbins & Busby, sp. n.

Figs 27-28, 49, 62, 73

**Type material.** Holotype ♂ [Venezuela, Aragua], Choroni, 1980 ix[Sep]-[19]69 [leg.] C[.] F[.] R[omero]. Deposited MIZA (Fig. 27). [Handwritten white label, red holotype label].

Paratypes. (2♂ 1♀). Venezuela, Aragua: 2♂ Choroni, Jul 1967 (FROM), Sep 1968 (USNM); 1♀ Rancho Grande, Portachuelo Pass, 1100m, 13 Sep 1976, leg. F. Fernandez Y., J.A. Clavijo (MIZA).

**Diagnosis and recognition as a distinct species.** Structure of the male genitalia differentiates *T. romero* from *T. eronos*, *T. pilosa*, and *T. gabriela*, but not from *T. balzabamba* (Figs. 46-50). However, the ventral forewing of *T. romero* has almost no iridescent blue while that of *T. balzabamba* has a large conspicuous patch of iridescent blue scales (Figs. 27, 29). There is no indication that these wing patterns intergrade geographically. Ventral forewing pattern among the five males of *T. balzabamba* from western Ecuador, central Colombia, and western Venezuela is essentially invariant. Likewise, there is virtually no ventral forewing pattern variation among the three known males of *T. romero*. Based on current evidence, *T. romero* appears to be a distinct, allopatric species.

**Description of Male.** Mean forewing length 11.90 mm, SD=0.954, N=3. Wing pattern (Fig. 27) and genitalia (Fig. 49) illustrated. Androconia are typical of the *T. eronos* group.

**Variation.** The vestigial postmedian line on the ventral hindwing (Fig. 27) is absent in the most "worn" male.

**Description of Female.** Mean forewing length 11.4 mm, N=1. Wing pattern (Fig. 28) and genitalia (Fig. 62) illustrated.

**Reasons for associating males and females.** *Timaeta romero* is the only *Timaeta* species known from the coastal mountains of northern Venezuela. The ventral hindwing postmedian line on the female (Fig. 28) is the same as the remnant postmedian line on the ventral hindwing of males (Fig. 27).

**Etymology.** This species is named in honor of the late Francisco Romero, who collected the three known males. The name is a masculine noun in apposition and is indeclinable and non-latinized.

**Type locality.** Choroni is a 1700m pass through the mountains to the north of Maracay, Aragua, Venezuela. It is about 15 km to the east of the better known Portachuelo Pass (Beebe 1949). Romero collected butterflies at Choroni for many decades, mostly from about 1300-1700m. We are grateful to his son for making these specimens available for examination.

**Distribution** (Fig. 73). Northern Venezuela.

**Habitat and elevation.** Montane forest from 1100 to about 1700m elevation.

**Material examined.** 3 males (2 genitalic dissections) and 1 female (1 genitalic dissection).

### *Timaeta balzabamba* (Goodson)

Figs 29, 50, 73

*Thecla balzabamba* Goodson 1945: 187. D'Abnera 1995: 1134 "holotype ♂" from "?Venezuela, Prov. Bolivar, Balzapampa [sic]" but the male was a syntype in 1995 from Ecuador, Bolivar, Balzabamba, as noted by Goodson.

*Trochusinus balzabamba* K. Johnson et al. 1997b: 8 comb. n., lectotype ♂ from Ecuador, Balzabamba in BMNH with stylized figure of its genitalia.

*Timaeta balzabamba* Robbins 2004b: 121 ♂ lectotype examined

**Diagnosis and recognition as a distinct species.** The male genitalia of *T. balzabamba* are distinct except for those of *T. romero* (Figs. 49, 50). The reasons for considering it to be a distinct from *T. romero* are discussed under that species. *Timaeta balzabamba* is sympatric with *T. eronos* without evidence of intergradation of distinguishing morphological characters. There is no evidence that *T. balzabamba* is a geographical form of *T. pilosa* or *T. gabriela*.

**Description of Male.** Mean forewing length 11.57 mm, SD=0.493, N=3. Wing pattern (Fig. 29) and genitalia (Fig. 50) illustrated. Androconia are typical of the *T. eronos* group.

**Description of Female.** Unknown or unrecognized.

**Distribution** (Fig. 8). Western Venezuela, central Colombia, and western Ecuador. A male of *T. balzabamba* in SMF, which was illustrated in Draudt (1919-1920) as *Thecla eronos*, was collected by Fassl in Medina, Ost Colombia. It is labeled 1500m (with the "1" handwritten, preceding the printed "500"), but the elevation of Medina is less than 500m (Fassl 1918). We infer that it was collected at 1500m along the transect over the eastern cordillera illustrated in Fassl (1918), but it is unclear if it was collected on the eastern or western slope. The "dot" on the distribution map covers both slopes.

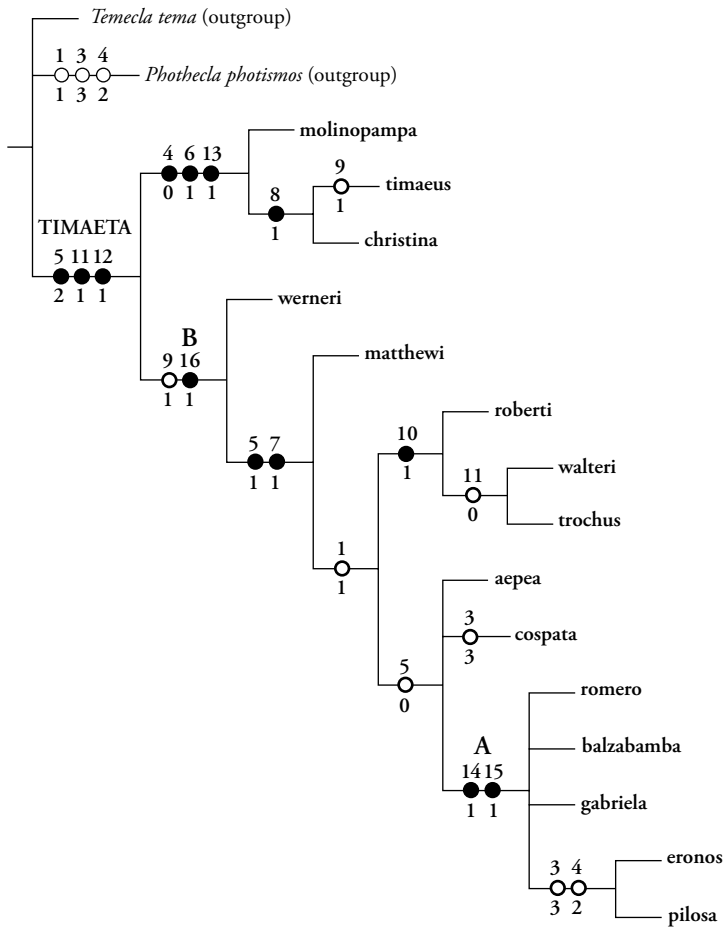
**Habitat and elevation.** Montane forest from 1500 to 1600m elevation.

**Male behavior.** A male appeared to set up a mating territory in the early afternoon 6m above the ground in a light gap (I. Aldas, pers. comm.).

**Material examined.** 3 males (2 genitalic dissections), the lectotype in the BMNH, and an image of a specimen from western Venezuela (BMNH).

### Unplaced females

Three *Timaeta* females cannot be identified with confidence. Either they are variants of one of the species treated or represent species for which we have not seen males. The data for these females are: 1♀ Ecuador, Napo, Baeza, 2000m (RCB); 1♀ Ecuador, Morona-Santiago, Nueve de Octubre, 1800m



**Figs 74.** First equal-weight most parsimonious cladogram for *Timaeeta* (30 steps). It is the same as the strict consensus tree. Character numbers are above nodes and character state numbers are below, optimized with the “unambiguous changes only” option. Node A is where androconia along the posterior edge of dorsal hindwing vein  $Cu_2$  and blue scaling on the distal edges of the frons in males was inferred to have evolved (characters 14 and 15). Node B is where hindwing vein  $M_2$  was inferred to be lost (character 16). See discussion of these characters in the text.

(RCB); 1 ♀ Ecuador, Pastaza, Rio Topo, 1400m (USNM).

### Phylogenetic analysis and biogeography

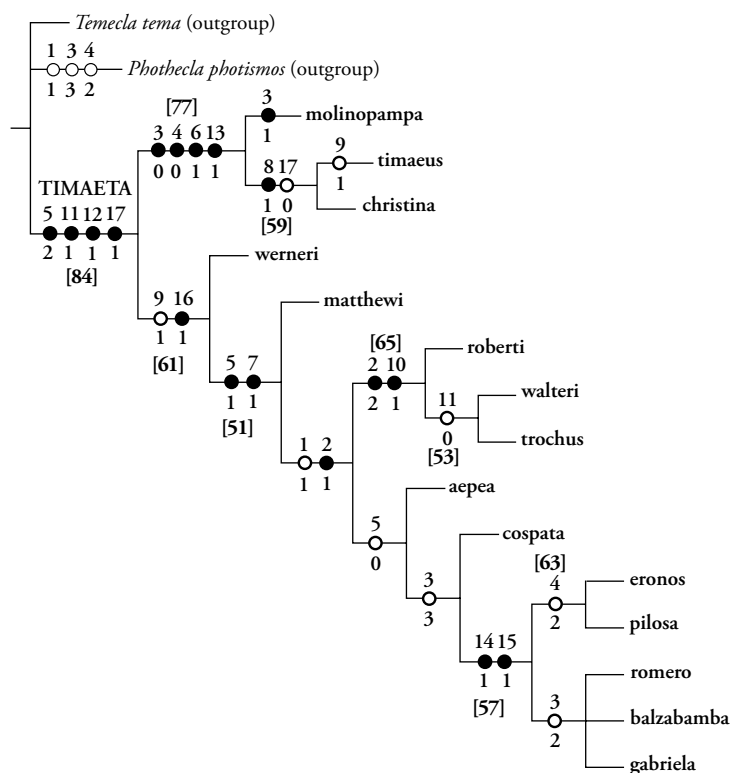
Characters for the phylogenetic analyses were derived from adult morphology because no *Timaeeta* species has been reared, so far as we are aware, and because DNA sequences are currently available for only two *Timaeeta* species (Quental et al., in prep.). Characters were coded primarily from males because females of some *Timaeeta* species are yet unknown or unrecognized. Dissections of 49 male genitalia and 16 female genitalia were examined. Male wing slides were made for 5 species following standard methods. For the other species, venation was examined by placing a drop of 95% ethanol on the ventral wings or by examination with a binocular microscope.

The terminal taxa are the 15 *Timaeeta* species

recognized in this paper (Table 2). The outgroups for the analysis are *Temecla tema* (Hewitson) and *Phothecla photismos* (H.H. Druce), the type species of their respective genera, for the reasons noted in the taxonomic history of *Timaeeta*.

The characters used in the phylogenetic analysis are listed in Table 1, and the state for each *Timaeeta* and outgroup species was recorded in Nexus Data Editor (web available software from R.D.M. Page) (Table 2). Uncertain character states were coded with a question mark (?), and all characters were unordered. We searched exhaustively for shortest trees using the implicit enumeration option of Hennig86 software (ie\*) to derive a most parsimonious cladogram. A strict consensus tree was determined. To test the assumption of equally weighted characters, successive weighting was performed (Farris 1969) and a consensus of the resulting trees was determined. Mapping of characters on trees was done with





**Fig. 75.** Second equal-weight most parsimonious cladogram for *Timaeta* (30 steps). Character numbers are above nodes and character state numbers are below, optimized with the “fast” option. Numbers in brackets are jackknife support values.

WinClada software (Nixon 2002) with the “unambiguous changes only” and “fast” options. Jackknife and bootstrap supports were determined in WinClada using Nona (1000 replications with mult\*10, memory 1000 trees).

Implicit enumeration yielded two 30-step trees with a consistency index of 73 and retention index of 86 (Figs. 74, 75), one of which was the same as the strict consensus tree (Fig. 74). Successive weighting resulted in two trees with the same topology as the original most parsimonious trees. Jackknife support for nodes (bootstrap supports were almost identical) was not especially high (Fig. 75) because we were able to code only 17 characters (39 states) for 15 ingroup species using adult morphology. However, most nodes were supported by unambiguous non-homoplastic character state changes (Fig. 74). A more robustly supported cladogram would require more characters than we were able to code.

Two of the 15 *Timaeta* species are elevationally allopatric/parapatric with their sister lineage in both most parsimonious cladograms (Figs. 74, 75). *Timaeta molinopampa* is recorded only above 2500m while its sister lineage (*T. timaeus* and *T. christina*) occurs only below 2200m. On the eastern slope of

the Andes, *T. aepea* is recorded from 900-1100m while the species in any possible sister lineage (*T. cospata* and the *T. eronos* group) occur above 1100m, with *T. gabriela* having been reliably recorded once as low as 1100m.

*Timaeta romero*, *T. balzabamba*, and *T. gabriela* form a monophyletic lineage of geographically allopatric species (Fig. 73) in the more resolved most parsimonious cladogram (Fig. 75). In the other cladogram (Fig. 74), the lack of phylogenetic resolution in the *T. eronos* group neither confirms nor falsifies this hypothesis. There is no other case in *Timaeta* in which a species is allopatric with its sister lineage.

## Discussion

### Morphology

Draudt (1919-1920) noted a “comb” of piliform-shaped androconia on the posterior edge of dorsal hindwing vein  $Cu_2$  in *T. eronos*, and we find that it also occurs in *T. balzabamba*, *T. romero*, *T. pilosa*, and *T. gabriela* (character 14, Tables 1, 2). The scales at the base of the piliform setae also appear to be androconia (Fig. 65). Optimization of character states on

**Table 1.** Coded characters.**Male Genitalia**

1. Shape of posterior valve tip (0) rounded, (1) tapered to a point.
2. Valve tips (0) with setae, (1) with a short (<0.05 mm) posteriorly pointing process lacking setae, (2) with a long (>1.5 mm) posteriorly pointing process lacking setae.
3. Saccus length (0) 1.3-1.7 mm, (1) 0.7-0.9 mm, (2) 0.3-0.6 mm, (3) 0.1-0.3 mm.
4. Saccus shape (0) length greater than width at middle, (1) length equal to width at middle, (2) length less than width at middle.
5. Posterior edge of labides in lateral aspect (0) most posterior dorsally, (1) most posterior ventrally, (2) dorso-ventrally flat.
6. Length of external penis to length of internal penis (0) less than 1.8, (1) more than 1.8.
7. Dorsal cornutus (0) more than half the length of the ventral cornutus, (1) less than half the length of the ventral one (it some cases, it is poorly sclerotized).
8. Ventro-lateral processes of posterior vinculum/tegumen (0) as long as wide, (1) significantly wider than long.

**Wing Shape and Pattern**

9. Male hindwing anal angle (0) lobe present, (1) rounded with no lobe.
10. Black scale tuft at anal angle on ventral hindwing (0) absent, (1) present.
11. Male ventral hindwing cubital spot (0) orange, (1) brown.
12. Male hindwing tails (0) present, (1) absent.

**Androconia.** Because male eumaeines often have more than one kind of androconia, we treat the following androconial characters separately.

13. Androconia at base of dorsal hindwing and ventral forewing (0) absent, (1) present.
14. "Comb"-like androconia along the posterior edge of dorsal hindwing vein  $Cu_2$  (0) absent, (1) present.

**Head**

15. Scales at lateral edge of the frons (0) white, (1) blue.

**Wing Venation**

16. Hindwing vein  $M_2$  (0) present, (1) absent.
17. Terminus of forewing vein  $R_1$  (as measured by a line perpendicular to vein 2A) (0) distal of end of discal cell, (1) basal of end of discal cell.

the cladogram suggest that this structure evolved once in *Timaeta* (node A in Fig. 74). It is unrecorded elsewhere in the Eumaeini.

Hindwing vein  $M_2$  lacking was recorded in some species of *Semonina* Robbins (*Erora* Section of the Eumaeini), but is otherwise unknown among the Eumaeini (Robbins & Duarte 2004). The "loss" of hindwing vein  $M_2$  occurred once within *Timaeta* (node B in Fig. 74). The vein is missing in both males and females, which facilitates the generic identification of females that have wing patterns similar to females in other genera. Forewing vein  $M_2$  is always present in *Timaeta*, but in male *T. gabriela* it may arise from the discal cell, from the origin of vein  $M_1$ , or from the "middle" of vein  $M_1$  (stalked). The forewing venation of *Timaeta* (Figs. 31-34) resembles that of *Micandra* Schatz (Schatz & Röber 1885-1892, Clench 1971) and may provide good characters for the *Micandra* Section of the Eumaeini. Vein  $R_1$  is located much closer to vein Sc than to vein  $R_2$ , and the lower disco-cellular vein is concave. The

forewing venation of *T. molinopampa* was illustrated with a recurrent vein (Bálint & Wojtusiak 2000), but this structure was not mentioned in the text and our wing vein slide of *T. molinopampa* (and some other *Timaeta*) revealed a vestigial fold, not a recurrent vein. Recurrent veins have been reported previously among eumaeines only in *Micandra* (Robbins 1986).

Sexual dimorphism in wing shape and pattern is pronounced in *Timaeta*. Dimorphism in the occurrence of hindwing tails in the Eumaeini (the male is the tailless gender in each case) occurs in *Timaeta*, *Micandra platyptera* (all other *Micandra* species have "tailed" males), and in some species of *Erora* (*Erora* Section). In each of these cases, the ventral wing pattern is also sexually dimorphic and associating the sexes has often been problematic. Whether the lack of tails in female *T. molinopampa* and *T. werneri* is a convergent reversal or a symplesiomorphy is unresolved on our cladogram.

A second unusual sexual dimorphism in *Timaeta* is

**Table 2.** Character matrix for *Timaeta*. The outgroups are *Temecla tema* and *Phothecla photismos*. Characters and their states are listed in Table 1.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Temecla tema</i>	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phothecla photismos</i>	1	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Timaeta timaeus</i>	0	0	0	0	2	1	0	1	1	?	1	1	1	0	0	0	0
<i>Timaeta christina</i>	0	0	0	0	2	1	0	1	0	0	1	1	1	0	0	0	0
<i>Timaeta molinopampa</i>	0	0	1	0	?	1	0	0	0	0	1	1	1	0	0	0	1
<i>Timaeta matthewi</i>	0	0	2	1	1	0	1	0	1	0	1	1	0	0	0	1	1
<i>Timaeta weneri</i>	0	0	2	1	2	0	0	0	1	0	1	1	0	0	0	1	1
<i>Timaeta walteri</i>	1	2	2	1	1	0	1	0	1	1	0	1	0	0	0	1	1
<i>Timaeta trochus</i>	1	2	2	1	1	0	1	0	1	1	0	1	0	0	0	1	1
<i>Timaeta roberti</i>	1	2	2	1	1	0	1	0	1	1	1	1	0	0	0	1	1
<i>Timaeta aepea</i>	1	1	2	1	0	0	1	0	1	0	1	1	0	0	0	1	1
<i>Timaeta cospata</i>	1	1	3	1	0	0	?	0	1	0	1	1	0	0	0	1	1
<i>Timaeta eronos</i>	1	1	3	2	0	0	1	0	1	0	1	1	0	1	1	1	1
<i>Timaeta pilosa</i>	1	1	3	2	0	0	1	0	1	0	1	1	0	1	1	1	1
<i>Timaeta romero</i>	1	1	2	1	0	0	1	0	1	0	1	1	0	1	1	1	1
<i>Timaeta balzabamba</i>	1	1	2	1	0	0	1	0	1	0	1	1	0	1	1	1	1
<i>Timaeta gabriela</i>	1	1	2	1	0	0	1	0	1	0	1	1	0	1	1	1	1

that the ventral hindwings of females have an orange cubital spot that is lacking in males except for *T. walteri* and *T. trochus* (an apparent “reversal”, Fig. 74). This dimorphism is otherwise unique within the *Micandra* Section of the Eumaeini. Finally, all male *Timaeta* have blue scaling on the ventral forewing (a few scattered blue scales in *T. romero*) while all females lack it. This dimorphism is widespread in the *Eumaeus*, *Brangas*, *Atlides*, and *Micandra* Sections of the Eumaeini (Robbins 2004a).

### Monophyly, stability, and generic nomenclature

Johnson et al.’s (1997a) concept of *Timaeta* was polyphyletic. It included *Thecla barba*, a species that belongs to *Porthocla* in the *Panthiades* Section (character evidence in Robbins & Duarte 2004), but did not include *T. lecroemi* (a synonym of *T. timaeus*), which was described in the unrelated genus *Androconia* K. Johnson, Eisele & MacPherson (*Erora* Section) (Robbins 2004b).

Johnson et al.’s (1997b) concept of *Trochusinus* was also polyphyletic. It included *Trochusinus elizabetha* Salazar, Vélez & K. Johnson, a species that belongs to *Salazarina* D’Abrera & Bálint, but did not include *T. neblina* (a synonym of *T. eronos*), which Salazar and K. Johnson (1997) described in *Micandra* (Robbins 2004b).

The description of the monotypic *Jagiello* (Bálint & Wojtusiak 2000) omitted mention of *Timaeta*. Recognition of *Jagiello* now would require new concepts for the genera *Timaeta* and *Trochusinus*. Further, the information content of monotypic genera, such as

*Jagiello*, is redundant (Farris 1976).

We adopt the classification in Robbins (2004b) because it is the only previous monophyletic classification of the butterfly species treated in this paper according to the phylogenetic results. The synapomorphies that characterize *Timaeta* in the phylogenetic results are posterior edge of labides in lateral aspect dorso-ventrally flat (character 5), male ventral hindwing cubital spot brown (character 11, “reversed” in *T. trochus* and *T. walteri*), and male hindwing tails absent (character 12). The node for this concept of *Timaeta* is the best supported node among these species as measured by jackknife values (Fig. 75).

### Biogeography

Diversity of Andean butterflies is still in the documentation phase. Eight of the 15 *Timaeta* species that we recognize in this paper were previously unnamed. This result is consistent with recent revisions of primarily Andean butterfly genera belonging to the Nymphalidae and Riodinidae, in which a third or more of the species had been undescribed (Willmott et al. 2001, Peña & Lamas 2005, Hall 2005).

Adams (1985) proposed a speciation model for Andean butterflies in which allopatric speciation in isolated mountain ranges was followed by parapatric speciation at different elevations. In a few cases in which many species are elevationally allopatric/parapatric, rapid speciation in the Andes has been contrasted with slower diversification in the lowlands (Hall 2005 for butterflies, Fjeldså & Rahbek 2006

for birds). Extensive current sympatry makes it difficult to determine the extent to which this model is applicable to *Timaeta*, but molecular sequence data (currently unavailable) could be used to determine the prevalence of allopatric/parapatric speciation (Barraclough & Vogler 2000, but see Losos & Glor 2003).

*Timaeta* is the first of the primarily montane Eumaeini to be revised, and most of its species are sympatric with their closest relatives. Among 15 *Timaeta* species, there are two species (*T. molinopampa*, *T. aepea*) that are elevationally parapatric with their sister lineage, and up to three species (*T. romero*, *T. balzabamba*, *T. gabriela*) that are geographically allopatric. This pattern is similar to that found among primarily lowland eumaeine genera (Robbins 1991, 2005, Robbins & Duarte 2005, Robbins & Busby In Press). As with *Hypanartia* Hübner in the Nymphalidae (Willmott et al. 2001), it is a distinct contrast to the repeated reports of elevationally parapatric species among Andean butterflies (Adams 1985, Pycrz & Wojtusiak 2002, Hall 2005, Bollino & Costa 2007).

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## References

Adams, M.J., 1985. Speciation in the pronophiline butterflies (Satyridae) of the northern Andes. – *Journal of Research on the Lepidoptera*. Supplement 1: 33-49.

Bálint, Z., & J. Wojtusiak 2000. *Jagiello molinopampa* gen. et sp. n. from Peru (Lepidoptera: Lycaenidae). – *Annales historico-naturales Musei nationalis hungarici* 92: 183-191.

Barraclough, T.G., & A.P. Vogler 2000. Detecting the geographical pattern of speciation from species-level phylogenies. – *American Naturalist* 155: 419-434.

Bates, J.M., & R.M. Zink 1994. Evolution into the Andes: molecular evidence for species relationships in the

genus *Leptopogon*. – *The Auk* 111: 507-515.

Beebe, W., 1949. Insect migration at Rancho Grande, north-central Venezuela. – *Zoologica*, New York 34: 107-110.

Bollino, M., & M. Costa 2007. An illustrated annotated check-list of the species of *Catantia* (s.l.) Butler (Lepidoptera: Pieridae) of Venezuela. – *Zootaxa* 1469: 1-42

Brehm, G., L.M. Pitkin, N. Hilt, & K. Fiedler 2005. Montane Andean rain forests are a global diversity hotspot of geometrid moths. – *Journal of Biogeography* 32: 1621-1627.

Clench, H.K., 1971. Two new hairstreaks from Mexico (Lepidoptera: Lycaenidae). – *Bulletin of the Allyn Museum*. 3: 6 pp.

Comstock, J.H., 1918. *The wings of insects*. – The Comstock Publishing Company, Ithaca, New York. 430 pp.

D'Abrera, B.L., 1995. *Butterflies of the Neotropical region*. Part VII. Lycaenidae. – Black Rock, Hill House, p. i-xi + 1098-1270.

Draudt, M., 1919-1920. Theclinae F. – In: A. Seitz (Ed). *Die Gross-Schmetterlinge der Erde*, vol. 5. Die amerikanischen Tagfalter, p. 744-812. – Stuttgart, Alfred Kernen.

Druce, H.H., 1907. On neotropical Lycaenidae, with descriptions of new species. – *Proceedings of the Zoological Society of London* 566-632, 6 plates

Eliot, J.N., 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. – *Bulletin of the British Museum (Natural History) Entomology* 28(6): 371-505.

Farris, J.S., 1969. A successive approximations approach to character weighting. – *Systematic Zoology* 18: 374-385.

Farris, J.S., 1976. Phylogenetic classification of fossils with recent species. – *Systematic Zoology*, 25: 271-282.

Fassl, A.H., 1918. Verbreitung der Lepidopteren in der Columbischen Ost Cordillere. – *Entomologische Rundschau* 35: 1-4.

Felder, C., & R. Felder 1865. *Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodore B. von Wüllerstorff-Urbair*. Zoologischer Theil. Zweiter Band. Zweite Abtheilung: Lepidoptera. – Wien, Carl Gerold's Sohn. 2: [2] + 137378 pp, pls. 2247.

Fjeldså, J., & C. Rahbek 2006. Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. – *Integrative and Comparative Biology* 46: 72-81.

Goodson, F.W., 1945. Notes and descriptions of new species of American Theclinae contained in the British Museum (Natural History) (Lep. Lycaenidae). – *Entomologist* 78(990): 169-171, (991): 184-187.

Hall, J.P.W., 2005. Montane speciation patterns in *Ithomiola* butterflies (Lepidoptera: Riodinidae): are they consistently moving up in the world? – *Proceedings of the Royal Society B* 272: 2457-2466.

Johnson, K., R.C. Eisele, & B.N. MacPherson 1993. *Genera for the small green hairstreak butterflies of the*

- Neotropical realm (Lepidoptera, Lycaenidae, Theclinae). – Reports of the Museum of Natural History, University of Wisconsin (Stevens Point) 39: 1-16.
- Johnson, K., J.J. Kruse & K.R. Kroenlein 1997a. The Macusiina, a new infratribe of the Eumaeini with description of ten new genera (Lycaenidae). – Review of Colombian Theclinae 2 (13): 37 pp.
- Johnson, K., J.A. Salazar, and J.H. Vélez 1997b. New species of *Micandra* Staudinger from Colombia with distinction of *Trochusinus*, a new genus of the Eumaeini. – Review of Colombian Theclinae 2 (15): 15 pp.
- Klots, A.B., 1970. Lepidoptera. In S.L. Tuxen (ed.), Taxonomist's glossary of genitalia in insects. pp. 115-130, – Munksgaard, Copenhagen.
- Losos, J.B., & R.E. Glor 2003. Phylogenetic comparative methods and the geography of speciation. – Trends in Ecology and Evolution 18: 220-227.
- Nixon, K.C., 2002. WinClada ver. 1.00.08. – Published by the author, Ithaca, NY.
- Peña, C., & G. Lamas 2005. Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). – Revista peruana de biología 12 (1): 5-48.
- Pyrz, T.W., & J. Wojtusiak 2002. The vertical distribution of pronophiline butterflies (Nymphalidae, Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. – Global Ecology & Biogeography 11: 211-221.
- Raguso, R.A., & O. Gloster 1996. Preliminary checklist and field observations of the butterflies of the Maquipucuna Field Station (Pichincha Province, Ecuador). – Journal of Research on the Lepidoptera 32: 135-161.
- Remsen, J.V. Jr., & S.W. Cardiff, 1990. Patterns of elevational and latitudinal distribution, including a “niche switch,” in some guans (Cracidae) of the Andes. – The Condor 92(4): 970-981.
- Robbins, R.K., 1986. Evolution and identification of the New World hairstreak butterflies (Lycaenidae: Eumaeini). I. Eliot's *Trichonis* Section and *Trichonis* Hewitson. – Journal of the Lepidopterists' Society 40: 138-157.
- Robbins, R.K., 1991. Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). – Smithsonian Contributions to Zoology. #498, 64 pp.
- Robbins, R.K., 2004a. Introduction to the checklist of Eumaeini (Lycaenidae). In: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea – Papilionoidea. In: Heppner, J.B. (Ed.), Atlas of Neotropical Lepidoptera. Volume 5A, pp. xxiv-xxx. – Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- Robbins, R.K., 2004b. Lycaenidae. Theclinae. Tribe Eumaeini. In: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea – Papilionoidea. In: Heppner, J.B. (Ed.), Atlas of Neotropical Lepidoptera. Volume 5A, pp. 118-137. – Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- Robbins, R.K., 2005. Phylogenetic relationships among the species of *Panthiades* Hübner (Lycaenidae: Theclinae: Eumaeini). – Proceedings Entomological Society of Washington 107: 501-509.
- Robbins, R.K., & R.C. Busby In Press. Updated Phylogeny, Taxonomy, and Diversification of *Janthecla* Robbins & Venables (Lycaenidae: Theclinae: Eumaeini). – Journal of Research on the Lepidoptera.
- Robbins, R.K., & M. Duarte 2004. Descriptions of new butterfly genera. Lycaenidae, Eumaeini. In: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea – Papilionoidea. In: Heppner, J. B. (Ed.), Atlas of Neotropical Lepidoptera. Volume 5A, pp. 275-282. – Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- Robbins, R.K., & M. Duarte 2005. Phylogenetic analysis of *Cyanophrys* Clench, a synopsis of its species, and the potentially threatened *C. berthae* (Jones) (Lycaenidae: Theclinae: Eumaeini). – Proceedings Entomological Society of Washington 107:398-416.
- Salazar, J.A., & K. Johnson 1997. A new genus of Neotropical hairstreaks utilizing bird excrement as their protective color substrate (Eumaeini; Macusiina). – Review of Colombian Theclinae 2 (13): [ii] + 1-10, 2 figs.
- Schatz, E., & J. Röber 1885-1892. Die Familien und Gattungen der Tagfalter. In Exotische Schmetterlinge. Ed. O. Staudinger & E. Schatz. – Lowensohn, Furth, Bavaria, 284 pp., 50 pl.
- Snodgrass, R.E., 1935. Principles of insect morphology. – McGraw-Hill Book Co., New York, 667 pp.
- Willmott, K.R., J.P.W. Hall, & G. Lamas 2001. Systematics of *Hypanartia* (Lepidoptera: Nymphalidae: Nymphalinae), with a test for geographical speciation mechanisms in the Andes. – Systematic Entomology 26: 369-399.

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