

Phylogeny and Taxonomy of the Neotropical *Thepytus* (Lepidoptera: Lycaenidae: Theclinae)

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> Abstract

The Neotropical lycaenid hairstreak genus *Thepytus* Robbins and its eight species are revised. Species treatments summarize nomenclature, distribution, habitat, behavior, and diagnostic traits, as well as noting why each species is considered distinct under a biological species concept. An identification key for males and a checklist are included. *Beatheclus* Bálint & Dahners **new synonym** is synonymized with *Thepytus*, and *Thepytus beatrizae* (Bálint & Dahners) is a **new combination**. Other nomenclatural actions include the description of *Thepytus jennifer* Busby & Robbins **new species**, *Thepytus nancyana* Busby & Robbins **new species**, and *Thepytus carmen* Robbins & Duarte **new species**. A lectotype is designated for *Thecla thyrea* Hewitson, 1867, to ensure stability of this name. A phylogenetic analysis based on 22 coded morphological characters yields one equal weight most parsimonious 39-step tree. Implied weighting does not change the tree topology. Unambiguous changes in elevation optimized on the cladogram show that a montane lineage of *Thepytus* colonized the lowlands in at least one instance. The use of *T. echelta* (Hewitson) as a biological control agent for *Psittacanthus* (Loranthaceae) is discussed.

> Key words

Andes, *Beatheclus*, biological control, colonization of lowlands, implied weighting.

1. Introduction

The primarily Neotropical Eumaeini (Lycaenidae: Theclinae) is one of the most species rich tribes of true butterflies with 1,150 species (ROBBINS 2004a). Although some genera contain only montane species (e.g., ROBBINS & BUSBY 2008) or only lowland species (e.g., ROBBINS 1991), most have a mix of montane endemics and lowland taxa. When lowland butterfly lineages colonize the mountains, they may diversify quickly (HALL 2005), although this amplified diversification has not been found in those eumaeine genera for which there are inferred phylogenies (ROBBINS & DUARTE 2005; ROBBINS 2005; ROBBINS & BUSBY 2009).

Alternately, primarily montane butterfly lineages can colonize the lowlands, as was recently shown for two genera of ithomiine butterflies (ELIAS et al. 2009). To date, there are no documented cases of a montane eumaeine lineage colonizing the lowlands. Possible reasons are that such colonizations are infrequent, as noted by ELIAS et al. (2009), and that primarily montane eumaeine genera have been understudied (ROBBINS & BUSBY 2008).

A revision of the Neotropical *Thepytus* Robbins is potentially significant for a variety of reasons, even though most of the species are poorly represented in

museum collections. Preliminary data suggests that the widespread lowland *Thepytus echelta* (Hewitson) and an undescribed lower montane species were derived from a lineage of montane species and might provide a first documented example in the Eumaeini of a lowland colonization. Second, *Thepytus* was described in the *Panhiades* Section of the Eumaeini for seven Neotropical species, including three unnamed montane species (ROBBINS 2004b; ROBBINS & DUARTE 2004). BÁLINT & DAHNERS (2006) proposed a new genus and species (*Beatheclus beatrizae*) for one of these montane species, but did not specifically differentiate *Beatheclus* from *Thepytus*. As a result, the generic classification of these butterflies needs to be resolved. Finally, *T. echelta* is being investigated as a biological control agent for *Psittacanthus* (Loranthaceae) (UCHÔA & CAIRES 2000).

The purpose of this paper is to infer phylogenetic relationships among the seven species of *Thepytus* listed in ROBBINS (2004b) plus a subsequently discovered eighth species. *Thepytus* species-level taxonomy is reviewed, including the description of three new species from the mountains of South America. We use the phylogenetic results to show that at least one lineage in *Thepytus* has colonized the lowlands; possible biological consequences of this colonization are discussed very preliminarily. The results provide a phylogenetic basis for the classification of *Thepytus*. Finally, we note reasons why *Thepytus* is unlikely to be an effective biological agent for controlling *Psittacanthus*, but if incorrect, the results provide a phylogenetic framework that may be useful as research on this topic progresses.

2. Materials and methods

The genus and species level taxonomy is based on an analysis of morphological variation among 53 male and 37 female pinned specimens of *Thepytus* from various museum and private collections, as noted below, plus images of an additional four specimens. Species accounts include notes on nomenclature, morphological variation, elevation, habitat, larval food-plants, behavior, and other biological characteristics for which there is information. The evidence supporting the hypothesis that each available name represents a distinct species under a biological species concept is discussed. The known distribution of each species is mapped. Forewing lengths were measured with a vernier caliper from the base to the apex of the forewing. Months are abbreviated by their first three letters.

A wing pattern key is presented to facilitate identification of males. A summary of the new classification is presented in the format of the previous checklist for the Eumaeini (ROBBINS 2004b). Brackets are used for information not explicitly noted on type labels and for descriptions of the labels. Paratype labels are light blue. Citations for all original descriptions from before 1995 can be found in LAMAS et al. (1995).

Genitalic terms follow those in KLOTS (1970), as modified for the Eumaeini in ROBBINS (1991). Wing vein names follow COMSTOCK (1918), androconial terminology follows ROBBINS (1991), and abdominal 'brush organ' terminology follows ELIOT (1973).

Characters for the phylogenetic analyses are limited to adult morphology because published information on immature stages of hairstreak butterflies species is minimal (cf. DUARTE et al. 2005), and DNA sequences are currently unavailable for any *Thepytus* (Quental and coworkers, in prep.). Dissections of 19 male and 11 female genitalia were examined. The terminal taxa are the five described and two undescribed species that were placed in *Thepytus* by ROBBINS (2004b) plus a subsequently discovered species. The outgroup taxa for the analyses are representatives of three other *Panhiades* Section genera: *Olynthus narbal* (Stoll), *Parrhasius polibetes* (Stoll), and *Michaelus ira* (Hewitson). The characters used in the phylogenetic analysis are listed in section 5.1., and the state for each *Thepytus* and outgroup species was recorded in Nexus Data Editor (web available software from R.D.M. Page, <http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html>) (Tab. 1). All characters were analyzed non-additively (unordered).

We searched exhaustively for shortest trees using the implicit enumeration option of TNT software (GOLOBOFF et al. 2008) to derive most parsimonious equal weight cladograms. To test the assumption of equally weighted characters, we used the implied weighting option with implicit enumeration in TNT (values of $K = 1, 25, 50, 100, 500, 1000$) to find most parsimonious implied weight trees. Mapping of characters on trees was done with WinClada software (NIXON 2002) with the "unambiguous changes only" options. Bootstrap support was determined in WinClada (1000 replications with mult*10, memory 1000 trees).

Following ELIAS et al. (2009), we classified the habitat of each *Thepytus* species as lowland (0–1,200 m), lower montane (500–1,700 m), or montane (>1,300 m), but *T. echelta* was classified as both lowland and lower montane because of its wide elevational range. We optimized these elevation ranges on the resulting cladogram using unambiguous changes only.

3. Abbreviations for collections

AMNH	American Museum of Natural History, New York, USA
BMNH	Natural History Museum, London, UK
DZUP	Universidade Federal do Paraná, Curitiba, Paraná, Brazil
FIOC	Fundação Instituto Oswaldo Cruz, Rio de Janeiro, Rio de Janeiro, Brazil
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia
JHKW	Jason Hall and Keith Willmott Collection, Smithsonian Institution, Washington, DC, USA
JYG	Jean-Yves Gallard Collection, Cayenne, French Guiana
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil
RCB	Robert C. Busby Collection, Andover, MA, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany

4. Taxonomy

4.1. Wing pattern key to *Thepytus* males (All characters illustrated, Figs. 1, 3, 5, 7, 9–11, 13)

1. Dorsal surface of forewings with conspicuous postmedian black patches *T. echelta*
– Dorsal surface of forewings without conspicuous postmedian black patches 2
2. Ventral forewing postmedian line composed of a series of black dots and dashes 3
– Ventral surface of forewing with a white postmedian line 4
3. Ventral surface of hindwing with an orange-red cubital spot *T. epytus*
– Ventral surface of hindwing without an orange-red cubital spot *T. thyrea*
4. Ventral surface of forewing with white postmedian and submarginal lines (somewhat indistinct in *T. carmen*) 5
– Ventral surface of forewing without white submarginal line 7
5. Dorsal surface of forewing violet with black outer margin narrow at the tornus *T. carmen*
– Dorsal surface of forewing blue or green with black outer margin broad at the tornus 6

6. Ventral surface of hindwing anal lobe without orange-red scales, dorsal surface of forewing with a distinct greenish hue *T. beatrizae*
– Ventral surface of hindwing anal lobe with orange-red scales, dorsal surface of forewing blue *T. nancyana*
7. Ventral hindwing basal mark short with the postmedian line anterior segment (cell Sc+R₁-Rs) displaced toward the outer margin *T. arindela*
– Ventral hindwing basal mark long with the postmedian line anterior segment (cell Sc+R₁-Rs) colinear with the other segments *T. jennifer*

4.2. Checklist

THEPYTUS Robbins, 2004

Beatheclus Bálint & Dahners, 2006, **new synonym**

epytus (Godman & Salvin, 1887) (*Thecla*) – Panama

thyrea (Hewitson, 1867) (*Thecla*) – French Guiana; Brazil (Pará)

arindela (Hewitson, 1874) (*Thecla*) – Nicaragua

jennifer Busby & Robbins, **new species** – Ecuador

beatrizae (Bálint & Dahners, 2006) (*Beatheclus*), **new combination** – Colombia

nancyana Busby & Robbins, **new species** – Ecuador

carmen Robbins & Duarte, **new species** – Brazil (Rio de Janeiro)

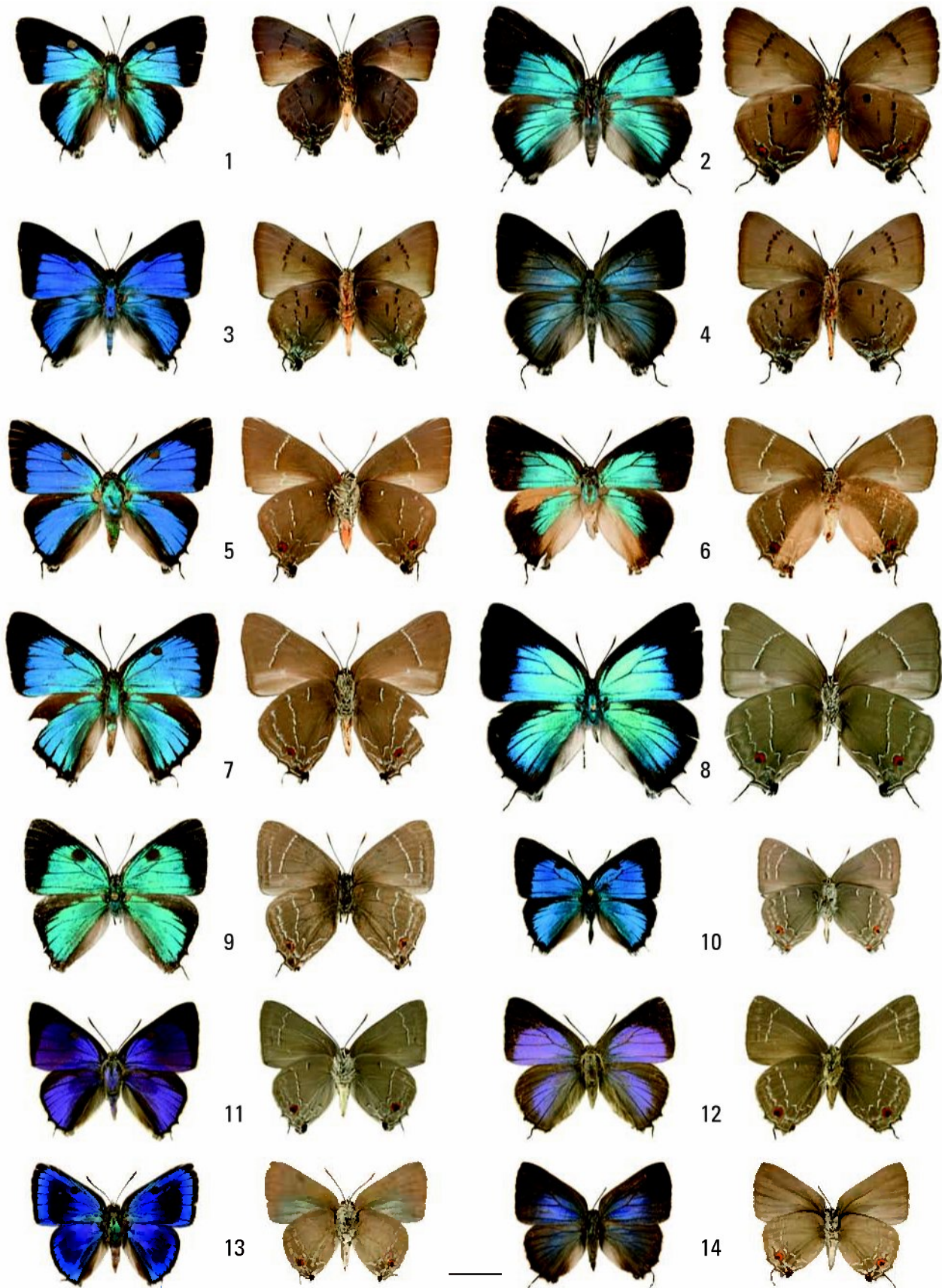
echelta (Hewitson, 1867) (*Thecla*) – Brazil (Pará)

4.3. *Thepytus* Robbins, 2004

Thepytus Robbins, 2004: 280 (in ROBBINS & DUARTE 2004), **type species**: *Thecla epytus* Godman & Salvin, 1887 (by original designation).

Beatheclus Bálint & Dahners, 2006: 146, **type species**: *Beatheclus beatrizae* Bálint & Dahners, 2006 (by original designation); new synonym.

Diagnosis, recognition as a distinct genus, and synonymy. The synapomorphies that characterize *Thepytus* in the phylogenetic results (unambiguous changes only, Fig. 33, see below) are lack of a curved structure at the dorsal base of the male genitalia valvae (Character 12, state 1; the presence of this structure in a related taxon is illustrated in NICOLAY 1982) and the upturned anterior end of the female ductus bursae (Character 20, state 1; arrow in Fig. 24). Both characters were noted in the original description of the genus. The first synapomorphy is widespread in the Eumaeini, which means that it is diagnostic for *Thepytus* only in relation to the outgroup taxa that we selected. The second synapo-



Figs. 1–14. Adults of *Thepytus*, dorsal (left), ventral (right). 1: ♂ *T. epytus* (Panama). 2: ♀ *T. epytus* (western Ecuador). 3: ♂ *T. thyrea* (southern Brazil). 4: ♀ *T. thyrea* (eastern Ecuador). 5: ♂ *T. arindela* (Panama). 6: ♀ *T. arindela* (Panama). 7: ♂ *T. jennifer* (southeastern Perú, paratype). 8: ♀ *T. jennifer* (eastern Ecuador, holotype). 9: ♂ *T. beatrizae* (eastern Ecuador). 10: ♂ *T. nancyana* (eastern Ecuador, holotype). 11: ♂ *T. carmen* (southern Brazil, paratype). 12: ♀ *T. carmen* (southern Brazil, paratype). 13: ♂ *T. echelta* (southern Brazil). 14: ♀ *T. echelta* (southern Brazil). Scale bar 1 cm.

morphy, however, is unique in the *Panthiades* Section. Recognition of the monotypic *Beatheclus*, as proposed by BÁLINT & DAHNERS (2006), would leave *Thepytus* paraphyletic in all equal weight and implied weight most parsimonious trees (Fig. 33). If the concept of *Beatheclus* were modified to include *T. echelta* and the newly described *T. carmen* and *T. nancyana*, the bootstrap support of 49 for the remaining four species is lower than the support of 57 for *Thepytus* as originally proposed (Fig. 33). For these reasons, *Beatheclus* is treated as a junior synonym of *Thepytus*.

Wing pattern identification and sexual dimorphism. *Thepytus* cannot be distinguished by wing pattern characters alone; genitalic characters are needed to confirm generic identification. Although each species within *Thepytus* can be distinguished from the other *Thepytus* species by wing pattern (cf. identification key), wing pattern resemblances with species of *Parrhasius*, *Michaelus*, and *Olynthus* can make identification difficult. For this reason, we note when appropriate those wing pattern characters that distinguish a *Thepytus* species from those in other genera with similar wing patterns. Finally, associating the sexes in *Thepytus* does not pose a problem, unlike many other genera (DUARTE et al. 2005; ROBBINS & BUSBY 2008), because the ventral wing patterns of *Thepytus* species are not sexually dimorphic.

Androconia and brush organs. All *Thepytus* species have a scent pad composed of androconia at the origin of forewing veins R_3 and M_1 (Figs. 1, 3, 5, 7, 9–11, 13), as is also the case in *Parrhasius* Hübner, *Olynthus* Hübner, *Ignata* Johnson, and *Michaelus* Nicolay. A distinctive patch of dark scales in the distal half of the dorsal surface of the forewing of *T. echelta* (Fig. 13), which is similar in appearance to that in some species of *Parrhasius* and *Panthiades* Hübner, may also be composed of androconia. *Thepytus epytus* and *T. thyrea* have brush organs that lie on the dorsal surface of the vinculum (Fig. 16). BÁLINT & DAHNERS (2006) reported and illustrated a brush organ in *T. beatrizae*, but we found no brush organs in the specimen that we dissected nor could we see one in their photograph of a putative brush organ. No other species of the *Panthiades* Section is reported to have brush organs.

Genitalia. The strongly curved and twisted penis of *Thepytus* (Figs. 15–22) is shared within the *Panthiades* Section with *Olynthus*, which has differently shaped valvae, as illustrated by NICOLAY (1982). The anterior edge of the vinculum is strongly convex in the lateral view (Figs. 15–22), in contrast to some related genera, such as *Oenomaus* (FAYNEL 2006). The upturned anterior end of the female ductus bursae of *Thepytus* is unique within the *Panthiades* Section (Figs. 23–28).

Habitat. *Thepytus echelta* and *T. thyrea* are the two most widespread species in the genus and occur in

wet and dry forest, but the other *Thepytus* species are recorded only from wet forest. *Thepytus jennifer*, *T. beatrizae*, and *T. nancyana* are restricted to montane forest above 1,500 m elevation while the other species are lowland and/or lower montane inhabitants.

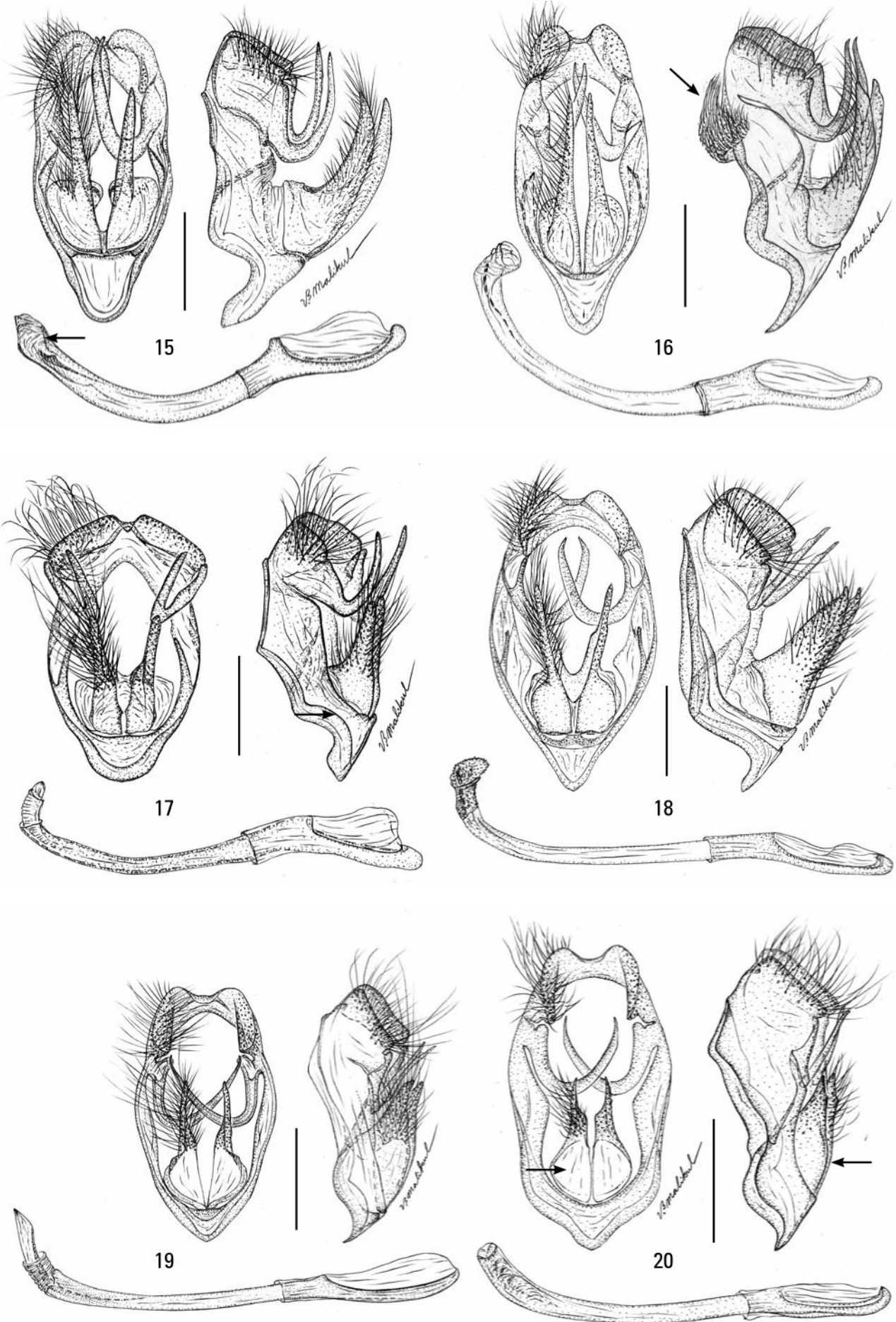
Larval foodplants and immature stages. *Thepytus echelta* has been reared from the fruits of *Psittacanthus* (Loranthaceae) in Costa Rica (JANZEN & HALLWACHS 2009) and Brazil (UCHÔA & CAIRES 2000). At the latter locality, this species is being tested as a possible biological control agent (UCHÔA & CAIRES 2000). A pre-pupal larva and pupa of *T. thyrea* were illustrated, but the foodplant was unknown (ZIKÁN 1956).

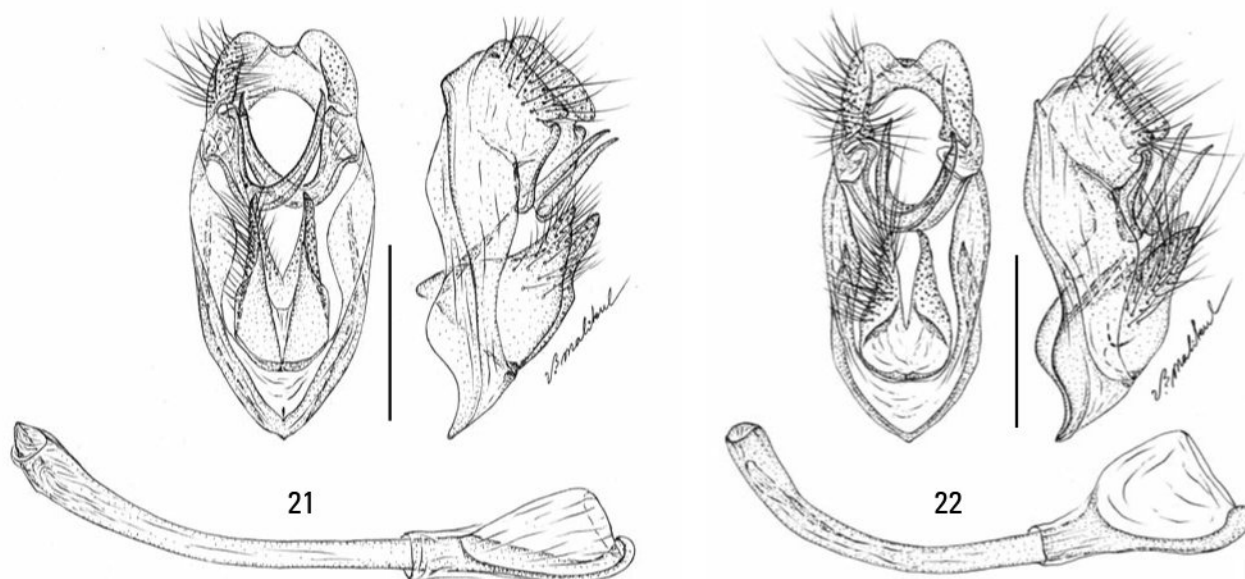
Behavior. Males of four *Thepytus* species have been recorded setting up mating territories on hilltops and ridge tops during the early afternoon from about 12:00 to 15:00 hours. Females of two species have been found on traps baited with rotting fish.

4.4. *Thepytus thyrea* species complex: *T. thyrea* and *T. epytus*

Thepytus epytus and *T. thyrea* are sisters in the phylogenetic results and are the only *Thepytus* with black postdiscal bars on the ventral surface of forewing and hindwing and with a series of black spots forming the postmedian line of the ventral surface of the forewing (Figs. 1–4). They do not differ genitally (assessed in the species account for *T. epytus*), but have always been treated as distinct species because *T. epytus*, which occurs from Panama to western Ecuador, and *T. thyrea*, which occurs widely in South America east of the Andes, have distinctly different wing patterns. One difference is that a conspicuous orange cubital spot occurs on the ventral surface of the hindwing in *T. epytus* but is entirely absent in *T. thyrea* (Figs. 1–4). A second is that the male dorsal forewing dark border is considerably wider in *T. epytus* than in *T. thyrea*. A third is that the dorsal iridescent color in females is shining blue-green in *T. epytus* and dull chalk-blue in *T. thyrea*.

All specimens in the *T. thyrea* complex east of the Andes have wing patterns typical of *T. thyrea*, except for two from eastern Ecuador that have the dorsal wing pattern of *T. epytus* and the ventral hindwing orange cubital spot reduced to a few orange scales. These individuals are sympatric with others that have the typical *T. thyrea* wing pattern. One likely hypothesis is that *T. epytus* and *T. thyrea* are distinct, sympatric species in eastern Ecuador with occasional hybridization, represented by these two ‘questionable’ specimens. Another likely hypothesis is that *T. epytus*





Figs. 15–22. Male genitalia of *Thepytus*, ventral (left), lateral (right), and penis lateral (bottom). **15:** *T. epytus* (Panama), dorsal brush organ removed, arrow points to slender second cornutus. **16:** *T. thyrea* (southern Brazil), arrow points to dorsal brush organs. **17:** *T. arindela* (Panama), arrow points to groove on outer surface of vinculum. **18:** *T. jennifer* (Perú). **19:** *T. beatrizae* (eastern Ecuador). **20:** *T. nancyana* (eastern Ecuador), arrows point to basal process of valvae that is smooth and lacking setae. **21:** *T. carmen* (southern Brazil). **22:** *T. echelta* (Mexico). Scale bars 1 mm.

and *T. thyrea* hybridize widely in eastern Colombia and Ecuador and should be considered one species. A less likely third hypothesis is that the eastern Ecuadorian specimens with the ‘questionable’ wing pattern represent a third species that is sympatric with *T. thyrea*. We have insufficient evidence to falsify any of these hypotheses. For this reason, we do not alter the long established classification that recognizes *T. epytus* and *T. thyrea* as distinct species, but note the variation represented by these two ‘questionable’ individuals.

4.5. *Thepytus epytus* (Godman & Salvin)

Figs. 1, 2, 15, 23, 29

Thecla epytus Godman & Salvin, 1887: 41 from Bugaba and Chiriquí, Panama.

Thepytus epytus; ROBBINS 2004b: 134, ♂ syntype from Bugaba in BMNH (B.M. type No. Rh. 663) examined. Photograph of ♀ syntype from Chiriquí in ZMHB examined.

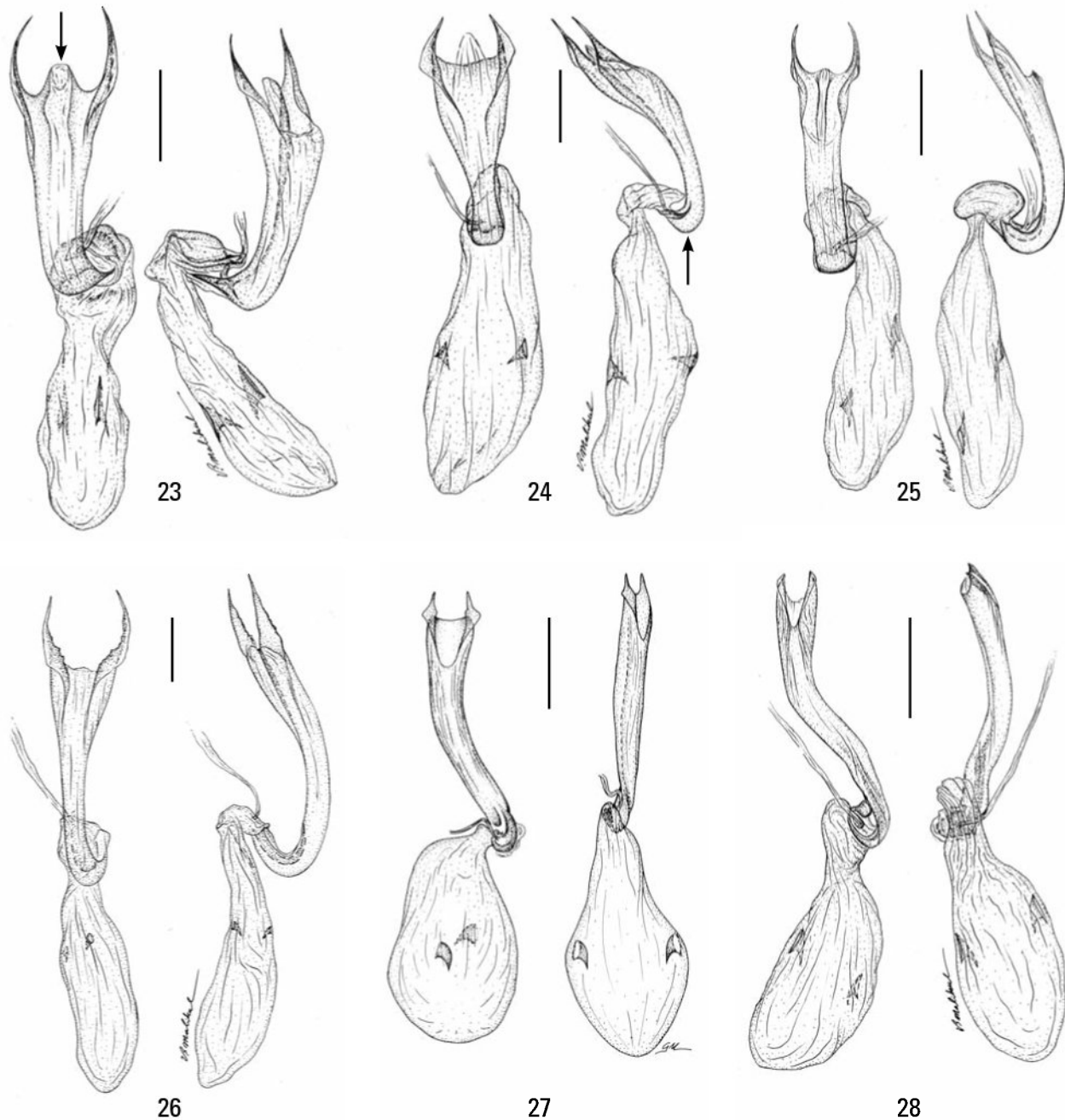
Diagnosis and recognition as a distinct species. The recognition of *T. epytus* from *T. thyrea* is addressed in section 4.4.

Genitalic variation of the *T. thyrea* complex. We assess the genitalic variation of *T. epytus* and *T. thyrea* together because we cannot distinguish them and because *T. epytus* is rare in collections. Genitalic preparations (Figs. 15–16) were chosen to illustrate variation in the complex rather than between the species. Based

on a comparison of nine male genitalia from Panama, western Ecuador, French Guiana, eastern Ecuador, Perú, central Brazil (Distrito Federal) and southern Brazil (Santa Catarina), all males have brush organs, which is otherwise unique in the *Pantheiades* Section (cf. generic account above). The shape of the vinculum in lateral aspect (especially the dorsal half) varies as illustrated (Figs. 15–16). A slender second terminal cornutus occurs in a male from Panama (Fig. 15) and a male from Perú but is vestigial or absent in the others (Fig. 16). The width of the anterior valves in ventral aspect varies as illustrated (Figs. 15–16). Shape of the saccus varies similarly to that documented for another eumaeine species (ROBBINS 1990). As noted, there is no indication in the male genitalia of more than one species.

As with the males, we compared 6 female genitalic preparations from Panama, eastern Ecuador, Perú, and southern Brazil (Santa Catarina). The length, width, and degree of curvature of the posterior-pointing spines of the lamella postvaginalis are highly variable, more so than the differences illustrated (Figs. 23–24). Width of the ductus bursae in ventral aspect is similarly variable. However, the medial process of the lamella postvaginalis is clearly developed in *T. epytus* (Fig. 23), but poorly developed to absent in the four females from east of the Andes (Fig. 24). Possibly this structure could be used to distinguish *T. epytus* and *T. thyrea*. The one female from eastern Ecuador with an ambiguous wing pattern had this structure poorly developed.

Wing pattern variation. Dorsal shining iridescence in females is green-blue in Panama and a somewhat



Figs. 23–28. Female genitalia of *Thepytus*, ductus copulatrix in ventral aspect (left) and lateral aspect (right). **23:** *T. epytus* (Panama), arrow points to process on medial lamella postvaginalis. **24:** *T. thyrea* (southern Brazil), arrow points to the upturned anterior ductus bursae. **25:** *T. arindela* (Panama). **26:** *T. jennifer* (eastern Ecuador). **27:** *T. carmen* (southern Brazil). **28:** *T. echelta* (southern Brazil). Scale bars 1 mm.

darker blue in Ecuador. The ventral surface of the hindwing anal lobe has a few orange scales in Panama, may or may not have them in western Ecuador, and lacks them in the ‘questionable specimens’ from eastern Ecuador. As already noted, the ventral hindwing orange cubital spot in specimens from eastern Ecuador is reduced to a few orange scales.

Wing pattern similarity with species in other genera. The ventral wing patterns of *T. epytus* and *T. thyrea* are sometimes confused in museum collections with that of *Parrhasius polibetes*, perhaps because

the ventral forewing postmedian line is broken into dark spots or dashes. However, *T. epytus* and *T. thyrea* have charcoal-colored postdiscal bars on the ventral surface of the wings (Figs. 1–4) that are lacking in *P. polibetes*.

Habitat and elevation. *Thepytus epytus* is a lowland species that inhabits wet forest from 250 to 1,100 m.

Distribution. *Thepytus epytus* occurs from Chiriquí, Panama to western Ecuador with two questionable specimens from eastern Ecuador (Fig. 29). D’ABRERA (1995) illustrated the dorsal wing surface of a female

from Guatemala, but positive identification requires characters of the ventral wing surface or genitalia, which we have not seen.

Study series. We examined three males (three dissected) and five females (three dissected) from Panama and Ecuador (including dissections of the questionable male and female), as well as the male syntype and a photograph of the female syntype.

4.6. *Thepytus thyrea* (Hewitson)

Figs. 3, 4, 16, 24, 29

Thecla thyrea Hewitson, 1867: 99 from Tapajós, Amazonas, Pará, Brazil and from Cayenne, French Guiana.

Thepytus thyrea; ROBBINS 2004b: 134, ♀ lectotype, designated herein, from Tapajós in BMNH (B.M. type No. Rh. 661).

Lectotype designation. Described from a female from the Amazon that was collected by Bates along the Rio Tapajós, Pará, which is segregated in the BMNH type collection, and a male from Cayenne in the collection of Boisdual (not found, maybe in MNHN). The male has not been noted in recent papers on eumaeine types in MNHN (JOHNSON 1991; FAYNEL & BÁLINT 2004). To insure the stability of this name, we designate the female from Tapajós as a lectotype.

Diagnosis and recognition as a distinct species. The recognition of *T. thyrea* from *T. epytus* is addressed in section 4.4.

Variation. Darkness of the ventral wing ground color shows some minor, non-geographical variation, as does the extent of the light blue iridescent submarginal scales from the inner margin to vein Cu₁. Genitalic variation is assessed under *T. epytus*, section 4.5.

Wing pattern similarity with species in other genera. See account for *T. epytus*, section 4.5.

Immature stages. ZIKÁN (1956) found a larva in a pile of rotting sugar cane peels, where it appeared to be preparing for pupation. It pupated 17 Apr 1929 and eclosed 21 May 1929. ZIKÁN (1956) described and illustrated the pre-pupal larva and pupa, which had a double-thread girdle. The pupa and adult are deposited in FIOC. We note that a pupa of *T. echelta* has only a single-thread girdle (deposited in USNM), so the unusual double-thread girdle would not seem to be a characteristic of *Thepytus*.

Behavior. Robbins recorded a territorial male on the summit of Morro do Chapéu, Bahia, Brazil (1,475 m) at 14:20 hours on 24 Apr 1991 (voucher in USNM). Busby caught a female on a trap baited with rotting fish on 4 Oct 2007 at 10 km Los Encuentros – El Panqui Rd, Zamora Chinchipe, Ecuador (1,050–1,200 m) (voucher in RCB). Adults of both sexes were recorded

nectaring on *Cordia schomburgkii* A. DC. (Boraginaceae) in French Guiana (FAYNEL 2003).

Habitat and elevation. *Thepytus thyrea* is a lowland species that inhabits wet forest, occasionally drier habitats, from sea level to about 1,500 m. One specimen from Mendoza, Perú in MUSM collected by Benigno Calderon is labeled 1,800 m, but we suspect that it was actually found at a lower elevation. Calderon collects at a wide range of elevations near his home in Mendoza, and a number of Calderon specimens subsequently labeled 1,800 m in Lima are otherwise unrecorded above 1,500 m. An 1,800 m elevation for *T. thyrea* is an outlying data point that needs confirmation.

Distribution. *Thepytus thyrea* occurs east of the Andes in South America from the Guianas to the Amazon Basin to southern Brazil (Fig. 29). It was recorded once from Panama (DRAUDT 1919–1920) without attribution, probably a misidentification of *T. epytus* or a ‘clerical’ mistake.

Study series. We examined 21 males (six dissections) and 18 females (three dissections) from five countries, including five Brazilian states, plus the Brazilian female lectotype.

Remarks. Although widespread in South America, *T. thyrea* is a very rare species except in the vicinity of Joinville, Santa Catarina, Brazil, where Herbert Miers found it commonly on flowering plants (specimens in USNM, MZSP, DZUP).

4.7. *Thepytus arindela* (Hewitson)

Figs. 5, 6, 17, 25, 30

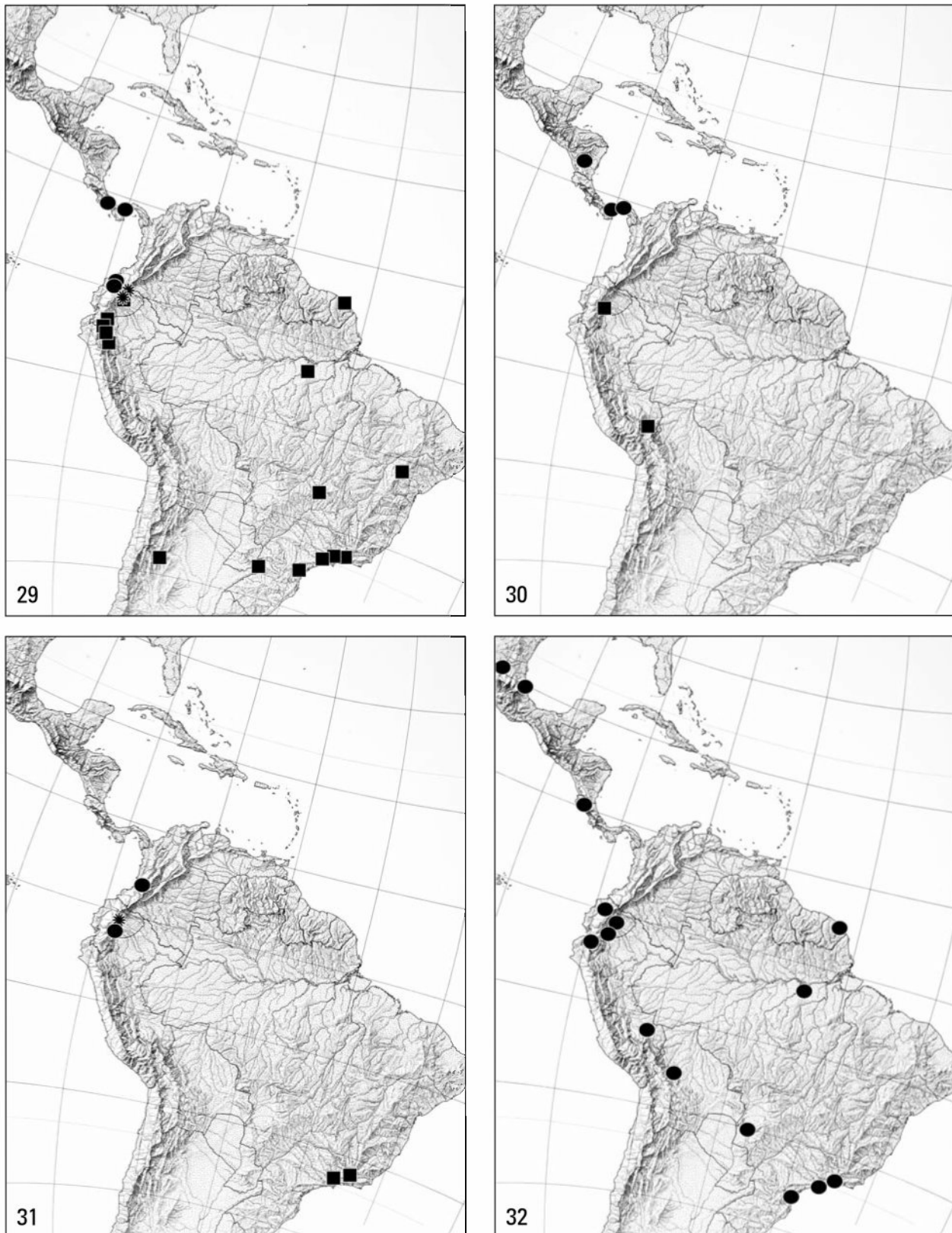
Thecla arindela Hewitson, 1874: 172 from Chontales, Nicaragua.

Thepytus arindela; ROBBINS 2004b: 134, ♂ holotype from Nicaragua in BMNH (B.M. type No. Rh. 662) examined.

Diagnosis and recognition as a distinct species.

Thepytus arindela forms a clade with *T. epytus* and *T. thyrea*, but differs from them by lacking a ventral hindwing dark discal bar and by having a white ventral forewing postmedian line. It is sympatric with *T. epytus* without any evidence of intergradation. The wing patterns of *T. arindela* and *T. jennifer* are similar (Figs. 5–8), but distinguishing characters are given in the identification key.

Wing pattern similarity with species in other genera. The ventral wing patterns of *T. arindela* and *T. jennifer* resemble that of an Andean undescribed species of *Olynthus*. The latter has red scales at the base of the ventral wings that are lacking in *T. arindela* and *T. jennifer*, and has a darker brown ventral ground color. The ventral wing patterns of *T. arindela*



Figs. 29–32. Distribution of *Thepytus*. The species combined in figures 30 and 31 do not form monophyletic lineages, see cladogram Fig. 33. 29: *T. epytus* (circles), *T. thyrea* (squares), ‘questionable’ *T. epytus/thyrea* specimens (stars in eastern Ecuador). 30: *T. arindela* (circles), *T. jennifer* (squares). 31: *T. beatrizae* (circles), *T. nancyana* (star), *T. carmen* (squares). 32: *T. echelta* (circles).

and *T. jennifer* are also superficially similar to those of *Parrhasius selika* (Hewitson), *P. urraca* Nicolay, and *P. moctezuma* (Clench). However, the ventral fore-

wing postmedian line in *Parrhasius* is more inclined and is located in the middle of the wing rather than in the distal half, as in *T. arindela* and *T. jennifer*.

Habitat and elevation. A wet-forest, lowland species that occurs from 300 to 850 m elevation at localities that are often covered with clouds. The holotype from Chontales, Nicaragua was probably collected in the vicinity of Santo Domingo (BATES 1872; BELT 1874), which is wet forest at about 600 m elevation. The three Panamanian specimens were collected by the late Gordon Small. A male labeled “Colon, 1000” is from the Santa Rita Ridge at 1,000 ft elevation in Colon Province (approximately 09°22'N 79°43'W, this locality is discussed in RIDGELY 1976); it does not refer to the populated town of Colon (09°21'N 79°54'W), which is at sea level. (Those specimens from Small labeled “Colon, 1500” were collected a few miles further east on the Santa Rita Ridge.) A male and female of *T. arindela* from Cerro Campana were collected in wet montane forest on the continental divide at about 850 m elevation with approximate coordinates 08°41'N 79°55'W. This locality is discussed in RIDGELY (1976) and ROBBINS & SMALL (1981).

Distribution. Nicaragua and Panama (Fig. 30).

Study series. We examined two males (dissected) and one female (dissected) from Panama and the male holotype from Nicaragua.

Remarks. So far as we are aware, these are the only four specimens collected in the past 135 years. KIRBY (1879) listed this species from Ecuador with no further data. DYAR (1916) described *Thecla arindela rinde* from Guerrero, but ROBBINS (2004b) transferred *rinde* to *Parrhasius*, where it is a synonym of *P. polibetes* (Stoll). D'ABRERA (1995) listed *T. arindela* from Costa Rica with a question mark and no further data.

4.8. *Thepytus jennifer* Busby & Robbins, new species

Figs. 7, 8, 18, 26, 30

Type material. Holotype: ♀, *Thepytus jennifer* Busby & Robbins [printed red label]. ECUADOR, Morona[-]Santiago Province/ 14 km. W. of Macas (1,600m)/ 23. ix. 1998 Rio Abanico/ leg. Robert C. Busby [printed white label]. GENITALIA No./ 2007: 30♀/ R. K. Robbins [printed green label]. Deposited USNM (Fig. 8). – Paratype: ♂, Perú, [Puno], Inca Mines [“lies in the outskirts of Santo Domingo” at 5,000 ft. according to LAMAS 1976], 2 Oct 1900, H.H. Keys Collection. Deposited AMNH (Fig. 7).

Etymology. This strikingly large and beautiful species is named for Jennifer Busby, daughter of Robert Busby, who first recognized this species as distinct. The name is a non-latinized noun in apposition and is indeclinable.

Diagnosis and recognition as a distinct species. The ventral wing pattern of *T. jennifer* is very similar to

that of *T. arindela* (Figs. 5–8), for which reason we thought that they might be geographical forms of one species. However, their genitalia are quite distinct, especially the vinculum in lateral aspect (Figs. 17, 18) and the posterior end of the ductus bursae (Figs. 25, 26). *Thepytus jennifer* is the sister taxon of a clade comprising three *Thepytus* species, including *T. arindela*, suggesting that the wing pattern similarities are symplesiomorphies.

Size. Forewing length in male 21.1 mm (N=1), in female 24.1 mm (N=1).

Variation. The ventral wing patterns of the male and female types are very similar (Figs. 7, 8), which is the reason why we associate them. However, the underside ground color of the holotype female is gray and the underside of the paratype male has a brownish hue. There is insufficient information to determine if these differences are due to individual, sexual, geographical, seasonal, or interspecific variation.

Wing pattern similarity with species in other genera. See account for *T. arindela*.

Type locality. The type locality is along the road that goes from Macas west into the mountains. It is a logging trail on the west side of the Rio Abanico.

Habitat and elevation. *Thepytus jennifer* is a wet-forest montane species known from 1,525 and 1,600 m elevation.

Behavior. The holotype female was collected on a trap baited with rotting fish.

Distribution. *Thepytus jennifer* occurs in eastern Ecuador and Perú (Fig. 30).

Study series. We examined the female holotype (dissected) from Ecuador and male paratype (dissected) from Perú.

4.9. *Thepytus beatrizae* (Bálint & Dahners), new combination

Figs. 9, 19, 31

Beatheclus beatrizae Bálint & Dahners, 2006: 149 from S. Antonio, R. Agucatal [sic], Valle, Colombia in ICN.

Diagnosis and recognition as a distinct species. *Thepytus beatrizae* is a phylogenetically distinct species (Fig. 33) that occurs in eastern Ecuador, as does its sister lineage, specifically *T. nancyana*. The dorsal color of males has more of a greenish hue than other *Thepytus* males, but the green dorsal color of the female illustrated by BÁLINT & DAHNERS (2006) is the same, or nearly so, as the dorsal color of females of *T. arindela* and *T. epytus* from Panama (Figs. 2, 6). The male genitalia of *T. beatrizae* possess the male synapomorphy for *Thepytus* and are exceed-

ingly similar to those of *T. nancyana*, *T. carmen*, and *T. echelta*.

Habitat and elevation. *Thepytus beatrizae* is a wet-forest montane species that occurs from 1,800 m to 2,200 m elevation.

Behavior. According to BÁLINT & DAHNERS (2006), males set up mating territories between 12:00 and 14:30 hours. Busby likewise found two “territorial” males in the early afternoon along ridges west of Macas, Morona-Santiago, Ecuador (1,800–2,100 m).

Distribution. *Thepytus beatrizae* occurs from western Colombia to eastern Ecuador (Fig. 31).

Study series. We examined two males (one dissected) from Ecuador plus the original description of *T. beatrizae*.

4.10. *Thepytus nancyana* Busby & Robbins, new species

Figs. 10, 20, 31

Type material. Holotype: ♂, *Thepytus nancyana* / Busby & Robbins [printed red label]. ECUADOR: Napo/ 10 km El Chaco – El Reventador Rd/ 0°16.5'S, 77°45.6'W/ 13 January 2007 1800–1900m/ Robert C. Busby. leg. [printed white label]. GENITALIA No./ 2007: 87♂/ R. K. Robbins [printed green label]. Deposited USNM (Fig. 10). – Paratype: ♂, same data as holotype except “11 Jan 2007” and “GENITALIA No./ 2007: 20♂/ R. K. Robbins”. Deposited RCB.

Etymology. This beautiful species is named for Nancy Busby in celebration of her 90th birthday. She is the mother of Robert Busby, who discovered this species. Nancy introduced Robert to the study of butterflies in the early 1950s in Tenafly, New Jersey. The name is a feminine noun in apposition.

Diagnosis and recognition as a distinct species. *Thepytus nancyana* co-occurs in eastern Ecuador with *T. echelta* and *T. beatrizae*, but is readily distinguished without any evidence for introgression. The unusual smooth process without setae on the ventral valvae is shared with *T. echelta*, *T. carmen*, and *T. beatrizae* (Figs. 19–22). Two ventral forewing white lines are shared only with *T. beatrizae* and *T. carmen* (but less reduced) while a red spot at the ventral hindwing anal angle is shared with *T. echelta* and *T. carmen*.

Size. Male forewing lengths are 15.9 mm (holotype) and 16.7 mm (paratype).

Variation. Other than size, there is little evident variation between the two known males.

Type locality. The type locality is a long ridge with a fairly steep, heavily forested slope on one side and a gentle slope on the other, which has been partly cut for pasture.

Habitat and elevation. *Thepytus nancyana* is a wet-forest montane species that occurs at 1800–1900 m elevation.

Behavior. The two known males set up mating territories on the same tree about 6 m above the ground at 13:30 and 15:00 hours.

Distribution. *Thepytus nancyana* is known only from the type locality (Fig. 31).

Study series. We examined the two male types (dissected) from Ecuador.

4.11. *Thepytus carmen* Robbins & Duarte, new species

Figs. 11, 12, 21, 27, 31

Type material. Holotype: ♂, *Thepytus carmen* / Robbins & Duarte [printed red label]. Independência 900m/ Petropolis-E.[estado] do Rio/ 21-2[Feb]-1938/ Gagarin [printed white label with the date in pencil]. Ex Col. Gagarin [printed white label]. DZ 3565 [printed white label]. GENITALIA No./ 1992: 3 ♂/ R. K. Robbins [printed green label]. Deposited DZUP (DZ 3565). – Paratypes: 2♂♂ 6 Jun 1946, 15 May 1941 and 2♀♀ 22 May 1945, 14 May 1941 [Brazil, Rio de Janeiro State, Parque Nacional do Itatiaia] (Figs. 11–12). Deposited FIOC. Specimens from Itatiaia in the Zikán Collection in FIOC and in USNM lack “Itatiaia” locality labels. J.F. Zikán worked for many years as the Park Naturalist (Márcio Zikán, pers. comm.), which may be the reason for the lack of locality labels on Itatiaia specimens. However, these four paratypes were curated in FIOC under the name *Thecla selica* [sic], and all specimens of *T. selica* in the Zikán collection were from Itatiaia (ZIKÁN & ZIKÁN 1968). Further, the paratypes have a handwritten “Poins.” label, which likely refers to the many flowering poinsettia (*Euphorbia pulcherrima*) bushes near the main park station (~700 m elevation) that are covered with nectaring bees (FERRAZ 1997) and hairstreaks (R.K. Robbins unpubl.) in May and June.

Etymology. This beautiful species is named in memory of Carmen Lúcia Buck in recognition of the gracious support of science that she and her husband Peter have provided to the Smithsonian Institution’s National Museum of Natural History. She grew up and lived for many years in Minas Gerais and Espírito Santo, and loved the forests where *Thepytus carmen* flies. The name is a feminine noun in apposition.

Diagnosis and recognition as a distinct species. *Thepytus echelta* and *T. carmen* both occur in southern Brazil and are sister species with nearly indistinguishable genitalia (Figs. 21–22, 27–28), but they have distinctly different wing patterns (Figs. 11–14).

Size. Forewing length in males 18.0 mm (holotype) and 17.1 mm, in female 18.3 mm. We were unable to measure the other two paratypes for this paper.

Type locality. Curtis Callaghan lived for many years in Independência and writes “Independência consists of a series of hilltops at the top of the escarpment of

the Serra do Mar south of the town of Petropolis at 900 m. Once a famous type locality for numerous taxa and covered by pygmy subtropical forest, it has since been destroyed and replaced by a shantytown."

Habitat and elevation. *Thepytus carmen* is a wet-forest lower montane species that occurs from 700 to 900 m elevation.

Distribution. *Thepytus carmen* is known only from Independência and Itatiaia and is likely endemic to the Serra do Mar and Serra da Mantiqueira (Fig. 31).

Study series. We examined the three male (one dissected) and two female (one dissected) types from Brazil.

4.12. *Thepytus echelta* (Hewitson)

Figs. 13, 14, 22, 28, 32

Thecla echelta Hewitson, 1867: 109 from Tapajós, Amazon, Pará Brazil.

Thepytus echelta; ROBBINS 2004b: 134, ♂ presumed holotype from Tapajós in BMNH (B.M. type No. Rh. 673) examined.

Diagnosis and recognition as a distinct species. The dorsal wing pattern of the male is unique in the Eumaeini, with little variation that we can detect from Mexico to southern Brazil. *Thepytus echelta* is sympatric with its phylogenetic sister, *T. carmen*, although the two have not been found at exactly the same locality.

Variation. Male dorsal blue color in the study series is slightly lighter in Central America and western Ecuador than in South America east of the Andes, but this variation may be due to a small sample size. The genitalia from Central America and South America are the same.

Wing pattern similarity with species in other genera. *Thepytus echelta* females have wing patterns that are very similar to those of *Michaelus ira* and *Olynthus fanci*, but they lack submarginal orange-red scales in ventral hindwing cell Cu₂-2A that are possessed by females of *M. ira* and *O. fanci*. The only certain means of identification, however, is by dissecting the female genitalia.

Male *T. echelta* have conspicuous patches of black scales on the dorsal forewing surface that resemble patches of dark scales that occur on the male forewings of a few species of *Panhiades* and *Parrhasius*. The occurrence of these patches is homoplastic.

Habitat and elevation. *Thepytus echelta* inhabits wet and dry forest. It is a lowland and lower montane species that occurs from sea level to 1,500 m elevation. It has been found once at 2,200 m on a wind-blown ridge in southwestern Ecuador; its regular occurrence above 1,500 m needs confirmation.

Larval foodplant and immature stages. On 2 Jan 1979 Janzen (JANZEN & HALLWACHS 2009: 79-SRNP-7) found a larva eating the fruits of *Psittacanthus calyculatus* G. Don in Santa Rosa National Park, Guanacaste, Costa Rica (10.83764°N 85.61871°W). A female eclosed 2 Feb 1979. "Found as tiny red larva feeding through red fruit wall into the seed; by 10 Jan was 17 mm long and red (as in color of the unripe fruit); over night of 12 Jan ate entire contents of one black ripe fruit plus seed." Voucher with pupal case in USNM.

UCHÔA & CAIRES (2000) collected six late instar larvae on unripe and mature fruits of *Psittacanthus* (Loranthaceae) that were parasitizing *Cecropia* (Cecropiaceae) and *Anadenanthera* (Mimosaceae) trees between Jul 1998 and Sep 1999 in Aquidauana (20°30'S 55°48'W, 173 m) and Anastácio (20°29'S 55°49'W, 170 m), Mato Grosso do Sul, Brazil. Caterpillars ate the cotyledons, embryo, and surrounding tissues, hindering the germination of the seeds. Duarte identified the adults (four vouchers in DZUP).

Behavior. Robbins recorded a territorial male on the summit of a small hill in Villa Nova, near Joinville, Santa Catarina, Brazil (200 m) at 14:31 hours on 23 Mar 1991 (voucher in USNM). Jean-Yves Gallard found a pair in copula on a French Guiana hilltop at about 15:00 hours on 28 Feb 1990 (Faynel, pers. comm.).

Distribution. *Thepytus echelta* occurs from Mexico to southern Brazil (Fig. 32).

Study series. For this paper, we examined 16 males (three dissected) and nine females (two dissected) from Mexico, Costa Rica, Ecuador, Perú, Bolivia, and southern Brazil plus the male Amazonian presumed holotype in BMNH. We also have seen images of the copulating pair from French Guiana (deposited JYG).

Remarks. *Thepytus echelta* is a rare species despite being widespread. For example, according to previous butterfly compendia (DRAUDT 1919–1920; D'ABRERA 1995), it had been collected once in Brazil and once in Mexico.

5. Phylogenetic and biogeographical analyses

5.1. Characters used in phylogenetic analysis

01. Color of dorsal surface of wings in female (Figs. 2, 4, 6, 8, 12, 14) (0) shining green-blue (1) muted pale blue.

Tab. 1. Data matrix for *Thepytus*. Dimorphisms are denoted by “A” (= states 0 and 1), unknown states with a question mark (?), and inapplicable characters with a dash (-).

Taxa	0 1	0 2	0 3	0 4	0 5	0 6	0 7	0 8	0 9	1 0	1 1	1 2	1 3	1 4	1 5	1 6	1 7	1 8	1 9	2 0	2 1	2 2
<i>Michaelus ira</i>	1	0	0	0	0	2	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Parrhasius polibetes</i>	1	A	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Olynthus narbal</i>	0	1	0	0	-	-	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0
<i>Thepytus epytus</i>	0	1	1	0	1	1	A	0	1	0	0	1	0	1	1	0	0	1	1	1	1	0
<i>Thepytus thyrea</i>	1	0	1	0	1	1	0	0	1	0	0	1	0	1	1	0	0	1	1	1	1	0
<i>Thepytus arindela</i>	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0
<i>Thepytus jennifer</i>	0	0	0	0	0	0	0	2	1	0	0	1	0	1	1	1	0	0	0	1	1	0
<i>Thepytus beatrizae</i>	0	0	0	1	0	1	0	2	0	0	1	1	1	1	0	1	1	0	0	?	?	?
<i>Thepytus nancyana</i>	?	0	0	1	0	1	1	2	0	1	0	1	1	1	A	1	1	0	0	?	?	?
<i>Thepytus carmen</i>	0	0	0	1	0	1	1	1	0	1	1	1	1	0	0	1	1	0	0	1	2	1
<i>Thepytus echelta</i>	1	0	0	0	0	2	A	1	0	1	1	1	1	0	0	1	1	0	0	1	2	1

02. Ventral surface of hindwing with orange-red cubital spot (Figs. 1–14) (0) present (1) absent.
03. Conspicuous black bar at end of the discal cell on the ventral surface of the forewing and hindwing (Figs. 1–14) (0) absent or very faint (1) present.
04. White submarginal line on ventral surface of forewing (in addition to the postmedian line) (Figs. 1–14) (0) absent (1) present.
05. Color of postmedian line on ventral wing surfaces (Figs. 1–14) (0) mostly white (1) mostly black.
06. Position of postmedian line on ventral surface of the forewing (Figs. 1–14) (0) median (1) postmedian (2) submarginal.
07. Orange-red scales on ventral surface of hindwing anal lobe (Figs. 1–14) (0) absent (1) present.
08. Basally displaced postmedian line segment in cell Sc+R₁-Rs on ventral surface of hindwing (Figs. 1–14) (0) primarily black circle within the cell (1) part black, part white line within the cell (does not touch vein Rs) (2) part black, part white, the entire width of the wing cell (touching vein Rs).
09. Ventral surface of abdomen (Figs. 1–14) (0) yellow-white (1) orange-white.
10. Position of basally displaced postmedian line segment in cell Sc+R₁-Rs on ventral surface of hindwing (Figs. 1–14) (0) at or basal of origin of vein M₁ (1) distinctly distal of the origin of vein M₁.
11. Base of forewing costa on ventral surface (0) orange-red (1) yellow-gray.
12. Sclerotized curved structure at the dorsal edge of the anterior base of the male valva (0) present (1) absent.
13. Basal part of male valva with the ventral surface smooth and without setae (cf. Fig. 20) (0) absent (1) present.
14. Groove on outer surface of vinculum (not to be confused with the ridge on the inner surface of the vinculum) ventral of the vinculum strut (cf. Fig. 17) (0) without angles (1) forms an angle, about 90° or greater.

15. Groove on outer surface of vinculum dorsal of the vinculum strut (cf. Fig. 17) (0) without angles (1) forms an angle, greater than 90°.
16. Ridges on inner surface of dorsal tegumen (0) terminating laterally at apex of lateral window (1) terminating dorsal of the apex of the lateral window.
17. Penis tip (0) straight (1) twisted about 90° to the right side of the butterfly.
18. Saccus (Figs. 15–22) (0) as wide as or wider than long (1) longer than wide (see length in lateral aspect in Fig. 16).
19. Brush organs on the dorsal surface of the vinculum (Fig. 16) (0) absent (1) present.
20. Anterior end of female ductus bursae (Figs. 23–28) (0) straight (1) upturned.
21. Pair of posteriorly pointing spines on the lamella postvaginalis (Figs. 23–28) (0) absent (1) long (cf. Figs. 23–26) (2) short (cf. Figs. 27–28).
22. Ductus bursae (Figs. 23–28) (0) straight to barely twisted (1) twisted 90° so that when the posterior end is in ventral aspect, the posterior end is in lateral aspect.

5.2. Results of analyses

There was one most parsimonious 38-step equal weight tree with CI=65 and RI=73 and with bootstrap support for nodes as noted (Fig. 33). Each implied weight most parsimonious tree with K varying from 1 to 1,000 resulted in one tree with the same topology.

Mapping of elevation on the cladogram suggests that *T. echelta* and *T. carmen* colonized lower elevations from the montane *T. beatrizae* and *T. nancyana* (Fig. 34). It is possible that the lineage *T. epytus* + *T. thyrea* + *T. arindela* also colonized the lowlands, but the data are equivocal (Fig. 34).

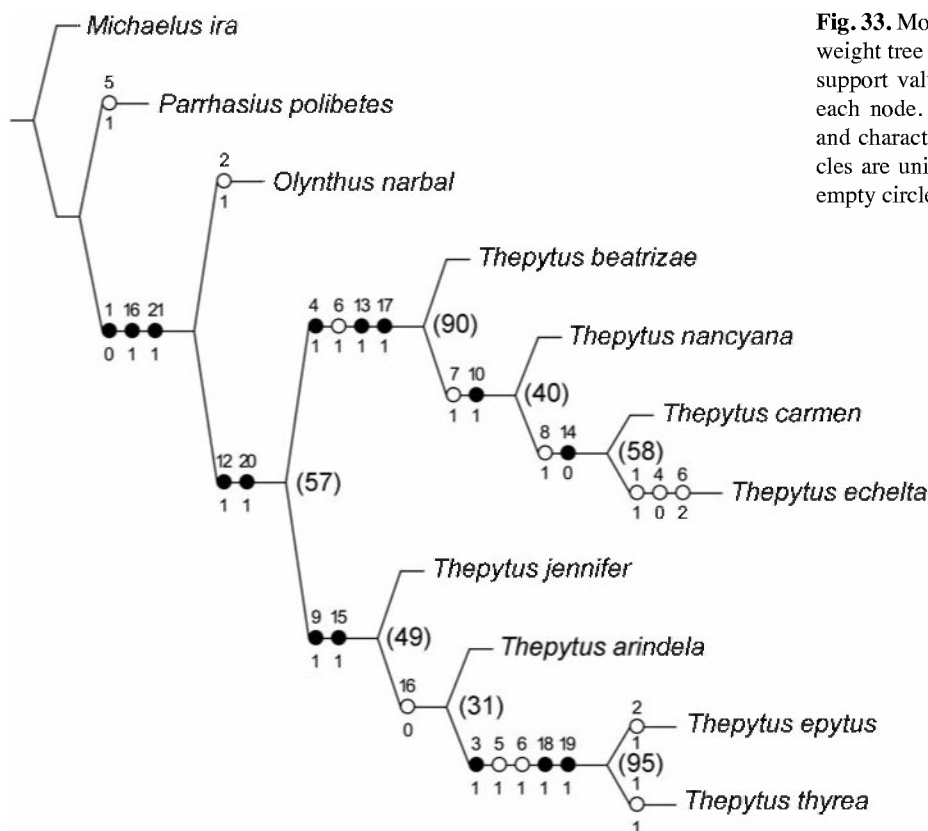


Fig. 33. Most parsimonious equal and implied weight tree (38 equal weight steps). Bootstrap support values in parentheses to the right of each node. Character numbers above circles and character state numbers below. Solid circles are unique character state changes while empty circles are homoplastic changes.

6. Discussion

6.1. Biogeography

The result (Fig. 34) that *Thepytus carmen* and *T. echelta* colonized lower montane and lowland forest is the first documented case of such a colonization in the Eumaeini. It might be reasonably argued that the montane *T. nancyana* and *T. beatrizae* are poorly known taxa, casting doubt on this result, but lower elevations have been well-collected historically. For example, the four lowland *Thepytus* species were described prior to 1900 while the montane and lower montane *Thepytus* species were described after 2000. Further, the butterfly fauna at the localities where *T. nancyana* and *T. beatrizae* were collected in eastern Ecuador contain virtually no lowland species (R. Busby unpubl. results).

Thepytus echelta and *T. thyrea* are the most widespread species in *Thepytus*, and both inhabit lowland habitats. In general, lowland species appear to be more widely distributed on average than montane species, but we are unaware of any attempt to quantify this anecdotal hypothesis, at least for butterflies. If correct, colonization of lowlands might be accompanied by an increase in distribution range, as appears to be the case for *T. echelta*.

6.2. Generic taxonomy

The genitalia of *Thepytus* are similar to those of *Olynthus*, and these genera may be sister groups. If so, we suspect that further phylogenetic analyses will confirm the monophyly of each because both the male and female genitalia are relatively homogeneous within each genus (compare Figs. 15–28 with figures in NICOLAY 1982).

BÁLINT & DAHNERS (2006) described *Beatheclus* in the *Panthiades* Section of the Eumaeini (ROBBINS 2004b). They did not compare *Beatheclus* to *Thepytus* even though the sole included species belonged to *Thepytus* as originally described (ROBBINS & DUARTE 2004). Their concept of *Beatheclus* as a monotypic genus leaves *Thepytus* paraphyletic in equal and implied weight most parsimonious trees (Fig. 33). Because recognition of *Beatheclus* would needlessly destabilize the taxonomy of the *Thepytus*, we herein synonymize *Beatheclus* with *Thepytus*.

6.3. Intergeneric wing pattern resemblances

The ventral wing patterns of some *Thepytus* species tend to closely resemble those of more common sym-

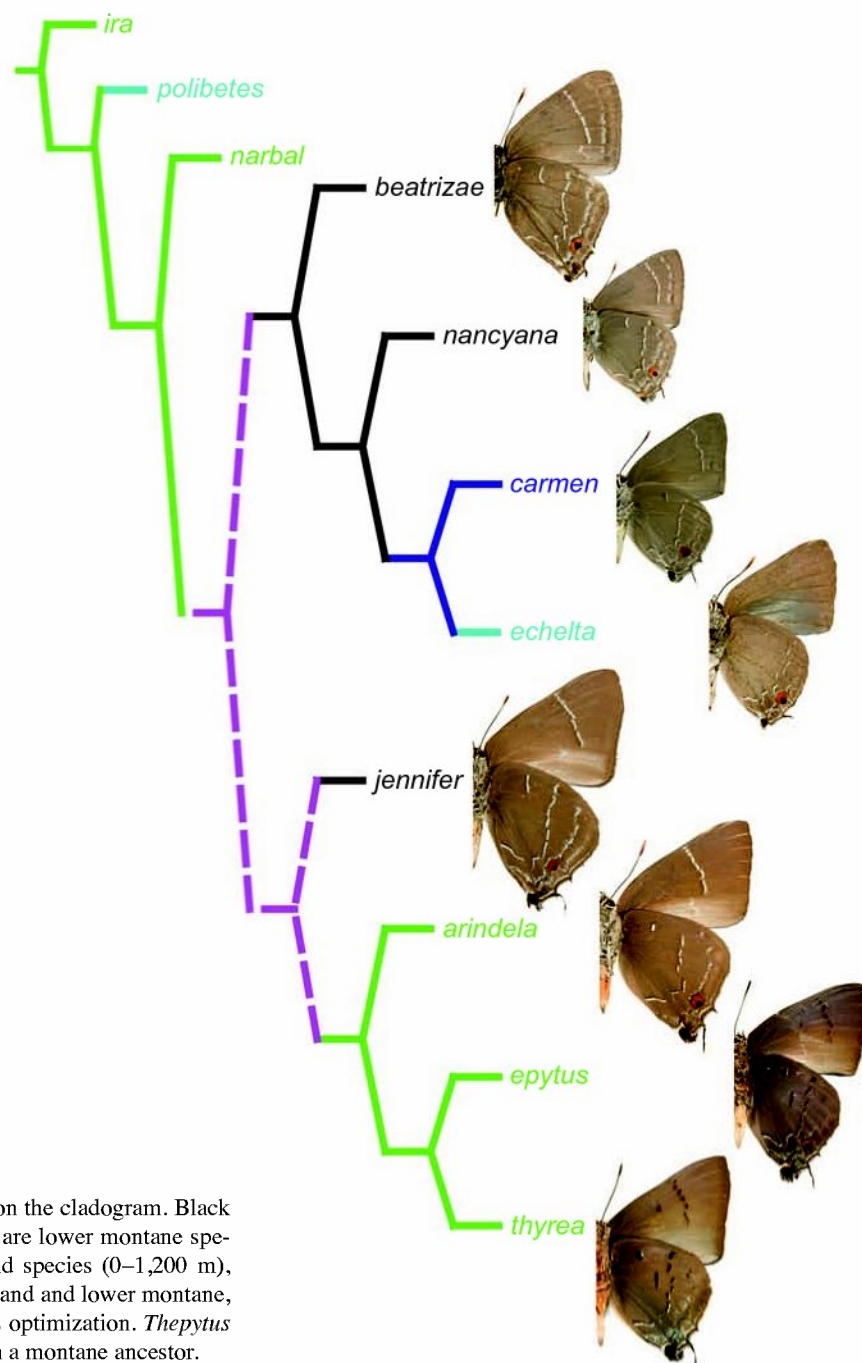


Fig. 34. Elevation changes optimized on the cladogram. Black are montane species (>1,300 m), blue are lower montane species (500–1,700 m), green are lowland species (0–1,200 m), turquoise are species that are both lowland and lower montane, and dashed-pink represents ambiguous optimization. *Thepytus carmen* and *T. echelta* are derived from a montane ancestor.

patric species that belong to other genera. Examples are *T. epytus* / *T. thyrea* and *Parrhasius polibetes*, *T. jennifer* and an undescribed species of *Olynthus*, and *T. echelta* and *Michaelis ira*. We note the occurrence of these resemblances with the thought that they may not be the result of coincidence.

6.4. Biological control

Eumaeini caterpillars characteristically feed on buds, flowers, and fruits rather than mature leaves (CHEW &

ROBBINS 1984). For this reason, they are often reared by biologists looking for predatory biological control agents, as appears to be the case with *T. echelta* on *Psittacanthus* (Loranthaceae) (UCHÔA & CAIRES 2000). Despite the apparent specificity of *T. echelta* for *Psittacanthus* from Costa Rica to Brazil, we are skeptical that this species is likely to be an effective control agent. In Mato Grosso do Sul, *Psittacanthus* remains a common weed despite the presence of *T. echelta*, and *T. echelta* remains a rare species despite the abundance of its larval food plant. Indeed, UCHÔA & CAIRES (2000) found only six *Thepytus* larvae among 23,916 examined fruits, suggesting that factors other than larval food plant abundance determine this butterfly's density.

7. Acknowledgments

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