



Phylogenetic Classification of the *Atlides* Section of the Eumaeini (Lepidoptera, Lycaenidae)

ANANDA REGINA P. MARTINS^{1,2,4}, MARCELO DUARTE¹ & ROBERT K. ROBBINS³

¹Museu de Zoologia, Universidade de São Paulo, Avenida Nazaré 481, Ipiranga, 04263-000, São Paulo, SP, Brazil.

²Department of Biology, McGill University, Redpath Museum, 859 Sherbrooke Street West, Montreal, Québec, Zip code: H3A2K6, Canada

³Department of Entomology, PO Box 37012, NHB Stop 105, Smithsonian Institution, Washington, DC 20013-7012, USA.

⁴Corresponding author. E-mail: ananda.pereiramartins@mail.mcgill.ca

Abstract

This paper provides the first phylogenetic classification of the *Atlides* Section (Lycaenidae: Theclinae, Eumaeini). It is based on a recently published morphological phylogenetic study, in which the *Atlides* Section proved to be monophyletic in all analyses. In particular, that study identified a hindwing cleft anal lobe in all members of the *Atlides* Section that is lacking in all other Eumaeini (except for some species of *Panthiades* Hübner). The included genera are *Theritas* Hübner; *Arcas* Swainson; *Lucilda* d'Abrera & Bálint; *Pseudolycaena* Wallengren; *Brangas* Hübner; *Atlides* Hübner; and *Denivia* K. Johnson. Each is characterized by synapomorphies. *Margaritheclus* Bálint and *Dabrerus* Bálint are **new generic synonyms** of *Lucilda* and *Brangas*, respectively. We recognize 71 species. Distribution and habitat are provided for each, and nomenclature is updated. *Atlides centralis* Salazar & Henao is a **new synonym** of *Atlides browni* Constantino, Salazar & K. Johnson; *Brangas contrastus* Bálint is a **new synonym** of *Brangas felderi* (Goodson); *Denivia grava* Bálint, K. Johnson & Kroenlein is a **new synonym** of *Denivia deniva* (Hewitson); *Denivia ponsanota* Bálint, K. Johnson & Kroenlein is a **new synonym** of *Atlides zava* (Hewitson); *Denivia striata* Bálint, K. Johnson & Kroenlein is a **new synonym** of *Atlides zava* (Hewitson); *Margaritheclus boliboyeri* Bálint & Wojtusiak is a **new synonym** of *Margaritheclus boliboyerus* Bálint & Wojtusiak; and *Theritas gozmanyi* Bálint & Wojtusiak is a **new synonym** of *Theritas paupera* (C. Felder & R. Felder). **New combinations** are *Lucilda margaritacea* (Draudt), *Lucilda danaus* (C. Felder & R. Felder), *Lucilda dabrerus* (Bálint), *Lucilda boliboyerus* (Bálint & Wojtusiak), *Denivia curitabaensis* (K. Johnson), *Denivia augustinula* (Goodson), *Denivia theocritus* (Fabricius), *Denivia augustula* (W.F. Kirby), *Denivia arene* (Goodson), *Denivia monica* (Hewitson), *Denivia hemon* (Cramer), *Denivia phegeus* (Hewitson), *Denivia acontius* (Goodson), *Denivia chalumna* (Schaus), *Denivia viresco* (H.H. Druce), *Denivia silma* (Martins, Faynel & Robbins), and *Denivia lisus* (Stoll).

Key words: *Arcas*, *Atlides*, *Brangas*, *Denivia*, *Lucilda*, *Pseudolycaena*, *Theritas*

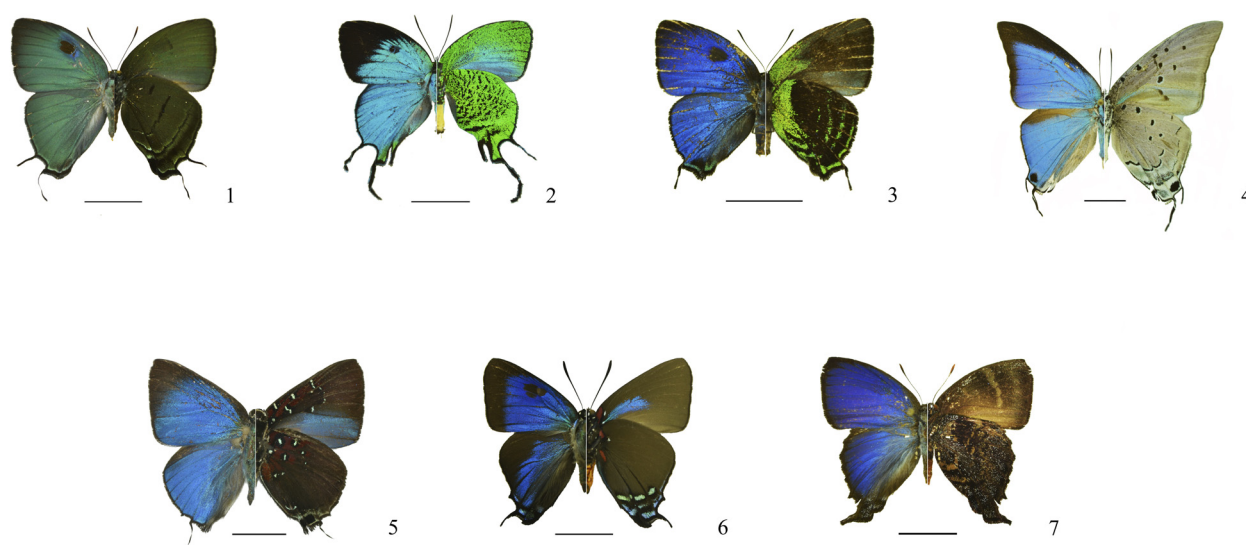
Introduction

Godman and Salvin (1887–1901) discovered a great variety of male secondary sexual organs among the New World hairstreak butterflies (Lycaenidae, Eumaeini), especially among those species currently placed in *Atlides* and related genera (Figs. 1–7). They proposed a classification that was based, in large part, on these organs. The significance of these organs was ignored for decades until their fine structure was detailed using scanning electron micrographs and wing slides (Robbins 1991; Robbins *et al.* 2012; Martins *et al.* 2016). Based on these studies, scent pads, scent patches, scent pouches, and brush organs were characterized (summarized in Martins *et al.* 2018). Using the morphological results in Godman and Salvin as a foundation, Martins *et al.* (2018) performed phylogenetic analyses of *Atlides* and related genera.

The purpose of this paper is to update the taxonomy of the *Atlides* Section based on the phylogenetic analysis in Martins *et al.* (2018) (Fig. 8). In particular, we describe morphological evidence for recognizing the *Atlides* Section, including the genus *Brangas* Hübner, which was not included in the section by Robbins (2004b). We partition the *Atlides* Section into monophyletic genera, characterize each phylogenetically, and update the species level classification of each genus.

Classification History. Robbins (2004b) preliminarily grouped *Atlides* Hübner, *Arcas* Swainson, *Theritas* Hübner, and *Pseudolycaena* Wallengren in the *Atlides* Section of the Eumaeini (56 described species recognized). Classification is scanty. *Arcas* is the only genus to have been the subject of phylogenetic revision, based on morphology (Robbins *et al.* 2012). The small genus *Pseudolycaena* was the subject of conflicting, non-phylogenetic taxonomic papers (e.g., Clench 1964; Austin *et al.* 2007). The taxonomy of parts of *Theritas* (sensu Robbins 2004b) has been addressed (Balint 2002, 2006). Recently, the taxonomy of *Theritas lisus* (Stoll) and close relatives, including association of the dimorphic sexes, was updated using morphology and mitochondrial DNA sequence data (Martins *et al.* 2016).

A phylogenetic study of exemplar Eumaeini taxa using 3,863 DNA base pairs (Quental, unpublished dissertation) differed in two respects from the morphological checklist classification of the *Atlides* Section. First, *Brangas* was excluded from the *Atlides* Section in the checklist, but was included in the *Atlides* Section in the molecular phylogeny results. Second, the genus *Theritas* in the checklist was used as a catchall for those *Atlides* Section species that did not belong to one of the other readily recognized genera. *Theritas* was paraphyletic in the molecular phylogeny results, but only 12 of the proposed species of the section were included in the molecular phylogeny.



FIGURES 1–7. Male wing pattern in the *Atlides* Section. Dorsal and ventral surfaces. 1. *Theritas mavors*. 2. *Arcas imperialis*. 3. *Lucilda crines*. 4. *Pseudolycaena marsyas*. 5. *Brangas caranus*. 6. *Atlides halesus*. 7. *Denivia deniva*.

Material and methods

The data matrix and phylogenetic analyses are available on Martins *et al.* 2018. The matrix in nexus format, including the characters, is available electronically in Morphobank (https://morphobank.org/index.php/Projects/ProjectOverview/project_id/3345). According to Martins *et al.* (2018), there was a single most parsimonious tree (Fig. 8). Implied weight analysis with concavity constant (k) 500, 100 and 50 yielded one tree with the same topology. Analyses with $k = 10$ and $k = 3$ each yielded one tree that differed slightly (2 or 3 steps longer assuming equal weight), but the *Atlides* Section and each of its constituent genera were monophyletic in all trees.

Species level decisions were made based primarily upon an analysis of morphological variation among 240 specimens of the 44 species in the matrix. We also examined cursorily all species of *Atlides* and *Brangas*. Specimens were examined in the American Museum of Natural History, New York, USA; The Natural History Museum [formerly British Museum (Natural History)], London, UK; Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil; Fundação Instituto Oswaldo Cruz, Rio de Janeiro, RJ, Brazil; Museo del Instituto de Zoología Agrícola, Maracay Venezuela; Museu Nacional, Universidade do Rio de Janeiro, RJ, Brazil; Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil; Private collection of Robert C. Busby, Andover, MA, USA; National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

The phylogenetic results are incorporated into the proposed classification, which is updated from Robbins (2004b), Robbins *et al.* (2012) and Martins *et al.* (2016). New combinations are noted. New synonymies for names proposed after 2003 are indicated, when appropriate. Name changes necessitated by subsequent ICZN rulings are noted.

Information on the distribution and habitat for each species was accumulated from the literature, from museum collections studied (listed above), and from our fieldwork. States in Brazil and the United States are noted by their two-letter postal codes. Those in Mexico by their three-letter codes. The Transandean, Amazonian, and Atlantic biogeographic regions follow Brown (1982).

Results and discussion

The *Atlides* Section

Six synapomorphies characterize the *Atlides* Section in the phylogenetic results (Table 1, Fig. 8), including a cleft anal angle of the hindwing (Martins *et al.* 2018). This trait was used historically to characterize the group (Godman & Salvin 1887–1901; Robbins 2004a). It occurs in all species of the *Atlides* Section (illustrated for each genus, Figs. 9–15). The cleft anal angle occurs at vein 2A, which usually terminates on the distal side of the indentation. Indentations are unreported in other Eumaeini, except for two species of *Panthiades* (Godman & Salvin 1887–1901). The depth of the cleft anal angle was treated as three states in the phylogenetic analysis (Martins *et al.* 2018). As noted by Godman & Salvin (1887–1901), a deep indentation occurs in *Arcas* (Fig. 9), a shallow indentation occurs in *Brangas* (Figs. 10), and an “intermediate” indentation occurs in all other members of the *Atlides* Section (Figs. 11–15).

TABLE 1. List of synapomorphies from the phylogenetic analysis of the *Atlides* Section (Martins *et al.* 2018).

<i>Atlides</i> Section
Male, frons, color: muted green
Male, paraocular area, color: muted green
Female, hindwing, ventral surface, submarginal region, red band: absent
Hindwing, outer margin split at intersection with vein 2A: present
Male, hindwing, number of tails: two tails (M3-Cu1 and Cu1-Cu2)
Valvae, posterior margin, lateral view: rounded
<i>Theritas</i>
Forewing, dorsal surface, scent patch distal of the discal cell between veins M1 and M3, not intermixed with regular wing scales: present
Male, forewing, ventral surface, discal cell band: present
Male, forewing, origin of vein R2: discal cell apex
Female, forewing and hindwing, dorsal surface, ground color: brown
Male, hindwing, ventral surface, postmedian band in cell Sc+R1-Rs: basally displaced
<i>Arcas</i>
Male, frons, color: emerald green
Male, paraocular area, color: emerald green
Male, forewing, ventral surface, postmedian band: absent
Female, forewing, ventral surface, postmedian band: absent
Male, hindwing, ventral and dorsal surface, cell Cu1-Cu2 submarginal macule: present
Hindwing, anal region, size of split at vein 2A: reaching postmedian region
Male, hindwing, shape of anal lobe structure: triangular
Saccus, length (cm): Long (0.30 - 0.40)
Ductus bursae, shape: in S shape

.....continued on the next page

TABLE 1. (Continued)

Ductus bursae, posterior region, membranous area: present

Lucilda

Male, hindwing, number of tails: One tail (Cu1-Cu2) and one stub (M3-Cu1)

Brush-organ: absent

Vinculum, dorsal projection: absent

Pseudolycaena

Male, forewing, outer margin: Concave

Male, forewing, apex of cell R2-M1: acute

Male, forewing, ventral surface, submarginal band, color: black macules with white outline

Female, forewing, ventral surface, submarginal band, color: black macules with white outline

Male, hindwing, ventral and dorsal surface, cell Cu1-Cu2 submarginal macule: present

Male, thorax covered by white bristles: present

Male, abdomen, ventral surface, ground color: white

Brangas

Male, forewing, costal margin: straight

Male and female, forewing ventral surface at the base, red scaling between vein Sc and the discal cell: present

Male and female, hindwing ventral surface at the base, red scaling between vein Sc+R1 and the discal cell: present

Male, hindwing, ventral surface, cell 2A-3A with a small pencil of hairs: present

Hindwing, anal region, size of split at vein 2A: not reaching submarginal region

Valvae, posterior margin, lateral view: finger-like

Saccus, length (cm): short (0.05 0.07)

Vinculum, dorsal projection, location and shape: lies under and on the inner edge of brush organs

Atlides

Forewing, dorsal surface, scent patch distal of the discal cell between veins M1 and M3, not intermixed with regular wing scales: present

Forewing, dorsal surface, scent pad: present

Male, hindwing, ventral surface, veins covered by black scales: all veins

Male, hindwing, postmedian band: absent

Male, abdomen, ventral surface, ground color: orange

Denivia

Ductus bursae, posterior region, membranous area: present

We do not propose a subtribe name for the *Atlides* Section. It is one of numerous unresolved clades with long branches (Quental, unpublished dissertation). Genomic sequencing currently in progress may resolve eumaeine subtribe classification, but it is currently premature to propose a more extensive higher classification. For now, we adhere to Eliot's (1973) classification based on sections.

Robbins (2004a, b) excluded *Brangas* from the *Atlides* Section based on morphological differences of the genitalia and male secondary sexual traits. As noted, *Brangas* possesses a hindwing anal cleft, and the phylogenetic results strongly support the inclusion of *Brangas* (*B. caranus* and *B. getus*) in the *Atlides* Section as the sister of *Atlides*. The morphological differences that distinguish *Brangas* from the other *Atlides* Section genera appear to be autapomorphies.

The phylogeny based on DNA sequences in Quental (unpublished dissertation) was rooted on the lineage leading to *Pseudolycaena*. If one roots the Quental phylogeny where the tree of Martins *et al.* (2018) was rooted, the cladograms are the same, albeit with significantly fewer species in Quental. This congruence lends support to the phylogenetic results of Martins *et al.* (2018). Despite the different placement of the root, which may be due to the different ingroup sampling densities, the genera that we recognize are monophyletic in all analyses.

We here treat the *Atlides* Section as consisting of seven genera containing 71 described species.

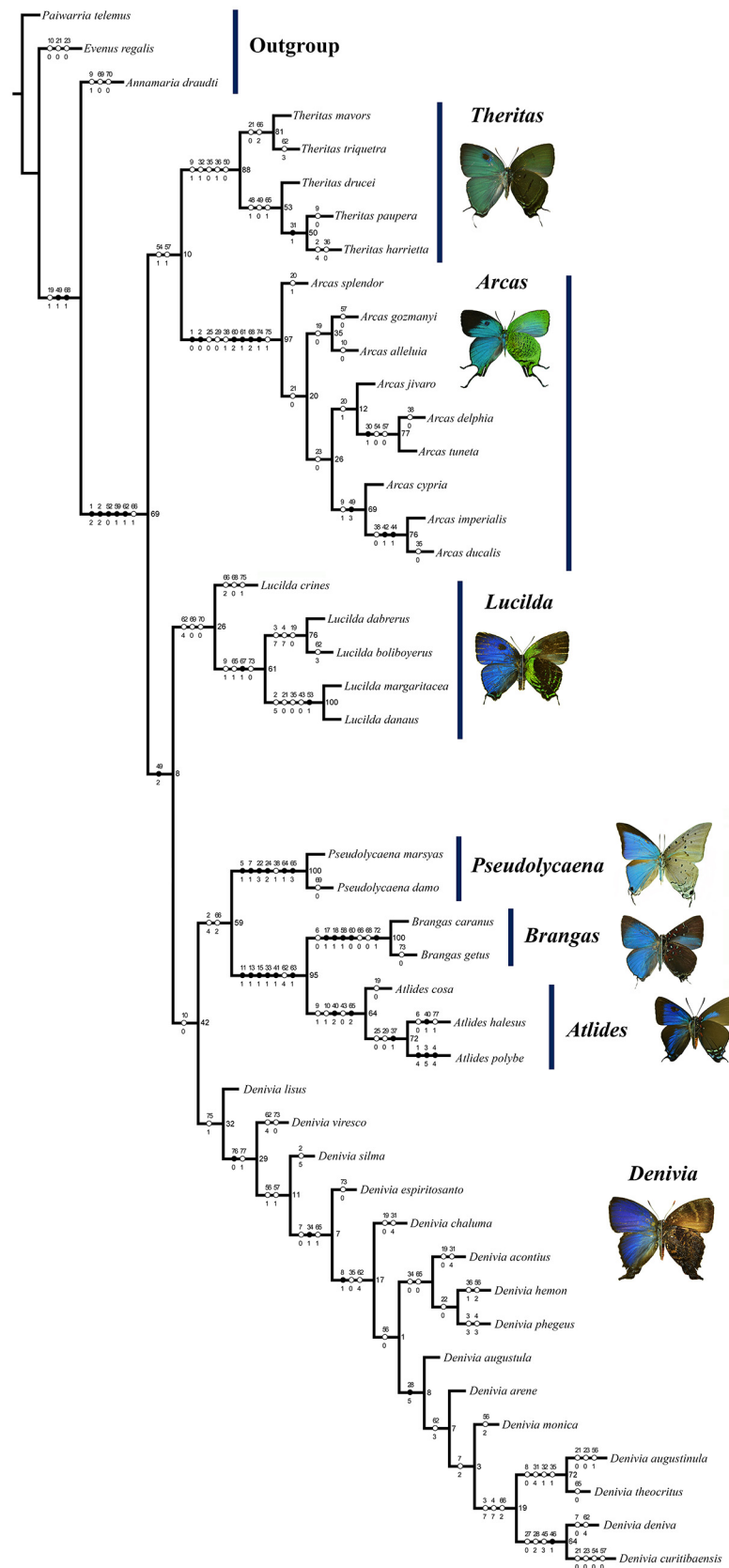
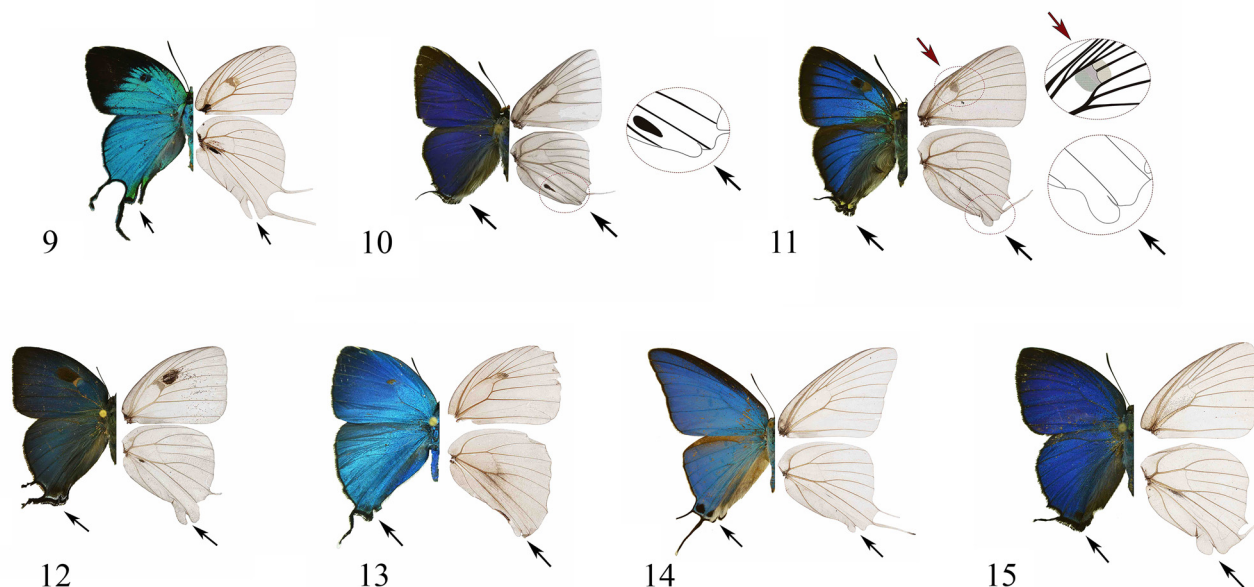


FIGURE 8. Cladogram modified from Martins *et al.* (2018).

Theritas sensu Robbins is not monophyletic

Robbins (2004b) used *Theritas* as a catchall for those *Atlides* Section species that did not belong to the readily recognized *Arcas*, *Pseudolycaena*, or *Atlides*. It is polyphyletic in our results (Fig. 8). To maintain the taxonomic stability of *Arcas*, *Pseudolycaena*, and *Atlides*, *Theritas* is partitioned into *Theritas*, *Denivia* K. Johnson and *Lucilda* d'Abrera & Bálint. New generic names are not needed.



FIGURES 9–15. Hindwing anal lobe cleft (black arrows). 9. *Arcas imperialis*, 10. *Brangas getus*, 11. *Atlides cosa* (with a forewing double scent pad in the discal cell—red arrow), 12. *Theritas drucei*, 13. *Lucilda danaus*, 14. *Pseudolycaena damo*, 15. *Denivia silma*.

Theritas Hübner, 1818

Type species: *Theritas mavors* Hübner

Theritas as reclassified here is a small, widespread Neotropical genus of five species. *Theritas mavors* and *T. triquetra* are common, primarily lowland forest species that replace each other geographically. *Theritas paupera*, *T. harrietta*, and *T. drucei* are South American montane forest species that also replace each other geographically.

Theritas is sister to *Arcas* and is characterized by five synapomorphies (Table 1, Fig. 8). It is most readily recognized by the color of its wings, despite the substantial variability within species. Males are greenish-blue dorsally and have a distinctive muted green ground color ventrally (Figs. 1 and 12). *Denivia phegeus* is the only other *Atlides* Section species with superficially similar male coloration. Females have brown scaling dorsally and ventrally (except for *T. harrietta*). In flight, the brown females somewhat resemble satyrine butterflies (Nymphalidae). *Denivia hemon* is the only other *Atlides* Section species with similar female coloration.

Theritas mavors Hübner, 1818, type locality: Surinam

kalikimaka (Clench, 1944) (*Thecla*), type locality: Mexico (VER)

lotis (Goodson, 1945) (*Thecla*), type locality: Venezuela

Distribution and Habitat. Mexico to central Brazil (Transandean and Amazonian Regions) in wet and dry lowland forest, occasionally in lower montane forest.

Theritas triquetra (Hewitson, 1865) (*Thecla*), type locality: Brazil

Distribution and Habitat. The Atlantic Region in wet and dry lowland forest, occasionally in lower montane forest.

Theritas paupera (C. Felder & R. Felder, 1865) (*Pseudolycaena*), type locality: Colombia

ella (Draudt, 1919) (*Thecla*), type locality: Colombia

chione (Goodson, 1945) (*Thecla*), type locality: Colombia; "Amazon", an incorrect type locality.

gozmanyi Bálint & Wojtusiak, 2007, **New Synonym**, type locality: Ecuador

Distribution and Habitat. Venezuela to southern Peru (Cosñipata Valley) in montane forest.

Synonymy. Bálint and Wojtusiak (2007) proposed that *T. paupera* consists of two species distinguished by the presence/absence of a dorsal forewing scent pad and by color of the ventral wings. In the study series for this paper, the scent pad varies from absent to a few scales at the posterior disco-cellular vein (cannot be seen without the aid of a microscope) to enough scales to cover the lower disco-cellular vein to sufficient scales to cover both the lower and middle disco-cellular veins. Bálint and Wojtusiak did not address the hypothesis that scent pad size in *T. paupera* is variable, including absence. Further, Bálint and Wojtusiak suggested that presence of a scent pad was correlated with wing color, but we found no correlation in the study series. The description of *T. gozmanyi* was also problematic for another reason. The authors claimed without evidence that the male of *T. paupera* lacks a scent pad, but the holotype of *T. paupera* is a female. Even if there were two distinct biological species—and we know of no compelling evidence to support such a hypothesis—we do not know to which species the name *T. paupera* would apply.

Theritas harrietta (A.G. Weeks, 1901) (*Thecla*), type locality: Bolivia

Distribution and Habitat. Southern Peru (Cosñipata Valley) to Bolivia in montane forest.

Theritas drucei (Lathy, 1926) (*Thecla*), type locality: Brazil (SC)

Distribution and Habitat. Brazil in montane forest from RJ to SC. It occurs at lower elevations in the south of its range.

***Arcas* Swainson, 1832**

Type species: *Papilio imperialis* Cramer

The species currently placed in *Arcas* have been recognized as a distinct and widespread Neotropical group for more than a century (Godman & Salvin 1887–1901; Draudt 1919–1920). Nicolay (1971) first revised the genus, recognizing seven species. In the ensuing decades, other names were proposed, leading to the phylogenetic revision in Robbins *et al.* (2012) and the recognition of nine species.

The study of Martins *et al.* (2018) identified ten synapomorphies for *Arcas* (Table 1, Fig. 8), but the emerald green ventral wings, long hindwing tails, and deep anal lobe cleft are conspicuous characterizing traits (Fig. 2 and 9). The genus can also be recognized by its male and female genitalic structures.

The phylogenetic results in Martins *et al.* (2018) differ from those in Robbins *et al.* (2012) in the position where the genus is rooted. The grouping *A. splendor* + *A. alleluia* + *A. gozmanyi* was a monophyletic lineage previously, but because of the changed rooting, is now a paraphyletic group.

Arcas imperialis (Cramer, 1775) (*Papilio*), type locality: Surinam

actaeon (Fabricius, 1775) (*Papilio*), type locality: ?, suppr. (ICZN, Op. 1058)

venus (Fabricius, 1781) (*Papilio*), type locality: Surinam, repl. name

oakesii (Butler, 1884) (*Theritas*), type locality: Colombia

magnifica Austin & K. Johnson, 1995, type locality: Brazil (RO)

Distribution and Habitat. Mexico to Argentina and southern Brazil in wet lowland forest up to about 1,000 m elevation.

Arcas ducalis (Westwood, [1851]) (*Thecla*), type locality: Brazil

Distribution and Habitat. Brazil from RJ to RS in wet lower montane forest in the north and at lower elevations in the south.

Arcas cypria (Geyer, 1837) (*Theritas*), type locality: Mexico (YUC)

paphia (C. Felder & R. Felder, 1865) (*Pseudolycaena*), type locality: Colombia

publica (Röber, 1923) (*Thecla*), type locality: Colombia

Distribution and Habitat. Mexico to Venezuela and Colombia in wet lowland forest.

Arcas jivaro Nicolay, 1971, type locality: Ecuador

Distribution and Habitat. Ecuador to Bolivia in wet lower montane forest.

Arcas delphia Nicolay, 1971, type locality: Costa Rica

katia Salazar, 2001, type locality: Colombia, nom. nud.

katia K. Johnson & Salazar, 2002, type locality: Colombia

Distribution and Habitat. Costa Rica to western Ecuador in wet lowland forest.

Arcas tuneta (Hewitson, 1865) (*Thecla*), type locality: [Brazil (AM)]

marginata Austin & K. Johnson, 1995, type locality: Brazil (RO)

viriditas Austin & K. Johnson, 1995, type locality: Brazil (RO)

arcadia Bálint, 2002, type locality: Brazil (SC)

Distribution and Habitat. The Guianas to southern Brazil in wet lowland forest up to lower montane elevations.

Arcas gozmanyi Bálint, 2006, type locality: Panama

Distribution and Habitat. Costa Rica to western Ecuador in wet lower montane forest.

Arcas splendor (H.H. Druce, 1907) (*Thecla*), type locality: Colombia

nicolayi Salazar & Constantino, 1995, type locality: Colombia

lecromi Salazar & Constantino, 1995, type locality: Colombia

Distribution and Habitat. Colombia and Ecuador in montane forest (mapped in Robbins *et al.* 2012).

Arcas alleluia Bálint, 2002, type locality: Peru

Distribution and Habitat. Eastern Peru in montane forest.

***Lucilda* d'Abrera & Bálint, 2001**

ICZN Opinion 2358 (2015)

type species: *Thecla crines* Druce

Margaritheclus Bálint, 2002, **New Synonym**

type species: *Pseudolycaena danaus* C. Felder & R. Felder

Lucilda crines (Druce) has been traditionally grouped with species now placed in *Denivia* (Druce 1907; Draudt 1919–1920). In all analyses of Martins *et al.* (2018), *L. crines* formed a monophyletic lineage with four other species characterized by three synapomorphies (Table 1). In particular, these five are the only species in the *Atlides* Section lacking a dorsal process on the male genitalia vinculum (Figs. 16–17). We do not place *L. crines* in its own genus (*Margaritheclus* Bálint 2002) because the information content of monotypic genera is redundant (Farris 1979) and because monotypic genera are not testable hypotheses.

As characterized, *Lucilda* consists of five species that inhabit wet forest. The type species (Fig. 3) occurs in lowlands under 800 m while the others inhabit montane forest above 1,000 m. Among the *Atlides* Section genera, *Lucilda* is the most poorly represented in museum collections. The genus occurs from Costa Rica to Bolivia.

Lucilda margaritacea (Draudt, 1919) (*Thecla*), type locality: Colombia, **New Combination**

Distribution and Habitat. Western Colombia and Ecuador in montane forest.

Lucilda danaus (C. Felder & R. Felder, 1865) (*Pseudolycaena*), type locality: Venezuela, **New Combination**

belus (Bálint, 2002) (*Margaritheclus*), type locality: Peru

Distribution and Habitat. Venezuela to eastern Peru in montane forest.

Lucilda dabrerus (Bálint, 2002) (*Margaritheclus*), type locality: ?, **New Combination**

Distribution and Habitat. Ecuador in montane forest.

Lucilda boliboyerus (Bálint & Wojtusiak, 2006) (*Margaritheclus*), type locality: Bolivia, **New Combination**

boliboyeri (Bálint & Wojtusiak, 2006) (*Margaritheclus*), **New Synonym**, type locality: Bolivia.

Nomenclature. The original description contained two different spellings for this name. As first revisers, we choose *boliboyerus* as the senior synonym.

Distribution and Habitat. Southern Peru and Bolivia in montane forest.

Lucilda crines (H.H. Druce, 1907) (*Thecla*), type locality: Colombia

wernerii (Hering, 1925) (*Thecla*), type locality: Colombia

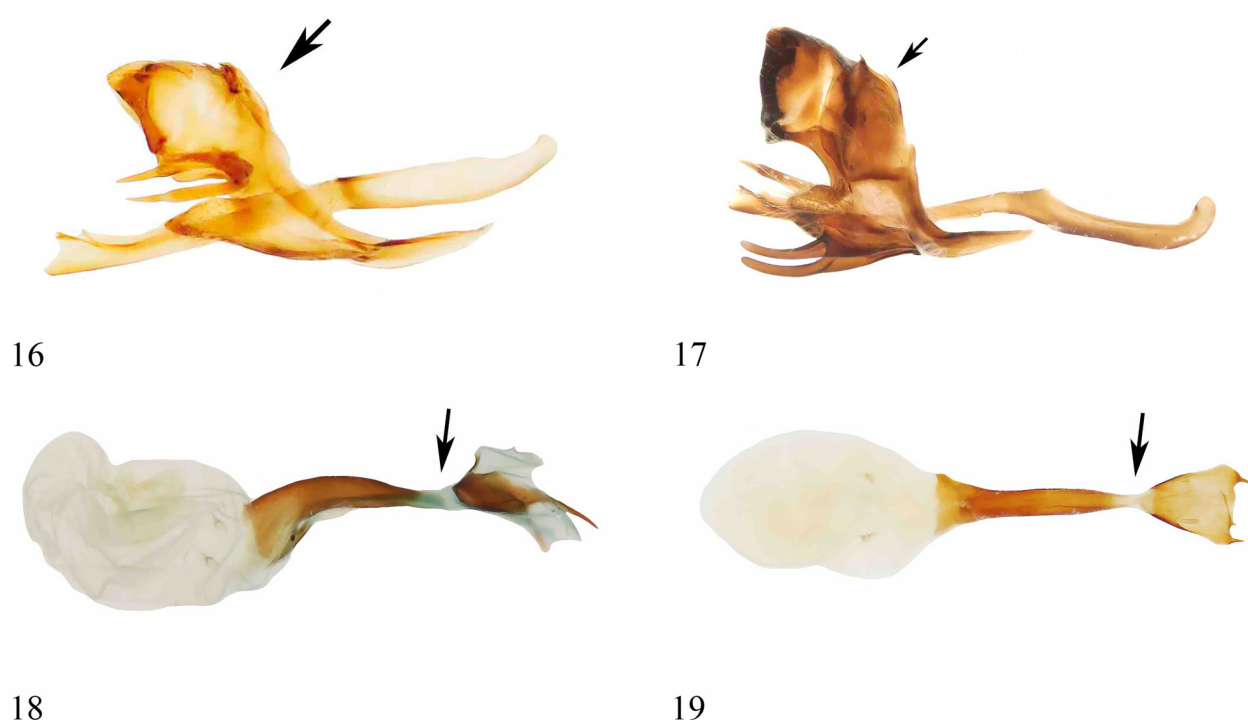
Distribution and Habitat. Costa Rica to western Ecuador in wet lowland forest.

Pseudolycaena Wallengren, 1858

type species: *Papilio marsyas* Linnaeus

Two *Pseudolycaena* species have been recognized traditionally (Godman & Salvin 1887–1901; Draudt 1919–1920; Robbins 2004b). Clench (1964) recognized one species, and Austin *et al.* (2007) recognized five species in two different groups based on a character matrix that was not analyzed phylogenetically. We used some of the newly proposed characters in Austin *et al.* (2007) in our phylogenetic analyses (Martins *et al.* 2018), as they were informative, but could not confirm the validity of others because of excessive intraspecific variation. We follow the traditional two species taxonomy but note that the name *P. dorcas* (Druce) refers to populations that appear to be a hybrid mix of the two species. The genus occurs almost everywhere in the Neotropics, but the two species are allopatric or parapatric in all parts of their range except for a few scattered records of *P. marsyas* and *P. damo* on the wet Caribbean coast of Central America.

Pseudolycaena is characterized by seven synapomorphies (Table 1), but the conspicuous disjointed spotting on the ventral wing patterns, the size, and the wing shape make this genus immediately recognizable (Figs. 4 and 14).



FIGURES 16–17. Male genitalia in lateral aspect (posterior of butterfly to right) showing no process on the dorsal vinculum (black arrows). 16. *Lucilda crines*. 17. *Lucilda margaritacea*.

FIGURES 18–19. Female genitalia ductus copulatrix (posterior of butterfly to the right) showing the transparent membranous area in the ductus bursae (arrow). 18. *Denivia deniva* lateral aspect. 19. *Denivia espiritosanto* ventral aspect.

Pseudolycaena damo (H. Druce, 1875) (*Thecla*), type locality: Panama

dorcas (H.H. Druce, 1907) (*Thecla*), type locality: Peru [appears to be a “hybrid taxon” that could have been synonymized under *P. marsyas*.]

Distribution and Habitat. Mexico to Panama in wet and dry lowland habitats with two presumably disjunct populations in South America. Western Ecuador in dry scrub coastal vegetation around Guayaquil south to Tumbes, Peru. Dry scrub vegetation in the Rio Marañon Valley of Peru south of 5°S latitude.

Pseudolycaena marsyas (Linnaeus, 1758) (*Papilio*), type locality: In calidis regionibus [no locality given].

cybele (Godman & Salvin, 1896) (*Thecla*), type locality: St. Vincent

nellyae Lamas, 1981, type locality: Peru

described as *Pseudolycaena marsyas nellyae*.

Distribution and Habitat. The entire Amazonian and Atlantic Regions in many kinds of habitats. Western

Colombia and western Ecuador in forest (not in scrub vegetation along the coast). Southwestern Ecuador and western Peru (Atacama Desert) in valleys with vegetation. Occasional records from the very wet Atlantic coast of Central America, where it overlaps the previous species, but it is not known if these records refer to this species, to wing pattern variants of *P. damo*, or to hybrids.

***Brangas* Hübner, [1819]**

type species: *Papilio caranus* Stoll

Dabreras Bálint, 2008, **New Synonym**

type species: *Thecla teucris* Hewitson

Brangas is characterized by eight synapomorphies (Table 1), but they are exceedingly tentative because we included only two *Brangas* species in the phylogenetic analyses. However, every *Brangas* species has a male genitalia dorsal vinculum process that lies under and inside of its associated brush organs, a trait that occurs nowhere else in the Eumaeini. There are sixteen described and three undescribed species of *Brangas*. The genus occurs from Mexico to southern Brazil and northern Argentina.

Robbins (2004b) placed *Thecla teucris* Hewitson in *Brangas* while Bálint & Faynel (2008) moved *Brangas teucris* to the monotypic genus *Dabreras*. *Brangas teucris* possesses a shallow hindwing anal lobe cleft similar to that in *Brangas*. Males of *B. teucris* have a male genitalia dorsal vinculum process that lies under and inside of its associated brush organs, as it does in *Brangas*. Finally, the genitalia of *B. teucris* and *B. rita* (Goodson) are almost indistinguishable.

Brangas teucris (Hewitson, 1868) (*Thecla*), type locality: Brazil

Distribution and Habitat. The Amazonian Region in wet lowland forest.

Brangas rita (Goodson, 1945) (*Thecla*), type locality: Colombia

Distribution and Habitat. Costa Rica to western Colombia and Ecuador in wet lowland forest.

Brangas dydimaon (Cramer, 1777) (*Papilio*), type locality: Surinam

Distribution and Habitat. The Amazonian Region in wet lowland forest.

Brangas neora (Hewitson, 1867) (*Thecla*), type locality: Guatemala

Distribution and Habitat. Mexico to southern Brazil in wet and dry lowland forest, occasionally occurring in montane habitats.

Brangas moserorum Bálint & Faynel, 2008, type locality: Brazil (SP)

Distribution and Habitat. Paraguay and southern Brazil, from MT, DF, and MG to RS.

Brangas coccineifrons (Godman & Salvin, 1887) (*Thecla*), type locality: Nicaragua; Colombia

Distribution and Habitat. Mexico to western Ecuador in wet lower montane forest, at lower elevations in the north.

Brangas torfrida (Hewitson, 1867) (*Thecla*), type locality: Brazil (PA)

Distribution and Habitat. The Amazonian and Atlantic regions in wet lowland forest to lower montane forest.

Brangas carthaea (Hewitson, 1868) (*Thecla*), type locality: Mexico

Distribution and Habitat. Mexico to western Ecuador in wet montane forest, but at lower elevations in the north.

Brangas getus (Fabricius, 1787) (*Papilio*), type locality: Surinam, repl. name

pelops (Stoll, 1781) (*Papilio*), type locality: Surinam, preocc. (not Drury, 1773)

Distribution and Habitat. Mexico to Argentina, Paraguay, and southern Brazil in wet and dry lowland forest.

Brangas caranus (Stoll, 1780) (*Papilio*), type locality: Surinam

Distribution and Habitat. From western Ecuador to French Guiana, south to southern Brazil (ES) in wet lowland forest.

Brangas rambutorum Bálint & Faynel, 2008, type locality: Colombia

Distribution and Habitat. Venezuela and Colombia in dry forest.

Brangas neildonatus Bálint & Faynel, 2008, type locality: Venezuela

Distribution and Habitat. Venezuela. Dry lowland forest along the Venezuelan northern coast.

Brangas silumena (Hewitson, 1867) (*Thecla*), type locality: ?

Distribution and Habitat. Paraguay and Brazil from RJ to RS in montane forest, but at lower elevations in the south.

Brangas felderi (Goodson, 1945) (*Thecla*), type locality: Colombia; Ecuador

contrastus Bálint, 2008, **New Synonym**, type locality: Ecuador

Distribution and Habitat. Colombia to Peru in montane forest.

Synonymy. The differences between *B. felderi* and *B. contrastus* mentioned by Bálint (width of the dorsal forewing border, amount of ventral blue iridescence) represent a small part of continuous variation in the series of more than 25 males that we have examined from eastern Ecuador.

Brangas polonus Bálint, 2008, type locality: Peru

Distribution and Habitat. Peru to Bolivia in montane forest.

Brangas insolitus Bálint & Faynel, 2008, type locality: Peru

Distribution and Habitat. Ecuador to Peru in montane forest.

***Atlides* Hübner, [1819]**

type species: *Papilio halesus* Cramer

Riojana d'Abrera & Bálint, 2001, ICZN Opinion 2358 (2015)

type species: *Thecla thargelia* Burmeister

Atlides in the phylogenetic results is characterized by five synapomorphies (Table 1), but as with *Brangas*, they are tentative because we included only three *Atlides* species in the phylogenetic analyses. A double scent pad in the discal cell (Fig. 11) is a trait that appears to be unique to *Atlides*, but we do not yet know if it is a synapomorphy. The type species of *Atlides* and *Riojana* share this trait.

There are eighteen described and four undescribed species in *Atlides*. The species *A. halesus* is unique in the *Atlides* Section in that it occurs widely in the temperate parts of North America (south in the mountains to Costa Rica). *Atlides thargelia* occurs widely in subtropical parts of southern South America.

Atlides and *Brangas* have traditionally been considered close relatives because of ventral wing pattern similarity (Draudt 1919–1920). The results in Quental (unpublished dissertation) and here support a sister group hypothesis. However, because the taxon sampling for this paper was incomplete for *Atlides* and *Brangas*, it is yet premature to conclude whether the wing pattern similarities between these two genera are due to inheritance from a common ancestor or to convergence.

Atlides halesus (Cramer, 1777) (*Papilio*), type locality: USA (VA)

dolichus Hübner, [1819], type locality: ?, nom. nud.

dolichos Hübner, 1823, type locality: USA (GA)

juanita (Scudder, 1868) (*Thecla*), type locality: USA (FL)

cynara (Godman & Salvin, 1887) (*Thecla*), type locality: Mexico (OAX)

corcorani Gunder, 1934, type locality: USA (CA)

described as *Atlides halesus* tr. f. *corcorani*.

estesi Clench, 1942, type locality: USA (CA)

described as *Atlides halesus corcorani* f. *estesi*.

Distribution and Habitat. Temperate parts of the United States to Mexico, south in the mountains to Guatemala and Costa Rica.

Atlides gaumeri (Godman, 1901) (*Thecla*), type locality: Mexico (YUC)

Distribution and Habitat. Mexico to Panama in deciduous forest.

Atlides polybe (Linnaeus, 1763) (*Papilio*), type locality: ["Indiis"], an incorrect type locality.

Distribution and Habitat. Mexico to southern Brazil in wet and dry lowland forest, occasionally in lower montane forest.

Atlides dahnersi Bálint, Constantino & K. Johnson, 2003, type locality: Colombia

Distribution and Habitat. Western Colombia in montane forest.

Atlides carpophora (Hewitson, 1868) (*Thecla*), type locality: Mexico.

- Distribution and Habitat.** Mexico to western Ecuador in forest in both lowlands and lower montane forest. Northern Venezuela to eastern Peru in lower montane and montane forest.
- Atlides inachus* (Cramer, 1775) (*Papilio*), type locality: "West Indies", an incorrect type locality.
baeton (Sepp, [1829]) (*Papilio*), type locality: Surinam
- Distribution and Habitat.** The Amazonian Region in wet lowland forest.
- Atlides cosa* (Hewitson, 1867) (*Thecla*), type locality: ?
- Distribution and Habitat.** Eastern Brazil from BA to RS in lowland and montane forest.
- Atlides misma* D'Abrera, 1995, type locality: Brazil (PR)
- Distribution and Habitat.** Eastern and central Brazil from DF and PE to RS in lowland and montane forest.
- Atlides atys* (Cramer, 1779) (*Papilio*), type locality: Surinam
scamander Hübner, [1819], type locality: Surinam, repl. Name
- Distribution and Habitat.** Costa Rica to southern Brazil in wet lowlands.
- Atlides halljasoni* Bálint, Kertész, & Wajtusiak, 2006, type locality: Ecuador
- Distribution and Habitat.** Colombia to Peru in wet montane forest.
- Atlides bacis* (Godman & Salvin, 1887) (*Thecla*), type locality: Panama
vulnerata (Staudinger, 1888) (*Thecla*), type locality: Colombia
melidor (H.H. Druce, 1909) (*Thecla*), type locality: Peru
- Distribution and Habitat.** Costa Rica to southern Brazil in wet lowlands.
- Atlides carpasia* (Hewitson, 1868) (*Thecla*), type locality: Mexico
- Distribution and Habitat.** Mexico to Panama in lower montane forest, at lower elevations in the north.
- Atlides browni* Constantino, Salazar & K. Johnson, 1993, type locality: Colombia
centralis Salazar & Henao, 2004, **New Synonym**, type locality: Colombia
described as *Atlides browni centralis*.
- Distribution and Habitat.** Colombia and Ecuador in montane forest.
- Synonymy.** A biological hypothesis that *A. centralis* is a distinct geographic form is premature because there are only two known males of the "*centralis*" phenotype.
- Atlides rustan* (Stoll, 1790) (*Papilio*), type locality: "China", an incorrect type locality.
macaria (Swainson, 1822) (*Thecla*), type locality: Brazil (PE)
- Distribution and Habitat.** Mexico to southern Brazil in wet and dry lowland forest, up to lower montane forest.
- Atlides polama* (Schaus, 1902) (*Thecla*), type locality: Brazil (PR; RJ)
- Distribution and Habitat.** Eastern Brazil from MG to SC in montane forest.
- Atlides havila* (Hewitson, 1865) (*Thecla*), type locality: Colombia
- Distribution and Habitat.** Colombia to Peru in montane (usually dry) forest.
- Atlides zava* (Hewitson, 1878) (*Thecla*), type locality: ?
iracema (J. Zikán & W. Zikán, 1968) (*Thecla*), type locality: Brazil (RJ; MG), nom. nud.
striata (Bálint, K. Johnson & Kroenlein, 1998) (*Denivia*), type locality: Brazil (SP), **new synonym**
ponsanota (Bálint, K. Johnson & Kroenlein, 1998) (*Denivia*), type locality: Brazil (SP), **new synonym**
- Distribution and Habitat.** Eastern Brazil from MG to SC in montane forest.
- Synonymy.** The male holotypes of *striata* and *ponsanota* have a double discal cell scent pad, a trait that is restricted to *Atlides*. Their description in *Denivia* was incorrect. We find no characters to differentiate these holotypes from *A. zava*.
- Atlides thargelia* (Burmeister, 1878) (*Thecla*), type locality: Argentina
- Distribution and Habitat.** Bolivia to Uruguay in subtropical forest.

***Denivia* K. Johnson, 1992**

type species: *Thecla deniva* Hewitson

Denivia consists of fifteen Neotropical species and one species provisionally placed here. Some lowland species are common in museum collections, such as *D. hemon* (Fig. 20), and some are rare, such as *D. acontius*. Similarly,

some montane species are common in museum collections, such as *D. monica*, and some are relatively rare, such as *D. curitabaensis*. *Denivia lisus* and *D. hemon* are widespread, occurring from Mexico to southern Brazil. Within *Denivia*, the female of *D. hemon* is the only one that is entirely brown dorsally and ventrally, so that it resembles females of *Theritas*.

Denivia in the results is characterized by a membranous area in the female ductus bursae (Table 1, Figs. 18–19). Although the occurrence of this character is homoplastic, *Denivia* is monophyletic in all analyses. There is no evident way to divide the genus into better-supported genera. The original description of *Denivia* (Johnson 1992) included species that are currently placed in *Denivia*, *Lucilda*, and *Atlides*, but most of the species listed below have not previously been placed in *Denivia*.

The most conspicuous trait of *Denivia* is the dorsal forewing scent patch in which neutral-colored androconia are intermixed with iridescent blue wing scales (Fig. 20). According to Martins *et al.* (2018) (Fig. 8), this trait evolved within *Denivia* and was lost evolutionarily once.

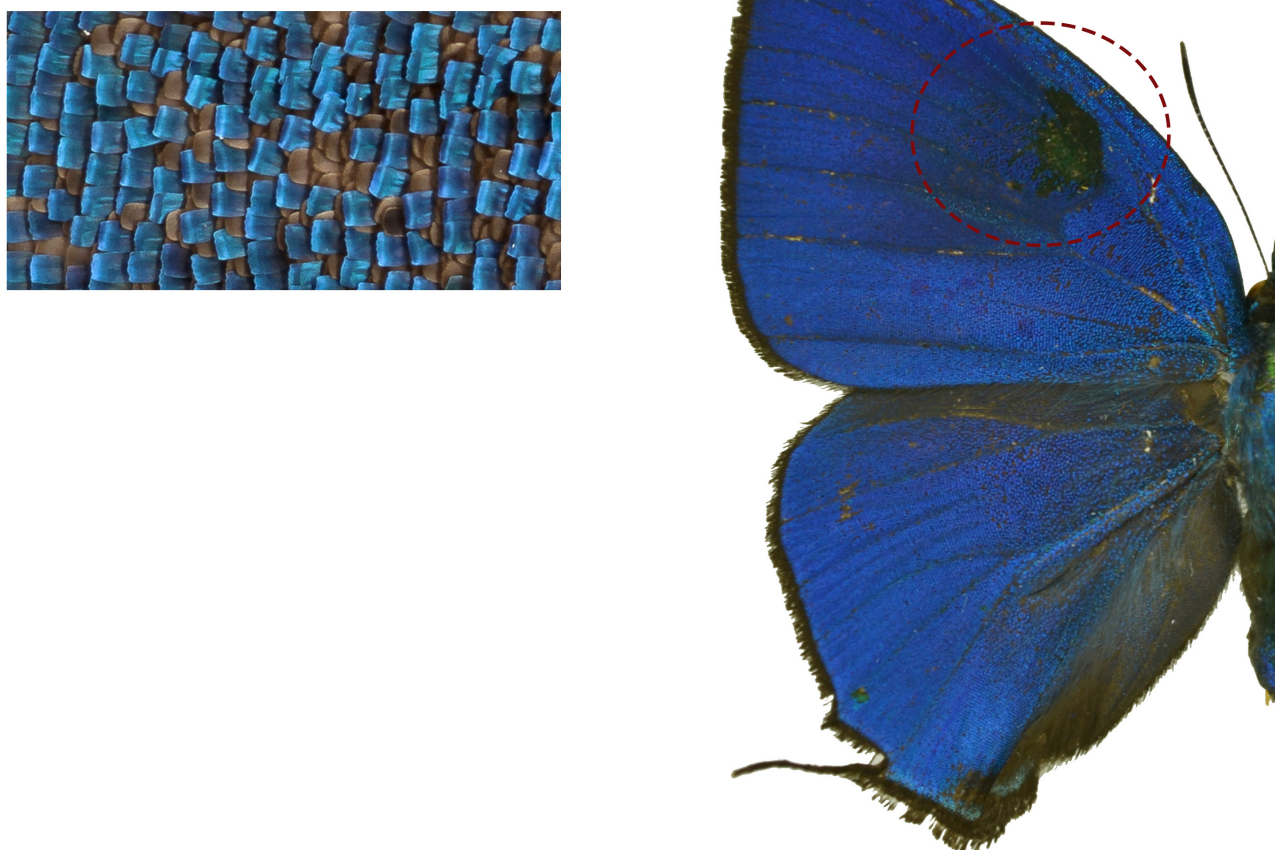


FIGURE 20. Scent patch of *Denivia hemon* scent patch. Note tan colored androconia mixed with iridescent blue wing scales.

Denivia deniva (Hewitson, 1874) (*Thecla*), type locality: Brazil

maggae K. Johnson, 1992, type locality: Argentina

grava Bálint, K. Johnson & Kroenlein, 1998, type locality: Brazil (SP), **new synonym**

Distribution and Habitat. Argentina and Southern Brazil from MG and ES to SC in lowland and lower montane wet forest.

Synonymy. *Denivia grava* was mistakenly placed as a synonym (Robbins 2004) of the following species. The jagged hindwing outer margin of the holotype is the reason for its placement here.

Denivia curitabaensis (K. Johnson, 1992) (*Radissima*), type locality: Brazil (PR), **New Combination**

Distribution and Habitat. We have seen three museum specimens of this species from the plateau in central PR and the mountains of SP. It is recorded further south in RS (Giovenardi *et al.* 2008; Iserhard *et al.* 2010),

but we have not seen the specimens on which these records are based. *Denivia curitabaensis* is a poorly known species that may be easily confused with *D. deniva*. It differs in lacking the jagged hindwing outer margin of *D. denivia*.

Denivia augustinula (Goodson, 1945) (*Thecla*), type locality: Costa Rica, **New Combination**

augustinula (Strand, 1916) (*Thecla*), type locality: Costa Rica

described as *Thecla augustula* ab.? *augustinula*.

Distribution and Habitat. Mexico to northern Colombia in wet lower montane forest, but at lower elevations to the north.

Denivia theocritus (Fabricius, 1793) (*Hesperia*), type locality: "Indiis", an incorrect type locality, **New Combination**

nepia (Godman & Salvin, 1887) (*Thecla*), type locality: Guatemala; Nicaragua; Panama

Distribution and Habitat. Mexico to western Ecuador in lowland forest. Specimens from eastern Colombia and Ecuador have larger spots on the ventral wings.

Denivia augustula (W.F. Kirby, 1877) (*Thecla*), type locality: Costa Rica, repl. name, **New Combination**

augustinus (Butler & H. Druce, 1872) (*Mithras*), type locality: Costa Rica, preocc. (not Westwood, 1852) (ICZN Art. 59.3)

Distribution and Habitat. Costa Rica and Panama to western Ecuador in lower montane forest.

Denivia arene (Goodson, 1945) (*Thecla*), type locality: Peru, **New Combination**

Distribution and Habitat. Ecuador and Peru in montane forest.

Denivia monica (Hewitson, 1867) (*Thecla*), type locality: Venezuela, **New Combination**

crinella (Strand, 1918) (*Thecla*), type locality: Ecuador

described as *Thecla crines* var. ? *crinella*.

electryon (Goodson, 1945) (*Thecla*), type locality: Ecuador; Peru; Colombia

Distribution and Habitat. Venezuela to Bolivia in lower montane and montane forest.

Denivia hemon (Cramer, 1775) (*Papilio*), type locality: Surinam, **New Combination**

acmon (Cramer, 1775) (*Papilio*), type locality: Surinam

aemon (Cramer, 1776) (*Papilio*), type locality: Surinam, missp.

gispa (Hewitson, 1865) (*Thecla*), type locality: Brazil ([PA])

callirrhoe (Goodson, 1945) (*Thecla*), type locality: ?

Distribution and Habitat. Everywhere in Neotropical continental forests below 1,000 m elevation.

Denivia phegeus (Hewitson, 1865) (*Thecla*), type locality: Brazil (BA); Amazon, **New Combination**

laudonia (Hewitson, 1867) (*Thecla*), type locality: Brazil

Distribution and Habitat. The Amazonian Region to southern Brazil (RJ) in wet lowland forest.

Denivia acontius (Goodson, 1945) (*Thecla*), type locality: Colombia, **New Combination**

Distribution and Habitat. Panama south to the Amazonian Region in wet lowland forest.

Denivia chaluma (Schaus, 1902) (*Thecla*), type locality: Brazil (SC), **New Combination**

hamila (Jones, 1912) (*Thecla*), type locality: Brazil (PR)

secunda Bálint, K. Johnson & Kroenlein, 1998, type locality: Brazil (SP)

Distribution and Habitat. Central and southern Brazil from DF and ES to SC in lower montane and montane forest.

Denivia viresco (H.H. Druce, 1907) (*Thecla*), type locality: Brazil (MA), **New Combination**

photeinos (H.H. Druce, 1907) (*Thecla*), type locality: Guyana

Distribution and Habitat. Amazonian Region in wet and dry lowland forest.

Denivia silma (Martins, Faynel, & Robbins, 2016) (*Theritas*), type locality: French Guiana, **New Combination**

Distribution and Habitat. Amazonian Region south to Paraguay and Brazil (MG) in wet low land forest.

Denivia espiritosanto Bálint & Moser, 2007, type locality: Brazil (RJ)

Distribution and Habitat. Eastern Brazil from RJ to SC in wet lowland forest up to 800 m elevation.

Denivia lisus (Stoll, 1790) (*Papilio*), type locality: Surinam, **New Combination**

orsina (Hewitson, 1877) (*Thecla*), type locality: Bolivia

hisbon (Godman & Salvin, 1887) (*Thecla*), type locality: Guatemala; Costa Rica; Panama

Distribution and Habitat. Mexico to southern Brazil in wet and dry lowland forest, occasionally in lower montane forest.

Denivia adamsi (H.H. Druce, 1909) (*Thecla*) (generic placement uncertain), type locality: Peru

Distribution and Habitat. Presumably lower montane or montane forest.

Generic Placement. We were unable to examine the male holotype of *Thecla adamsi* Druce for this project. We know of no other male museum specimen. Based on its ventral wing pattern, this species is tentatively placed in *Denivia* so that it has a generic name.

Excluded from the *Atlides* Section. *Thecla anna* Druce “belongs to a group by itself” (Druce 1907: 39) and has been described as “an entirely isolated animal” (Draudt 1919–1920: 750). Robbins (2004b) provisionally placed it in *Theritas* based on superficial similarities in brush organ structure. Balint *et al.* (2006) removed it from the *Atlides* Section because it lacked a hindwing anal cleft. This species did not cluster with the *Atlides* Section in an exemplar phylogeny based on DNA sequences (Quental, unpublished dissertation). There is no compelling evidence of which we are aware that it belongs to the *Atlides* Section.

Conclusion

This paper provides the first classification of the *Atlides* Section based on phylogenetic analyses, in accord with the general lycaenid taxonomic scheme in Eliot (1973). It provides character evidence for the scattered historical remarks suggesting relationships among the included taxa (Godman & Salvin 1887–1901; Clench 1964; Nicolay 1971). For the first time, genera are characterized using phylogenetic evidence. The new classification of the *Atlides* Section is now updated with a considerable amount of data on distribution and habitat.

Acknowledgements

We thank the São Paulo Research Foundation – FAPESP, Brazil (grants: 2002/13898–0, 2010/14682–8, 2011/50225–3, 2012/03854–8, 2013/00952–1 and 2016/50384–8) and the National Council for Scientific and Technological Development - CNPq/Brazil (grants: 563332/2010–7, 305905/2012–0 and 311083/2015–3) for financial support.

We are grateful to R.C. Busby, D. Dolibaina, C. Faynel, L. Gibson, J. Glassberg, G. Lamas, and M. McInnis for providing specimens, information, images, and/or specimen loans. For reviewing the manuscript, in whole or part, with great insight, we thank R.C. Busby, C. Faynel, M. Greenfield, G. Lamas, K. Willmott, and an anonymous reviewer. For specific help with nomenclature, we are grateful to C. Faynel and G. Lamas. For technical assistance, we acknowledge Karie Darrow, Brian Harris, Renato Oliveira, and Scott Whittaker. We acknowledge the Hennig Society for making TNT software freely available. We are very grateful to all museum curators who provided access to collections. Thanks to D. Grimaldi from the American Museum of Natural History (New York - USA), B. Huertas from the Natural History Museum (London, UK), M. M. Casagrande from the Universidade Federal do Paraná (Curitiba, Brazil), J. M. Costa from the Fundação Instituto Oswaldo Cruz (Rio de Janeiro, Brazil), M. M. Barrios from the Museu Nacional (Rio de Janeiro, Brazil), J. Clavijo from the Museo del Instituto de Zoología Agrícola (Maracay, Venezuela), G. Lamas from the Museo de Historia Natural (Lima, Peru), and R. C. Busby for access to his private collection (Andover, USA).

Literature cited

- Austin, G.T., Miller, L.D. & Miller, J.Y. (2007) Taxonomic comments on *Pseudolycaena* Wallengren (Lepidoptera: Lycaenidae: Theclinae: Eumaeini). *Bulletin of the Allyn Museum*, 149, 1–22.
- Bálint, Z. (2002) Miscellaneous notes on *Arcas* Swainson, 1832 (Lepidoptera: Lycaenidae, Eumaeini). *Annales Historico-Naturales Musei Nationalis Hungarici*, 94, 141–161.
- Bálint, Z. (2006) *Arcas* Swainson, 1832 is revisited: review of some species-group names, identification of the sister group and a key for species (Lepidoptera, Lycaenidae: Eumaeini). *Annales Historico-Naturales Musei Nationalis Hungarici*, 98, 147–158.
- Bálint, Z. & Faynel, C. (2008) Review of the genus *Brangas* Hübner, 1819 (Lepidoptera: Lycaenidae) with description of a new genus. *Annales Historico-Naturales Musei Nationalis Hungarici*, 100, 271–306.

- Brown, K.S. (1982) Historical and ecological factors in the biogeography of aposematic neotropical butterflies. *American Zoologist*, 22, 2, 453–471.
<https://doi.org/10.1093/icb/22.2.453>
- Clench, H.K. (1964) A synopsis of the West Indian Lycaenidae with remarks on their zoogeography. *Journal of Research on the Lepidoptera*, 2 (4), 247–270.
- Cong, Q., Shen, J., Borek, D., Robbins, R.K., Opler, P.A., Otwinowski, Z. & Grishin, N.V. (2017) When COI barcodes deceive, complete genomes reveal introgression in hairstreaks. *Proceedings of the Royal Society B*, 284, 20161735.
<https://doi.org/10.1098/rspb.2016.1735>
- Draudt, M. (1919–1920) Theclini F. In: Seitz A (Ed.), *Die Gross-Schmetterlinge der Erde, Vol. 5. Die amerikanischen Tagfalter*. Alfred Kernen, Stuttgart, pp. 744–812.
- Druce, H.H. (1907) On Neotropical Lycaenidae, with descriptions of new species. *Proceedings of the Zoological Society of London*, 1907, 566–632.
- Eliot, J.N. (1973) The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. *Bulletin of the British Museum (Natural History) Entomology*, 28, 371–505.
<https://doi.org/10.5962/bhl.part.11171>
- Giovenardi, R., Di Mare, R.A., Sponchiado, J., Roani, S.H., Jacomassa, F.A.F., Jung, A.B. & Porn, M.A. (2008) Diversidade de Lepidoptera (Papilionoidea e Hesperioidea) em dois fragmentos de floresta no município de Frederico Westphalen, Rio Grande do Sul, Brasil. *Revista Brasileira de Entomologia*, 52 (4), 599–605.
<https://doi.org/10.1590/S0085-56262008000400010>
- Godman, F.D. & Salvin, O. (1887–1901) *Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera. Fam. Lycaenidae*. London, Dulau & Co., Bernard Quaritch, 2, 112 pp.
- Iserhard, C.A., Quadros, M.T., Romanowski, H.P. & Mendonça Jr, M.S. (2010) Borboletas (Lepidoptera: Papilionoidea e Hesperioidea) ocorrentes em diferentes ambientes na Floresta Ombrófila Mista e nos Campos de Cima da Serra do Rio Grande do Sul, Brasil. *Biota Neotropica*, 10 (1), 309–320.
<https://doi.org/10.1590/S1676-06032010000100026>
- Johnson, K. (1992) Genera and species of the Neotropical "elfin"-like hairstreak butterflies (Lepidoptera, Lycaenidae, Theclinae). *Reports of the Museum of Natural History, University of Wisconsin (Stevens Point)*, 22 (1), 1–279.
- Martins, A.R.P., Faynel, C. & Robbins, R.K. (2016) Variation of male secondary sexual structures and the taxonomy of *Theritas lisus* and relatives (Lepidoptera, Lycaenidae, Eumaeini). *Proceedings of the Washington Entomological Society*, 118 (4), 555–573.
<https://doi.org/10.4289/0013-8797.118.4.555>
- Martins, A.R.P., Duarte, M. & Robbins, R.K. (2018) Evolution of male secondary sexual organs in hairstreak butterflies (Lepidoptera, Lycaenidae). *Cladistics*, 1–25.
- Nicolay, S.S. (1971) A review of the genus *Arcas* with descriptions of new species (Lycaenidae, Strymonini). *Journal of the Lepidopterists' Society*, 25 (2), 87–108.
- Quental, T.B. (2008) *Systematics, sexual selection and evolution of secondary sexual characters in Neotropical Eumaeini butterflies (Lepidoptera: Lycaenidae)*. Dissertation, Harvard University, 226 pp.
- 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*. Association for Tropical Lepidoptera, Scientific Publishers, Gainesville, pp. xxiv–xxx.
- 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*. Association for Tropical Lepidoptera, Scientific Publishers, Gainesville, pp. 118–137.
- Robbins, R.K., Martins, A.R., Busby, R.C. & Duarte, M. (2012) Loss of male secondary sexual structures in allopatry in the Neotropical butterfly genus *Arcas* (Lycaenidae: Theclinae: Eumaeini). *Insect Systematics & Evolution*, 43 (1), 35–65.
<https://doi.org/10.1163/187631212X626195>
- West-Eberhard, M.J. (1983) Sexual selection, social competition, and speciation. *The Quarterly Review of Biology*, 58 (2), 155–183.
<https://doi.org/10.1086/413215>