

COMMENTS ON THE SYSTEMATICS AND NATURAL
HISTORY OF AVEEXCRENOTA, A GENUS OF RARE ANDEAN
EUMAEINE LYCAENIDAE (LEPIDOPTERA)

BÁLINT, ZS.¹, BOYER, P.², DAHNERS, H. W.³, SALAZAR-ESCOBAR, J. A.⁴ & KERTÉSZ, K.⁵

¹*Department of Zoology, Hungarian Natural History Museum
H-1088 Budapest, Baross utca 13, Hungary, E-mail: balint@nhmus.hu*

²*Lotissement l'Horizon, Le Puy Sainte Réparate, F-13610, France*

³*Universidad del Valle, Departamento de Ciencias Fisiológicas, A. A. 25.360, Cali, Colombia*

⁴*Colección de Historia Natural, Universidad de Caldas
Sede Central, Calle 65, No. 26–10, Manizales, Colombia*

⁵*Research Institute for Technical and Materials Science, Hungarian Academy of Sciences
H-1121 Budapest, Konkoly Thege út 29–33, Hungary*

The original description and type material of the nominal taxon *Thecla anna* DRUCE, 1907 has been investigated. The specimen which served as the basis for the original description is holotype by monotypy. The figure accompanying the original description is partly hypothetical, and actually resembles the female phenotype, which has been discovered almost one century later. The nominal taxon *Aveexcrenota mimianna* SALAZAR et JOHNSON, 1997 proved to be a junior synonym of *A. anna*, which has been hitherto reported only from the Colombian Andes. Recently *Aveexcrenota* has been found also in Ecuador and Peru. The only known Peruvian specimen (from departament Amazonas, Pomachocha) is diagnosed on the basis on qualitative and quantitative wing characters. The genus *Aveexcrenota* SALAZAR et JOHNSON, 1997 (type species: *Thecla anna* DRUCE, 1907, by original designation) seems to be most closely related to the monotypic Pan-American *Evenus* HÜBNER, 1818 based on wing spectral and internal structural characters. Previous placements in “*Thecla*” or “*Theritas*” are considered unsupported by current evidence. The hypothetical cladogram for the *Evenus* genus group is given on the basis of wing androconia, color, pattern and shape characters considered apomorphies or synapomorphies. The clade of *Thecla coronata* HEWITSON, 1865 is diagnosed as *Suneve* BÁLINT, **gen. n.** The males of *A. anna* are hilltoppers, where females may be also found. They are reported from virgin cloud forests between 1800–2300 m in the Cordillera Occidental (Cali) and the Cordillera Central (Manizales) of Colombia throughout the year having one flight peak in temporal distribution.

Key words: *Evenus* genus group, genera, spectral reflectance, Eumaeini, Andes

INTRODUCTION

The nominal species *Thecla anna* was described from Colombia (H. H. DRUCE 1907). The phenotype of the species is so unusual amongst South American eumaeine lycaenids that DRAUDT (1919) erected a monotypic group for it. Almost a century then passed before the species was collected again (SALAZAR 1993).

When new material turned up, SALAZAR and JOHNSON (1997) erected the genus *Aveexcrenota* with the type species *Thecla anna*. They also described a sister species, *A. mimianna*, which they considered synchronic and sympatric with the type species of *Aveexcrenota*. The females of the taxa remained unknown at that time. In giving such a “smelly” generic name for such a beautiful species, SALAZAR and JOHNSON wanted to stress their hypothesis that both *A. anna* and *A. mimianna* possess a kind of cryptic hind wing ventral pattern which mimics bird droppings. Subsequent to the paper of SALAZAR and JOHNSON the female of *A. anna* was collected and described (SALAZAR 2000) and the female of *A. mimianna* also figured (SALAZAR 2002).

In a checklist concerning *Aveexcrenota anna* ROBBINS (2004) proposed the following, without any comment or supportive data. (1) He synonymized *Aveexcrenota* with *Theritas* HÜBNER, 1818 (type species: *Theritas mavors* HÜBNER, 1818). (2) He presented the new combination *Theritas anna* (DRUCE, 1907). (3) He considered *Aveexcrenota mimianna* as junior synonym of *Theritas anna*. (4) He placed *Theritas anna* between the taxa *Theritas adamsi* (DRUCE, 1909) [new, unjustified combination] and *Theritas hemon* (CRAMER, 1775) d’ABRERA, 1995 [new combination].

The aim of the present paper is to: (1) review the nomenclature and type material of *Thecla anna*; (2) address the taxonomic validity of the putative sister species *A. mimianna* based on a material larger by one magnitude (see Appendix) and characterize the Peruvian population by wing pattern and spectroscopic characters; (3) review whether previous and most recent systematic placements of the species reflect probable phylogenetic relationships; and (4) summarize experience with the species from the field, reporting briefly on the behaviour, flight period, habitat and lycaenid butterfly community of *A. anna*.

MATERIALS AND METHODS

We approach the subject taxon by applying traditional as well as new methods. We discriminate it from related taxa and hypothesize its phylogenetic relationship by reference, among other things, to scale nanostructures (how its wings manipulate light, an essential element in life) and how adults interact with their environment, enhancing their fitness (BÁLINT *et al.* 2005a, b).

We have examined 71 male and 2 female *Aveexcrenota* individuals. In descriptive text, with regard to dissecting and microscopic investigations, we use and apply traditional lepidopterological terminology (KUDRNA 1991) and methods (WINTER 2000). Through facilities at his scientific institute, novel spectroscopic investigations were carried out by K. KERTÉSZ using an Avantes 2048 fiber optic spectrometer in the ultraviolet – visual – near infrared range (200–1000 nm). Measurements were taken from the left forewing dorsal discal centre of every individual sample in normal incidence. Material examined for comparative and spectroscopic studies is listed in the Appendix.

Throughout the text we use the following abbreviations (listed in alphabetical order; curators of the museums involved are listed and acknowledged here): BMNH = The Natural History Museum, (London, UK: Mrs KIM GOODGER and Mr PHILLIP ACKERY), CHD = collection of HANS DAHNERS (Cali, Colombia), CJS = collection of JULIAN SALAZAR-ESCOBAR (Manizales, Colombia); HNHM = Hungarian Natural History Museum (Budapest, Hungary), NMW = Naturhistorisches Museum (Wien, Austria: Drs SABINE GAÁL-HASZLER and MARTIN LÖDL), PBC = collection of PIÉRRÉ BOYER (Sainte Réparate, France), ZSM = Zoologische Staatssammlung des Bayerischen States (München, D: Dr. AXEL HAUSMANN) and ICZN = International Code on Zoological Nomenclature (1999).

NOMENCLATURE AND TYPIFICATION

The nominal species *Thecla anna* was described by HAMILTON H. DRUCE on the basis of the male “Type” (= holotype by monotypy, ICZN 73.1.1.) taken in “Interior of Colombia” originating from “Wheeler”, and deposited in the “Museum Godman”. The holotype was figured in colour in plate 33 as fig. 2 showing in dorsal and ventral aspect. According to the figure, the “male” specimen possesses long tail-like projections at vein termini CuA1 and CuA2. However, DRUCE stated that the actual specimen was “worn toward the anal angle of the hind wing”; therefore the figure was obviously somewhat hypothetical. The butterflies of F. D. WHEELER were auctioned via the mercantile company C. J. STEVENS (HORN *et. al.* 1991: 420), so the specimen was almost certainly purchased by FREDERICK DU CANE GODMAN (1834–1919) in London in this manner. Subsequently the “type” was deposited in the BMNH as part of the GODMAN-SALVIN collection in 1919 as attested by one of the curatorial labels of the holotype (see Appendix).

In the SEITZ series – the figures supplemented as DRAUDT’s account (1919, plate 147, row d, figs. “anna”) – the dorsal and ventral figures provided for the original description were faithfully copied. Actually, DRAUDT probably did not read the original description since he wrote: “Sie (*Thecla anna*) tragen ziemlich lange und breite Schwänze” (= They (*Thecla anna*) bear rather long and broad tails) (translated by Zs. B.).

The holotype was first catalogued in the BMNH as “B.M. Type No. Rh. 531” by FREDERICK W. GOODSON (1945) (BÁLINT 2005*a*), then figured in colour by d’ABRERA (1995). This individual specimen is in good condition contradicting the statement of DRUCE who stated that it is worn. The HNHM possesses by donation an almost identical specimen from Colombia. In any event, DRUCE’s suspicion that the vein termini lack tails led to a misleading supposition, guiding the artist to “supplement” supposedly broken parts of the wings. Subsequent to the figure of d’ABRERA, the holotype was dissected in the early 1990s by KURT JOHNSON and the structures were illustrated (SALAZAR & JOHNSON 1997: fig. 1a), thus demonstrating that the holotype is indeed a male as DRUCE stated.

All the males collected recently perfectly match the type figured (Fig. 1). Therefore DRUCE was mistaken in considering that it is a worn male specimen. The supposition that the original specimen was probably a female (J. SALAZAR, *pers. comm.*), because the holotype was shown as tailed in the original figures, can also now be dismissed since there was no other “*Thecla anna*” specimen in the GODMAN-SALVIN collection. Consequently, we are of the opinion that the specimen figured by d’ABRERA (1995: 1118) does represent the true holotype of *Thecla anna*.

The female of *Aveexcrenota anna* was discovered and figured in dorsal aspect by J. SALAZAR (2000, 2002). It is identical to the male in coloration and pattern but the hind wing vein CuA2 terminus possesses a tail of approximately 10 mm.

TAXONOMY

Aveexcrenota anna (DRUCE, 1907) (Figs 1–6)

Thecla anna DRUCE, 1907: 577, holotype male: “Interior of Colombia”, pl. 33, fig. 2 (holotype dorsum, ventrum colour drawings); DRAUDT 1919: 750, “Columbien”, pl. 147, row d, figs “anna” (reproduction of DRUCE’s drawings in colour); SALAZAR 1993: 48, “Cordilleras Occidental y Central Colombia” (fig. 6, male dorsum (Manizales) and ventrum (Riosucio) in half tone).

“*Thecla*” *anna* DRUCE, d’ABRERA 1995: 1118, figs (holotype dorsum, ventrum in colour), 1119 “Colombia”.

Aveexcrenota anna (DRUCE), SALAZAR & JOHNSON, 1997: 7–8, “Colombia: Caldas, Cerro Aguacatal (Riosucio), Quinchia Risaralda”, fig. 1a (holotype genital structures), photoplate xv/A (male dorsum, ventrum in colour); SALAZAR 2000: 103, “Caldas, Villamaría” and “Manizales city”; SALAZAR 2002: 213, “Aguacatal, Caldas, Riosucio”, fig. 2 (female dorsum in half tone).

Aveexcrenota mimianna SALAZAR & JOHNSON, 1997: 8, holotype male: “Colombia, Dept. Caldas, Riosucio, Cerro Ingrumá, 2200 m”, photoplate XIII A, fig. G (holotype male dorsum and ventrum in half tone); SALAZAR, 2002: 213, “Aguacatal, Caldas, Riosucio”, fig. 2 (female dorsum in half tone), **syn. n.**

Theritas anna (DRUCE), ROBBINS, 2004: 120.

Aveexcrenota in Colombia (Figs 1–4)

In the material examined by SALAZAR & JOHNSON (1997) there are listed three specimens of *Aveexcrenota anna* (holotype and two new samples) and two *A. mimianna* (holotype plus one paratypic male) specimens. They distinguished *A. anna* and *A. mimianna* on the basis of the following characters. (1) Size: *A. anna* is slightly larger than *A. mimianna*. (2) Dorsal wing coloration: Dorsal wing colour is more aquamarine than green: *A. anna* (older specimens greener); dorsal ground



Figs 1–6. Recently collected *Aveexcrenota anna* (DRUCE, 1907) individuals. 1–2: male individual from Cali, Colombia (CHD), 1= in dorsal, 2= in ventral aspects. 3–4: female individual from Caldas, Colombia (CJS), 3 = in dorsal, 4 = ventral aspects (the individual is dissected; see fig. 9). 5–6: male individual from Amazonas, Peru (PBC): 5 = in dorsal, 6 = in ventral aspects

colour is more emerald green in fresh specimens: *A. mimianna*. (3) Ventral wing pattern: Hind wing ventral black blotches are interspersed most abundantly in the medial and submarginal area in *A. anna*; in contrary, on the hind wings blotches are abundant in distocostad on medial and submedial areas from cell Sc + R1 to M2, and appearing to form a line directed mediocostad then curves outwards cell M2, M1 and Sc+R1 in *A. mimianna*. (4) Male genital structures: The male genital capsules are differing in shape: *A. anna* with vinculum is sloped to saccus, while *A. mimianna* has an angled vinculum; *A. anna* valva shape is delicate, elongate and sculptured with shorter length to aedeagus and saccus compared to its congener; *A. mimianna* valva shape is robust, widely parabolic with longer length to aedeagus and saccus compared to its congener.

In our examined material we list 70 male (plus the holotype) individual specimens and two female individuals from Colombia (see Appendix). We came to the following conclusions (1): Within 58 specimens of *A. anna* from Cali (CHD) fore wing costal length is distributed between 15 and 22 mm with a mean = 20,0 mm and a SD = 1,3 mm. The distribution is skewed to the right with a symmetrical part between 18 and 22 mm and two dwarfs with values of 15 and 16 mm, respectively, lying more than three SD's below the mean. Therefore, size cannot be a distinguishing character between *anna* and *mimianna*. (2) Dorsal wing colour changes according to the angle of the falling light (a) if the angle is steep (more than 45 degrees) the scale structures generate greenish emerald green, (b) if the angle is flat (less than 45 degrees) the scale structures generate aquamarine blue. (3) On the basis of hind wing ventral pattern it is impossible to recognise any distinctive character, therefore this is certainly not diagnostic. The black elements of the hind wing pattern are rather variable, and almost all individuals differ somehow in this respect. (4) The genital valva in size shows intermediate figures comparing the figures of SALAZAR and JOHNSON (1997) regarding the length of aedeagus. We were not able find distinguishing characters. However, we were able to visualize the more robust *mimianna* habitus by pressing the dissected organ, or see the delicate shape emphasized for *anna* when the capsule was left untouched floating in glycerol on the microscopic slide.

In sum, ROBBINS' unsupported action has merit concluding that the nominal taxon *mimianna* is a junior subjective synonym of the nominal taxon *anna*. Therefore, we formalize here the synonymy *Thecla anna* H. H. DRUCE, 1907 = *Aveexcrenota mimianna* SALAZAR et JOHNSON, 1997, subjective junior synonym.

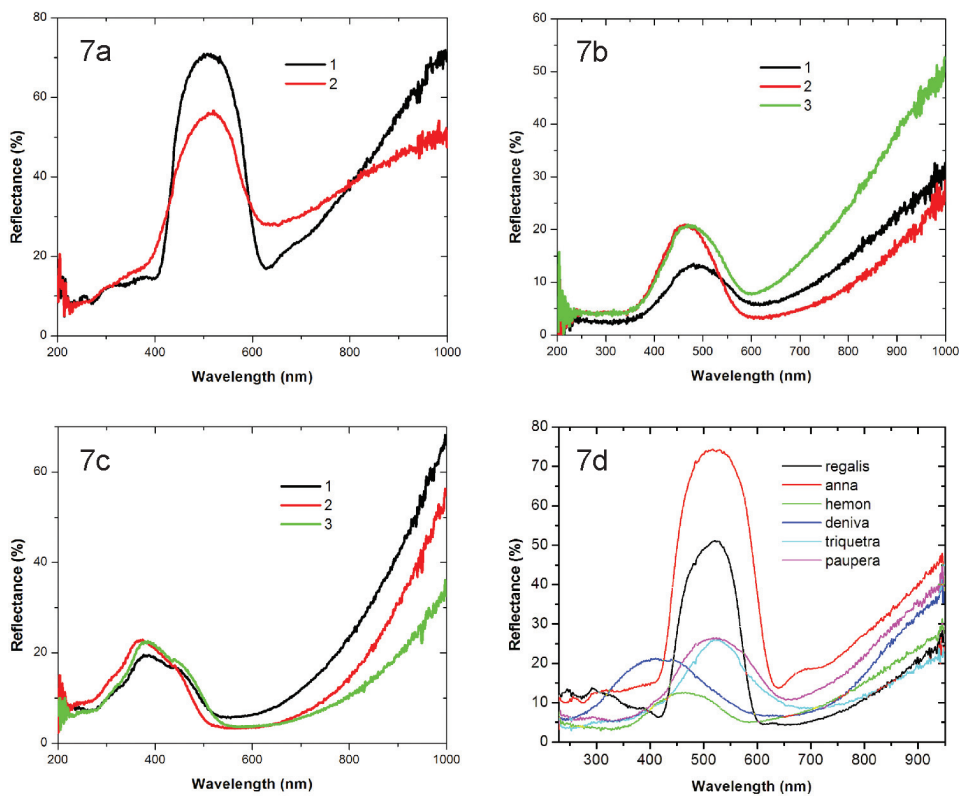
Aveexcrenota in Peru (Figs 5–6)

Hitherto, *A. anna* was exclusively known from a single Peruvian locality where the one male specimen was collected while hilltopping. We examined this specimen and were able to distinguish the following characters in comparison with Colombian individuals: (1) the fore wing cubital veins CuA1 and CuA2 are shorter in the Peruvian specimen than in *A. anna* resulting a different wing shape; (2) the dorsal hind wing antemarginal area in the Peruvian specimen between veins M3 and 1A+2A is blue, whilst this area in *A. anna* is black; (3) the presence of the postmedial line on the Peruvian specimen's fore wing verso is unique, none of our *A. anna* specimen possesses this conspicuous trait; (4) the yellow-brown blotches on the Peruvian specimen's hind wing verso are merged, creating a continuous pattern, whilst these blotches in *A. anna* are not so numerous and isolated; (5) the hind wing vein tails at vein CuA1 and CuA2 in the Peruvian specimen seems to be acute, while in *A. anna* they are more rounded, shovel-shaped; (6) and the dorsal structural colour displays different reflectivity in the Peruvian specimen than in *A. anna* from Columbia; indeed, the Peruvian specimen possesses distinctive qualities (Fig. 7a).

Character evaluation

(1): Different wing shape is often a useful character, especially when longer series are available. This was demonstrated for example for the genus *Paraspiculatus* JOHNSON et CONSTANTINO, 1997 (BÁLINT 2002, 2004). (2): The extension of dorsal hind wing black markings is also a helpful character, as it is most probably involved in thermal regulation (BÁLINT, *in prep.*). In the case of the genus *Thecloxurina* JOHNSON, 1992 species discrimination was based on this trait for one obvious case (BÁLINT & WOJTUSIAK 2003). However this trait most probably cannot be restricted to male individuals for discrimination, as *A. anna* females obviously possess it (*c.f.* Fig. 3). (3): The quantitative and qualitative aspects of the fore wing postmedial pattern are also important characters for species discrimination as is the case in many large eumaeine hairstreaks (*c.f.* BÁLINT 2005b). And, (4), (5): Characters based on hind wing blotch-pattern and tail-shape can be used only if fresh specimens are involved. One of the main characters of the subjective synonym *A. mimianna*, based on hind wing blotches, turned out to be erroneous and hind wing tails are often broken in museum specimens.

We were informed that specimens originating from eastern Ecuadorian populations (Morona-Santiago and Zamora-Chinchipe) share certain characters with the Colombian specimens while other characters are identical with the ones found in the Peruvian specimen (K. WILLMOTT, *pers. comm.*). However, since we were



Figs 7–8. 7 = Spectral reflectance of various eumane lycaenids: a = *Aveexcrenota* from Colombia (black) and from Peru (red); b = *Denivia hemon* (CRAMER, 1775) from Peru, San Martin (black) and Loreto (green), Costa Rica, Bugaba (red); c = *Thecloxurina chachapoya* BÁLINT et WOJTUSIAK, 2003 individuals from Peru, Amazonas, 3000 m (black and red) and Apurímac (green); d = species from genera *Aveexcrenota* (*anna*), *Denivia* (*deniva*, *hemon*), *Evenus* (*regalis*) and *Theritas* (*paupera*, *triquetra*). 8 = Male hind wing ventral androconia in Eumaeini: a = *Theritas mavors* HÜBNER, 1818, b = *Arcas imperialis* (CRAMER, 1775)

not able to study any Ecuadorian material, we were unable to make any conclusion on the taxonomic status of *Aveexcrenota* south of Colombia.

We hypothesize that the genus can be viewed as (1) monotypic, and its type species *A. anna* is a polytypic species of relatively wide distribution in the Andes from Colombia to Peru; or (2), polytypic with various populations representing allopatric sister taxa. This remains to be resolved.

SYSTEMATICS

Previous placements

The discoverer of “*Thecla anna*” placed the species between two distinctive, distantly related eumaeine lycaenids: *Thecla thara* HEWITSON, 1867 (present combination and placement: *Enos thara* (HEWITSON, 1867) JOHNSON, KRUSE & KROENLEIN, 1997) and *Thecla candor* DRUCE 1907 (present combination, placement and status: *Abloxurina amatista* (DOGNIN, 1895) (JOHNSON, 1992), emphasizing, regarding “*Thecla anna*”, that “this beautiful species is not nearly allied to any described and belongs to a group by itself” (DRUCE 1907: 577–578). Obviously, DRUCE did not consider *T. anna* as closely related to “large and showy” eumaeines like *Arcas* SWAINSON, 1832 (type species: *Papilio imperialis* CRAMER, 1775) and *Evenus* HÜBNER, 1819 (type species: *Papilio endymion* FABRICIUS, 1781 = *Papilio regalis* CRAMER, 1775) which were discussed much earlier in his paper (pp. 571–573).

Superficially it seems that DRAUDT (1919) was more attentive to relationships. DRAUDT moved *Thecla anna* creating the “13. Anna Gruppe” between his *Deniva*- and *Mavors*-groups indicating a closer relationship to these large eumaeines. It is worthwhile to mention that the terminal taxon of the “*Deniva*-group” is *Thecla zava* HEWITSON, 1874, placed before *A. anna* in the Draudtian system, and which possesses cryptic hind wing ventral patterns somewhat similar to that of *T. anna*. This system is clearly reflected in the BMNH general collection, where F. W. GOODSON curated “*Thecla anna*” between “*Theritas zava*” and “*Theritas mavors*” (d’ABRERA 1995: 1118–1119). Despite the fact that GOODSON diverged in many cases from the arrangements of DRAUDT (*c.f.* BÁLINT 2005), in this case it seems that the hypothesis of DRAUDT was clearly accepted. However, in modern view there is no supporting character for the tight (sister) relationship of these groups; the classification of DRAUDT was based purely on phenotypic (“Gestalt”) philosophy.

Salazar and Johnson's placement

According to the title of their paper SALAZAR and JOHNSON (1997) placed the genus *Aveexcrenota* in the “infratribe” *Macusiina* (JOHNSON *et al.* 1997), but the paper itself lacks any indication to the actual placement of *A. anna* in the “infratribe”.

Robbins' placement

Subsequently, *Macusiina* was regarded as a paraphyletic entity according to ROBBINS (2004: xxviii), who considered *Aveexcrenota* as junior synonym of *Theritas* and placed the nominal taxon *anna* into an unsupported new combination *Theritas anna* between *Theritas adamsi* (H. H. DRUCE, 1907) and *Theritas hemon* (CRAMER, 1775). The placement of ROBBINS suggests that the *Aveexcrenota* male has an androconial fold in the median part of their hind wing ventra in cell CuA1 and CuA2 (as documented by GODMAN & SALVIN 1887 and d' ABRERA 1995) as both, *adamsi* and *hemon*, possess this distinctive trait. But the taxon *anna* does not. Consequently, the three taxa do not represent monophyly or, alternately, the presence or absence of the hind wing androconial fold has no importance in the system of lycaenids, contrary to the general consensus among lepidopterists that androconia have great importance in classification (*c. f.* VANE-WRIGHT & BOPPRÉ 1993). Surveying the androconia of Riodinidae, considered as the sister group of Lycaenidae, HALL and HARVEY (2002: 192–193) wrote the following: “Once an androconial character is derived in a riodinid clade it seems to be rarely lost”. We hypothesise (see below), that the clade which includes *Aveexcrenota* never evolved androconia.

Actually, the taxa *adamsi* and *hemon* belong to the *hemon* species group of the genus *Denivia* JOHNSON, 1992 (type species: *Thecla deniva* HEWITSON, 1874, by original designation), which can be distinguished by the characters of a (1) male fore wing dorsal “visual brand” (*sensu* ELIOT 1973: 400) and (2) filamentous hind wing tails. All *Denivia* species possess the hind wing ventral androconial pouch (see above) plus a heavily sclerotized bipartite female anterior ductus with an assymmetrically spined anal terminus (Fig. 9d; *c. f.* JOHNSON 1992: Figs 236–239) (BÁLINT & MOSER, *in prep.*). *Aveexcrenota* does not share any of these characters with *Denivia*; therefore its placement between *adamsi* and *hemon* or as a species of *Theritas* *sensu* d' ABRERA or ROBBINS is not supported.

The placement of *Aveexcrenota* amongst the relatives of “*Theritas*” *sensu stricto* is also erroneous by the reasons we present in the following brief review. We characterize the genus *Theritas* by the presence of the male ventral hind wing androconial scales situated along the basal part of the cubital vein (Fig. 8a) plus a

long and straight tubular female genital ductus with simple anal terminus (Fig. 9c; c.f. JOHNSON 1992: Fig. 241). Certain *Theritas* taxa have an additional dorsal fore wing discoidal scent patch and/or pad. On the basis of the hind wing ventral androconia we consider *Arcas* SWAINSON, 1832 (type species: *Papilio imperialis* CRAMER, 1775) as sister group of *Theritas* (Fig. 8b). None of these characters we regard to be important are present in *Aveexcrenota*. Therefore, from this aspect *Theritas* sensu ROBBINS with *Denivia* and *Aveexcrenota* is polyphyletic, and does not reflect monophyly as it was contended (ROBBINS 2004: xxv). Moreover, we do not consider *Aveexcrenota* to be a taxon which belongs to the “*Atlides* Section” as defined by ROBBINS, characterized by having “the anal lobe cleft... (modified from GODMAN & SALVIN, 1887)”. *Aveexcrenota* has an anal lobe indeed, but that is not a cleft, which is an independent flap resulting from an extended hind wing vein according to our definition (ROBBINS did not give any). Because of its different form, with a remarkable larger tail, the *Aveexcrenota* hind wing anal lobe cannot be considered to have the same three dimensional termite-like shape imitating with two large eyes with antennae as the *Atlides* cleft (c.f. FAYNEL 2005: Fig.10). We consider this lobe as an analogy and not as homology, especially if we take into consideration that it is sexually dimorphic in *Aveexcrenota*. Consequently, we remove *A. anna* from the tentative “*Atlides* Section” of ROBBINS.

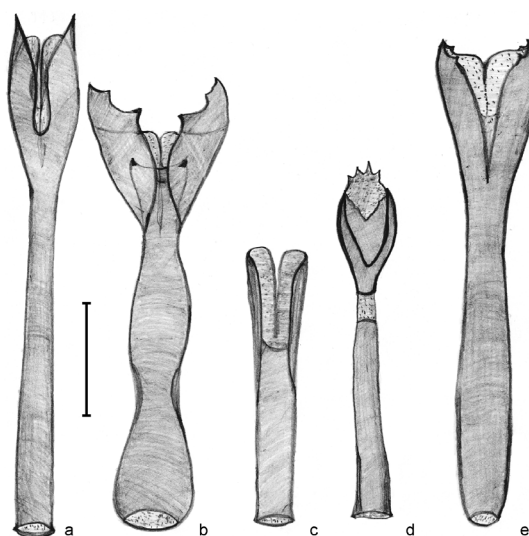


Fig. 9. Female genital ductus of eumaeine lycaenids in ventral aspect: a = *Aceexcrenota anna* (DRUCE, 1907) (gen. prep. BÁLINT, HNHM 998), b = *Evenus regalis* (CRAMER, 1775) (gen. prep. BÁLINT, HNHM 886), c = *Theritas mavors* HÜBNER, 1818 (gen. prep. BMNH 5792), d = *Denivia hemon* (CRAMER, 1775) (gen. prep. BÁLINT, HNHM 1087), e = *Suneve coronata* (HEWITSON, 1865) (gen. prep. BÁLINT HNHM 1088). Same magnification (scale bar = 1 mm)

Aveexcrenota as valid genus

We consider *Aveexcrenota* as a valid genus according to the following characters: (1) sexual dimorphism marked by considerable longer extension of female vein terminus CuA₂, (2) hind wing ventral pattern cryptic with heavy black mottled melanization with a white or yellow discoidal patch. Both characters are unique in the tribe. Regarding character (1), sexually dimorphic vein termini are present in many qualitatively different cases in the tribe. For example genus *Pons* JOHNSON, 1992 (Type species: *Pons magnifica* JOHNSON, 1992) possesses non-tailed males with large anal lobe but two-tailed females (*c.f.* “browni-group” in HALL *et al.* 2005); or genus *Trichonis* HEWITSON, 1865 (type species: *Papilio theanus* CRAMER, 1777), where males are tailless, whilst females are tailed (d’ABRERA 1995: 1251). However, if the sexes are similarly tailed (= possessing extensions in the same vein termini) they display no quantitative difference. Amongst south American eumaeine hairstreaks the hind wing ventral pattern of the taxa *Atlides zava* (HEWITSON, 1878) ROBBINS, 2004 (an unjustified combination) and *Denivia deniva* (HEWITSON, 1874) JOHNSON, 1992 are somewhat similar in appearance to character (2) above. This is probably a clue to why DRAUDT put them in the same group (see above); however, none of the mentioned taxa possesses light brown or green scalings and a similarly coloured yellow discoidal patch on the hind wing ventra.

We consider *Aveexcrenota* to be most closely related to the genus *Evenus*. We base this hypothesis on the following considerations: (1) Highly similar dorsal wing structural colour and very similar spectral figures; and (2) similarly structured genital organs. Regarding (1): It was demonstrated that spectral reflectance can be used as tool in polyommata lycaenids for hypothesizing their phylogeny and consequent taxonomy (KERTÉSZ *et al.* 2005). We have checked this phenomenon among several eumaeine lycaenid groups and have noted the same results (BÁLINT & KERTÉSZ, *in prep.*). For example, in the case of *Denivia hemon* and *Thecloxurina chachapoya* BÁLINT *et* WOJTUSIAK, 2003, all the conspecific individuals examined possess quantitatively the same spectra (Fig. 7b–c). The spectra of *Evenus* and *Aveexcrenota* are strikingly similar, whilst that of *Denivia* and *Theritas*, plus *Thecloxurina* are distinctive (*c.f.* Fig. 7d). The highest reflectance of *Aveexcrenota* and *Evenus* is produced between the wavelength 500–550 nm as noted by a drastically emerging, and extremely ascending, high peak. The reflectance peak of *Theritas* is in the same wavelength region, but is noted as a smooth curve. The reflectance of *Denivia* is the lowest with the peak of the investigated taxa appearing well below 500 nm. The peak of *Thecloxurina* reflectance is shifted to the region slightly below 400 nm. On the basis of this character *Aveexcrenota* and *Evenus* are more closely related than the other investigated genera.

Regarding (2): Qualitative difference can be detected in male and female genitalia. The *Aveexcrenota* male and female genitalia are structurally close to those of *Evenus regalis*, and are divergent in many traits from *Denivia* and *Theritas*. *Theritas* females generally possess a long sclerotized ductus bursal tube with practically no anal plates, whilst *Denivia* female genital ductus bursae is divided by a membranous area having a pair of large asymmetrical anal plates which are often bristled. *Aveexcrenota* male and female genitalia very much resemble that of *E. regalis* (for genitalia structure documentation see BRÉVIGNON 2002) with its sclerotized tube and heavily sclerotized anal plates which are pointed (Fig. 9). We consider this character as synapomorphy of *Aveexcrenota* and *Evenus*, which is supported by their spectral character.

Consequently, we consider the combination *Theritas anna* (DRUCE, 1907) (ROBBINS 2004) not only unjustified but erroneous and we resurrect *Aveexcrenota* from synonymy with *Theritas* resulting in the recovered combination *Aveexcrenota anna* (DRUCE, 1907) SALAZAR et JOHNSON, 1997.

The Evenus genus group

We have removed *Aveexcrenota* from the “*Atlides* section” of ROBBINS and place in the “genus” *Evenus* sensu ROBBINS. The monophyly of genus *Evenus* was based on “similar genitalia, unique androconial structures... and larvae... that eat leaves of trees in the plant family Sapotaceae” by ROBBINS (2004: xxv). According to this definition *Aveexcrenota* can be placed in *Evenus* only on the basis of genital structures as it does not possess any unique androconial structures and there is no information about the early stages. However we are of the opinion that *Aveexcrenota* and *Evenus* s. str. are in sister relationship based on the character spectral reflectance as synapomorphy. We consider the extended vein Cu1 terminus and the cryptic ventral wing pattern as an apomorphy of *Aveexcrenota* being the terminal taxon of the clade, while *Evenus* s. str. is in basal position.

The sister of the lineage *Evenus-Aveexcrenota* is the clade comprised of the species *Thecla coronata* HEWITSON, 1865 and its undescribed sister (BÁLINT & NEILD, in prep.). The *coronata* lineage warrants a generic name. The sister group of *Aveexcrenota-Evenus*-gen. n. is the rest of the genus *Evenus* sensu ROBBINS including genera *Ipocia* BRÉVIGNON (2000; type species: *Papilio gabriela* CRAMER, 1775) (= *Poetukulumna* BRÉVIGNON, 2002), *Macusia* KAYE, 1904 (type species: *Thecla satyroides* HEWITSON, 1865) and *Cryptaenota* JOHNSON, 1992 (type species: *Thecla latreilleii* HEWITSON, 1874). We build the hypothetical cladogram for the *Evenus* genus group on the basis of wing androconia, colour, pattern, and shape characters considered as unique synapomorphies (nodes) and apomorphies (in ter-

minal taxa) (Fig. 10). Phenotypes of the genera are fully illustrated in the book of d'ABRERA (1995), the distribution of the characters in the genera is given as Table 1.

Characters and genera

- (1) Dorsal fore wing tornal lobe with large blue red spot.
- (2) Hind wing margin between veins M3-CuA1 and CuA1-CuA2 terminus c-shaped basally with rigid short (less than 5 mm) vein CuA1 terminal and long (more than 10 mm) vein CuA2 tail-like extension.
- (3) Hind wing vein terminus CuA2 sexually dimorphic: *Aveexcrenota*.
- (4) Fore wing vein R3 as long as veins R4 and R5: *Evenus* s. str.
- (5) Fore wing with androconial scales in basal part of the costa.
- (6) Hind wing dorsum with scent patch in the subbasal costal area of cell Sc+R1: *Suneve* BÁLINT, **gen. n.** (type species: *Thecla coronata* HEWITSON, 1865) (Fig. 11).
- (7) Fore wing dorsa with androconial scales in basal part of the costa comprised of long and tightly attached scales without green structural colour.
- (8) Hind wing ventra with short-range ordered matt green structural colour (*c.f.* KERTÉSZ *et al.* 2006): *Ipocia*.
- (9) Fore wing dorsal androconial scales heavily melanized along vein Sc.
- (10) Hind wing pattern satyrioid with large discoidal streak: *Macusia*.
- (11) Hind wing anal margin recurrent with conspicuous lobe: *Cryptaenota*.

Character discussion (from above)

- (1) This character is unique. The tornal lobe in eumaeines is often pigmented differently than the other part of the wings, but generally it is coloured orange, grey or blue.
- (2) This character is unique. However, there are certain genera which possess similar but not identical character, for example the closely related *Ipocia*, but in this latter case vein terminus CuA2 possesses a filamentous, not rigid tail.
- (3) This character is unique in the lineage and supported by a wing ventra with melanized ground colour and cryptic pattern.
- (4) This character is unique in the lineage resulting in a peculiar wing shape for *E. regalis*. All the other genera possess a more round fore wing shape because of shorter radial veins.
- (5) This character is unique in the tribe and goes through a transformation in the more derived genera.

Table 1. Character distribution in the genera of *Evenus* genus-group. Genera are listed in alphabetic order. Characters are listed and discussed in the main body of the text. No. = number of character discussed; 1 = presence of the character, 0 = absence of the character

Genus	1	2	3	4	5	6	7	8	9	10	11
<i>Aveexcrenota</i>	0	1	1	0	0	0	0	0	0	0	0
<i>Cryptaenota</i>	0	0	0	0	1	0	1	0	1	0	1
<i>Evenus</i>	1	1	1	0	0	0	0	0	0	0	0
<i>Ipocia</i>	1	0	0	0	1	0	1	1	0	0	0
<i>Macusia</i>	0	0	0	0	1	0	1	0	1	1	0
<i>Suneve</i>	1	1	0	1	1	1	0	0	0	0	0

(6) This character is unique and with a peculiar tuft of erect gleaming scales in the frons (“crown” *sensu* HEWITSON 1865: 70).

(7) This character is a transformation of character 5, as we regard the gleaming condition as relatively plesiomorphic.

(8) This is unique in the lineage but obviously widely apparent in South American eumaeines where there are analogies in many different, not closely related, genera. Apparently it is very rare among the lycaenids of the Palaeotropics as the only genus which possesses this trait is *Anartia* HÜBNER, 1819 (type species: *Papilio jatrophae* LINNAEUS, 1763).

(9) This is the most derived state of the character (5).

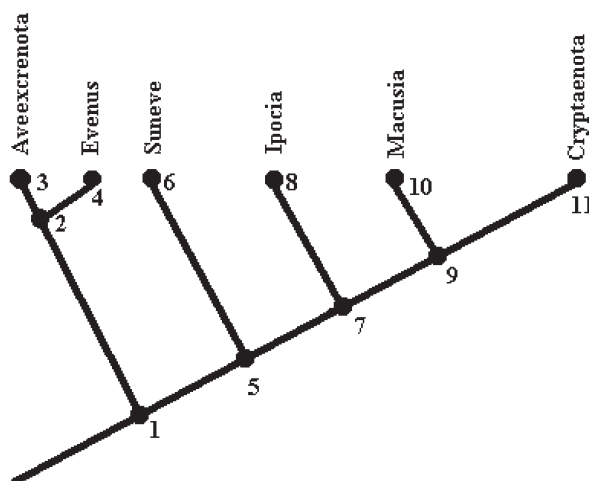


Fig. 10. Hypothetical cladogram for the *Evenus* genus group. Characters are listed and discussed in the text

(10) This pattern is unique in the lineage. Similar conditions occur in the sister species pair of *Ipocia floralia* (DRUCE, 1907) and *I. tagyra* (HEWITSON, 1865) but the discoidal streaks and hind wing marginal spots are missing.

(11) This unique character is supported by a cryptic pattern of the wing ventrum, which is analogous to the superficially similar *Aveexcrenota* pattern.

BIOLOGY

Habitat in Colombia and the accompanying lycaenids

All 58 specimens of *A. anna* in CHD were collected during the years 1998 to 2004 at two neighbouring peaks of the Cerro San Antonio (about 2200 m) in the Western Cordillera near the City of Cali (Colombia).

The top of the mountain's main peak is formed by a flat area covered with shrubs, ferns and a few trees. The hilltopping site at the main peak, where most of our *A. anna* specimens have been captured, measures about 17×12 m with tree heights below 7.50 m, and the nearby antenna site has only an extension of 4×3 m. There is some competition for the perching sites within this strata among various eumaeini taxa, namely (listed in alphabetical order according their generic placement) *Atlides dahnersi* BÁLINT, CONSTANTINO et JOHNSON, 2003, *Aubergina hesychia* (GODMAN et SALVIN, 1887), *Brangas caranus* (STOLL, 1780), *Cyanophrys pseudolongula* (CLENCH, 1944), *Laothus tolmides* (FELDER et FELDER, 1865), and others. Below this strata flies and perches *Theritas paupera*, while the upper strata above 3 m, which includes the tree tops, is populated by *Atlides browni* CONSTANTINO, SALAZAR et JOHNSON, 1993, *Atlides polybe* (LINNAEUS, 1763), *Cyanophrys agricolor* (BUTLER et H. DRUCE, 1872), *Parrhasius* sp. n., *Erora* sp. n. and occasionally *Atlides scamander* HÜBNER, 1819 and *Brangas coccineifrons* (GODMAN et SALVIN, 1887).

The top of the secondary peak is covered by telecommunication antennae complex and several buildings. Here, hilltopping butterflies gather at a hillock which lies a few meters downward on the slope and shows a somewhat rugged topography, where meter high bush can be found at the same level as the top of a 20 m tall adjoining tree. At this site no clear stratification of perching sites can be noted, except for *Theritas paupera*, which still flies around in the lower vegetation.



Fig. 11. *Suneve* gen. n. apomorphy (indicated by arrow)

Male flight period and behaviour

Male individuals are present at those sites throughout the year, the numbers peaking in July/August and with two more minor numerical peaks in February/March and October/November (Fig. 12).

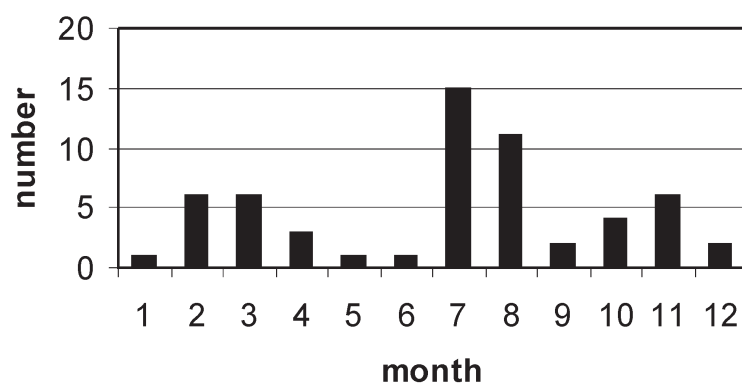


Fig. 12. Monthly distribution of male *Aveexcrenota anna* (DRUCE, 1907) individuals collected near Cali, Colombia

On a sunny day the first specimens appear at about 10 am; the presence of clouds delays daily appearance. The males alight on certain preferred perching sites, occasionally engaging in mating flight attempts wherein they return either to the same perch or to another one. After noontime, activity drops and after 2 pm there are hardly any individuals visible at the two sites.

Perching *Aveexcrenota anna* align their body axis at an angle so that their heads point down from the horizontal towards the ground. When a cloud blankets the sun they shift the position of their folded wings to an angle that favours the capture of solar radiation by the dark underside of their wings. If the overcast period is prolonged, they will fly away and – if its not too late in the day – eventually return. On few occasions, and well after activity hours at about 4 pm, *A. anna* males were encountered near their usual perching sites in a peculiar pose: lying flat in the middle of a leaf with the wings folded, exposing the brown and grey mottled underside of the hind wings. The two tail-like appendices were arranged so that they were pointing downhill with respect to the leaf surface, offering to the human eye a perfect imitation of a fresh bird dropping. Nevertheless, there is no observation in the natural environment that further supports the hypothesis that this kind of behaviour plays the role suggested by JOHNSON and SALAZAR (1997).

Females

The two females we have reported were collected at 2200 m on flowering trees locally known as Arrayán and Arboloco. They showed no sign of hilltopping behavior. We have no further records regarding nectaring and ovipositing. The larval host plant is also unknown, but it supposedly belongs to Sapotaceae (*c.f.* ROBINS 2004).

By the way, we had some luck capturing the first female *A. anna* in S. Antonio in late 2005 by applying a male rarefaction method, i. e. by catching and temporarily storing all males. The female sat on a branch about 1m above ground level, which jibes with the males looking down from their perching sites at 2–3 m high.

*

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APPENDIX

Material examined

BMNH Type Material (Holotype male, BMNH(#) 266365, COLOMBIA, labelled as): (1) “Interior of Colombia, Wheeler” (printed), (2) “Godman-Salvin., Coll. 1919–93.” (3), “T. anna, ?, type, H. H. Druce” (handwritten), (4) “Type” (printed) (5) “B.M. Type, No. Rh. 531” (printed, numbers handwritten), (6) “B.M.(N.H.), Rhopalocera, V. No., 3840” (printed, numbers handwritten), (7)

“Holotype” (handwritten), “(8) Holotype, T. anna, Drc., (recto.) conf., Zs. Bálint, 11.IX.'98” (printed, handwritten). The specimen is in good condition, without abdomen (dissected).

CHD *Aveexcrenota anna* material (arranged in chronological order according to the collecting of the individual specimens; in brackets the DAHNERS collection inventory number: altogether 58 male individuals, all from COLOMBIA): Valle, R. Aguacatal, S. Antonio: 2300 m, 4.I.1998. (7504); 2300 m, 7.II.2001. (5519); 2300 m, 2.VII.2001. (6167, 6168); 2300 m, 24.VII.2001. (6246); 2300 m, 14.XII.2001. (6311); 2300 m, 24.VI.2002. (6366); 2300 m, 3.VIII.2002. (6520); 2300 m, 10.VIII.2002. (6630, 6631); 2200 m, 9.III.2003. (6813, 6814, 6815); 2200 m, 13.III.2003. (6828); 2200 m, 18.III.2003. (6844, 6845); 2200 m, 2.IV.2003. (6895); 2200 m, 6.IV.2003. (6922); 2200 m, 11.IV.2003. (6937); 2200 m, 2.V.2003. (6968); 2200 m, 2.VII.2003. (7142, 7143); 2200 m, 4.VII.2003. (7144); 2200 m, 13.VII.2003. (7184); 2200 m, 14.VII.2003. (7186); 2200 m, 17.VII.2003. (7187, 7188, 7189); 2200 m, 18.VII.2003. (7190, 7191); 2200 m, 21.VII.2003. (7502); 2200 m, 27.VII.2003. (7193); 2200 m, 4.VIII.2003. (7218); 2200 m, 16.VIII.2003. (7232); 2200 m, 19.VIII.2003. (7273); 2200 m, 23.VIII.2003. (7348); 2200 m, 26.VIII.2003. (7485); 2200 m, 31.VIII.2003. (7373, 7374); 2200 m, 16.IX.2003. (7398, 7399); 2200 m, 13.X.2003. (7418, 7419); 2200 m, 19.X.2003. (7445); 2200 m, 25.X.2003. (7476); 2200 m, 1.XI.2003. (7500, 7501); 2200 m, 2.XI.2003. (7503, 9153); 2200 m, 16.XI.2003. (7520, 7521); 2200 m, 19.XI.2003. (7522); 2200 m, 16.XII.2003. (7523); 2200 m, 1.II.2004. (7549); 2200 m, 9.II.2004. (7637); 2200 m, 12.II.2004. (7660); 2200 m, 14.II.2004. (7661, 7662).

MHNUC *Aveexcrenota anna* material (3 males all from COLOMBIA): Caldas: Western slopes of Central Cordillera, Manizales, Cerro Sancancio, 2100 m, 10.X.1994, leg. J. Salazar (MHN-UC 232, male). Caldas: Eastern slopes of Occidental Cordillera, Manizales, 2150 m, 10.XI.1997, leg. F. Cardona (MHN-UC 256, male). Caldas: Eastern slopes of Occidental Cordillera, Riosucio, Cerro Ingrumá, 2200 m, XI.1999, leg. J. Salazar (MHN-UC 259, male).

CJS *Aveexcrenota anna* material (7 males, 2 females, all from COLOMBIA): Caldas: Western slopes of Central Cordillera, Chipre, 2200 m, 10.XI.1984, leg. J. Salazar (two males). Caldas: Western slopes of Central Cordillera, Monte León, 2300 m, 7.XII.1997, leg. J. Salazar (male). Caldas: Eastern slopes of Occidental Cordillera, Riosucio, Cerro Ingrumá, 2200 m, 10.VII.1994, leg. J. Salazar (two males). Caldas: Riosucio, Cerro Aguacatal, 1700 m, no date, leg. J. Salazar (male). Caldas: Manizales, La Linda, 1800 m, 2004, observed, without capture (male); Villmarca, El Roble, leg. J. I. Vargas (two females).

HNHM *Aveexcrenota anna* material (2 males): COLOMBIA: Caldas, Cerro Ingrumá, Riosucio, 2200 m, 31. XII.1994, leg. J. Salazar (male). Valle, Cali, Santonio, 2180 m, 25.IX.2005 (male). PERU: Amazonas, Pomacocha 2150 m, 13. VI. 2000, leg B. Calderon (male) (PBC).

Genital dissections

All dissections are kept in plastic vial containing glycerol with the relevant specimens. Taxa are listed in alphabetical order according to their generic placements. Genital dissections prepared by the senior author are inventoried in the BMNH and in the HNHM; when voucher specimens are kept in a different collection, their acronyms are given in parentheses.

Aveexcrenota anna: “Colombia, Manizales” (CJS) (HNHM 998, female); “Caldas” (HNHM 1073, male).

Evenus regalis: “Brazil” (BMNH 5850, male); “Brazil” (HNHM 886, female). *Denivia adamsi*: “Ecuador” (BMNH 5818, female); *D. chaluma*: Brazil, Ararás” (NMW) (HNHM 902, male).

D. deniva: “Brazil, Rio Grande do Sul” (NMW) (HNHM 903, male); “Petropolis” (NMW) (HNHM 904, female). *D. sp. n.*: “Peru” (NMW) (HNHM 900, m). : *D. hemon*: “Brazil, Rio” (NMW) (HNHM 905, male); “Brazil, Ivoti” (HNHM 1087, female). *D. monica*: “Colombia, Bogotá” (NMW) (HNHM 901, female). *D. theocritus*: “Colombia, Bogotá” (BMNH 5851, female).

Suneve coronata: “Ecuador, Baños” (HNHM 885, male); “Colombia, Cali” (HNHM 1088, female).

Theritas mavors: “Guatemala, Guazacapan” (BMNH 5792, female), “Brazil, Amazon” (NMW) (HNHM 913–15, males); *T. paupera*: “Columbien” (NMW) (HNHM 910, male); *T. triquetra*: “Brazil, Tijuco” (BMNH 5791, female), “Petropolis” (NMW) (HNHM 911, female, 912 female).

Spectroscopy

Material examined for spectroscopic investigations presented in this paper, all male individuals, are listed in alphabetic order according to generic placements of taxa:

Aveexcrenota anna – COLOMBIA: Caldas, Cerro Ingrumá, 2200 m (HNHM); PERU: Amazonas, Pomacocha, 2105 m.

Denivia deniva – BRAZIL: Paraná, Pien, 900 m; Rio Grande do Sul, Morro Reuter, 700 m (HNHM).

Denivia hemon – COSTA RICA: Bugaba (ZSM). BRAZIL: PERU: San Martín, Juanjui, 400m; Loreto, Iquitos, 100 m (HNHM).

Evenus regalis – BRAZIL: Amazonas, Santarem (NMW).

Thecloxurina chachapoya – PERU: Amazonas, Chachapoyas, 3000 m (2 specimens); Apurímac, Quebrada Yanaccacca, 3300 m (PBC)

Theritas paupera – COLOMBIA: Caldas, Cerro Ingrumá, 2270 m (HNHM).

Theritas triquetra – BRAZIL: Santa Catarina, São Bento do Sul, 600 m (HNHM).