A NEW GENUS OF "ELFIN" BUTTERFLIES FROM THE NORTHERN HIGH ANDES (LEPIDOPTERA: LYCAENIDAE)

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ABSTRACT.—Podanotum n. gen. (tribe Eumaenini, infrafamily Theclixurina, a new genus of high Andean "elfin"-like hairstreak butterflies, is described from two new species recently discovered in Colombia and Ecuador: Podanotum clarissimus n. sp. and Podanotum metalicus n. sp. The morphology of Podanotum places the genus in the "loxurina" subclade of the infrafamily and is highly autapomorphic, but its wing shape more closely resembles that of the sister "arrina" subclade. Brilliant dorsal "tinfoil"-like iridescence in the new genus strongly resembles that of certain sympatric species of Lymanopoda Westwood, [1851] (Nymphalidae, Satyrinae). The adaptive significance of this dorsal iridescence is discussed in the light of field observations and current data concerning possible cases of mimicry in Lymanopoda.

RESUMEN.—Podanotum (tribu Eumaenini, infrafamilia Theclixurina), un género nuevo de mariposas licencíadas del grupo de las "elfines" procedente de las grandes alturas Andinas, es descrito a partir de dos especies nuevas recientemente descubiertas en Colombia y Ecuador. La muy estensible morfología autapomorfa de Podanotum permite colocarlo en el subclado "loxurina" de la infrafamilia. Sin embargo, la forma de las alas se parece más a la del subclado hermano "arrina". El brillo iridíscido de la superficie dorsal semejante a papel metálico en el nuevo género le confieren un marcado parecido a simpáticas especies de Lymanopoda Westwood, [1851] (Nymphalidae, Satyrinae). Se discute el significado adaptativo de la iridiscencia dorsal considerando las observaciones de campo y los datos recientes sobre posibles casos de mimetismo en Lymanopoda.

KEY WORDS: Abloxurina, Caeroofethra, Candora, Chlorosmyron, Colombia, Ecuador, Eumaenini, hilltopping, Lymanopoda, mimicry, morphology, Neotropical, Podanotum n. gen., Podanotum clarissimus n. sp., Podanotum metalicus n. sp., Pons, Pseudolucia, Rhamna, Shapiroana, taxonomy.

Nearly simultaneously in 1995, Torres (in Colombia) and Hall and Willmott (in Ecuador) discovered species of brilliantly colored "elfin" butterflies (Lycaenidae, tribe Eumaenini, infrafamily Theclixurina) representing a previously unrecognized lineage of generic worth. Interestingly, the dorsal colors in these "elfins" resemble the bright "tinfoil" hues of some sympatric and synchronic species of Lymanopoda Westwood, [1851] (Nymphalidae, Satyrinae), and we discuss the possibility of mimicry between these two genera.

The purpose of this paper is to describe these new entities. The paper follows terminology in Johnson’s (1992) monograph of Andean "elfins" and a subsequent paper (Salazar and Constantino, in press) describing another new genus from this eumaenine infrafamily. This includes use of VFW, VHW and DFW, DHW for ventral and dorsal fore- (FW) and hindwings (HW), respectively.

*Tribe Eumaenini (sensu Elliot, 1973)
Infracervice Theclixurina (sensu Johnson, 1992)

**PODANOTUM** Torres & Johnson, new genus

Fig. 2a-d, 3a-d; 5a-d, 6a-f, 7a-d, 8a-f

Type species: Podanotum clarissimus Hall, Willmott & Johnson, new sp.

**Diagnosis.**—Wings: compared to all other Theclixurina, the dorsal wing surfaces are brilliant "tinfoil" green with black borders of various width; males lack scent brands; ventral surfaces light green-hued to gray-hued brown, each wing showing a submarginal spotband of blackish brown lunules or chevrons and, medially, a variously undulate line blackish brown band. HWs show only a slight anal lobe, if at all.

Morphology: females with notable bipartite genital habitus, uniquely sclerotized in terminal element only; male genitalia most resembling the genus Candora Johnson, 1992 (vinctulum venter elliptic, arc of vinculum fully filled by valvae, saccus small), but with saccus and valvae in Podanotum more reduced, valve bilobes and caudal extensions of about equal length, and acedeagus with unique ventro-terminal keel.

**Description.**—Adult: tagmata blackish brown with profuse gray hairs and with occasional patches of bright iridescent blue-green scales; frons predominantly white with some brown scaling and long brown hairs; antennae typically eumaenine, finely striped white and black. MALE: lacking external secondary sexual marks in known species. DFW, DHW shape broad with outer margins convex, HW anal angle completely rounded or with only slight anal lobe; structural color brilliant "fine-grained" (sensu Johnson, 1992) silver-hued green of "tinfoil-like" intensity; borders blackish and of various width, wider at FW apex. VFW, VHW ground color green-hued to gray-hued brown, FW with arc of 4-7 blackish-brown lunules (or chevrons) across submargins paralleled basally by a narrow undulate medial band of varying intensity (basally blackish or brown, distally with white scales); HW with arc of 6-7 prominent blackish-brown lunules (or chevrons) across submargins paralleled basally by narrow undulate medial band of varying intensity (basally blackish or brown, distally with white scales) across medial area and, sometimes, a less apparent dark brown line across the postbasal
area. FEMALE: similar to male but with somewhat duller structural color and wider blackish wing borders.

Morphology: terminal tergites of both sexes normal (i.e., without subordinate incised posterior cavity ["spic", sensu Johnson, 1991, 1992]); brush organs lacking in known species. Male genitalia (Fig. 5a-d, 7a-d): vinculum elliptic (sensu Johnson, 1991) marked by broad, but very short saccus. Valvae with bilobed area and caudal extensions both apparent, of about equal length and, together, filling most of the vincular arc (similar to thechloxurine with prominent valvae [like Candora Johnson, 1992], not taxa with reduced valvae or without caudal extensions [like Abloxxurina Johnson, 1992]). Aedeagus short (length exceeding genitalia by only part of caudal length); caudal slightly arched and comprising about one-third of aedegal length; shatt generally straight, terminating with a sculptured central keel and one peneulate conusulus. Female genitalia (Fig. 6a-f, 8a-f): bipartite in structure with prominently sclerotized, fluted, and distally toothed terminal element joined by a transparent, membranous juncture to a hardly sclerotized, flexible, anterior tube (of about equal length) extending to ovate corpus bursae; cervix bursae lacking prominent hood typical of most Theclouxurina; corpus bursae with two extremely large, plate-like, signa (comparable to some large structures in the theclouxurine genus Pons Johnson, 1992).

Etymology: The name Podanotum combines the Latin suffix meaning "marked like" to the prefix "Podo," alluding to the satyrine genus Lymanopoda, and refers to the external resemblance of these two butterfly genera; considered masculine.

Discussion: Considering the brilliant coloration of this genus, taxa of Podanotum n. gen. resemble other theclouxurines only in the hindwing shape and ventral markings (which are most reminiscent of Shapiroana Johnson, 1992). Notably, Shapiroana is a member of the "arrina subclade" of the Theclouxurina, which lacks clear tubular elements in the female genitalia. Podanotum belongs to the "luxurina subclade" of the Theclouxurina whose members show a tubular female genital habits. However, of the genera in this group (see Johnson, 1992), Podanotum is alone in having fully sclerotized tubelike elements of the ductus bursae in only the terminal element. Among members of the "luxurina subclade," only members of Abloxxurina Johnson, 1992, also exhibit a distinctly bipartite female genitalia (these heavily sclerotized in both the posterior and anterior elements). Neither the male genitalia nor wing pattern of Abloxxurina are similar to Podanotum. It appears most likely that Podanotum is a sister group of the "luxurina subclade" genus Candora Johnson, 1992. This new genus is a highly autapomorphic sister group, however, considering not only the morphological characters of Podanotum, but the possibility that it may be involved in mimicry (see final discussion). Members of Candora vary notably in wing shape (some with elongate anal lobes, others without) and at least one species lacks scent brands in males. The male genitalia of Podanotum most closely resemble those of Candora (in valvae and vinculum/saccus) while the terminal element in the female genitalia of Podanotum resembles the entire tubal configuration in Candora. No species of Candora, however, have extremely bright dorsal coloration.

Notably, the terminus of the female genitalia in one species of Podanotum is asymmetrical, a condition noted only in a few other theclouxurines (e.g., Shapiroana matuski Johnson, 1992) which show extreme autapomorphies of both wing and morphological characters. Moreover, S. matuski (an orange species in an otherwise blue and purple genus) appears to be the "orange mimicry ring" described recently by Benyamini (1995) based on the toxic polyommatine lycaenid species Pseudolucia chilensis (Blanchard, 1852) (see final discussion). It is noteworthy, concerning autapomorphy in Podanotum, that in the Eumaeini reduction of anterior genital sclerotic features (or reversion to a membranous state) has only been noted in either extremely insular taxa (e.g., certain Chlorestromyn species [Johnson 1989, 1990]) or genera characterized by extreme overall apomorphy (e.g., Caerofethra Johnson, 1991). This genital characteristic in Podanotum forms an interesting parallel with the new genus's insularity and possible mimicetic involvement.

**Podanotum clarissimus** Hall, Willmott & Johnson, new sp.

Fig. 2a-d, 5a-d, 6a-f

Diagnosis: Wings: differs from *P. metallicus* n. sp. (see below) by possessing much wider (postmedial distal) dorsal black borders in both sexes and, on the ventral surface, a green-hued light brown ground color (of less suffusive appearance) with more prominent pattern elements in both the medial and submarginal areas and elements of the latter often appearing more chevron-like than lunulate.

Morphology: the male differs from *P. metallicus*, among other characters, in the far less angulate shape of the valvae, and broadly elliptic bilobes which terminate in short tapered caudal extensions. The female differs from *P. metallicus* by being less robust, having a symmetrical ductus bursae terminus, and a much shorter anterior ductal element.

Description: MALE: HW with slight anal lobe. DFW, DHW brilliant iridescent green (blue-green at an oblique angle) with blackish borders extending distally from the postmedial area. VFW, VHW ground color light green-hued brown without extensive overlay of suffusive scales; FW and HW with 6-7 succinct submarginal black lunules or chevrons (particularly costa) and basally, a prominent, succinct and (on the HW only) greatly undulate mediococ pearl framing a slightly brown ground color within. Male genitalia (Fig. 5a-d): typical of the genus, differing from its congener *P. metallicus* in showing a more convex outline to the vinculum (ventral view), having valvae with elliptic bilobes and gradually tapered caudal extensions of about equal length, and little to no arch to the caecum of the aedegus.

FEMALE: similar to male but with duller green dorsal iridescence and slightly wider black borders on both wings. Female genitalia (Fig. 6a-f): bipartite habitus divided into a heavily sclerotized, fluted, and distally toothed terminal element connected by a transparent juncture to a shorter (about half the length of the posterior) anterior element which is weakly sclerotized, flexible and extends to the corpus bursae; cervix bursae without notable sclerotic development; corpus bursae with two very large and shield-like signa, robust and inwardly toothed in the lateral view; papillae anales typical of the Eumaeini, in this species with apophyses extending the full length of the ductal tube.

Types: Holotype &: EDUARDO - Loja Prov., km 27 Loja-Cuenca, Cerro Palma, 3000m, 4 Aug 1995 (K. R. Willmott). Allotype &: same data as above. Both to be deposited in the American Museum of Natural History, New York, USA (AMNH).

Paratypes: 1 &, 2 &, same data as above. In the collection of J. B. Hall and K. R. Willmott.

Etymology: This species name is derived from the Latin for "very bright, shining" in reference to its unusually brilliant dorsal surface.

Discussion: The type locality of Cerro Palma is a prominent conical hill in the center of the Andean mountain chain. Its upper slopes are clothed in patchy high-altitude elfin forest and bamboo,
but the flat summit is devoid of vegetation. This proved to be a very diverse site for highland "elfin"-like lycaenids, and 19 species (including several undescribed species) were captured during only two days fieldwork. Like most of the other species present, both sexes of *Podanotum clarissimus* n. sp. could be found hilltopping in this cleared summit. Individuals were active in the afternoon between approximately 1300-1530h, when they would occasionally be seen flying rather rapidly across this small field, only alighting fleetingly on the surrounding vegetation.

*Podanotum metallicus* Torres & Johnson, new sp.

**Fig.** 3a-d, 7a-d, 8a-f

**Diagnosis.**—Wings: differs from *P. clarissimus* (see above) by the more brilliant silver-green dorsal iridescence which limits the black borders to only narrow areas of FW submargin and HW margin in the male (wider in female); ventral surface suffused with silver-gray scales over a light brown ground color, markings less emphatic than in *P. clarissimus* with prominence limited to a FW medial band, and a HW submarginal arc of 6-7 prominent blackish-brown spots; HW without anal lobe.

Morphology: male differs from *P. clarissimus*, among other characters, by having a narrower and more angulate valvae shape (bilobes narrowly elliptic with membranous distal outline, caudal extension undulate along inner and outer margin); female with more robust habitus, a distinctively asymmetrical terminus to the ductus bursae, and a relatively long anterior ductal element compared to *P. clarissimus*.

**Description.**—MALE: DFW, DHW extremely brilliant iridescent silver-green (blue-green at an oblique angle) with very narrow and irregular blackish borders limited to FW submargin and HW margin. VFW, VHW with suffusive gray-scales over light brown; FW with light, suffusive arc of 5-7 blackish-brown spots across submargin, paralleled basally by a bipartite (basally blackish-brown, distally white-scaled) medial band from costa to cell C4; HW with arc of 5-6 prominent blackish-brown spots across submargin paralleled basally by a lightly defined, blackish medial line framing a darker ground color within, and in postbasal area some hint of a more darkly blackish line. *Male genitalia* (Fig. 7a-d): typical of the genus, differing from its congener *P. clarissimus* in having a more angulate outline to the vinculum (ventral view), having more angulate valvae (bilobes narrowly elliptic with membranous distal outline, caudal extension angulate along inner and outer margins, latter slightly longer than former), and a prominent arch in the caecum of the aedeagus.

FEMALE: similar to male, although with wider marginal and apical black borders, slightly less brilliant dorsal iridescence and a more falcate-shaped forewing. *Female genitalia* (Fig. 8a-f): bipartite habitus divided into a heavily sclerotized, robust, elliptic and asymmetrically toothed terminal element connected by a transparent juncture to a robust anterior element (of about equal length) which is weakly sclerotized, flexible and extends to the corpus bursae; cervix bursae without notable sclerotal development; corpus bursae with two very large and shield-like signa (although less robust than in the Ecuadorian sister species), inwardly toothed in the lateral view; papillae anales typical of the Euinaeini in this species with apophyses only about three-quarters of the ductus bursae length.


**Paratypes:** 1♂, same data as holotype but, 17 Dec 1994. Deposited in the AMNH.

**Etymology.**—This species is named after the Latin for "metallic" in reference to the brilliant "tinfoil"-like iridescence of the dorsal surface.

**Discussion.**—Torres and students under his supervision have been conducting a biodiversity survey of the Santuario de Flora y Fauna de Iguaque, in Colombia, for several years. In addition to *Podanotum metallicus* n. sp., they have collected two new *Rhamma* species, and a new species of *Heoda* (Strymonina) whose description is in press.

**DISCUSSION**

**Discovery of the genus**

Torres collected the initial samples of this genus in a survey of the Lycaenidae of the Santuario de Flora y Fauna de Iguaque, Boyacá, in the Cordillera Oriental of Colombia. He noted the general similarity of the external features to taxa of *Rhamma* Johnson, 1992, and *Shapiroana* Johnson, 1992, and forwarded two males to the AMNH for morphological study. Johnson noted some similarity in the male morphology to *Codora* Johnson, 1992, but additional sister species, and particularly females, were needed to confirm such a placement. Caution was warranted because Johnson (1991, 1992) had cited numerous in-
stances where external facies of Andean "elfins" (wing shape, color, and pattern) were misleading as to generic placement, particularly in an infratribe like the Thecloxurina where the two subclades ("loxurina" and "arria") differ so radically in the female genitalia.

About one month after the discovery by Torres in Colombia, Hall and Willmott sent photographs of the Ecuadorian entity to Johnson as part of a general inquiry about unidentified high Andean Theclinae. Their female specimens showed that the morphology of these new "elfins" reflected a distinct lineage among the Thecloxurina (at most identifiable as a sister lineage of Candora). This view was further supported when Torres later captured a female of the Colombian entity.

**Adaptive significance of the dorsal coloration**

Hall and Willmott (in the field) and Johnson (from specimens provided by Torres) immediately noted the superficial resemblance on the dorsal surface of species of *Podanotum* to certain similarly brightly colored satyryines of the genus *Lymanopoda*. Such extreme iridescence is not found among other high Andean Theclinae and it is unusual in the genus *Lymanopoda*, which consists of predominantly brown colored species. In Ecuador, Hall and Willmott recorded *P. clarissimus* n. sp. flying with *Lymanopoda hazelana* Brown, 1943 (see Fig. 4), while in Colombia, Torres found *P. metallicus* n. sp. flying with *Lymanopoda samius* Westwood, [1851]. These observations led us to speculate that there might be a mimetic relationship.

Tomasz Pyrce (Zoological Museum of the Institute of Zoology, Jagiellonian University, Kraków, Poland), who is revising the genus *Lymanopoda*, noted (in litt. to Johnson, 30.10.1995) that there seem to be many examples of mimicry between *Lymanopoda* and other butterflies.
"Some Lymanopoda are true Batesian mimics, such as Lymanopoda (or Trophonina) acracida Butler, 1868, which mimics distasteful species of Actinoptera (Nymphalidae, Acraeinae), and the white Lymanopoda paramera Adams & Bernard, 1979, nevada Krüger, 1924, and viveniata (Apolinar, 1924), which are nearly perfect copies of Tatochila piersis. There may also be mimicry between possibly distasteful pronophtilines, for instance Lymanopoda mariana Staudinger, 1897, and Cheimas opalinus (Staudinger, 1897)."

Pyrcz also informed us that, despite their phenotypic similarity, Lymanopoda samius and Lymanopoda hazelana are only loosely related, belonging in different lineages. This suggests that, for whatever reason, these two species have converged on a bright green dorsal surface.

Benyamini (1995), working in Chile, documented a "ring" or "guild" involving approximately twenty Lycaenidae (Polyommatini and Eumaeini) and day-flying moths showing various patterns of bright dorsal orange coupled with cryptic ventral surfaces. The proposed model, whose identity was deduced by considering life histories, patterns of local sympathy and synchrony, and comparative geographic distributions, appears to be among the smallest taxa of the ring — the polyommatine Pseudolucia chilensis (Blanchard, 1852), which feeds on Cuscuta chilensis Ker. (Cuscutaceae), a parasite of the poisonous bush Colliguaja odorifera Mol. (Euphorbiaceae).

Although the above evidence suggests that a mimetic relationship might be possible between Lymanopoda and Podanotum, as Benyamini (1995) notes, without foodplant data it is nearly impossible to guess which among a group of compellingly similar (but phylogenetically diverse) butterfly taxa may constitute a distasteful model. Unfortunately, no foodplant information is available for these two genera. At Cerro Palma, in Ecuador, Lymanopoda hazelana is spatially more widespread and more common than P. clarissimus, and unlike the lycaenid it is known to us from several other sites in the country. Thus the rarer P. clarissimus is unlikely to be the sole model in this case. It is possible that species of Podanotum with Lymanopoda samius and Lymanopoda hazelana might be part of a larger mimetic "ring," involving other Andean "elfin" lycaenids with similarly brilliant dorsal iridescence, whose potential model is unknown. However, without further ecological information, it also seems possible that the brilliant dorsal coloration in these taxa could be due to coincidence or the result of convergent evolution on an adaptive flash color pattern.

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LITERATURE CITED

Benyamini, D.

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SUMARIO

Casi simultáneamente en 1995, Torres (en Colombia) y Hall y Willmott (en Ecuador) descubrieron especies de mariposas "elfín" (Lycanidae, tribu Eumaeini, infrafamilia Theclurina) de colores brillantes, representantes de un linaje de rango genético justificable y hasta el momento desconocido. Los colores dorsales más sobresalientes en estas "elfín" semejan el matiz luminoso del papel metálico de algunas especies de Lymanoptera Westwood, [1851], un género de Satyrinae (Nymphalidae), documentado como simpátrico y sincrónico con estas elfín. Estos dos géneros pueden estar envueltos en una relación mimética (ver discusión final).

El propósito de este artículo es describir estas nuevas entidades. El trabajo sigue la terminología de Johnson (1992) en su monografía de los "elfín" Andinos y de un trabajo posterior (Salazar y Constantino, en prensa) describiendo otro género nuevo de esta infrafamilia de eumaeinos. Aquí también se incluye el uso de VFW, VHW, y DFW, DHW para las alas anteriores y posteriores, ventral y dorsal respectivamente.

**PODANOTUM** Torres & Johnson, new genus

Fig. 2a-d, 5a-d, 6a-f, 7a-d, 8a-f

Type species: *Podanotum clarissimus* Hall, Willmott & Johnson, new sp.

**Diagnosis.**—Alas: diferen de *P. metallicus* n. sp. (ver más adelante) por lo mucho más ancho (postmedial distal) de los bordes dorsales negros en ambos sexos; superficie ventral matizada de verde claro sobre un color de fondo café (de apariencia menos suturativa) con unos elementos del patrón más prominentes, en las áreas médiales y submarginales; los elementos de esta última tienen más apariencia de galones que de lúnulas.

Morfología: el macho difiere de *P. metallicus*, entre otros caracteres, por la forma de la valva, mucho menos angulosa, bilobulada bastante elíptica, terminando en extensiones caudales cortas y acinatadas. La hembra difiere de *P. metallicus*, por ser menos robusta, tener un terminación del ductus bursae simétrico y por tener la porción anterior del ductus mucho más corta.

**Podanotum metallicus** Torres & Johnson, new sp.

Fig. 3a-d, 7a-d, 8a-f

**Diagnosis.**—Alas: diferen de *P. clarissimus* (ver arriba) por exhibir una iridiscencia dorsal verde plateado más brillante con bordes negros limitados a solo áreas angostas del submargen de la FW y margen de la HW; ventralmente fusión con escamas gris plata, sobre un fondo café claro, marcas menos acentuadas que en *P. clarissimus* con prominencia limitada a la banda medial de la FW y en la HW un arco submarginal de 6-7 manchas café negruzcas; HW sin lóbulo anal. Morfología: macho difiere de *P. clarissimus*, entre otros caracteres, por tener valvas mas angulosas (bilobuladas elípticas y angostos con tronco distal membranoso; extensiones caudales unduladas a lo largo de los márgenes externo e interno); hembra con habitos mas robusto; terminación del ductus bursae claramente asimétrico y la porción anterior del ductus relativamente larga comparado con *P. clarissimus*. 

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