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Expanded Phenotypic Diagnoses for 24 Recently Named New Taxa of Hesperiidae (Lepidoptera)

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Expanded phenotypic diagnoses for 24 recently named new taxa of Hesperiidae (Lepidoptera)

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ABSTRACT. Expanded diagnoses by phenotypic characters for the 24 new taxa named in the article "Genomes of skipper butterflies reveal extensive convergence of wing patterns" by Li, W., Cong, Q., Shen, J., Zhang, J., Hallwachs, W., Janzen, D.H. and Grishin, N.V., 2019 and published in the Proceedings of the National Academy of Sciences of the United States of America on March 15, 2019 are provided and illustrated. More detailed diagnoses will help identifying these phylogenetic groups by their wing patterns and shapes and other morphological characters including the structures of antennae and genitalia using this single publication, instead of obtaining the sequences or inspecting additional works referenced in the original diagnoses for brevity.

Key words: taxonomy, classification, genomics, phylogeny, Evans.

ZooBank registration: http://zoobank.org/D0BA0046-6ACA-47B4-9E00-B0FD90A99555

INTRODUCTION

Recently, we published genomics-based analysis of Hesperiidae that suggested 24 new taxa: 6 tribes, 6 subtribes, 9 genera, and 3 subgenera (Li *et al*., 2019). We and others have argued that the best way to define a higher level taxon (above species level) is by a clade in a phylogenetic tree that has strong statistical support (Talavera *et al*., 2012; Li *et al*., 2019). While the exact criteria for matching the ranks (e.g. genus vs. subgenus) to clades can be debated, if the taxa are desired to be monophyletic, the only way to increase the probability of that would be by using reliable phylogenetic trees. While the definition of a taxon by a branch in a tree is aimed at having it monophyletic to the best of our knowledge, such definition does not agree with how the taxon has to be defined according to the ICZN Code (ICZN, 1999). The Code requires defining "characters," i.e. some features of an organism that enable us to diagnose it as belonging to a particular taxon. A list of characters should be provided as a "diagnosis" when a new name is proposed. If an animal possesses these characters (individually or in combination), it belongs to the taxon. While such definitions are reasonable and practically useful, they have obvious limitations. Most importantly, it is challenging to extrapolate to yet undiscovered taxa. Thus some characters shared by the currently know taxa may not hold for a new taxon to be discovered, which nevertheless belongs to the group by the criterion of monophyly. The challenges are more severe in animals that experience high frequency of phenotypic convergence, for instance Hesperiidae. To protect the name itself from the problems with reporting characters that do not actually hold for the entire group, ICZN does not require the characters to be meaningful, just "purported to differentiate" is sufficient. Thus, in principle, any statement of any characters would be enough, even if they are wrong. While such an approach does not sound appealing, it is not easy to suggest a better alternative.

Nevertheless, researchers strive to find characters that are most meaningful given the current knowledge. The best character would be a conserved synapomorphy, i.e. some feature that originated in the common ancestor of the entire group before that group has diversified, and stayed in all member of the group (i.e. "conserved" in the group). Thus, only the group that has this character and no animal outside the group possesses it. An example would be osmeterium in Papilionidae (Cong *et al*., 2015). However, it is challenging to find such characters, and they may not even exist in some groups due to rapid evolution reflected in character losses and gains. To address the problem of possible phenotypic convergence and rapid divergence, and keeping in mind that the best way to define a higher-level taxon is from a phylogenetic tree, we can look for possible synapomorphies in DNA that was used to construct the tree. Such DNA-based characters are likely to be more reliable as diagnoses than phenotypic characters. An approach to predict conserved synapomorphies in genomic sequences was described in the SI Appendix to Li *et al*. (2019) and was used to find such characters for the new taxa proposed in that publication. These potential synapomorphies were listed as a part of diagnoses in Tables 1 and 2 (Li *et al*., 2019), and actual sequences from the reference genome with positions highlighted (to prevent mishaps with position numbers) were given in the SI Appendix.

While the DNA characters are expected to be more reliable in diagnosing the taxon, they are not easy to use, because they require sequencing that is not available to everyone. Therefore, in addition to DNA-based diagnoses, morphology-based diagnoses were also provided for each taxon in Tables 1 and 2 (Li *et al*., 2019). Due to the need to fit the article into 6 pages, these diagnoses, while far from being random, were brief and mostly referred to published statements in literature (Williams and Bell, 1934; Evans, 1937; Evans, 1949; Evans, 1951; Evans, 1952; Evans, 1953; Evans, 1955; Burns, 1996). The majority of diagnoses referenced the comprehensive Evans volumes. In Evans, diagnostic characters were given as identification keys (he described dozens of new taxa by means of these keys), which may be a better way of presentation, because a key allows comparisons of the alternatives. However, these keys may not be straightforward to use, and Evans books are not readily accessible to everyone, similar to sequencing. Here, I use the opportunity to elaborate on the diagnoses and rephrase the Evans keys. These morphological characters (while not being original, but discovered by Evans and others) are put together in this article that would be easier to use than going through the Evans volumes. In addition, many essential characters are illustrated here, which was not possible in the original article due to space constraints. The main value of this work is educational and I hope that this article, while not very original, is nevertheless useful in the studies of Hesperiidae.

EXPANDED DIAGNOSES OF THE 24 TAXA

Here are the 24 standardized sections, each giving the name of the taxon; its type genus or species, ZooBank registration, diagnosis that explains how the taxon was defined in the original diagnosis and expands it to rephrase characters given in the referenced publication, all members placed in the taxon in the original description (genera or species), and the parent taxon of the next rank. Species names are given with their original genus in its original spelling ([sic] indicates spelling errors). Collating all this information from the main text, tables and SI Appendix of the original publication (Li *et al*., 2019) and rephrasing characters from the publications referenced in the original diagnoses (Williams and Bell, 1934; Evans, 1937; Evans, 1949; Evans, 1951; Evans, 1952; Evans, 1953; Evans, 1955; Burns, 1996) makes this information more accessible and usable.

Tribe Entheini Grishin, 2019

Type genus: *Entheus* Hübner, [1819].

ZooBank registration: 303C1FD0-07CB-4919-900E-EA3D6347E5DD

Diagnosis: The tribe was defined as a clade from about 40-45 Mya that contains the genus *Entheus*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this tribe would key to B.3a in Evans (1952), excluding B.9. Diagnosed by unusual palpi (Fig. 1): 3rd segment divergent, stout, spatulate and set on the outer edge of the 2nd segment; and regular-shaped, not produced at vein M_3 hindwing. The hindwing character needs to be added to avoid inclusion of *Phareas* Westwood, 1852 (hindwing produced at vein M_3), which apparently converged to this unusual shape of palpi, but is not monophyletic with Entheini as revealed by genomic trees (Li *et al*., 2019).

Fig. 1. Entheini. Head of *Entheus aureolus* Austin, O. Mielke & Steinhauser, 1997 ♂, Brazil: AM, with divergent 3rd segment of palpi.

Genera included: *Drephalys* E. Watson, 1893, *Udranomia* A. Butler, 1870, *Phanus* Hübner, [1819], *Hyalothyrus* Mabille, 1878, *Entheus* Hübner, [1819], *Augiades* Hübner, [1819], and *Tarsoctenus* E. Watson, 1893.

Parent Taxon: Subfamily Eudaminae Mabille, 1877.

Subtribe Loboclina Grishin, 2019

Type genus: *Lobocla* Moore, 1884.

ZooBank registration: C606FC35-323D-4E55-AF5A-A86C6366BAFA

Diagnosis: The subtribe was defined as a clade from about 30 Mya that contains the genus *Lobocla*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this subtribe would key to B.4 in Evans (1949) or C.5, C.10a, C.15.2 or C.18 in Evans (1953). Genera in this tribe are unified by the long forewing cell, at least 2/3 of costa, lobed or tailed hindwing, short, non-divergent palpi with the 2nd segment touching the face and the 3rd not protruding beyond the 2nd (except *Zestusa*). Most genera could be diagnosed by single character and possible synapomorphy: broadly arcuate antennal clubs (Fig. 2). Additionally, hyaline spot in forewing cell R_2-R_3 present even in species with hooked antennae. In species with hooked antennae that lack the spot, genitalic valvae asymmetrical and very broad. Typically (except *Aguna*), valvae rather broad, somewhat rectangular, with harpe narrow, long upturned, hook-like, leaving a deep space between harpe and ampulla, uncus divided.

Fig. 2. Loboclina. Above: arcuate antennal club of *Lobocla proximus* (Leech, 1891), China: Yunnan Province. Below: hooked antennal club of *Aguna coeloides* Austin & O. Mielke, 1998, Brazil: Para.

Genera included: *Aguna* R. Williams, 1927, *Zeutus* Grishin, 2019, *Lobocla* Moore, 1884, *Lobotractus* Grishin, 2019, *Codatractus* Lindsey, 1921, *Zestusa* Lindsey, 1925, *Ridens* Evans, 1952, and *Venada* Evans, 1952.

Parent Taxon: Tribe Eudamini Mabille, 1877.

Subtribe Cephisina Grishin, 2019

Type genus: *Cephise* Evans, 1952.

ZooBank registration: 22B59811-F174-4FDF-A9D2-799897F4D44E

Fig. 3. Cephisina. Head of *Cephise cephise* (Herrich-Schäffer, 1869) ♂, ventral view showing lateral projections of scales from palpi near eyes (by antennae).

Diagnosis: The subtribe was defined as a clade from about 30 Mya that contains the genus *Cephise*, and putatively synapomorphic DNA characters for this clade were given (Li *et al.*, 2019). Phenotypically, species in this subtribe would be diagnosed by "genitalia and palpi as described by Burns (1996: 182-183) for *Cephise*" (Li *et al.*, 2019). Note that this statement refers to the characters of genitalia and palpi (they are "as described . . . for *Cephise*"), not to the genus *Cephise*. Thus, the referenced publication could have been describing the characters of any other genus. Not the genus is relevant here, but the characters themselves, some of which are the following: uniquely short, truncate uncus with a couple of teeth at each distal corner, harpe extending distad, separated from the valva by a U-shaped notch; the first segment of palpi below the eyes with a shelf-like projection of scales that looks like a triangle below the eyes (Fig. 3), more developed in males than in females.

Genera included: *Cephise* Evans, 1952.

Parent Taxon: Tribe Eudamini Mabille, 1877.

Subtribe Telemiadina Grishin, 2019

Type genus: *Telemiades* Hübner, [1819].

ZooBank registration: 4AE0E59C-8B92-4C84-8651-E7A1C45C93C1

Fig. 4. Telemiadina. Wing bases of *Ectomis cythna cythna* (Hewitson, 1878) ♂, French Guiana, below, showing the tuft of scales and expanded costal area of hindwing.

Diagnosis: The subtribe was defined as a clade from about 30 Mya that contains the genus *Telemiades*, and putatively synapomorphic DNA characters for this clade were given (Li *et al.*, 2019). Phenotypically, species in this subtribe would key to B.2, C.3, C.7a (exclude C.7.6b), E.6a, or E.9 in Evans (1952, 1953). Includes a phenotypically diverse array of Hesperiidae that were not brought together before this study and do not possess an obvious phenotypic synapomorphy. Many species included here have a prominent tuft of long scales from a polished area near the base and inner margin of forewing below, and correspondingly widened costal area of hindwing to cover the tuft (Fig. 4). No such tufts on hindwing. If forewing tufts missing then forewing apex not truncate, recurrent vein in the discal cell on forewing present and ends at the origin of vein M_3 (not before it), no spot in cell R_2-R_3, antennae angled (bent beyond ticker part of club), discal cell about 2/3 of costa length. If discal cell longer, about 3/4 of costa, then antennae hooked, short, not reaching the origin of vein CuA_1, and no hyaline spots around mid costa or in cell CuA2-1A+2A.

Genera included: *Ectomis* Mabille, 1878, *Telemiades* Hübner, [1819], and *Polygonus* Hübner, [1825].

Parent Taxon: Tribe Eudamini Mabille, 1877.

Tribe Oileidini Grishin, 2019

Type genus: *Oileides* Hübner, [1825].

ZooBank registration: CF9C3D29-523A-4D17-B140-9A69CFA98731

Diagnosis: The tribe was defined as a clade from about 40-45 Mya that contains the genus *Oileides*, and putatively synapomorphic DNA characters for this clade were given (Li *et al.*, 2019). Phenotypically, species in this tribe would key to C.6, D.9.2a, D.9.4, E.2, E.4, E.5b, or E.10 in Evans (1952, 1953). A possible synapomorphy of the group: tufts of longer scales placed in a groove at the base of hindwing near anal fold. The tufts present either on dorsal or ventral side (Fig. 5), but not both. If tufts below, then antennae bent not beyond the thickest part of the club, the club more slender and uncus divided.


Fig. 5. Oileidini. Wing bases of *Oileides amazonensis renta* (Evans, 1952) ♂, Peru, ventral view, showing tufts of scales (peach color) inside grooves by veins.

Genera included: *Oileides* Hübner, [1825], *Typhedanus* A. Butler, 1870, *Oechydrus* E. Watson, 1893, *Cogia* A. Butler, 1870, *Nerula* Mabille, 1888, and *Marela* Mabille, 1903.

Parent Taxon: Subfamily Eudaminae Mabille, 1877.

Subtribe Typhedanina Grishin, 2019

Type genus: *Typhedanus* Butler, 1870.

ZooBank registration: B4D56F93-67F9-476F-B69C-133D98BFBD58

Diagnosis: The subtribe was defined as a clade from about 30 Mya that contains the genus *Typhedanus*, and putatively synapomorphic DNA characters for this clade were given (Li *et al.*, 2019). Phenotypically, species in this subtribe would key to C.6, E.2, E.4, E.5b, or E.10 in Evans (1952, 1953). Diagnosed by tufts of longer scales placed in a groove at the base of hindwing near anal fold, on dorsal side (Fig. 6), no tufts on ventral side.


Fig. 6. Typhedanina. Wing bases of *Typhedanus ampyx* (Godman & Salvin, 1893) ♂, Mexico: Veracruz, dorsal view, showing the tuft of scales (yellow) inside grooves by veins.

Genera included: *Typhedanus* A. Butler, 1870, *Oechydrus* E. Watson, 1893, *Cogia* A. Butler, 1870, *Nerula* Mabille, 1888, and *Marela* Mabille, 1903.

Parent Taxon: Tribe Oileidini Grishin, 2019.

Tribe Netrocorynini Grishin, 2019

Type genus: *Netrocoryne* C. & R. Felder, [1867].

ZooBank registration: DE61F048-02CF-4F8E-9392-D18A4618BABD

Diagnosis: The tribe was defined as a clade from about 40-45 Mya that contains the genus *Netrocoryne*, and putatively synapomorphic DNA characters for this clade were given (Li *et al.*, 2019). Phenotypically, species in this tribe would key to B.2, C.1, or C.15 in Evans (1949). Unexpected assemblage of genera without obvious synapomorphies (Fig. 72). Previously placed in tribe Tagiadini Mabille, 1878, but can be distinguished from them by the following somewhat convoluted combination of choices. If palpi erect, then mid and hind tibiae without spines and antennae not less than half of costa length in males, forewing vein M_3 originates midway between veins CuA_1 and M_1 (not M_2). If palpi porrect, then antennal club not flattened or twisted, apiculus tapered to a point (not blunt), palpi long, sometimes longer than head, and if club angled or hooked towards apiculus, then forewing cell not sorter than outer margin, forewing produced and truncate at apex, and hindwing produced at the end of vein 3; if the club arcuate or obtuse from the thickest part, then apiculus short, nudum with less than 17 segments, and hindwing costa produced at apex and longer than outer margin.

Fig. 7. Netrocorynini. Representatives of all 3 genera in the tribe (left to right): *Netrocoryne repanda* C. & R. Felder, [1867], *Chaetocneme denitza* (Hewitson, 1867), and *Exometoeca nycteris* Meyrick, 1888, all ♂♂ from Australia.

Genera included: *Netrocoryne* C. Felder & R. Felder, [1867], *Chaetocneme* Felder 1860, and *Exometoeca* Meyrick, 1888.

Parent Taxon: Subfamily Tagiadinae Mabille, 1878.

Tribe Jerini Grishin, 2019

Type genus: *Jera* Lindsey, 1925.

ZooBank registration: AF3B5CEA-880A-4CB2-AF40-E6D87C39C040

Diagnosis: The tribe was defined as a clade from about 40-45 Mya that contains the genus *Jera*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this tribe would key to E.3 in Evans (1953) and can be distinguished from all other Hesperiidae by unique wing shape (Fig. 8): forewing outer margin concave in the cell M_3-CuA_1, hindwing produced with a short and stout bifurcated tail extending cell CuA_1-CuA_2 and a lobe at tornus, antennal club blunt without apiculus, palpi long, forewing cell longer than 3/5 of costa.

Fig. 8. Jerini. Unique wing shape of *Jera tricuspidata* (Mabille, 1902) ♂, Ecuador.

Genera included: *Jera* Lindsey, 1925.

Parent Taxon: Subfamily Pyrrhopyginae Mabille, 1877.

Subtribe Pythonidina Grishin, 2019

Type genus: *Pythonides* Hübner, [1819].

ZooBank registration: CB890271-5483-4B5A-A7BC-27DBC5E23DE5

Diagnosis: The subtribe was defined as a clade from about 30 Mya that contains the genus *Pythonides*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this subtribe would key to E.44a, E.49.1, or, if uncus undivided, then to E.37a or 40d in Evans (1953). A heterogeneous assembly of mostly small and frequently brightly patterned Hesperiidae not easily diagnosed morphologically. In all genera, palpi porrect, antennae not shorter than 1/2 costa, forewing without recurrent vein and hindwing costal margin not shorter than anal margin. Includes two subgroups by uncus morphology. If (1) uncus deeply divided (Fig. 9), then 3rd segment of palpi as long as

2nd segment, antennal club nearly arcuate at its middle, apiculus not shorter than unbent portion of the club. If uncus undivided, and if (2) antennal apiculus shorter than unbent region of the club, then apiculus obtuse, not hooked, hindwing about triangular in shape, not quadrate, palpi not longer than head, or if (3) antennal club nearly arcuate at its middle and apiculus not shorter than unbent portion of the club, then 3rd segment of palpi shorter than 2nd segment.

Genera included: *Ouleus* Lindsey, 1925, *Zera* Evans, 1953, *Quadrus* Lindsey, 1925, *Gindanes* Godman & Salvin, 1895, *Pythonides* Hübner, [1819], *Haemactis* Mabille, 1903, *Atarnes* Godman & Salvin, 1897, *Eburuncus* Grishin, 2012, *Milanion* Godman & Salvin, 1895, *Paramimus* Hübner, [1819], and *Charidia* Mabille, 1903.

Parent Taxon: Tribe Achlyodini Burmeister, 1878.

Fig. 9. Pythonidina. Long uncus arms in *Eburuncus hierax* (Hopffer, 1874), Peru (top left); palpi (long 3rd segment) of *E. unifasciata* (C. & R. Felder, 1867), Costa Rica (top right); antennae, bottom left: *Ouleus calavius* (Godman & Salvin, 1895), Panama (above), *Pythonides lerina* (Hewitson, 1868), French Guiana (below); palpi (short 3rd segment) of *Gindanes brebisson panaetius* Godman & Salvin, 1895, Panama (bottom right).

Subtribe Clitina Grishin, 2019

Type genus: *Clito* Evans, 1953.

ZooBank registration: 971884E2-E5F7-46A3-B182-657729B6A778

Diagnosis: The subtribe was defined as a clade from about 30 Mya that contains the genus *Clito*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this subtribe would key to E.52 or E.13.8 in Evans (1953). A possible synapomorphic character is a conspicuously long sheath of aedeagus that distinguishes this subtribe from its relatives. In addition, a combination of the following characters is diagnostic: uncus undivided, tapered, apiculus arcuate at its center, sharply pointed, nudum not equally partitioned, 3/13: apiculus much longer than the club, mid tibiae with spines, wings produced, forewing inner margin straight, hindwing anal margin longer than costal margin, outer margin irregular, hindwing without hyaline spots but frequently with white areas (Fig. 10).

Fig. 10. Clitina. Characteristic wing shape and pattern in *Clito palotchka* Grishin, 2014, Ecuador (left) and *Clito mnemon* (Schaus, 1913), Panama (right).

Genera included: *Clito* Evans, 1953.

Parent Taxon: Tribe Erynnini Brues & Carpenter, 1932.

Tribe Butleriini Grishin, 2019

Type genus: *Butleria* Kirby, 1871.

ZooBank registration: D621EF81-FA65-4858-9450-E0C041598D7A

Diagnosis: The tribe was defined as a clade from about 40-45 Mya that contains the genus *Butleria*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this tribe would key to H.4 and H.5 in

Fig. 11. Butleriini. Apiculus of antenna (top left), hind leg (bottom left), and characteristic wing shape (right) of *Argopteron aureipennis* (Blanchard, 1852), Chile

Evans (1955). Belongs to the subfamily Heteropterinae and differs from the nominotypical tribe by the blunt somewhat flattened apiculus, compressed at the blunt tip, antennae not shorter than 1/2 costa, and hind tibiae with upper spurs (sometimes short) (Fig. 11).

Genera included: *Butleria* Kirby, 1871 and *Argopteron* E. Watson, 1893.

Parent Taxon: Subfamily Heteropterinae Aurivillius, 1925.

Tribe Pericharini Grishin, 2019

Type genus: *Perichares* Scudder, 1872.

ZooBank registration: 94B68BD2-7F83-4E58-80E1-7F5AC8C56511

Diagnosis: The tribe was defined as a clade from about 32 Mya that contains the genus *Perichares*, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this tribe would key to K.27a in Evans (1955). Belongs to the "K. Carystus group" (not a monophyletic assemblage) of Evans, characterized by the broad "quadrantic" palpi, inner side of 2nd segment longer than the side contacting head in dorsal view and the 3rd segment short and stout, nipple-like, antennae not constricted before apiculus, nudum 10-16 segments, its portion on the club shorter than the long apiculus. Distinguished from others within this group by forewing discal cell not shorter than inner margin, and vein CuA_1 opposite to vein R_1 (not R_2 or R_3) at their origins (Fig. 12).

Fig. 12. Pericharini. Characteristic palpi, antennae, and long forewing cell in *Perichares aurina* Evans, 1955 ♂, Brazil: Parana.

Genera included: *Perichares* Scudder, 1872, *Alera* Mabille, 1891, *Orses* Godman, 1901, *Lycas* Godman, 1901, *Lychnuchoides* Godman, 1901, *Pseudorphe* A. Warren & Dolibaina, 2015, and *Orphe* Godman, 1901.

Parent Taxon: Subfamily Hesperiinae Latreille, 1809.

Genus *Tekliades* Grishin, 2019

Type species: *Thymele ramanatek* Boisduval, 1833.

ZooBank registration: 081564BA-DA0C-4C46-AEAB-6C00131AC8BD

Diagnosis: The genus was defined as a clade from about 15 Mya that contains the species *Thymele ramanatek* Boisduval, 1833, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to I.1.9 in Evans (1937). The distinction of this genus from *Coeliades* Hübner, 1818 was not obvious before DNA studies due to similarity in appearance and genitalia. Distinguished from other genera of Coeliadinae by undivided uncus, bulkier gnathos and aedeagus, notch at the distal end of valva, white hindwing fringes, and a white postdiscal band on hindwing below (Fig. 13).

Fig. 13. *Tekliades*. Uniquely characteristic ventral wing pattern of *Tekliades ramanatek*.

Species included: *Thymele ramanatek* Boisduval, 1833.

Parent Taxon: Subfamily Coeliadinae Evans, 1937.

Genus *Salantoia* Grishin, 2019

Type species: *Eudamus eriopis* Hewitson, 1867.

ZooBank registration: 3F82E9DE-A5A2-44B3-A13D-53CF8A673FAE

Diagnosis: The genus was defined as a clade from about 15 Mya that contains the species *Eudamus eriopis* Hewitson, 1867, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to D.3.2 or D.3.3 in Evans (1952). Previously placed in *Sarmientoia* Berg, 1897, but distinguished from it by rectangular, not hook-shaped harpe in male genitalia and a lack of white spot in cell M_2-M_3 on forewing above. Either character is diagnostic (Fig. 14).

Fig. 14. ***Salantoia***. Valva of *Sarmientoia phaselis* (Hewitson, 1867), Colombia (top right) compared to valva of *Salantoia eriopis*, Brazil: PA (top left) and its forewing (bottom).

Species included: *Sarmientoia dinka* (Evans, 1952) and *Eudamus eriopis* (Hewitson, 1867).

Parent Taxon: Tribe Phocidini Tutt, 1906.

Genus *Spicauda* Grishin, 2019

Type species: *Goniurus procne*, Plötz, 1881.

ZooBank registration: 14D26B57-940C-407B-8E70-4E25203044B8

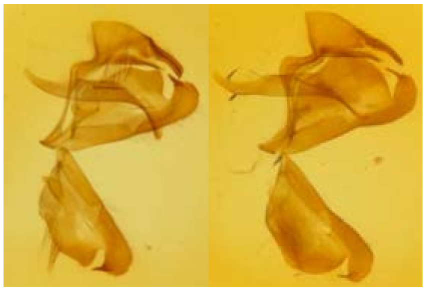

Fig. 15. ***Spicauda***. Diagnostic shape of valva with the spike in *Spicauda procne*, Guatemala (left) and *Spicauda teleus*, Mexico, Ver. (right).

Diagnosis: The genus was defined as a clade from about 15 Mya that contains the species *Goniurus procne*, Plötz, 1881, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to C.13.13c in Evans (1952). Previously placed in *Urbanus* Hübner, [1807] owing to long hindwing tails, but distinguished from it by unique shape of genitalic harpe that is upturned and with a spike-like process (or two) at its dorsal margin (Fig. 15). Externally, can be distinguished from other Eudaminae with long tails by a combination of the following characters: wings and body brown, without extensive green scales; fringes not checkered, brown or paler, but not white; if forewing cell M_3-CuA_1 with hyaline spot, it forms part of the discal band, not detached from it.

Species included: *Goniurus teleus* Hübner, 1821, *Urbanus tanna* Evans, 1952, *Urbanus ambiguus* de Jong, 1983, *Urbanus cindra* Evans, 1952, *Goniurus zagorus* Plötz, 1881, *Papilio simplicius* Stoll, 1790, and *Goniurus procne* Plötz, 1881.

Parent Taxon: Subtribe Eudamina Mabille, 1877.

Subgenus *Urbanoides* Grishin, 2019

Type species: *Goniurus esmeraldus* Butler, 1877.

ZooBank registration: 20FAC3B6-F038-40A0-B182-3C7F32A40702

Diagnosis: The subgenus was defined as a clade from about 12 Mya that contains the species *Goniurus esmeraldus* Butler, 1877, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this subgenus would key to C.13.6a in Evans (1952). Member of this subgenus are diagnosed by an apparent synapomorphy: dorsally directed process on genitalic valvae, lacking in the nominotypical subgenus, where valva may have a small "nose"-shaped projection (Fig. 16).

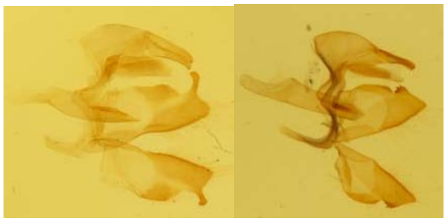
Fig. 16. *Urbanoides*. Valva with a process in *Urbanus* (*Urbanoides*) *esmeraldus*, Brazil: MG (left), compared to valva with a "nose" in *Urbanus* (*Urbanus*) *proteus* (Linnaeus, 1758), Brazil: RS.

Species included: *Goniurus esmeraldus* A. Butler, 1877, *Urbanus esma* Evans, 1952, *Urbanus prodicus* E. Bell, 1956, *Urbanus elmina* Evans, 1952, *Urbanus evona* Evans, 1952, *Urbanus esta* Evans, 1952, *Urbanus viridis* H. Freeman, 1970.

Parent Taxon: Genus *Urbanus* Hübner, [1807].

Genus *Zeutus* Grishin, 2019

Type species: *Cecropterus zeutus* Möschler, 1879.

ZooBank registration: 75715B9C-46AB-40F5-B738-420DABD56B63

Diagnosis: The genus was defined as a clade from about 15 Mya that contains the species *Cecropterus zeutus* Möschler, 1879, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would have genitalia as those described for *zeutus* by Williams & Bell (1934: 27). More specifically, uncus arms shorter than in *Calliades* Mabille & Boullet, 1912 where this species resided formerly; valvae asymmetrical, broad, diamond-shaped; both harpes narrow, deeply separated from the rest of valvae; aedeagus widens toward its apex, with a rounded flange on its dorsal side (Fig. 17).

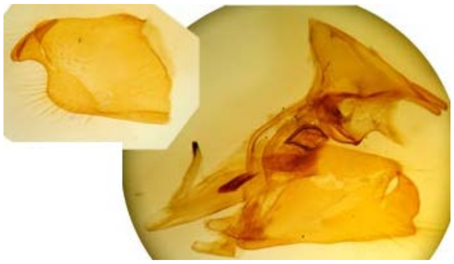
Fig. 17. *Zeutus*. Unique shape of asymmetric valvae in *Zeutus zeutus*, French Guiana, aedeagus seen in the center.

Species included: *Cecropterus zeutus* Möschler, 1879.

Parent Taxon: Subtribe Loboclina Grishin, 2019.

Genus *Lobotractus* Grishin, 2019

Type species: *Eudamus valeriana* Plötz, 1881.

ZooBank registration: C6E5B5DF-1C74-4DBD-85C3-7285209F6F03

Diagnosis: The genus was defined as a clade from about 15 Mya that contains the species *Eudamus valeriana* Plötz, 1881, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, diagnosis for this genus is the same as given for the "cyda group" by Burns (1996: 196). The following combination of characters unifies all known species in the genus and distinguishes them from all other genera: 3rd segment of palpi long, longer than in *Codatractus* (Fig. 18); costal fold absent; uncus undivided, in dorsal view longer than wide and slightly concave terminally and on the sides ("scalloped" per Evans (1952)), but not prominently bilobed; tegumen humped in lateral view; shorter, fan-like cornutus with many sharp branches; valvae with a fang-like harpe bending dorsad and enlarged, rounded ampulla protruding caudad to reach the end of harpe; lamella antevaginalis expanded in two large plates, each on the side of ostium bursae, plates reach the end of lamella postvaginalis and protrude further narrowing towards the middle into a sharp tooth, plates fully separated mid-ventrad exposing ostium bursae ventrally. All these characters are illustrated in Burns (1996), who discovered them and described in detail.

Fig. 18. *Lobotractus*. 3rd segment of palpi longer in *Lobotractus* (left) than in *Codatractus* (right): *L. cyda*, Honduras, vs. *C. melon* (Godman & Salvin, 1893), Mexico: Gro.

Species included: *Eudamus valeriana* Plötz, 1881, *Thorybes uvydixa* Dyar, 1914, and *Heteropia cyda* Godman, 1901.

Parent Taxon: Subtribe Loboclina Grishin, 2019.

Subgenus *Caudatractus* Grishin, 2019

Type species: *Eudamus alcaeus* Hewitson, 1867.

ZooBank registration: DF0F3C91-F56E-4B65-B86C-385A36F9D7FD

Diagnosis: The subgenus was defined as a clade from about 7 Mya that contains the species *Eudamus alcaeus* Hewitson, 1867, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this subgenus would key to C.11.1b in Evans (1952). These species share the following characters of *Codatractus*: broadly arcuate antennae, forewing with conjoined apical spots just beyond of discal cell in cells R_2-R_3 and R_3-R_4, spot in forewing cell M_3-CuA_1 midway between the discal band and outer margin, ventral hindwing with 3 dark irregular bands. Species in this subgenus are distinguished from all other *Codatractus* species by the tail near hindwing tornus (Fig. 19). Species from the nominotypical subgenus lack tails, but their hindwing may be lobed at tornus.

Fig. 19. *Caudatractus*. Left: *Codatractus* (*Caudatractus*) *aminias*, Brazil: MG, with tailed hindwing vs. right: *Codatractus* (*Codatractus*) *imalena* (A. Butler, 1872), Brazil, AM.

Species included: *Codatractus carlos* Evans, 1952, *Codatractus rowena* Evans, 1952, *Eudamus alcaeus* Hewitson, 1867, *Codatractus apulia* Evans, 1952, *Codatractus yucatanus* H. Freeman, 1977, and *Eudamus aminias* Hewitson, 1867.

Parent Taxon: Genus *Codatractus* Lindsey, 1921.

Subgenus *Asina* Grishin, 2019

Type species: *Eudamus asine* Hewitson, 1867.

ZooBank registration: B3B7A6F6-A95C-4A2E-B9FB-80A7A8F86761

Diagnosis: The subgenus was defined as a clade from about 14 Mya that contains the species *Eudamus asine* Hewitson, 1867, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this subgenus would key to C.7.2a in Evans (1952). The following

Fig. 20. ***Asina***. Diagnostic pattern of spots near forewing margin above in *Ectomis* (*Asina*) *gyges* ♂, Peru.

characters distinguish them from other Hesperiidae except some *Ectomis*: antennal club angled, hindwing elongated with a long tail by the tornus, apical spots on forewing in a straight line, spot in forewing cell M_3-CuA_1 near discal band and farther from outer margin, males with costal fold. The following characters differentiate species in this subgenus from the nominal *Ectomis*: head a thorax above brown (without extensive green scales), forewing above with a dark spot about 1/3 from the base of cell CuA_2-1A+2A, no spot in this cell past the discal band, but 2 small spots (one frequently hyaline) under the pale spot from the discal band in cell CuA_1-CuA_2 (Fig. 20), ventrally, aedeagus with a terminal spine projected to the left.

Species included: *Polythrix gyges* Evans, 1952, *Goniuris* [sic] *hirtius* A. Butler, 1870, *Polythrix roma* Evans, 1952, *Eudamus asine* Hewitson, 1867, and *Polythrix mexicanus* H. Freeman, 1969.

Parent Taxon: Genus *Ectomis* Mabille, 1878.

Genus *Tiana* Grishin, 2019

Type species: *Ebrietas niger* Williams & Bell, 1940.

ZooBank registration: B9382699-24FB-4466-B39B-94E6B544C425

Fig. 21. ***Tiana***. *Tiana platypterus*, Honduras (left) and *Tiana niger*, Colombia (right).

Diagnosis: The genus was defined as a clade from about 10 Mya that contains the species *Ebrietas niger* Williams & Bell, 1940, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to F.7.3 or F.7.4 in Evans (1953). Combination of the following characters is diagnostic of the genus (Fig. 21): forewing discal cell very short, outer margin of both wings evenly convex, palpi short, antennal shaft plain and club slender, nudum of 21-24 segments, males with costal fold on forewing, no tibial tufts, both wings dark, almost unmarked or with two paler, ochreous brown bands above cut by dark veins without violet sheen, below distal half of hindwing paler with darker veins. Differing from *Tosta* Evans, 1953 and *Iliana* E. Bell, 1937 by uncus without projections, either undivided or with very short knob-like arms, harpe simple, without processes, almost rectangular, unturned with serrated dorsal margin, not prominently separated from the ampulla.

Species included: *Ebrietas niger* Williams & Bell, 1940 and *Anastrus platypterus* Mabille, 1895.

Parent Taxon: Tribe Carcharodini Verity, 1940.

Genus *Chirgus* Grishin, 2019

Type species: *Hesperia limbata* Erschoff, 1876.

ZooBank registration: 7B1905F1-9471-4BBF-90BF-32360783AB1E

Diagnosis: The genus was defined as a clade from about 10 Mya that contains the species *Hesperia limbata* Erschoff, 1876, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to G.1.2e or G.1.9 in Evans (1953). Similar to *Pyrgus* and *Burnsius* in checkered appearance, produced wings: forewing costa longer than outer margin, hindwing costa about the same length as outer margin, short, extensively scaled palpi with inconspicuous 3rd segment, but differ in the following characters (Fig. 22): tibial tuft present, no costal fold in males, forewing with a white spot at the base of cell CuA_1-CuA_2, hyaline spots in cells R_3-R_4, R_4-R_5, and R_5-M_1 not produced into cell R_2-R_3, and (1) if cell R_1-R_2 without a spot between the apical spots and discal cell spot, then forewing lacks hyaline dot at base of cell R_3-R_4 between apical spots and discal cell spot, hindwing apex somewhat produced and outer margin slightly concave in cell CuA_2-1A+2A, no submarginal white spots on wings; or (2) if cell R_1-R_2 with a hyaline spot by the costa midway between the cell spot and apical spots, then no streaks marginally from the forewing discal cell spot and no discal spots in cells M_1-M_2 and M_2-M_3.

Fig. 22. *Chirgus*. Variation in the genus: *C. limbata*, Chile, *C. bocchoris trisignatus*, Peru, and *C. veturius*, Brazil: BA (left to right), all ♂♂.

Species included: *Hesperia* (*Syrichthus* [sic]) *limbata* Erschoff, 1876, *Syrichthus* [sic] *nigella* Weeks, 1902, *Pyrgus barrosi* Ureta, 1956, *Pyrgus fides* Hayward, 1940, *Syrichtus bocchoris* Hewitson, 1874, and *Pyrgus* (*Scelothrix* [sic]) *veturius* Plötz, 1884.

Parent Taxon: Tribe Pyrgini Burmeister, 1878.

Genus *Burnsius* Grishin, 2019

Type species: *Syricthus* [sic] *communis* Grote, 1872.

ZooBank registration: 48996B74-3AB1-4DEA-9A64-B8F112E62343

Fig. 23. *Burnsius*. Wing pattern of *B. albescens* ♂, USA: Texas, typical for the genus.

Diagnosis: The genus was defined as a clade from about 10 Mya that contains the species *Syricthus* [sic] *communis* Grote, 1872, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to G.1.5, G1.8, or G.1.10a in Evans (1953). Similar to *Pyrgus* and *Chirgus* in checkered appearance, produced wings: forewing costa longer than outer margin, hindwing costa about the same length as outer margin, short extensively scaled palpi with inconspicuous 3rd segment, but differ in the following characters (Fig. 23): forewing with a white spot at the base of cell CuA_1-CuA_2, hyaline spots in cells R_5-M_1, R_4-R_5, R_3-R_4 not produced into cell R_2-R_3, and (1) if cell R_1-R_2 without spot between the apical spots and discal cell spot, then forewing with hyaline dot at base of cell R_3-R_4 between apical spots and discal cell spot, but (2) if no such dot, then hindwing outer margin evenly convex, not produced apically and white bar at the end of discal cell absent both above and below; or (3) if cell R_1-R_2 with hyaline spot by the costa midway between the cell spot and apical spots, then forewing with pale streaks marginally from the forewing discal cell spot and discal spots in cells M_1-M_2 and M_2-M_3.

Species included: *Syrichtus notatus* Blanchard, 1852, *Pyrgus crisia* Herrich-Schäffer, 1865, *Syricthus* [sic] *communis* Grote, 1872, *Pyrgus albescens* Plötz, 1884, *Pyrgus adepta* Plötz, 1884, *Hydraenomia orcynoides* Giacomelli, 1928, *Pyrgus chloe* Evans, 1942, *Hesperia titicaca* Reverdin, 1921, *Pyrgus philetas* W. H. Edwards, 1881, *Papilio oileus* Linnaeus, 1767, *Papilio orcus* Stoll, 1780, and *Pyrgus brenda* Evans, 1942.

Parent Taxon: Tribe Pyrgini Burmeister, 1878.

Genus *Duroca* Grishin, 2019

Type species: *Hesperia duroca* Plötz, 1882.

ZooBank registration: 476FE13C-5895-4139-BB11-44F835E21565

Fig. 24. ***Duroca***. *D. duroca duroca* ♂, Brazil: RJ, dorsal (left) and ventral (right) views.

Diagnosis: The genus was defined as a clade from about 7 Mya that contains the species *Hesperia duroca* Plötz, 1882, and putatively synapomorphic DNA characters for this clade were given (Li *et al*., 2019). Phenotypically, species in this genus would key to J.39.5a in Evans (1955) and a combination of the following characters is diagnostic: antennae about half of costa length, nudum 2/9 to 4/9, palpi narrow, 3rd segment short, conically shaped, mid tibiae with spines, males with broad tripartite stigma from base of vein CuA_1 to vein 1A+2A, origin on vein CuA_2 on forewing is closer to the base than to vein CuA_1. Stigma longer than in *Lerema* Scudder, 1872 and reaches vein 1A+2A closer to the base of wing (Fig. 24). Uncus and gnathos deeply divided, and this genus best distinguished from other genera by broad valva with large harpe, upturned and shaped like a hook, being more similar to some *Phlebodes* Hübner, [1819] and *Saturnus* Evans, 1955 than to *Lerema*, but uncus and gnathos divided less deeply in these genera with hook-shaped harpe.

Species included: *Hesperia duroca* Plötz, 1882.

Parent Taxon: Subtribe Moncina A. Warren, 2008.

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