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Checking the checkered taxonomy of Plötz's checkered skippers (Hesperiidae: Pyrgini)

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ABSTRACT. We present an analysis of the names proposed by Carl Plötz in 1884 for the New World species in the genus *Pyrgus* Hübner, [1819] facilitated by the genomic sequencing of extant primary type specimens comparatively with a larger sample of more recently collected specimens of these species and their relatives. The changes to nomenclature suggested here are only caused by the identity of primary type specimens as revealed by their phenotypes or though genomic sequencing. All neotypes are designated to stabilize nomenclature in agreement with the current usage of these names, which in unison agrees best with the information available about them. **Lectotypes** are designated for the following 5 taxa: *Pyrgus (Scelothrix* [sic]*) bellatrix* Plötz, 1884 (type locality Argentina: Buenos Aires), *Pyrgus (Pyrgus) willi* Plötz, 1884 (type locality in Brazil: Minas Gerais), *Pyrgus (Pyrgus) albescens* Plötz, 1884 (type locality in Mexico), *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884 (type locality in "Central America", likely southern Mexico), and *Pyrgus occidentalis* Skinner, 1906 (type locality USA: Texas, San Antonio). **Neotypes** are designated for the following 4 taxa: *Pyrgus (Pyrgus) adepta* Plötz, 1884 (Herrich-Schäffer in litt.) (type locality Colombia: Bogota), *Pyrgus (Scelothrix* [sic]*) dion* Plötz, 1884 (type locality Colombia: Bogota), *Pyrgus (Scelothrix* [sic]*) adjutrix* Plötz, 1884 (Herrich-Schäffer in litt.) (type locality in Mexico: Nuevo Leon), *Pyrgus (Pyrgus) insolatrix* Plötz, 1884 (Herrich-Schäffer in litt.) (type locality in "Central America", likely southern Mexico). As a result, *P. lycurgus* and *P. insolatrix* are objective synonyms. The following are junior subjective synonyms: *P. dion* of *Burnsius adepta* (Plötz, 1884), *Pyrgus (Syrichthus* [sic]*) varus* Plötz, 1884 of *Burnsius orcus* (Stoll, 1780) and *P. adjutrix* of *Burnsius oileus* (Linnaeus, 1767). *Heliopetes (Heliopyrgus) willi* (Plötz, 1884) is a species-level taxon and not a subspecies of *Heliopetes (Heliopyrgus) domicella* (Erichson, [1849])). Genomic analysis of the lectotypes of *P. albescens*, *P. lycurgus*, and *P. occidentalis* establishes them as conspecific with *Burnsius communis* (Grote, 1872), thus depriving a distinct species currently identified as *Burnsius albescens* from its name, that becomes a name for *Burnsius communis albescens* (Plötz, 1884) in accord with its lectotype identity; *P. lycurgus* and *P. insolatrix* are its junior subjective synonyms, but *P. occidentalis* is a junior subjective synonym of *B. communis communis*. A new name *Burnsius albezens* Grishin **sp. n.** (type locality USA: Arizona, Cochise Co., Portal) is proposed for the species misidentified as *B. albescens*. Furthermore, genomic comparisons reveal two other new species and one new subspecies of *Burnsius* Grishin, 2019: *B. burnsi* Grishin **sp. n.** (type locality Mexico: Veracruz, Huatusco), *B. adepta inepta* Grishin **ssp. n.** (type locality Ecuador: Pichincha, Tandapi), and *B. orcynus* Grishin **sp. n.** (type locality Curaçao: Hato Field) that are cryptic and can be confidently identified only by their genotype.

Additional key words: nomenclature, stability, taxonomy, classification, genomics, biodiversity, butterflies.

ZooBank registration: http://zoobank.org/1AC1F3FB-603E-46A0-B8C2-BB9DE88B46BB

INTRODUCTION

Carl Plötz named several hundred Hesperiidae species in a short span of 8 years right before his death, developed and published identification keys for the Worldwide Hesperiidae fauna as he understood it, and prepared drawings for nearly all Hesperiidae species he knew and had access to. Unfortunately, a large number of species proposed by Plötz could not be traced to primary type specimens, his drawings were not published and their whereabouts remain unknown, and his keys were neither detailed nor accurate enough to allow unambiguous identification. For these reasons, it has been a challenge to figure out the attribution of Plötz names, and many of them were either incorrectly synonymized or used for species they were not meant for.

To partly alleviate the problem, copies of some of Plötz's drawings were arranged by Godman for the species he could not confidently recognize and attribute to specimens in his collection (Godman 1907). This compilation was largely focused on Neotropical species, but included a number of Old World species as well. These drawings that are not particularly precise and look more like sketches (it is unclear whether the originals were any more accurate), remain unpublished and are in the library of the Natural History Museum, London, UK (BMNH). At least a second copy of some of these drawings was also made, because similar drawings, cut into small cards, are pinned among the specimens of corresponding species in the collection of National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

In his treatment of checkered skippers Plötz placed in *Pyrgus* Hübner, [1819], a number of species that are now transferred to other genera, such as *Burnsius* Grishin, 2019, *Heliopetes* Billberg, 1820, *Muschampia* Tutt, 1906, *Favria* Tutt, 1906, *Spialia* Swinhoe, 1912, *Agyllia* Grishin, 2020, *Ernsta* Grishin, 2020, *Alenia* Evans, 1935, *Taractrocera* Butler, [1870], *Nervia* Grishin, 2019, and *Amblyscirtes* Scudder, 1872, assigned to 6 tribes (Pyrgini Burmeister, 1878, Carcharodini Verity, 1940, Celaenorrhinini Swinhoe, 1912, Astictopterini Swinhoe, 1912, Taractrocerini Voss, 1952, and Hesperiini Latreille, 1809) in 3 subfamilies (Pyrginae Burmeister, 1878, Tagiadinae Mabille, 1878, and Hesperiinae Latreille, 1809); and he proposed 12 new names that have been associated with the New World fauna (Plötz 1884). One of them, *Pyrgus (Syrichthus* [sic]*) argina* Plötz, 1884 (type locality Australia, Brisbane, in error), later found to be a junior subjective synonym of *Amblyscirtes (Stomyles) hegon* (Scudder, 1863) (Evans 1949; Evans 1955) (synonymy confirmed), belongs to the subfamily Hesperiinae Latreille, 1809 and was never truly associated with the "checkered skippers" later on. Here, we analyze the remaining 11 names together with others, trace some to their primary type specimens, and propose solutions to nomenclatural and taxonomic problems related to these names. The major new data presented here are: (1) unpublished copies of the Plötz's drawing of *Pyrgus (Syrichthus* [sic]*) varus* Plötz, 1884 and (2) genomic analysis of primary type specimens together with a series of more recently collected specimens, which calls for a number of taxonomic changes.

MATERIALS AND METHODS

The specimens were inspected and photographed/sampled for DNA in the following collections: American Museum of Natural History, New York, NY, USA (AMNH), Natural History Museum, London, UK (BMNH), Burke Museum of Natural History and Culture, Seattle, WA, USA (BMUW), Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH), Ernst Moritz Arndt Universität in Greifswald, Germany (EMAU), Field Museum of Natural History, Chicago, IL, USA (FMNH), Mississippi Entomological Museum, Starkville, MS, USA (MEM), Museum für Naturkunde, Berlin, Germany (MFNB), McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA (MGCL), Texas A&M University Insect Collection, College Station, TX, USA (TAMU), Bohart Museum of Entomology, University of California, Davis, CA, USA (UCDC), National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), Zoologische Staatssammlung München, Germany (ZSMC). Historical documents, such as unpublished drawings, were inspected in the following collections: Natural History Museum, London, UK (BMNH) and National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). Photographs of specimens and illustrations were taken with Nikon D800 camera through 105 mm macro lens and processed using Photoshop. Genomic sequencing and analysis was carried out using our developed protocols as previously described (Cong et al. 2021; Zhang et al. 2021). Sequence datasets obtained in this work are deposited in the NCBI database <https://www.ncbi.nlm.nih.gov/> as BioProject PRJNA832040 (BioSample entries of the project contain the locality and collection data of the sequenced specimens shown in the trees), and COI barcodes have GenBank accessions ON255697–ON255706. Exon sequences with diagnostic characters highlighted are also available from <https://osf.io/ru7bc/>. DNA characters are given as abbreviations, e.g., aly728.44.1: G672C means position 672 in exon 1 of gene 44 from scaffold 728 of *Cecropterus lyciades* (formerly in *Achalarus* Scudder, 1872, thus aly) reference genome (Shen et al. 2017) is C, changed from G in the ancestor. Similar notations are used for the COI barcode characters, e.g., A78G means position 78 is G, changed from A in the ancestor, or T264T(not C) means position 264 is T, unchanged from the ancestor, and not C as in sister taxon.

RESULTS AND DISCUSSION

At the end of his *Pyrgus* revision, Plötz acknowledged the difficulties he experienced with the project (translated from German): "several species are [known] only in a defective condition, from female specimens, or illustrations" (Plötz 1884). The issue with female specimens is that major divisions in Plötz's key are largely based on the two characters: costal fold and "hair pencil", i.e., a tuft of long, hair-like scales on hind-tibiae. Both of these characters are expressed only in males. "Defective condition" might refer to the absence of hindlegs in males, needed to check a "hair pencil" (although thoracic pouch presence is also an indicator of the pencil).

As a result, four subjective synonyms of a single species *Pyrgus ruralis* (Boisduval, 1852), all treated as separate species by Plötz, are scattered throughout his key: *Hesperia ricara* W. H. Edwards, 1865 is placed in the subgenus *Pyrgus* (hair pencil absent, costal fold present), *Syrichtus caespitatis* Boisduval, 1852 and *Syrichtus ruralis* Boisduval, 1852 are placed not near each other in the subgenus *Scelothrix* [sic] (hair pencil present, costal fold present in all but one species) and *Syrichtus petreius* W. H. Edwards, 1870 is placed in the subgenus *Syrichthus* [sic] (both hair pencil and costal fold are absent). The characters given in the key seem insufficient to confidently figure out which actual species were meant by Plötz. All these 4 taxa have costal fold and hair pencil in males. Therefore, Plötz either misidentified some of these species, or experienced other problems, like having only female specimens available for analysis (leaving the rest to guesswork), misidentifying females as males, or missing the presence of sometimes poorly developed costal fold. Judging from the information in his key, we hypothesize that, if Plötz inspected actual specimens of these taxa (instead of inserting them into the key based on literature and correspondence), both his "*ricara*" (males probably included) and "*petreius*" (likely only females) were variations of *Burnsius communis* (Grote, 1872) from Colorado and Nevada.

One of the more mysterious names, *Pyrgus (Scelothrix* [sic]*) dion* Plötz, 1884, was proposed on the basis of a female (likely a single specimen) from unknown locality, so its attribution to a subgenus defined by the two secondary sexual characters in males, was arbitrary. Regardless of these mistakes and problems, we undertook the task to figure out which presently known species were meant by the 11 names proposed by Plötz in this work for the New World taxa. From the example given above, we learned that we should not put much weight in Plötz's identification of species named before him and his judgment about the presence or absence of secondary sexual characters or the sex of a specimen. In our decisions, we largely relied on (1) the agreement between the description, more heavily weighted for the characters given in the paragraph just above the name, with the specimen(s) curated as the type(s) of this name, or with the copies of unpublished drawings; (2) Plötz's statements about general similarity between his taxa: for his n. 49 (*Lycurgus*), 50 (*Petreius*) and 51 (*Communis*), all 3 in the subgenus *Syrichthus* [sic], Plötz stated: "It is the same habitus as in § n. 5 [*Albescens*], 6 [*Ricara*], 7 [*Insolatrix*, all 3 in the subgenus *Pyrgus*] and §§§ n. 38 [*Adjutrix*, in the subgenus *Scelothrix* [sic]], but in basal area of the discal cell there is no white ray on forewing, and no spot on the hindwing"; (3) specimen localities, if MFNB and ZSMC (the two collections with Plötz's types) had many old specimens of a species from one locality.

We started from the names with extant syntype specimens: *Pyrgus (Pyrgus) willi* Plötz, 1884 (NVG-18057A03, ZSMC), *Pyrgus (Pyrgus) albescens* Plötz, 1884 (NVG-15033H10, MFNB), *Pyrgus (Scelothrix* [sic]*) bellatrix* Plötz, 1884 (NVG-15032B12, MFNB), and *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884 (NVG-15033H11, MFNB), one specimen per name found (Fig. 1a–d). For each of the four, we compared the specimen closely with the original description and found a good agreement in all cases. Therefore, we confirm them as syntypes, and stabilized nomenclature by lectotype designations below.

All four type specimens were sequenced and included in the genomic tree along with many more recently collected specimens. While *P. willi* and *P. bellatrix* indeed grouped with the specimens identified as such (the former is a species-level taxon, not a subspecies as in the current taxonomic arrangement), to our surprise, both *P. albescens* and *P. lycurgus* clustered within the species known today as *Burnsius communis* (Grote, 1872) (type locality in USA: central Alabama) and not in agreement with the current usage of these names (Table 1). This discrepancy prompted a more careful investigation into original descriptions of other seven taxa and analysis of additional information available about them.

For the two of these names, *Pyrgus (Pyrgus) aconita* Plötz, 1884 and *Pyrgus (Scelothrix* [sic]*) veturius* Plötz, 1884, we agree with the current taxonomic interpretation and hypothesize that the type locality of *P. veturius* might have been in Brazil: Bahia. For one name, *Pyrgus (Syrichthus* [sic]) *varus* Plötz, 1884, we inspected and photographed Godman's copies of Plötz's original drawings (Fig. 2c, d) that, in agreement with the original description, allowed us to identify this species as *Burnsius orcus* (Stoll, 1780), a change to the current synonymy. Furthermore, using this information, we found two female specimens in MFNB that are syntypes of *P. varus*, possibly the specimens illustrated by Plötz.

For the remaining four names, we analyze the original descriptions and designate neotypes to objectively define these names, because we were not able to find their syntypes and believe they were lost. The exceptional need for the neotype designations arises from the discovery of several cryptic species of *Burnsius* as revealed by genomic sequencing, and thus the necessity to apply names to them in accord with the ICZN Code (ICZN [International Commission on Zoological Nomenclature] 1999). In all four cases of neotype designations, we find that our choice is consistent with the current usage of these names, apparently the best decision that can be arrived at on the basis of available information and in the absence of syntypes. The neotypes are needed, however, to stabilize nomenclature, because the original descriptions are vague and at times inconsistent, some missing type localities.

After objectively defining Plötz's questionable names with lectotypes and neotypes, we find that the species currently known as *Burnsius albescens* (Plötz, 1884) does not have a name, because the primary types of all names previously assigned to it are *B. communis* and no other available name apparently applies. It has been a challenge to separate the now nameless species ("*B. albescens*") from *B. communis*. Over the course of more than a century, the entity called *albescens* has been widely and variously called a form, variety, race, geographical race, or subspecies of *communis*, or a separate species. Using differences in male genitalia, average size, and geographic distribution, Burns (2000) decisively documented its species status. Using genomics, we demonstrate that the trinomial *Burnsius communis albescens* should be retained but applied to an altogether different taxon: a Mexican subspecies of *B. communis*. So there are three valid taxa: *B. communis*, its Mexican subspecies *B. c. albescens*, and a species currently known as *B. albescens*.

It is unclear whether the ICZN should be approached to preserve the current usage of the name *B. albescens* by a neotype designation and to rename the true Mexican *albescens*. This matter is for the wider community of Lepidopterists to decide. To alleviate the problem for the time being, we propose a new

Table 1

New taxa, change of synonymy, and change in status are highlighted in green, yellow, and blue, respectively

First proposed as	Current treatment	Proposed herein
Pyrgus (Scelothrix [sic]*) veturius* Plötz, 1884	*Chirgus (Turis) veturius* (Plötz, 1884)	*Chirgus (Turis) veturius* (Plötz, 1884)
Pyrgus (Scelothrix [sic]*) bellatrix* Plötz, 1884	*Heliopetes (Heliopyrgus) americanus bellatrix* (Plötz, 1884)	*Heliopetes (Heliopyrgus) americanus bellatrix* (Plötz, 1884)
Pyrgus (Pyrgus) aconita Plötz, 1884 (Herrich-Schäffer in litt.)	*Heliopetes (Heliopyrgus) domicella domicella* (Erichson, [1849])	*Heliopetes (Heliopyrgus) domicella domicella* (Erichson, [1849])
Pyrgus (Pyrgus) willi Plötz, 1884	*Heliopetes (Heliopyrgus) domicella willi* (Plötz, 1884)	*Heliopetes (Heliopyrgus) willi* (Plötz, 1884)
Pyrgus (Pyrgus) adepta Plötz, 1884 (Herrich-Schäffer in litt.)	*Burnsius adepta* (Plötz, 1884)	*Burnsius adepta adepta* (Plötz, 1884)
Pyrgus (Scelothrix [sic]*) dion* Plötz, 1884	*Burnsius adepta* (Plötz, 1884)	*Burnsius adepta adepta* (Plötz, 1884)
Pyrgus (Syrichthus [sic]*) varus* Plötz, 1884	*Burnsius communis* (Grote, 1872)	*Burnsius orcus* (Stoll, 1780)
Pyrgus (Scelothrix [sic]*) adjutrix* Plötz, 1884 (Herrich-Schäffer in litt.)	*Burnsius oileus* (Linnaeus, 1767)	*Burnsius oileus* (Linnaeus, 1767)
Pyrgus (Pyrgus) albescens Plötz, 1884	*Burnsius albescens* (Plötz, 1884)	*Burnsius communis albescens* (Plötz, 1884)
Pyrgus (Syrichthus [sic]*) lycurgus* Plötz, 1884	*Burnsius adepta* (Plötz, 1884)	*Burnsius communis albescens* (Plötz, 1884)
Pyrgus (Pyrgus) insolatrix Plötz, 1884 (Herrich-Schäffer in litt.)	*Burnsius communis* (Grote, 1872)	*Burnsius communis albescens* (Plötz, 1884)
Pyrgus occidentalis Skinner, 1906	*Burnsius albescens* (Plötz, 1884)	*Burnsius communis communis* (Grote, 1872)
n/a	*Burnsius albescens* (Plötz, 1884) of Evans 1953 and Burns 2000	*Burnsius albezens* Grishin, sp. n.
n/a	*Burnsius adepta* (Plötz, 1884) in North and Central America	*Burnsius burnsi* Grishin, sp. n.
n/a	*B. adepta* and *orcynoides* in SW Colombia and Ecuador	*Burnsius adepta inepta* Grishin, ssp. n.
n/a	*Burnsius orcynoides* (Giacomelli, 1928) on islands off Venezuela	*Burnsius orcynus* Grishin, sp. n.

Fig. 1. Lectotypes and neotypes of *Heliopetes* and *Burnsius*. **a**. lectotype of *Pyrgus (Scelothrix* [sic]*) bellatrix* Plötz, 1884, now *Heliopetes (Heliopyrgus) americanus bellatrix*; **b**. lectotype of *Pyrgus (Pyrgus) willi* Plötz, 1884, now *Heliopetes (Heliopyrgus) willi*, stat. rest.; **c**. lectotype of *Pyrgus (Pyrgus) albescens* Plötz, 1884, now *Burnsius communis albescens*, stat. rev.; **d**. lectotype of *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884 and, simultaneously, neotype of *Pyrgus (Pyrgus) insolatrix* Plötz, 1884 (Herrich-Schäffer in litt.), now junior subjective synonyms of *Burnsius communis albescens*, stat. rev.; **e**. lectotype of *Pyrgus occidentalis* Skinner, 1906, now junior subjective synonym of *Burnsius communis communis* (Grote, 1872), end of its abdomen in left lateral view is shown on the right, scales removed to expose left valva and green arrows point at the two prongs of its expanded harpe, 0.5 mm scale bar refers to this image. Each specimen is separated from others by black lines; dorsal and ventral aspects are shown on the left and right, respectively. Labels and specimens are shown to scale with a 1 cm scale bar given. Synonyms are preceded with = sign and are placed in parenthesis. LT and NT denote lectotype and neotype, respectively. Specimen repository abbreviations are shown in blue font.

name for the current *albescens*. The new name is phonetically similar to *albescens* and would not sound like a change; and it replaces two letters (standing for the typically two-prong harpe of male genitalia in true *albescens*) with one letter (standing for what Evans (1953) called the "monodent" harpe of the unnamed species).

After this general overview summarized in Table 1, we present sections dealing with each name individually. These sections are ordered taxonomically unless the logic of presentation dictates a different order, which is adopted for clarity.

Pyrgus (Scelothrix [sic]*) veturius* Plötz, 1884 is confirmed as a valid (and type) species of *Turis* Grishin, 2022, a subgenus of *Chirgus* Grishin, 2019

We inspected specimens identified as *Pyrgus (Scelothrix* [sic]*) veturius* Plötz, 1884 (type locality not specified, could have been Brazil: Bahia, because this is one of the known localities with specimens collected at around that time, and Plötz named other species from there) in MFNB, an illustration of this species by Draudt (1921–1924) (which might have been a reproduction of the original drawing by Plötz that was included among the drawings copied by Godman's decision), and the original description given in a form of an identification key (Plötz 1884). Plötz diagnosed *P. veturius* by the absence of a central white band on hindwing that is replaced with disjoined spots, five in number, not reaching costal margin, and five spots in the submarginal area; two spots in forewing discal cell, one above the other, and pale dash between them and costa; a divided white spot in the postdiscal area of forewing cell 1 (CuA_2-1A+2A), with one of the parts of the spot displaced basad (i.e., actually two postdiscal spots in cell 1, one shifted basad comparatively to the other); a well-defined row of marginal white spots, but poorly developed submarginal spots; among other characters detailed in the original description (Plötz 1884).

One discrepancy with the original description is that this species lacks costal fold but stated to have one. It is possible that Plötz had only females at his disposal and made a guess that its males should have the fold, thus placing it in the subgenus *Scelothrix* [sic]. Alternatively, Plötz could have mistaken its somewhat expanded costal area for the fold. Regardless of the fold, this species is rather distinct from others, and the original description was detailed enough to allow its recognition even in the absence of illustrations and locality. Thus, we do not see problems with the current usage of this name, and simply confirm it as a valid species *Chirgus (Turis) veturius* Plötz, 1884 as it was identified and illustrated by Draudt (1921–1924) (reproduced here as Fig. 2i), Evans (1953), and subsequent workers in agreement with the original description. Therefore, we do not see an exceptional need to designate a neotype of this species.

Lectotype designation for *Heliopetes (Heliopyrgus) americanus bellatrix* (Plötz, 1884)

Described on the basis of at least two specimens from Argentina: Buenos Aires, *Pyrgus (Scelothrix* [sic]*) bellatrix* Plötz, 1884 is characterized by (interpretively translated from the original description): "dorsally, body and wing bases overscaled with gray hair-like scales, wings brown or blackish-gray with bright white spots, spot in cell 2 [CuA_1-CuA_2] square and not smaller than the spot in discal cell, which may have a ray towards the base; hindwings ventrally with gray bases and two strongly angular bands, the one by the base is broad in cell 7 [Sc+R_1-RS] and constricted before its middle" (Plötz 1884). Forewing length given as a range: 14–15 mm and the mention of "sometimes" referring to the discal cell white ray indicate that more than one specimen was described. This species is placed before *Heliopetes (Heliopyrgus) americanus americanus* (Blanchard, 1852) in the key, and therefore was likened to it by Plötz.

We were able to locate only a single syntype, but it agrees well with the original description and reflects the current application of this name. To ensure that this taxon is objectively defined, N.V.G. designates this syntype, in MFNB, shown in Fig. 1a, and bearing the following 8 labels: || Typus || Americanus | Buenos Ayres | 71 v. Ha[?]. || Bellatrix Plötz | taf 877 i l. | non Americanus || Coll. Weymer || Coll. Weymer || Bellatrix Plötz i l, | ~~Americanus Gay~~ | Buenos Ayres || {QR Code} http://coll.mfn-berlin.de/u/ | 44a0c5 || DNA sample ID: | NVG-15032B12 | c/o Nick V. Grishin || that can additionally be recognized by not fully expanded right hindwing near the outer margin around cell CuA_1-CuA_2 as the **lectotype** of *Pyrgus (Scelothrix* [sic]*) bellatrix* Plötz, 1884. Curiously, the drawing number 877 that appears on one of the lectotype labels is not mentioned in Godman (1907), or in the original description by Plötz, and as far as we can tell, is not available anywhere but from the original Plötz's drawing, further increasing the confidence that this specimen is from the type series. The COI barcode sequence of the lectotype (GenBank ON255697) is:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGTTTATTAATTCGTACTGAATTAGGAAATCCTGGATCATTAATTGGTGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTTTTTATAGTAATACCTATTATAATCGGAGGATTTGGAAACTGATTAGTTCCTTTAATACTAGGAGCTCCAGATATAGCATTTCCACGTA
TAAATAATATAAGATTTTGATTATTACCCCCATCTTTAACATTACTTATTTCGAGAAGTATTGTAGAAAATGGAGCAGGAACTGGATGAACAGTTTATCCCCCACTTTCATCTAATATTGC
TCATCAAGGCTCCTCTGTTGATTTAGCTATTTTCTCACTACATTTAGCAGGAATTTCATCTATTCTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATATATCA
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCTTTATTATTATTATTATCATTACCTGTCTTAGCTGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACTT
CATTTTTCGACCCAGCAGGAGGAGGAGATCCAATTTTATATCAACATTTATTT
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Genomic analysis places *P. bellatrix* as a close sister to *H. americanus americanus* (Fig. 3a) consistently with its current treatment as a subspecies *Heliopetes (Heliopyrgus) americanus bellatrix* (Plötz, 1884), their COI barcode sequences are only 0.3% (2 bp) different, and additional data are needed to study the relationship between the two subspecies.

Pyrgus (Pyrgus) aconita Plötz, 1884 (Herrich-Schäffer in litt.) is confirmed as a junior subjective synonym of *Heliopetes (Heliopyrgus) domicella domicella* (Erichson, [1849])

Pyrgus (Pyrgus) aconita Plötz, 1884 (Herrich-Schäffer in litt.) (type locality "Georgia", probably in error) was paired with the species currently known as *Heliopetes (Heliopyrgus) domicella* (Erichson, [1849]) by Plötz in his key (Plötz 1884), and differs from it by lacking the marginal (while still having submarginal) row of white dots on all wings and greener bands on ventral hindwing. Godman, who inspected the original unpublished Plötz's drawing, which had a number 871 not listed in the original description, commented that *P. aconita* was "very like *Heliopetes domicella* Er., but greener" (Godman 1907). We were not able to find any additional information about this taxon, but note that some populations of *H. domicella* are indeed darker and lack various rows of white spots, approaching the appearance of *Heliopetes (Heliopyrgus) domicella margarita* (E. Bell, 1937) at the extreme. Therefore, it is likely that *P. aconita* is a junior subjective synonym of *Heliopetes (Heliopyrgus) domicella domicella* (Erichson, [1849]), as currently presumed. Finally, we note that according to Plötz, the type(s) of *P. aconita* had the base of cell 3 (M_3-CuA_1) on forewing filled with white (not brown) and thus merged with the central band, something to watch for in re-discovering this taxon or its type specimens.

Heliopetes (Heliopyrgus) willi (Plötz, 1884), reinstated status

Genomic sequencing of *Pyrgus (Pyrgus) willi* Plötz, 1884 (type locality Brazil: Minas Gerais) syntype and a more recent specimen reveals prominent genetic differentiation of this taxon currently treated as a subspecies of *Heliopetes (Heliopyrgus) domicella* (Erichson, [1849]) (type locality Guyana) from the nominotypical subspecies (Fig. 3a). For instance, Fst/Gmin between them computed on the Z chromosome are 0.39/0.02 and COI barcodes between type specimens of *P. willi* and *H. domicella* differ by 1.7% (11 bp). Therefore, we reinstate it as a species *Heliopetes (Heliopyrgus) willi* (Plötz, 1884), **stat. rest**. However, despite differences in facies, *Heliopetes domicella margarita* (E. Bell, 1937) (type locality Venezuela: Margarita Island) clusters within *H. domicella* and therefore is left as its subspecies.

To define this species objectively, Olaf H. H. Mielke hereby designates a male syntype in the Zoologische Staatssammlung München, Germany (ZSMC) shown in Fig. 1b and bearing the following 5 labels: || Pyrgus | Willi | Plötz || Hesperia type | Willi Pl. Minas Geraes || Type || Lectotypus | Pyrgus | willi | Plötz, 1884 | Zool. Staatssammlg München | O. Mielke det. 1979 || DNA sample ID: | NVG-18057A03 | c/o Nick V. Grishin || as the **lectotype** of *Pyrgus (Pyrgus) willi* Plötz, 1884. This designation is only reflected on the label added to the specimen, but was not published previously, so it is formalized here. The COI barcode sequence of the lectotype (GenBank ON255698) is:

```
AACTTTATATTTTATTTTTGGAATCTGAGCAGGAATAGTAGGTACTTCATTAAGTTTATTAATTCGTACTGAATTAGGAAATCCTGGATCACTAATTGGAGATGACCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTCTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTAATTCCATTAATATTAGGAGCCCCAGATATAGCATTCCCCCGCA
TAAATAATATAAGATTTTGATTACTACCCCCATCTTTAACTTTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTATCCCCCTCTTTCAGCTAATATCGC
TCATCAAGGTTCTTCTGTAGATTTAGCTATTTTTTCTTTACATTTAGCAGGAATTTCTTCTATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATATATCT
TTTGATCAAATACCTTTATTTGTTTGAGCTGTAGGAATTACAGCATTATTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACTT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```

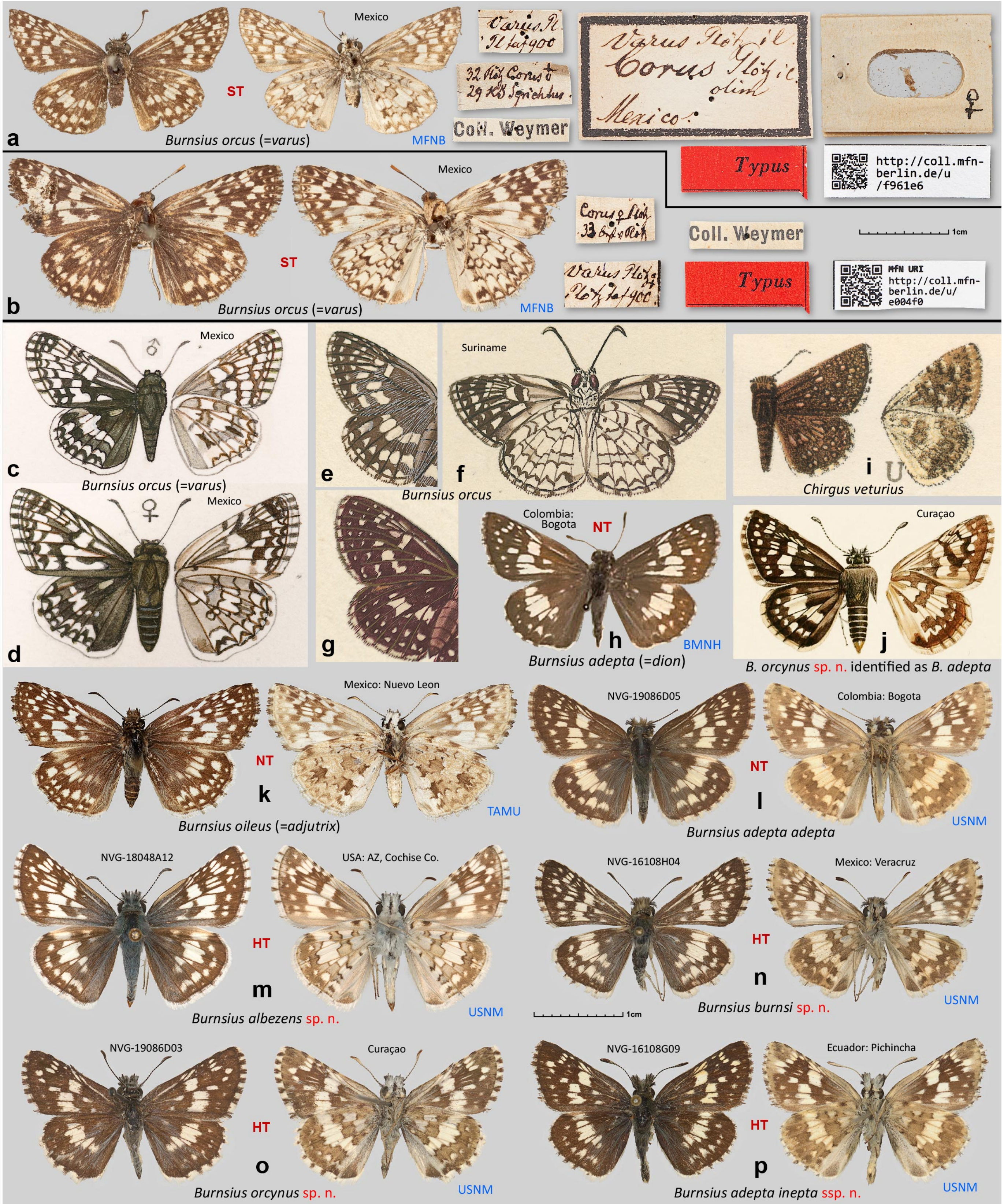

Fig. 2. Type specimens and illustrations of *Burnsius*. **a**, **b**. Syntypes of *Pyrgus (Syrichthus* [sic]*) varus* Plötz, 1884, now junior subjective synonym of *Burnsius orcus* (Stoll, 1780), with their labels separated between specimens by black lines; **c**, **d**. Godman's copies of unpublished Plötz's drawings of *P. varus* Plötz, 1884 from Mexico: no. 900 labeled as ♂ (actually ♀) and 900a ♀, respectively (to save space, sex symbols are pasted in from below the images, where they appear on the drawings); **e**, **f**, **g**. syntypes of *Papilio orcus* Stoll, 1780 (now in *Burnsius*) as drawn by Lambertz: ♂ dorsal, ♀ ventral, and ♀ dorsal aspects, respectively (sexes of specimens shown in dorsal aspects were switched in the original drawing and published engravings); **h**. neotype of *Pyrgus (Scelothrix* [sic]) *dion* Plötz, 1884, now junior subjective synonym of *Burnsius adepta adepta* (Plötz, 1884);

i. illustration of a possible syntype (if it is a copy of Plötz's drawing) of *Pyrgus (Scelothrix* [sic]*) veturius* Plötz, 1884, now *Chirgus (Turis) veturius* from Draudt (1921–1924), pl. 179 row a, images 4 and 5; **j**. illustration of a specimen identified as *Pyrgus adepta* by Snellen (1887: Pl. 2, Fig. 4), but actually *Burnsius orcynus* sp. n., image flipped (left-right inverted) from the original. **k**. neotype of *Pyrgus (Scelothrix* [sic]*) adjutrix* Plötz, 1884 (Herrich-Schäffer in litt.), now junior subjective synonym of *Burnsius oileus* (Linnaeus, 1767); **l**. neotype of *Pyrgus (Pyrgus) adepta* Plötz, 1884 (Herrich-Schäffer in litt.), now *Burnsius adepta adepta*; **m**. holotype of *Burnsius albezens* sp. n.; **n**. holotype of *Burnsius burnsi* sp. n.; **o**. holotype of *Burnsius orcynus* sp. n.; **p**. holotype of *Burnsius adepta inepta* ssp. n. Additional data in text. Dorsal and ventral aspects are on the left and right, respectively (if both are shown). Where available, DNA sample number and collecting locality are shown above dorsal and ventral images, respectively. Specimens are shown to scale with a 1 cm scale bar given. Synonyms are preceded with = sign. HT, ST, and NT denote holotype, syntype and neotype, respectively. Repository abbreviations are shown in blue font. Photographs a, b are by MFNB, k is by TAMU, and c–h are © The Trustees of the Natural History Museum London, and are made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/).

Neotype designation for *Burnsius adepta* (Plötz, 1884) affirming its current usage

Pyrgus (Pyrgus) adepta Plötz, 1884 (Herrich-Schäffer in litt.) (type locality Colombia: Bogota) presents two problems. First, this name is currently applied to a species lacking costal fold. However, the original description placed it in the subgenus *Pyrgus* that Plötz defined by the presence of costal fold and the lack of tibial tuft of long scales (Plötz 1884). Second, general appearance of what is currently presumed to be *Burnsius adepta* is more similar to *Burnsius communis* (Grote, 1872) and its close relatives than to *Heliopetes domicella* (Erichson, [1849]), with which *P. adepta* was grouped in the key by Plötz on the basis of a wide white central band on all wings, and differentiated from by white spots basad of this central band: two on the forewing and one on the hindwing (Plötz 1884).

Assuming that the type locality (Bogota in Colombia) is correct, the only species with costal fold that generally fits the description of *P. adepta* would be *H. domicella*. However, we could not find a specimen of *H. domicella* with white spots basad of the central band. Wing bases of *H. domicella*, even in the palest specimens, are always unspotted brown. Due to the white spots present at wing bases, *P. adepta* is not *H. domicella*. The only two other options, among species recorded from Colombia, would be either the species currently called *B. adepta*, or *Burnsius orcus* (Stoll, 1780) (type locality Suriname). The latter species is widely distributed in Colombia, has costal fold (as Plötz described for *P. adepta*) and tibial tuft (contrary to Plötz description). However, it reminds even less of *H. domicella* than a species currently called *B. adepta*. Indeed, in *B. orcus*, the forewing discal cell spot does not overlap much, if at all, with the spot in cell 2 (CuA_1-CuA_2), not giving an appearance of a band.

Therefore, we agree with Evans (1953), who applied the name *P. adepta* to the species identified today as *B. adepta*. It is conceivable to think that instead of separate spots, *P. adepta* possesses a continuous discal band through both wings, similar to that of *H. domicella*, although basal edges of discal cell spot and the spot in cell 2 (CuA_1-CuA_2) are not aligned as perfectly as in *H. domicella* and the spot in cell 2 is typically offset distad (or at least the basal edge of the band is more irregular), giving us an overall impression of *B. communis* rather than of *H. domicella*.

Minding the lack of the costal fold and assuming that Plötz didn't mix something up in his key, the type specimen(s) of *P. adepta* should have been female(s), or Plötz mistook his male type(s) for females, not seeing costal fold or tibial tuft. In either case, by likening *P. adepta* to *H. domicella*, Plötz might have deduced that *P. adepta* males would have costal fold. It is also conceivable that Plötz mistook convex in basal half forewing costa for the costal fold. A related discrepancy in Plötz's key is that in both *H. domicella* and *Heliopetes willi* (Plötz, 1884) tibial tuft is present, but they are placed in *Pyrgus* stated to lack the tuft. Because at least the lectotype of *H. willi* is a male, we hypothesize that hindtibiae might have been missing in the type specimen(s) during Plötz's inspection, as they are missing today in the lectotype. For the lack of a better option, Plötz might have presumed that the hindtibiae lacked the tuft, without having a chance to observe them.

Evans noted that there was an unpublished figure of *P. adepta* in the British Museum (Evans 1953), but the compilation of Godman's copies of Plötz's drawings did not include *P. adepta*. Moreover, Godman did not mention *P. adepta* in his listing of American species named by Plötz (Godman 1907). The source and whereabouts of the figure that Evans referred to remain unknown. However, in 1887, just

Fig. 3. Phylogenetic trees of *Burnsius* and its relatives constructed from protein-coding regions of the Z chromosome. **a**. Representatives of *Chirgus*, *Burnsius*, and *Heliopetes*. The clades of *Heliopetes willi* stat. rest. and *Heliopetes domicella* are shown in magenta and green, respectively. The clade highlighted in yellow is expanded into panel **b**., in which clades of different taxa are colored in different colors. Names of primary type specimens are shown in red font. Type status abbreviations are: HT - holotype; LT - lectotype; ST - syntype; PT - paratype; TT - topotype, which is not a true type, but is used as a symbol to indicate specimens from near type localities.

three years after the description of *P. adepta*, Snellen published its illustration from Curaçao (Snellen 1887), reproduced here as Fig. 2j (it likely to depict a new species described below), and the appearance of this species generally agrees with *P. adepta* of Evans, although Evans might have assigned it to his *Pyrgus communis orcynoides* (Giacomelli, 1928). Apparently, Snellen arrived at his identification independently, using Plötz's key, and was confused by the vague description of the ventral side.

In his key, Plötz portrayed *P. adepta* by the following combination of characters (translated and assembled from relevant sections): "forewing with costal fold; hindtibiae without a tuft of long scales; all wings with wide white central band, which on hindwing decreases rapidly from the middle to anal margin; basad of the discal band, forewing with two white spots, one in cell 1 [CuA$_2$-1A+2A], and the other at the base of cell 2 [CuA$_1$-CuA$_2$], hindwing with one spot, in discal cell; distad of forewing discal cell several evenly narrow spots, and before the outer margin of all wings a row of small roundish white spots; underside pale brownish-white, mostly only with pure white discal band on the forewing, the markings are brownish-gray?green ["gran"], the bases are gray, those of hindwings with a brown dot in cell 7 [probably viewed by Plötz as a union of cells Sc+R$_1$-RS and C-Sc+R$_1$]" (Plötz 1884). While the characters of the dorsal side are defined clearly, we found Plötz's description of the ventral side to be vague and difficult to interpret. Evans' *P. adepta* keys to G.1.10.(c), largely agreeing with Plötz's description, except for the lack of costal fold (Evans 1953). Above, we argued that Plötz and Evans referred to the same species. If *P. adepta* syntype(s) were mislabeled (i.e., were not from Bogota), then its males with costal fold and without the tibial tuft could have been *B. communis*. However, without locating syntypes or having strong evidence that they were mislabeled, it would be difficult to argue along these lines, especially in the interest of nomenclatural stability.

To learn more about this species, we searched for syntypes of *P. adepta* in the collections that are known to house Plötz's types: MFNB, ZSMC, and EMAU. We failed to find any candidate specimens. Although in MFNB there are specimens identified as *P. adepta* from Colombia: Bogota (conspecific with Evans' *P. adepta*), none was clearly identifiable as a syntype. Therefore, we believe that the syntypes of *P. adepta* are no longer extant. There is an exceptional need to designate a neotype of *P. adepta*, because of possible errors in Plötz's description and its general vagueness (costal fold, tibial tuft, ventral side), and the presence of new species from this group (see below), creating a potential for instability of nomenclature until the name is objectively defined, best in agreement with its current widespread application. To stabilize nomenclature, N.V.G. hereby designates a specimen from Bogota shown in Fig. 2l, a male, as the **neotype** of *Pyrgus (Pyrgus) adepta* Plötz, 1884. This neotype is consistent with both the present usage of the name and the original description of this taxon (including its locality), except that it lacks costal fold (see above). The COI barcode sequence of the neotype (GenBank ON255699) is:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCCGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTTTTCATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCATTCCCTCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTATCCCCCATTATCAGCTAATATTGC
TCACCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCCTTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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This neotype of *P. adepta* satisfies all requirements set forth by ICZN Article 75.3, namely: 75.3.1. It is designated to clarify the taxonomic identity of this taxon in the light of new species discovered by genomic sequencing; 75.3.2. The characters for the taxon have been given in its original description by Plötz (1884), subsequent work by Evans (Evans 1953) and are re-stated above; 75.3.3. The neotype specimen bears the following four labels || Bogota || EASmyth | Collection | 1947 || DNA sample ID: | NVG-19086D05 | c/o Nick V. Grishin || USNMENT | {QR Code} | 01588760 ||. 75.3.4. Our unsuccessful search for the syntypes is described above, leading us to conclude that they are lost; 75.3.5. As detailed above, the neotype is consistent with the original description of this taxon (except that it lacks costal fold, see discussion above), other information, such as subsequent published illustrations, and the current usage of this name; 75.3.6. The neotype is from Colombia: Bogota and the type locality given for *P. adepta* in the original description is "Bogota"; 75.3.7. The neotype is in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Neotype designation for *Pyrgus (Scelothrix* [sic]*) dion* Plötz, 1884 confirming it as a junior subjective synonym of *Burnsius adepta* (Plötz, 1884)

Pyrgus (Scelothrix [sic]*) dion* Plötz, 1884 was described from female(s) of unknown provenance (Plötz 1884) and, not being clearly attributed to the New World, was not included in the analysis of Godman (1907). Except being listed in several catalogs, this name was not discussed in publications, and Evans (1953) synonymized it with the species currently known as *Burnsius adepta* (Plötz, 1884). To learn more about *P. dion*, we turned to its original description, assembled from the Plötz's key and translated here: "Hindtibiae with a tuft of long scales. Abdomen beneath with a pit, and two almost straight, narrow, somewhat flat appendages arise from the base of abdomen ["hair pencil" and thoracic pouch define the subgenus *Scelothrix* [sic]]. Forewing with costal fold. Hindwing with a white, sometimes overscaled with brown or gray [this variation may refer to different species included in the corresponding part of the key, not necessarily to *P. dion*], central band that starts at the costal margin but does not reach anal margin: the band increases in width from the costal margin to discal cell and then tapers rapidly to cell 1 [CuA$_2$-

1A+2A]. Dorsal side black-gray with large, white, sharply defined, interconnected typical [for this genus] spots; in cell 1 [CuA_2-1A+2A] the typical [i.e., discal band] spot is connected along the vein 1 [1A+2A] with the spot by the base. The minor spots are small, at the base of hindwing there is a gray one. Ventrally, broad margin of hindwing and bases of all [wings] are green, spotted with white" (Plötz 1884).

Because *P. dion* was named from specimen(s) Plötz assumed to be female(s), statements in the description referring to secondary sexual characters (costal fold and tibial tuft) were Plötz's hypotheses about how males of this species might appear rather than actual observations, and therefore were not considered in our analysis. Plötz's description gives an impression of *P. dion* as a specimen with larger spots in the discal band (compared to most other "*Pyrgus*") contrastingly smaller submarginal spots, and hindwing band shaped more like an oval central spot. Out of all characters listed for *P. dion*, merging of the discal and the basal white spots in cell CuA_2-1A+2A into one along forewing vein 1A+2A is not found in many specimens, and can be used to constrain the set of possibilities in search for *P. dion*. Inspecting all checkered-patterned Hesperiidae worldwide that can possibly be attributable to the genus *Pyrgus* a century ago, we only found this merging present in several New World species, such as those in the *Burnsius communis* (Grote, 1872) group and the *Burnsius oileus* (Linnaeus, 1767) group. Specimens from the latter species group have smaller discal band spots on both wings and comparatively larger "minor" spots along wings' margins, thus contradicting the original description of *P. dion*, and therefore are less likely to be that taxon.

In the species of *B. communis* group other than *B. adepta*, the merging of spots in cell CuA_2-1A+2A is accompanied by even stronger merging of the two spots in cell CuA_1-CuA_2 (not mentioned in the description of *P. dion*), but most of the paler-patterned females of *B. communis* and *B. albescens* develop a pair of pale streaks in between the two spots in the middle of cell CuA_2-1A+2A, rather than these spots being merged along vein 1A+2A. Therefore, we concur with Evans that *P. dion* is most likely a junior subjective synonym of *B. adepta*, the placement not questioned since it was proposed (Evans 1953). *Burnsius adepta* was described by Plötz in the same work from specimen(s) from Colombia: Bogota, therefore he had specimens of this species from this locality. The specimen we found that agrees best with the original description of *P. dion* was a *B. adepta* variation that appears different enough from other specimens to suspect it was a distinct species, also from Bogota (Fig. 2h), which gave additional confidence in our association of the name *P. dion* with specimens.

One notable discrepancy of *B. adepta* with the original description of *P. dion* is the green color of ventral hindwing margin and base of the latter, as described by Plötz. First, there are no Hesperiidae worldwide with a truly green pattern like this. Second, Plötz used the word "green" [grün] to describe the color of hindwing bands of several other species in the same work (e.g., *Heliopetes domicella* (Erichson, [1849])), none of which are really green, but are more similar in color to *B. adepta*. Third, Godman mentioned for a number of Plötz drawings that they appeared greener than the species they represent, e.g., that *P. aconita* was "very like *Heliopetes domicella* Er., but greener" (Godman 1907). Therefore, we hypothesize that Plötz either worked under lighting conditions that did not allow accurate color perception and reproduction, or was at least partly color-blind. Therefore, we do not put much weight in Plötz's assessment of the ventral bands color as "green".

We searched for syntypes of *P. dion* in the collections that are known to house Plötz's types: MFNB, ZSMC, and EMAU. We failed to find any candidate specimens and believe that the syntypes of *P. dion* are no longer extant. There is an exceptional need to designate a neotype of *P. dion*, due to the presence of several new species in this complex and unknown type locality of this taxon creating a potential for instability of nomenclature in future. To stabilize nomenclature, N.V.G. hereby designates a specimen shown in Fig. 2h as the **neotype** of *Pyrgus (Scelothrix* [sic]*) dion* Plötz, 1884. This neotype confirms Evans' hypothesis that *P. dion* is a junior subjective synonym of *Burnsius adepta* (Plötz, 1884). The neotype is consistent with both the present usage of the name and the original description of this taxon (except that the ventral dark bands are not "green", but at best greenish-olive-brown).

This neotype of *P. dion* satisfies all requirements set forth by ICZN Article 75.3, namely: 75.3.1. It is designated to clarify the taxonomic identity of this taxon in the light of new species discovered by genomic sequencing; 75.3.2. The characters for the taxon have been given in its original description by

Plötz (1884) and are re-stated above as a translation of the original description; 75.3.3. The neotype specimen is labeled from "Bogota" and can be recognized by the merged discal and basal spots in forewing cell CuA_2-1A+2A, but separated in cell CuA_1-CuA_2, head tilted to the right, right antenna pointing anteriad and left antenna more aligned with the forewing costal margin. 75.3.4. Our unsuccessful search for the syntypes is described above, leading us to conclude that they are lost; 75.3.5. As detailed above, the neotype agrees with the original description of this taxon (except that the ventral dark bands are not "green") and the current usage of this name; 75.3.6. The neotype is from Colombia: Bogota and the type locality for *P. dion* was listed as unknown ("?") in the original description, but Plötz worked with specimens on this species (as its senior synonym) from "Bogota"; 75.3.7. The neotype is in the collection of the Natural History Museum, London, UK (BMNH).

***Pyrgus (Syrichthus* [sic]*) varus* Plötz, 1884 is a junior subjective synonym of *Burnsius orcus* (Stoll, 1780)**

Out of all 11 names proposed by Plötz (1884) and discussed here, only one was included in the compilation of Godman's copies of the original Plötz's drawings. *Pyrgus (Syrichthus* [sic]*) varus* Plötz, 1884 (type locality Mexico) was represented by two illustrations intended to depict a male (no. 900) and a female (no. 900a) (Fig. 2c, d). Attribution of this species to the subgenus *Syrichthus* [sic] by Plötz implied the absence of costal fold and tibial tuft in males that Plötz assumed were among his *P. varus* syntypes, illustrating one. For unclear reasons, Evans synonymized *P. varus* with *Burnsius communis* (Grote, 1872) (costal fold present) and not with *Burnsius adepta* (Plötz, 1884) (costal fold absent). Moreover, Evans mentioned these unpublished drawings of *P. varus*. Our inspection of the drawings reveals that they depict neither *B. communis*, nor *B. adepta*, but *Burnsius orcus* (Stoll, 1780).

This identification is based on four characters. First, there is a well-developed white spot on the forewing between the discal cell spot and the streaks in cells distad discal cell. Second, the row of marginal forewing spots is complete, with a spot in cell R_4-R_5. These two spots are depicted in both drawings (Fig. 2c, d). These spots are present only in the *B. oileus* group species and are (nearly always) absent (or very small) in the *B. communis* group species. Third, ventral hindwing lacks a brown spot at costa in the middle, characteristic of *B. oileus* and lacking in *B. orcus*, the only character given for by Evans (1953) to separate the former from the latter. Both drawings show no trace of the costal spots. Fourth, ventral hindwing pattern on the drawing is well-developed and therefore excludes *Burnsius philetas* (W. H. Edwards, 1881). These four characters imply that *P. varus* is a junior subjective synonym of *B. orcus*. Mexico as the locality for *P. varus* is consistent with this identification: it is the northern limit of *B. orcus* distribution.

Using this opportunity, we reproduce parts of the original drawings of *Papilio orcus* syntypes, from Suriname, by G. W. Lambertz in the Library of the Natural History Museum, London, that served as models for engravings published in Cramer volumes (1775–1780) (with Stoll) (Gilbert 2000) (Fig. 2e–g). The Lambertz drawings, which are typically more precise than stylized engravings, reveal additional details about the syntypes. The *P. orcus* drawings are similar to Plötz's *P. varus* (Fig. 2c, d), and the specimen illustrated in ventral view (Fig. 2f) lacks the brown spot on hindwing mid-costa. We also note that sexes of specimens shown in dorsal view were switched, both in the original Lambertz drawings and engravings published in Stoll (1780): the specimen labeled as a male (Fig. 2g) is a female (no gray overscaling, evenly convex forewing costa, smaller white spots), and the specimen labeled as a female (Fig. 2e) is a male instead (gray overscaling, slightly indented costa in the middle at the end of costal fold). The ventral image is labeled as a female (Fig. 2f), which may be correct due to an evenly convex forewing costal margin similar to Fig. 2g, and different from straightened in the middle costa of a male (Fig. 2e) reflecting its costal fold.

The only obstacle with the identification of *P. varus* as *B. orcus* is that according to Plötz, males of *P. varus* lack costal fold and tibial tuft, but *B. orcus* has both. However, the specimen on the drawing that depicts a male looks more similar to *B. orcus* female, because males have extensive gray overscaling on both wings, at least at the bases, and no such overscaling is visible on the drawing. If Plötz mistook female for a male, then he would find neither the fold, nor the tuft, and place this species in the subgenus *Syrichthus* [sic], as he did.

Curious about this reasoning, we searched for syntypes of *P. varus* in the collections that are known to house Plötz's types. We found two specimens in MFNB, both females, that match Godman's copies of Plötz's drawings rather well (Fig. 2a, b). Both specimens are from the Weymer collection according to their labels that refer to Plötz's taf[el] 900, labeled "varus", and the smaller specimen (marked as a male in old notation: ♁) bears a large label with locality "Mexico". The larger specimen exhibits fusion of discal and basal white spots in forewing cells CuA_2-1A+2A and CuA_1-CuA_2, exactly as the drawing 900a shows. This fusion is not that commonly observed, and additionally supports the hypothesis that this (or similar in appearance) specimen was used as a model of drawings no. 900a. The name "corus" on the labels of these specimens refers to an unpublished initial version of the name for this species conceived by Plötz.

The shapes of spots agree well between the specimens and the drawings, except that the white markings are broader in the drawings. We suspect that because these specimens are small and were drawn life-size, it was difficult to accurately outline the spots, therefore a more schematic image resulted, where dark lines were drawn to separated spots, rather than each spot being drawn individually. Therefore, the two specimens we found are syntypes of *P. varus* (the red "Typus" labels and specimen number labels with barcodes were added to them after our discovery, Fig. 2a, b), and they are identifiable as *B. orcus* confirming our hypothesis based on the drawings that *Pyrgus (Syrichthus* [sic]*) varus* Plötz, 1884 is a junior subjective synonym of *Burnsius orcus* (Stoll, 1780).

Neotype designation for *Pyrgus (Scelothrix* [sic]*) adjutrix* Plötz, 1884 (Herrich-Schäffer in litt.) confirming it as a junior subjective synonym of *Burnsius oileus* (Linnaeus, 1767)

Pyrgus (Scelothrix [sic]*) adjutrix* Plötz, 1884 (type locality Mexico) was named from at least 2 specimens, one male and one female. By attributing this species to the subgenus *Scelothrix* [sic], Plötz implied the presence of a tibial tuft (and thoracic pouch), and he placed it in the key with species having a costal fold. Provided that males were mentioned in the description, it is reasonable to assume that Plötz observed both costal fold and thoracic pouch with tibial tuft (and that's how they were identified as males), otherwise he would not have assigned this species to *Scelothrix* [sic]. He could not have mistook females for males in this case, because females lack secondary sexual characters, and such species would have been placed in the subgenus *Syrichthus* [sic], as Plötz did with *P. varus*. It is conceivable that the males lacked hindlegs making it impossible for Plötz to check the presence of the tibial tuft, but Plötz explicitly mentioned the pouch that should have been present in these specimens even in the absence of hindlegs. Therefore, unless some mistakes were made, *P. adjutrix* males should have had both the fold and the tuft. The only widely distributed Mexican species that generally agrees with the description of *P. adjutrix* and possesses both the fold and the tuft is *Burnsius oileus* (Linnaeus, 1767). This is likely the reason why Evans (1953) synonymized *P. adjutrix* with *B. oileus*. Moreover, Plötz placed *P. adjutrix* in the key following his *Papilio syrichtus* Fabricius, 1775, with which he synonymized *Papilio orcus* Stoll, 1780 among others, and listed specimens he inspected from South America. Therefore his concept of *P. syrichtus* was most likely based on specimens of *Burnsius orcus* (Stoll, 1780). Thus, if *P. adjutrix* is indeed synonymous with *B. oileus*, it seems logical that it was placed next after *B. orcus* in Plötz's identification key.

The original description of *P. adjutrix*, assembled and combined from segments of Plötz's key, can be translated as: "Hindtibiae with a tuft of long scales. Abdomen beneath with a pit, and two almost straight, narrow, somewhat flat appendages arise from the base of abdomen ["hair pencil" and thoracic pouch define the subgenus *Scelothrix* [sic]]. Forewing with costal fold. The white central band of dorsal hindwing begins at the costal margin and does not reach anal margin, but extends in the ♂ until in cell 1

[$\mathrm{CuA_2}$-1A+2A], in the ♀ until in cell 2 [$\mathrm{CuA_1}$-$\mathrm{CuA_2}$], is fairly broad and sometimes densely overscaled with brown. Dorsal side gray or brown; Forewing with the typical [for the genus *Pyrgus*] spots, sometimes predominantly white, the spot in the discal cell is almost square and continues to the costal margin, outwardly in cells 4 [$\mathrm{M_2}$-$\mathrm{M_3}$] to 6 [$\mathrm{R_5}$-$\mathrm{M_1}$] there are several white streaks, the typical spots in cells 1 [$\mathrm{CuA_2}$-1A+2A] and 2 [$\mathrm{CuA_1}$-$\mathrm{CuA_2}$] are fairly large, basewards in cell 1 [$\mathrm{CuA_2}$-1A+2A] there is sometimes missing [spot], at the base of cell 2 [$\mathrm{CuA_1}$-$\mathrm{CuA_2}$] there is a consistently-present white mark, in front of the outer margin there is not always a row of pale spots, but at the outer margin mostly fine points. Ventral hindwings white or yellowish with 3 broken, irregular bands composed of interconnected, square, green, black-edged spots, a black point near the base at the costal margin, several cap-shaped green spots at the outer margin and white or pale gray anal margin. [Forewing length] 13–14 mm. Mexico" (Plötz 1884).

Plötz's description mostly agrees with *B. oileus*, in particular, dense brown overscaling of the white hindwing discal band is characteristic of some *B. oileus* females, and "predominantly white" might have referred to dense pale overscaling present in *B. oileus* males, some of which may also have large white spots. The same refers to the description of the dorsal side as "gray" (likely for males) "or brown" (females), to which *B. oileus* is a good fit. The three broken and irregular bands on ventral hindwing may apply to the three brown spots at the costal margin, from which three band-like arrangements of spots can be traced towards the anal margin, developed in most specimens of *B. oileus*. The brown spot mid-costa is absent in *B. orcus*, which was the only character to distinguish between *B. orcus* and *B. oileus* given by Evans (1953). Thus, the ventral wing pattern of *B. orcus* is less likely to be described as having three bands, and therefore *P. adjutrix* is not *B. orcus*. In addition to these three costal spots that can be viewed as beginnings of the bands, *B. oileus* also possesses the fourth costal spot at the very base of hindwing, as mentioned in the description.

The only obvious contradiction is that the color of ventral hindwing bands and spots is not green ("grünen") in *B. oileus*. See discussion of "green" used by Plötz (1884) in the section dedicated to *Pyrgus dion* above. Apparently, Plötz used the term "green" to describe the color of ventral hindwing bands for a number of *Pyrgus* species in which these bands can at best be called olive-brown. Other possible problems with the fit of *B. oileus* to the description of *P. adjutrix* is not about what the description contains, but about what is missing from it. For instance, the description does not explicitly mention extensive gray overscaling in males, described by Plötz for *P. syrichtus* as "wing bases are hairy bluish-white". Then, there is no mention of the forewing white spot between the discal cell spot and streaks that for *P. varus* Plötz referred to as "there is also a spot at the end of the discal cell spot" (Plötz 1884). Finally, the forewing length of 13–14 mm may be on a smaller size of the spectrum for *B. oileus*. To study these possible contradictions, we analyzed other available sources.

The description of *P. adjutrix* refers to multiple specimens, detailing their variation (from nearly white to densely overscaled with brown). Although Godman didn't organize a copy of *P. adjutrix* drawing, he mentioned that there were more than one, and these drawings "were taken from Mexican specimens" in agreement with the original description (Godman 1907). Godman suggested that these drawings of *P. adjutrix* depicted "?=*Hesperia montivaga*", the same hypothesis as for *P. albescens* and *P. varus*. Godman's "*H. montivaga*" refers to *Burnsius communis/albescens*, as he treated these species in Biologia Centrali-Americana (Godman and Salvin 1899). Therefore, the drawings of the following three Plötz's taxa were similar to each other (they were like Godman's *H. montivaga*): *P. albescens*, *P. varus* and *P. adjutrix*. As shown above, *P. varus* is a junior subjective synonym of *B. orcus*, thus *P. adjutrix* could have been its close relative *B. oileus*. However, inclusion of *P. albescens* (and *P. communis*, by mentioning of "*H. montivaga*") in this group of similar-looking taxa deserves additional consideration.

The major disagreement between the species of the *B. communis* group and the description of *P. adjutrix* is in the lack of tibial tuft and thoracic pouch in the former. Only if Plötz has made a mistake in his assessment of the tuft/pouch, it is possible that males of the *B. communis* group species were among *P. adjutrix* syntypes. It is also possible that the type series included both species, i.e., some males had the tuft/pouch and were *B. oileus*, while others (which Plötz didn't check for the presence of the tuft/pouch) were from the *B. communis* group. It is also possible that some females in the type series of *P. adjutrix* were not *B. oileus* but species (may be several) from the *B. communis* group. However, in his description of *P. adjutrix*, Plötz mentioned brown overscaling of the discal hindwing band, which is more typical for *B. oileus* females than for the *B. communis* group females. For all these reasons, overall, the description and other information we gathered is more consistent with *P. adjutrix* being *B. oileus* (in agreement with Evans (1953) and the current synonymy), largely based on the costal fold and tibial tuft stated to be present in *P. adjutrix* per original description (Plötz 1884).

To further learn about *P. adjutrix*, we searched for its syntypes in the collections that are known to house Plötz's types: MFNB, ZSMC, and EMAU. We failed to find them, and believe that the syntypes of *P. adjutrix* were lost. There is an exceptional need to designate a neotype of *P. adjutrix* due to the generic nature of the original description that does not unambiguously point to a single species, a possibility of mistakes in the description (e.g., about the presence of tibial tuft), a possibility of a polytypic type series, and the presence of new cryptic species requiring objective definition of this name. To stabilize nomenclature, N.V.G. hereby designates a specimen shown in Fig. 2k, female, as the **neotype** of *Pyrgus (Scelothrix* [sic]*) adjutrix* Plötz, 1884. This neotype is consistent with both the present synonymy of the name as being conspecific with *B. oileus*, and the original description of this taxon (except that ventral hindwing bands and spots are not green).

This neotype of *P. adjutrix* satisfies all requirements set forth by ICZN Article 75.3, namely: 75.3.1. It is designated to clarify the taxonomic identity of this taxon in the light of new species that we found (see below); 75.3.2. The characters for the taxon have been given in its original description by Plötz (1884) and are also discussed above; 75.3.3. The neotype specimen bears the following 3 labels: || MEXICO: Nuevo Leon | ca. 5 mi. (8 km) | SSW Cola de Cabillo [sic!] | (horsetail falls) || coll. | 18 Mar 77 | Roy O. Kendall | and C. A. Kendall || HESPERIIDAE, | Pyrginae: | Pyrgus oileus | (Linnaeus, 1767) | det. R. O. Kendall | M. & B. No. 106 ||. 75.3.4. Our unsuccessful search for the syntypes is described above, leading us to conclude that they are lost; 75.3.5. As detailed above, the neotype is mostly consistent with the original description of this taxon (compare Fig. 2k with the description translated above, but the color of spots in hindwing ventral bands is not green) and the current synonymy of this name; 75.3.6. The neotype is from Mexico: Nuevo Leon and the type locality given for *P. adjutrix* in the original description is "Mexico"; 75.3.7. The neotype is in the Texas A&M University Insect Collection, College Station, TX, USA (TAMU). As a result of this neotype designation, *Pyrgus (Scelothrix* [sic]*) adjutrix* Plötz, 1884 remains a junior subjective synonym of *Burnsius oileus* (Linnaeus, 1767).

Burnsius communis albescens (Plötz, 1884), revised status

A single syntype of *Pyrgus (Pyrgus) albescens* Plötz, 1884, in the MFNB collection and labeled from "Mexico" (Fig. 1c), agrees well with the original description (Plötz 1884). Most notably, it is one of the smaller specimens, with the forewing length of 12 mm, at least by 1 mm smaller than any of the other 10 species of *Pyrgus* described by Plötz and analyzed here. Its general appearance is whiter than that of most other relatives, consistent with the name chosen by Plötz. In various details of wing pattern, this particular specimen is a nearly perfect fit to the original description (Plötz 1884).

For instance, Plötz starts with the following species-specific statement in his key: "The white band on the upper side of the hindwings is also quite wide towards the anal margin, the basal area is unspotted" (Plötz 1884). Indeed, compared to other specimens, some illustrated here (Fig. 1d, e), where the hindwing band narrows to nearly disconnected small spots and dots, in this specimen, the last spot of the band (in cell CuA_2-1A+2A) near the anal margin is almost square, and only slightly narrower than a spot in the cell M_3-CuA_1 (Fig. 1c). The entire dorsal hindwing area basad of discal band is unspotted in the syntype (paler in the middle) fitting the description, and can be contrasted with other specimens having a defined pale spot (Fig. 1d). The next character given by Plötz is that on "ventral side [of hindwing] at the base, in the discal cell and in cell 7 [$Sc+R_1$-RS], there is a cube-shaped, gray-nucleated spot, also the bands are mostly filled with gray", exactly as in the syntype, except that the color is more of a pale-brown hue than simply gray. Such color discrepancies are present throughout Plötz's works and indicate either suboptimal lighting conditions, color reproduction problems on his drawings (if descriptions were written from them), or color perception differences. The last species-specific character in Plötz's key is "the inner margin is gray [i.e., not white]" on ventral hindwing. The syntype has the entire area from at least vein 1A+2A to anal margin grayish-brown, different from paler anal margin area in other specimens (Fig. 1d, e).

Among characters that are shared with other species included in Plötz's key, and therefore not necessarily exactly applicable to this specimen or to *P. albescens*, several are nevertheless worth mentioning: "The bands on the ventral hindwing are composed of cube-shaped or crescent-shaped spots bordered with brown: the central spot of the first [discal] band is very narrow in front [anterior], broad behind; the outer [submarginal] band encloses a white spot in cell 6 [RS-M_1]; its spot in cell 4×5 [M_2-M_3 and M_1-M_2] forms a sharp angle inward. At the edge in cells 1c [CuA_2-1A+2A], 2 [CuA_1-CuA_2] and 3 [M_3-CuA_1] there are green lunules." All these characters are matched perfectly in the syntype, particularly the sharp, beak-like shape of the inner edge of the submarginal dark band along vein M_2 (in cell "4×5").

The combination of the small size (12 mm, exactly as given in the description), wing patterns closely matching the original description, separate locality label "Mexico" (not only on the identification label, in which case it may simply indicate type locality, not the locality of this specimen capture), identification label "*albescens*" mentioning drawing no. 889 (number not given in the original description, and possibly only available on the original drawing at the time this label was written, but the same number 889 is given for *albescens* by Godman (1907)), and the red label "Typus", implying that the specimen was curated as a type, strongly suggests that this specimen is indeed a syntype of *P. albescens.* Curiously, taf. 877 (not stated in the Plötz paper) is given on a label with similar handwriting on the lectotype of *bellatrix*, and this species is not mentioned in Godman (1907); therefore it is likely to be taken from the original drawing, giving further evidence that the *P. albescens* specimen is a syntype. Furthermore, two other specimens from the Weymer collection, labeled similarly from "Mexico", and curated in MFNB as types of *Thymelicus isidorus* Plötz, 1884 and *Apaustus euphrasia* Plötz, 1884, match their descriptions and agree with (available in this case) Godman's copies of Plötz's drawings for both species. This finding further increases our confidence in that this specimen is *albescens* syntype, because it was part of a similarly labeled series probably collected at the same locality (at least in the same country), and this series included type specimens of other Plötz names. All of these names were published in 1884, many of which were likely based on the Weymer collection specimens.

No other syntypes were found, and it is possible that none existed, because only a single length measurement (12 mm) was given in the description, not a range (e.g., 12–13 mm) as for a number of other species, and no mention of variation observed in other specimens was made (usually following the word "sometimes"). However, avoiding the assumption of the holotype, we proceed with a lectotype designation that is needed to objectively define this taxon. N.V.G. hereby designates a syntype illustrated in Fig. 1c, in the Museum für Naturkunde, Berlin, Germany (MFNB), bearing the following 11 labels: || Typus || Mexico || Gabinus Pltz | 130 best. v. Pltz. || Albescens Pl | Plötz taf 889 || 89:74 || Coll. Weymer || Albescens Pl. i. l. | Gabinus Plötz | olim. i l | Mexico || Präp. B. A | 658 || Pyrgus ♂ tessellata | det Alberti || {QR Code} http://coll.mfn-berlin.de/u/ | 80a6ef || DNA sample ID: | NVG-15033H10 | c/o Nick V. Grishin || that can additionally be recognized by the missing head and several terminal cleaned segments of the abdomen glued back to the specimen after genitalia dissection, as the **lectotype** of *Pyrgus (Pyrgus) albescens* Plötz, 1884. The COI barcode sequence of the lectotype (GenBank ON255700) is:

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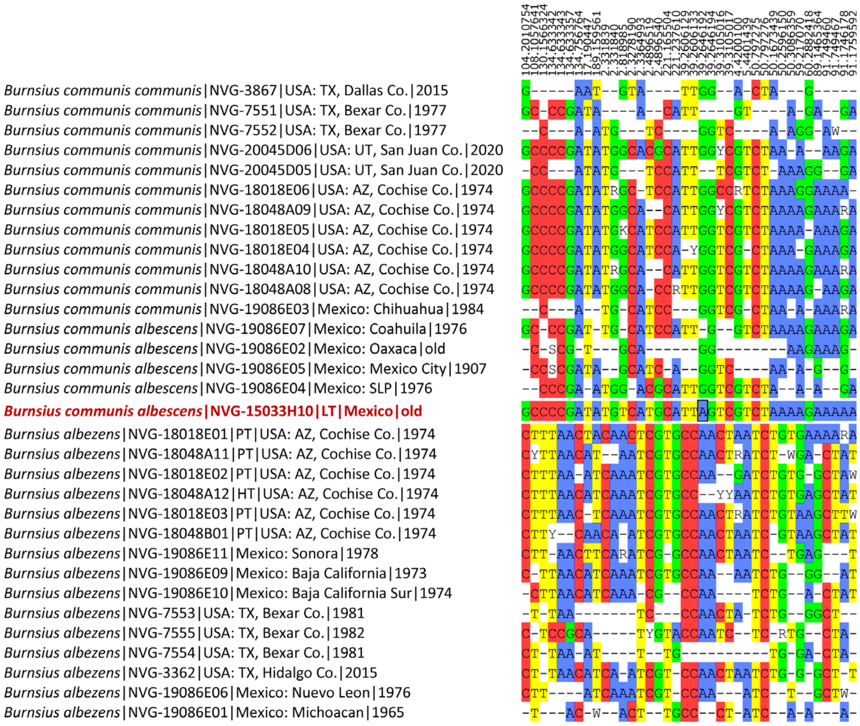
AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCCGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTTTTTATAGTCATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCATTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTACCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCATTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```

The label "89:74" refers to the genus and species numbers in Mabille (1904), which stand for *Hesperia albescens*, a species placed in his "species dubiae", simply referencing Plötz. According to two of its labels, the lectotype was identified by Plötz as *gabinus*: "*gabinus* best[immt] v[on] Pl[ö]tz". We attempted to understand how the name *gabinus* made it on the labels of this specimen. The only published *Hesperia gabinus* Plötz, 1882 (type locality Brazil: Rio de Janeiro), currently a junior subjective synonym of *Sodalia argyrospila* (Mabille, 1876), is a different-looking species (per description, illustration and an extant syntype) that cannot possibly agree with the description of *P. albescens*. Additionally, it is not from Mexico, suggesting that *gabinus* on the label refers to an unpublished name. Indeed, on another label, *gabinus* is followed by the word "olim", which is Latin for "once", "formerly", "some time ago". This label implies that previously this specimen was identified as *gabinus*, but the published name became *albescens*. We interpret this label as "*albescens*, formerly known as *gabinus*". Furthermore, we found another specimen, a likely syntype of *Nisoniades eusebius* Plötz, 1884, currently *Bolla eusebius*, labeled similarly to the *albescens* lectotype, and having the second name "*parna* Plötz" (and "olim") on its labels, a name not found in any publications. This *N. eusebius* specimen agrees with the original description, including its stated locality and forewing length measurement, and is a likely syntype of this taxon. Existence of this additional case of a double-named (with an unpublished, likely former manuscript name) syntype gives yet another evidence for the authenticity of the *albescens* lectotype.

Genomic tree places the lectotype of *P. albescens* within specimens of *B. communis* (Fig. 3b) implying that they are conspecific. To verify this unexpected result, we re-extracted DNA from the leg of the lectotype, prepared genomic libraries, and sequenced them for the second time. This second experiment was done with extra precautions to minimize cross-contamination, and no other *Burnsius* samples were prepared in the same batch with the lectotype. The results confirmed the initial conclusion that the lectotype of *P. albescens* is conspecific with *B. communis* and not with the species Burns (2000) called *P. albescens*. In addition to the tree, we assigned the lectotype of *P. albescens* to species using DNA characters. First, we "cleaned" the dataset of the lectotype to remove all sequences that did not match closely (fewer than 3 mismatches allowed) sequences of the species Burns called *P. albescens*. In addition to removing various contamination (e.g., from fungi and bacteria that were living on the specimen) present in century-old samples, this procedure biases the result towards Burns's "*P. albescens*" by selecting sequences that are closer to that species. Therefore, if the lectotype is still assigned to *B. communis* despite this bias, the result is easier to accept. Second, we selected positions in the lectotype that are covered by more than one sequencing read, thus increasing the reliability of such base pairs. Third, out of these positions, we selected those that discriminate best between the two species: *B. communis* and Burns's "*P. albescens*". Such a position should have a base pair present (and not missing due to low coverage sequencing) in more than 60% of samples of each species, and the most frequent base pair in this position should be different in the two species and present in more than 80% of samples of each species. As a result, we found 38 such discriminating positions (Fig. 4). In the lectotype of *P. albescens*,



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104.2010754 108.1057641 130.1563324 134.633342 134.633343 134.633357 134.756764 17.190447 189.159561 2.331839 2.331840 2.818985 2.3278190 2.3364993 2.4896519 2.4896540 221.165504 221.237610 39.2606129 39.2606133 39.2646192 39.2646194 39.3105016 39.3100017 4.4200100 5.4401439 50.797275 50.797276 50.1673439 50.2596150 50.3086359 59.210707 60.2882418 89.1465364 91.749460 91.749467 91.1746178 91.1759592

Burnsius communis communis|NVG-3867|USA: TX, Dallas Co.|2015                G-----AAT--GTA----TTGG--A-CTA---G-----
Burnsius communis communis|NVG-7551|USA: TX, Bexar Co.|1977                 GC-CCGATA----A--CATT----GT----A-GA--GA
Burnsius communis communis|NVG-7552|USA: TX, Bexar Co.|1977                 --C---A-ATG---TC----GGTC----A-AGG-AW--
Burnsius communis communis|NVG-20045D06|USA: UT, San Juan Co.|2020          GCCCCGATATGGCACGCATTGGYCGTCTAA-A--AAGA
Burnsius communis communis|NVG-20045D05|USA: UT, San Juan Co.|2020          -CC---ATATG---TCCATT--TCGTCT-AAAGG--GA
Burnsius communis communis|NVG-18018E06|USA: AZ, Cochise Co.|1974           GCCCCGATATRGC-TCCATTGGCCRTCTAAAGGAAAA-
Burnsius communis communis|NVG-18048A09|USA: AZ, Cochise Co.|1974           GCCCCGATATGGCA--CATTGGYCGTCTAAAAGAAARA
Burnsius communis communis|NVG-18018E05|USA: AZ, Cochise Co.|1974           GCCCCGATATGKCATCCATTGGTCGTCTAAAA-AAAGA
Burnsius communis communis|NVG-18018E04|USA: AZ, Cochise Co.|1974           GCCCCGATATGGCATCCA-YGGTCG-CTAAA-GAAAGA
Burnsius communis communis|NVG-18048A10|USA: AZ, Cochise Co.|1974           GCCCCGATATRGCA--CATTGGTCGTCTAAAAGAAARA
Burnsius communis communis|NVG-18048A08|USA: AZ, Cochise Co.|1974           GCCCCGATATGGCA-CCRTTGGTCGTCTAAAAG-AAGA
Burnsius communis communis|NVG-19086E03|Mexico: Chihuahua|1984              --C---A--TG-CATCC---GGTCG-CTAA-A-AAARA
Burnsius communis albescens|NVG-19086E07|Mexico: Coahuila|1976              GC-CCGAT-TG-CATCCATT-G--GTCTAAAAGAAAGA
Burnsius communis albescens|NVG-19086E02|Mexico: Oaxaca|old                 -C-SCG-T---GCA------GG--------AAGAAAG-
Burnsius communis albescens|NVG-19086E05|Mexico: Mexico City|1907           -CCSCGATA--GCATC-A--GGTC----AA-A-G--G-
Burnsius communis albescens|NVG-19086E04|Mexico: SLP|1976                   --CCCGA-ATGG-ACGCATTGGTCGTCTA--A-A--GA
Burnsius communis albescens|NVG-15033H10|LT|Mexico|old                      GCCCCGATATGTCATGCATTAGTCGTCTAAAAGAAAAA
Burnsius albezens|NVG-18018E01|PT|USA: AZ, Cochise Co.|1974                 CTTTAACTACAACTCGTGCCAACTAATCTGTGAAAARA
Burnsius albezens|NVG-18048A11|PT|USA: AZ, Cochise Co.|1974                 CYTTAACAT--AATCGTGCCAACTRATCT-WGA-CTAT
Burnsius albezens|NVG-18018E02|PT|USA: AZ, Cochise Co.|1974                 CTTTAA-ATCAAATCGTGCCAA--GATCTGTG-GCTAW
Burnsius albezens|NVG-18048A12|HT|USA: AZ, Cochise Co.|1974                 CTTTAACATCAAATCGTGCC--YYAATCTGTGAGCTAT
Burnsius albezens|NVG-18018E03|PT|USA: AZ, Cochise Co.|1974                 CTTTAAC-TCAAATCGTGCCAACTRATCTGTAAGCTTW
Burnsius albezens|NVG-18048B01|PT|USA: AZ, Cochise Co.|1974                 CTTY--CAACA-ATCGTGCCAACTAATC-GTAAGCTAT
Burnsius albezens|NVG-19086E11|Mexico: Sonora|1978                          CTT-AACTTCARATCG-GCCAACTAATC--TGAG---T
Burnsius albezens|NVG-19086E09|Mexico: Baja California|1973                 C-TTAACATCAAATCGTGCCAA--AATCTG--GG--AT
Burnsius albezens|NVG-19086E10|Mexico: Baja California Sur|1974             -CTTAACATCAAA-CG--CCAA----TCTG--A-CTAT
Burnsius albezens|NVG-7553|USA: TX, Bexar Co.|1981                          -T-TAA-------TC---CCAACTA-TCTG--GGCT--
Burnsius albezens|NVG-7555|USA: TX, Bexar Co.|1982                          C-TCCGCA-----TYGTACCAATC--TC-RTG--CTA-
Burnsius albezens|NVG-7554|USA: TX, Bexar Co.|1981                          CT-TAA-AT----T--TG----------TG-GA-CTA-
Burnsius albezens|NVG-3362|USA: TX, Hidalgo Co.|2015                        CT-TAACATCA-ATCGT-CCAACTAATCTG-G-GCT-T
Burnsius albezens|NVG-19086E06|Mexico: Nuevo Leon|1976                      CTT----ATCAAATCGT-CCAA---ATC--T--GCTW-
Burnsius albezens|NVG-19086E01|Mexico: Michoacan|1965                       -T---AC-W--ACT--TGCC--CT-ATC--A-A---A-
```

Fig. 4. Assignment of the lectotype of *Pyrgus albescens* to species by DNA characters. All 38 positions that are covered in the lectotype (coverage above 1) and discriminate best between the two species are shown as columns labeled above as {scaffold number}.{position number in the scaffold} (e.g., 2.331839 means position 331839 in scaffold 2) referring to the genomic assembly of *B. communis* specimen NVG-13311 (sequence not shown). The lectotype sequence (name in red font) is sandwiched between samples of the two species. Color highlight corresponds to the base type. Standard ambiguity codes (e.g., Y, R, S, etc.) denote heterozygous positions in the genomic sequences (different base pairs in mother and father copies). Dashes are used for data missing due to low coverage of sequencing. The only position that is inconsistent with the assignment of the *P. albescens* lectotype to *B. communis* is framed with black.

out of these positions, 34 (90%) match the most frequent base pair in *B. communis* (Fig. 4, above the lectotype sequence) and mismatch the most frequent base pair in Burns's "*P. albescens*" (Fig. 4, below the lectotype sequence), three positions are consistent with *B. communis* (i.e., base pair in them is present in at least one sequenced specimen of *B. communis*), and only one (39.2646192, Fig. 4, base pair framed in black) is inconsistent, and this base pair (A) is observed only in Burns's "*P. albescens*" among the specimens we sequenced. Therefore, despite biasing the lectotype sequences towards Burns's "*P. albescens*", the majority of positions assign the lectotype of *P. albescens* to *B. communis* in agreement with the phylogenetic tree analysis.

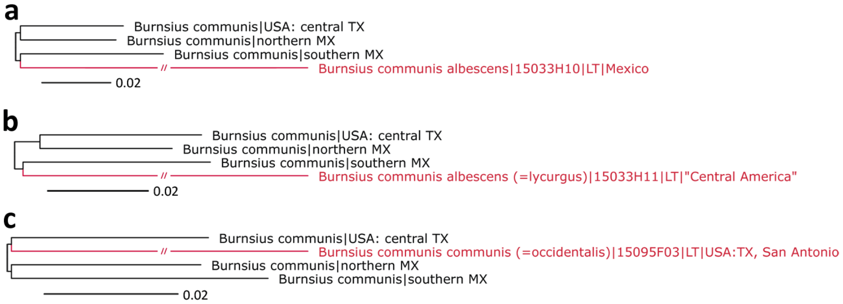

Fig. 5. Assignment of lectotypes to populations: **a**. *Pyrgus albescens*; **b**. *Pyrgus lycurgus*; **c**. *Pyrgus occidentalis*. TreeMix (Pickrell and Pritchard 2012) unrooted trees are shown. Three population are defined as: central TX (specimens 7551 & 7552 Bexar Co., 7549 Bandera Co., see also Fig. 3b), northern Mexico (19086E03 Chihuahua, 19086E04 San Luis Potosi, 19086E07 Coahuila), and southern Mexico (19086E02 Oaxaca, 19086E08 Veracruz, 19086E05 Mexico City). Each lectotype was analyzed separately to increase the number of positions used in the analysis, and placed in the context of the three populations. Terminal branches of lectotypes are colored in red and are longer than shown due to unique sequence variants in lectotypes compared to the averaged over three specimens branches leading to each population. The results are preliminary due to small number of specimens from each population, low coverage of sequencing, and too distant reference genome (*Burnsius philetas*, the closest available then) used for mapping of reads.

Furthermore, Alberti, who dissected the lectotype according to the label (Fig. 1c), identified it as "*Pyrgus tessellata*", which is an unavailable name (junior homonym) synonymous with *B. communis*. Genitalia Präp[arat] B[urchard] A[lberti] 658 was not located in the MFNB, and neither were other Alberti genitalia dissections despite a dedicated search by the collection manager. Genomic analysis reveals that many Mexican populations of *B. communis*, where *P. albescens* is placed, both by the locality label and genomic data (Fig. 5a), show some genetic differentiation from the specimens in the United States. Therefore, instead of synonymizing *P. albescens* under *B. communis*, we propose to treat it as a southern subspecies *Burnsius communis albescens* Plötz, 1884, **stat. rev**.

Pyrgus (Syrichthus [sic]*) lycurgus* Plötz, 1884 is a junior subjective synonym of *Burnsius communis albescens* (Plötz, 1884)

A single syntype of *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884 is curated in MFNB and agrees nearly perfectly with the original description, including its locality given as "Centr. Amer." on its label and size (forewing length 15 mm). More specifically, the original description, which is rather detailed and precise, mentions the following characters that can all be found in the syntype shown in Fig. 1d (translated here): "Forewing with a white outwardly curved central band, which consists of the square spot in the discal cell, the large one of cell 2 [CuA$_1$-CuA$_2$] and the almost split one in cell 1 [CuA$_2$-1A+2A]; a small, elongated spot is at the origin of cell 2 [CuA$_1$-CuA$_2$] and a similar one closer to the base in cell 1 [CuA$_2$-1A+2A]. The other typical [for the genus *Pyrgus*] spots are smaller. In submarginal area there is an interrupted row of small spots and at the margin there are dots, doubled in cell 1 [CuA$_2$-1A+2A]. In cells 4 [M$_2$-M$_3$] and 5 [M$_1$-M$_2$] distad of discal cell, there are two elongated white spots and in cells 6–9 [R$_5$-M$_1$–R$_2$-R$_3$] there are fine lines to the costal margin. Along the radius, a fine white line from the wing base to its center. The hindwings also have a broad white central band which ends in cell 1 [CuA$_2$-1A+2A] with a point, the point in cell 2 [CuA$_1$-CuA$_2$] is offset towards the base. In the submarginal area, there is a row of spots, some of which are cap-shaped [^], and sizable points at the outer margin. The ventral hindwings are yellowish-white with two jagged bands of olive-green, brown-rimmed patches; the inner one with a large central spot and two torn-off small side spots. By the outer margin in cells 1 [CuA$_2$-1A+2A], 2 [CuA$_1$-

CuA$_2$], 3 [M$_3$-CuA$_1$] and 6 [RS-M$_1$] there are cap-shaped spots and black dots at the margin" (Plötz 1884).

To stabilize nomenclature, N.V.G. hereby designates a female syntype in MFNB shown in Fig. 1d that bears the following 8 labels: || Typus || Centr. Amer || 89:76 || lycurgus Pltz | 129 best. v. Pltz || Coll. Weymer || Lycurgus Pltz | Amer, centr. 2 || {QR Code} http://coll.mfn-berlin.de/u/ | 80a6f0 || DNA sample ID: | NVG-15033H11 | c/o Nick V. Grishin || and a card with a genitalia capsule as the **lectotype** of *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884. The COI barcode sequence of the lectotype (GenBank ON255701) is:

```
AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCCGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTTTTTATAGTCATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCATTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTACCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCATTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
```

The label "89:76" refers to the genus and species numbers in Mabille (1904), which stand for *Hesperia lycurgus*, a species placed in his "species dubiae", simply referencing Plötz. Although currently associated with *B. adepta*, probably due to the lack of costal fold per original description (Plötz 1884) and its locality given as Central America, which by default may not always include Mexico, genomic sequencing reveals that the lectotype is placed among *B. communis* specimens from southern Mexico (Figs. 3b, 5b), either narrowing down its provenance, or suggesting that *B. communis* may have been found south of Mexico (unless the lectotype was mislabeled). Therefore, instead of synonymizing *P. lycurgus* under *B. adepta*, we propose that *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884 is a junior subjective synonym of *Burnsius communis albescens* (Plötz, 1884). The lectotype is a female, but it might have been misidentified as a male by Plötz, or associated with males incorrectly, because *B. communis* possesses a costal fold and P. *lycurgus* was placed by Plötz in the subgenus *Syrichthus* [sic] characterized by the lack of costal fold. Alternatively, Plötz might have been correct in identifying this specimen as a female, but may have had no males to pair with it, and hypothesized that this species lacked costal fold.

Neotype designation for *Pyrgus (Pyrgus) insolatrix* Plötz, 1884 (Herrich-Schäffer in litt.) confirming it as a junior subjective synonym of *Burnsius communis albescens* (Plötz, 1884)

Pyrgus (Pyrgus) insolatrix Plötz, 1884 (type locality in Mexico) did not enjoy a dedicated description as detailed as the one provided for *P. lycurgus* Plötz, 1884, and most of its characters were listed as shared with two other species: *P. albescens* Plötz, 1884 (type locality in Mexico) and *Hesperia ricara* W. H. Edwards, 1865 (Plötz 1884). Description of the latter was based on at least 2 specimens from Colorado, which judging from the characters given ("ventral hindwing at the base greenish-gray with two brown points at the costal margin") and locality were probably misidentified *Burnsius communis*. Moreover, as he stated on page 18 (1884), Plötz considered the following additional four taxa to be of a similar habitus as the abovementioned three: *P. lycurgus* Plötz, 1884, *Syrichtus petreius* W. H. Edwards, 1870 (probably misidentified *B. communis* from Nevada), *Syrichtus* [sic] *communis* Grote, 1872, and *P. adjutrix* Plötz, 1884. Furthermore, inspecting Plötz's original drawings, Godman suggested (1907) that *P. insolatrix* and *P. lycurgus* might have been "?=*Hesperia notata* [sic]". *Pyrgus insolatrix* and *P. lycurgus* were the only two of Plötz's *Pyrgus* species Godman identified as "*notata*" implying that the two drawings were rather similar to each other. This similarity is probably in being darker and having smaller white spots than other species, which was Godman's concept of "*notata*" as it was illustrated in Biologia Centrali-Americana (Godman and Salvin 1899), a misidentification of a species currently referred to as *B. adepta*.

Indeed, Plötz's descriptions of *P. insolatrix* and *P. lycurgus* are rather similar, for instance, in both species the white band on hindwing is much narrowed toward anal margin, versus being rather wide in *P. albescens*, a species paired with *P. insolatrix* + *H. ricara* (misidentified *B. communis*) in the key (Plötz 1884). Both *P. insolatrix* and *P. lycurgus* have bands on ventral hindwing composed of dark cube-shaped or crescent-shaped spots bordered with brown. According to Plötz's key, apart from semantic difference in words used to describe them (e.g., "cap-shaped spots" vs. "lunules") the only discernible difference between the two species is in the presence/absence of costal fold: present in *P. insolatrix* (as in *B. communis*), but absent in *P. lycurgus* (as in *B. adepta*). Due to this difference in costal fold, Evans (1953) synonymized *P. insolatrix* with *B. communis* and *P. lycurgus* with *B. adepta*. However, our genomic analysis of *P. lycurgus* lectotype, which is a female, and if it was the only specimen Plötz inspected, did not offer evidence about the costal fold presence, implies that it is *B. communis*, not *B. adepta* (Fig. 3b), further strengthening the tie between the two species named by Plötz.

Specifically for *P. insolatrix*, Plötz mentions that "ventral hindwing at the base with a green or gray angular cross-bar ["Querstrich"] and its anal margin is white [gray in *P. albescens*]" (Plötz 1884). Although no "cross-bar" or color of anal margin was mentioned in the description of *P. lycurgus*, its lectotype has such a bar at the base of ventral hindwing discal cell, and its ventral hindwing by the anal margin is relatively paler (not gray), agreeing with the description of *P. insolatrix*.

In summary, both Plötz (who described them) and Godman (who inspected Plötz's unpublished original drawings) thought that *P. insolatrix* and *P. lycurgus* are similar, their original descriptions are similar, they are both from the southern parts of North American continent: Mexico or "Central America" (which according to genomic analysis of *P. lycurgus* lectotype can be Mexico), and their forewing lengths are given as 15 mm for both. Evans synonymized *P. insolatrix* with *B. communis*, and genomic analysis of *P. lycurgus* lectotype reveals that it is *B. communis*. Therefore, we hypothesize that *P. insolatrix* is a *B. communis*-looking species.

Keeping this comparative analysis in mind, we searched for syntypes of *P. insolatrix* in the collections that are known to house Plötz's types: MFNB, ZSMC, and EMAU. We failed to find any candidate specimens, and believe that the syntypes of *P. insolatrix* were lost. There is an exceptional need to designate a neotype of *P. insolatrix* because of new cryptic species we found and the need to have an objective definition of this taxon, accompanied by genomic information about its primary type specimen. To stabilize nomenclature, N.V.G. hereby designates the lectotype of *Pyrgus (Syrichthus* [sic]*) lycurgus* Plötz, 1884, female, shown in Fig. 1d as the **neotype** of *Pyrgus (Pyrgus) insolatrix* Plötz, 1884, making the two names objective synonyms. The two "species" are very similar and are from the same biogeographical realm, as discussed above. The only marked difference between them we were able to tease out from the original description was the lack of costal fold in *P. lycurgus*, which turned out to be incorrect, provided our lectotype designation. Our neotype is consistent with both the present synonymy of the name as being conspecific with *Burnsius communis* (Grote, 1872) and the original description of this taxon, thus placing it as a junior subjective synonym of *Burnsius communis albescens* (Plötz, 1884).

This neotype of *P. insolatrix* satisfies all requirements set forth by ICZN Article 75.3, namely: 75.3.1. It is designated to clarify the taxonomic identity of this taxon in the light of possible new species that we found by genomic sequencing; 75.3.2. The characters for the taxon have been given in its original description by Plötz (1884) and are also discussed above; 75.3.3. The neotype specimen bears the following 8 labels: || Typus || Cent. Amer || 89:76 || lycurgus Pltz | 129 best. v. Pltz || Coll. Weymer || Lycurgus Pltz | Amer, centr. 2 || {QR Code} http://coll.mfn-berlin.de/u/ | 80a6f0 || DNA sample ID: | NVG-15033H11 | c/o Nick V. Grishin || and a card with a genitalia capsule. 75.3.4. Our unsuccessful search for the syntypes is described above, leading us to conclude that they are lost; 75.3.5. As detailed above, the neotype is consistent with the original description of this taxon, comments by Godman who examined Plötz's original drawing (Godman 1907), and the current synonymy of this name; 75.3.6. The neotype is from Central America (according to the genomic analysis it may have come from Mexico) and the type locality given for *P. insolatrix* in the original description is "Mexico"; 75.3.7. The neotype is in the collection of the Museum für Naturkunde, Berlin, Germany (MFNB).

Pyrgus occidentalis Skinner, 1906 is a junior subjective synonym of *Burnsius communis communis* (Grote, 1872)

A lectotype of *Pyrgus occidentalis* Skinner, 1906 was designated by Skinner and Williams (1923), who wrote: "We now select from the type material a male from San Antonio, Texas, as the single type." In the

Carnegie Museum of Natural History (CMNH), we found only one specimen labeled as "TYPE No. 7108 / Pyrgus / occidentalis / Henry Skinner". It is in the type collection, bears a label "SanAntonio / Tex.", and is the lectotype (Fig. 1e). Such dark-red "TYPE No." labels are characteristic of Skinner type specimens, and the presence of this label indicates authenticity of this specimen as the type. All other specimens attributed to the type series of *P. occidentalis* we found are labeled as "ALLO-TYPE" (1 female, in the type collection), and "PARA-TYPE" or "PARATYPE" (18 specimens in the general collection).

Bernard Hermier questioned this lectotype designation by Skinner and Williams because, while their work referred to a syntype ("we ... select from the type material"), mentioned their selection of "the single type", and gave a specific locality ("San Antonio, Texas") and sex ("male"), it did not provide information sufficient to unambiguously distinguish this particular "male from San Antonio" from other such syntypes, e.g., by some unique feature, such as a specimen photograph, number, or a unique label that would make the specimen recognizable on the basis of the Skinner and Williams publication alone. (Hermier pers. comm.). Some paralectotypes (labeled as paratypes in the collection) have the same locality label as the lectotype, and therefore they could not be distinguished from the specimen selected by Skinner and Williams as the lectotype without the presence of other labels. To alleviate this problem, N.V.G. hereby designates the only specimen of the type series with the label that states "TYPE" (and not "ALLO-TYPE", "PARA-TYPE" or "PARATYPE"), as the **lectotype** of *Pyrgus occidentalis* Skinner, 1906. This specimen from the collection of the Carnegie Museum of Natural History, Pittsburgh, PA, USA (CMNH) is the same specimen chosen as the lectotype by Skinner and Williams (1923), is illustrated here in Fig. 1e, and bears the following 2 labels: || SanAntonio | Tex. || TYPE No. 7108 | Pyrgus | occidentalis | Henry Skinner ||. Whichever of the two lectotype designation is considered valid, the type locality of *P. occidentalis* is USA: Texas, Bexar Co., San Antonio. A leg of the lectotype was sampled for genomic DNA sequencing, and the following label was added to the lectotype "DNA sample ID: | NVG-15095F03 | c/o Nick V. Grishin".

Whole genome shotgun sequence analysis of the lectotype (NVG-15095F03) unambiguously places it among specimens of *Burnsius communis communis* (Grote, 1872) (Fig. 3b), in agreement with Skinner's statement (1906) that *P. occidentalis* (initially proposed as a species), was "not a species, but only a form or geographical race of" *B. communis*, and confirming its provenance from Texas (Fig. 5c). Therefore, in accord with our genomic results and consistently with the opinion of the original author of the taxon, we propose that *Pyrgus occidentalis* Skinner, 1906 is a junior subjective synonym of *Burnsius communis communis* (Grote, 1872), **new placement**. The COI barcode sequence of the lectotype (GenBank ON255702) is:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCCGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTTTTTATAGTCATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCATTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTACCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCATTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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Accompanying their lectotype designation, Skinner and Williams (1923: Fig. 8) illustrated genitalia of a specimen they presumed to be *Hesperia tessellata* race *occidentalis* (the name they used for *P. occidentalis*) from Arizona: Tucson. However, as the genomic tree implies, genitalia of *P. occidentalis* lectotype would instead look more similar to Skinner and Williams Fig. 7, showing *Hesperia tessellata* (currently *B. communis*). Indeed, this is the case, see Fig. 1e here, for the *in situ* photograph of the left valva of *P. occidentalis* lectotype showing a more robust costa and a prominent bipartite terminal prong directed anterodorsad characteristic of *B. communis*. Apparently, genitalia in Skinner and Williams Fig. 8 are not of *P. occidentalis*, but belong to the taxon that Lindsey, Bell, and Williams (1931) and Evans (1953) called "*Pyrgus communis albescens*", which Burns (2000), with compelling evidence, treated as a species, status further supported by our genomic sequencing and analysis.

As a consequence of the analysis presented above, the species that Burns (2000) called "*Pyrgus albescens*" lost all of its names to other taxa: (1) the true *Pyrgus (Pyrgus) albescens* Plötz, 1884 is a subspecies of *B. communis*, and (2) *P. occidentalis* is a synonym of the latter. Moreover, we analyzed all names associated with *Burnsius* (see above), and none of these names applies to "*Pyrgus albescens*" of Burns. Therefore, a new name is proposed here for this morphologically and genetically distinct species.

Burnsius albezens Grishin, new species

http://zoobank.org/86633D04-9E08-4C9D-BC15-181A68DBB430

(Figs. 2m, 3 part, 4 part)

Description and diagnosis. Keys to G.1.10.(b). in Evans (1953) and is diagnosed by the shape of male genitalic valvae as described and illustrated by Burns (2000). In brief, males have costal fold and lack the tuft of long scales on hind tibiae; genitalia overall smaller than those of *B. communis*; relative to its length, valva shorter in dorsoventral dimension; harpe smaller and more rounded, without prominent dorsal expansions and prongs, but sometimes with 1 or 2 small teeth or bumps. In facies, basically indistinguishable from *B. communis*, but averages paler due to larger white spots, and smaller in overall size (see Burns 2000 figs. 376 and 377). It remains to be determined if females of this species can be separated from *B. communis* using methods other than DNA sequencing.

<u>Barcode sequence of the holotype</u>: Sample NVG-18048A12, GenBank ON255703, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCTGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTTTTTATAGTCATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCATTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTACCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCATTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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Type material. Holotype: ♂ (Fig. 2m), deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), bears five rectangular printed labels: four white [ARIZ.: COCHISE CO. | Portal 4800 ft | Chiricahua Mountains | VII-21-1974 | J. M. & S. N. Burns], [Pyrgus albescens | ♂ Ploetz | det. J. M. Burns 1986], [P-755], [DNA sample ID: | NVG-18048A12 | c/o Nick V. Grishin], and one red [HOLOTYPE ♂ | Burnsius | albezens Grishin]. **Paratypes** are all specimens identified as "*Pyrgus albescens*" by Burns with genitalia illustrated (Burns 2000 figs. 19, 24, 25, 27–29, 31–49, 52–67, 70–74, 77–82, 84, 85, 91, 92, 94, 103, 104, 107, 109–111, 266–374).

Type locality. USA: Arizona, Cochise Co., Chiricahua Mountains, Portal, ca. 4800 ft.

Etymology. The name is constructed to sound similar to *albescens*—the species epithet that was incorrectly applied to this taxon since Lindsey, Bell, and Williams (1931)—in order to ease this nomenclatural change by phonetic conservation of the name. Moreover, the spelling of the name replaces the two letters "sc" that stand for the two prongs of harpe typical for *Burnsius communis albescens*, with the one letter "z" that stands for the harpe that Evans described as "monodent" (actually, just more rounded and smaller) in *Burnsius albezens* sp. n. The name is a participle.

Distribution. This species is widely distributed in the southern United States and Mexico, as detailed and mapped by Burns (2000 figs. 21, 22, 375).

Burnsius burnsi Grishin, new species

http://zoobank.org/A97F5934-44AC-4D71-BFF9-BC325C393A07

(Figs. 2n, 3 part)

Description and diagnosis. North and Central American populations previously attributed to *B. adepta* reveal genetic differentiation from it suggesting a species-level distinction (Fig. 3). This new species lacks costal fold and keys to G.1.10.(c). in Evans (1953), together with *B. adepta*, and is distinguished from it by being paler, in particular around the tornal area of ventral forewing, by larger white spots and broader bands, and in males by typically heavier pale-gray overscaling at the wing bases, in particular on hindwing. However, due to significant individual variation, confident identification is currently possible only by DNA. A combination of the following DNA characters is diagnostic: aly2275.1.2:G183A, aly383.14.4:C75A, aly383.16.4:T54G, aly173.14.1:C1638T, and aly173.36.3:A51G. Fst/Gmin between the new species and *B. adepta* computed on the Z chromosome are 0.22/0.07. The COI barcodes differ between them by 0.9% (6 bp) and the barcode characters for the new species are T157T(not C), T163C, C238C(not T), C340C(not T), T367T(not C), and A400A(not C). The barcode of this species is different from *B. adepta* and its South American relatives, but is nearly the same as *B. communis* and *B. albezens* sp. n. Therefore, in mitochondrial DNA, this new species is like *B. communis* and *B. albezens* sp. n., but in nuclear DNA and phenotypic characters it is more similar to *B. adepta*. Partly due to this hybrid composition, this taxon is proposed as a species, but its genetic diversification from *B. adepta* is modest.

Barcode sequence of the holotype: Sample NVG-16108H04, GenBank ON255704, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCCGGCTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTCATTATAATTTTTTTTATAGTCATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGAGCTCCAGATATAGCATTCCCCCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTACCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCATTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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Type material. Holotype: ♂ (Fig. 2n), deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), bears four rectangular printed labels: three white [MEXICO: Veracruz | Huatusco 4500 ft. | 19.17°N, 96.97°W | 8-12 January 2007 | Leg. Sam Droege], [DNA sample ID: | NVG-16108H04 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00894458] and one red [HOLOTYPE ♂ | Burnsius | burnsi Grishin]. **Paratypes:** 1♂ (NVG-19086B09), Mexico: Campeche, 10 mi S Campeche, 28-Jul-1964, leg. Paul J. Spangler; 1♂ (NVG-19086B10) & 1♀ (NVG-16108G12), Mexico: Guerrero, Acapulco, Barra Vieja, reared on *Sida* sp. 5-Sep-1984, leg. Gillett & Miranda Segura; 1♀ (NVG-7701, genitalia NVG170108-32), Mexico, Oaxaca, 14 mi N Tonaltepec, 10-Jul-1981, leg. Schaffner, Bogar & Friedlander; 1♂ (NVG-19086B08), Mexico, Tamaulipas, Tampico, Sep-1965, leg. N. L. H. Krauss; 2♂♂ (NVG-19086C07 & NVG-19086C08, genitalia J. M. Burns 1978 X-467 & X-473, respectively) Mexico: Veracruz, 5 km SW La Tinaja, 6-Jul-74, leg. J. A. Chemsak & J. Powell; 1♂ (NVG-19086B07, genitalia J. M. Burns X-465, 1978), Mexico: Veracruz, Amate, 12-Aug-1974, leg. J. Chemsak, J. Powell, E. G. Linsley; 1♀ (NVG-19086C06), Belize: Orange Walk District, San Antonio Rio Hondo, 9-14-Oct-1975, leg. D. S. Puleston; 1♂ (NVG-19086C05), Guatemala: Izabal, Quirigua, elevation 800', 22-Sep-1969, James H. Baker collection; 1♂ (NVG-19086B11), El Salvador: San Salvador, 18-Jun-1952, leg. Stan Nicolay; 1♂ (NVG-19086B12), Honduras: Cortes, San Pedro Sula, Aug-1975, leg. N. L. H. Krauss; 1♀ (NVG-18014A04, 15-SRNP-70966), Costa Rica: Guanacaste Prov., Area de Conservacion Guanacaste, Sector Pitilla, Medrano, elevation 380 m, GPS 11.0160, −85.3805, eclosed on 24-May-2015, leg. Dinia Martinez; 1♂ (NVG-19086C01), Costa Rica: San Jose, Patarra, 9.883, −84.033, 25-Jun-1980, leg. Gordon B. Small; 1♂ (NVG-19086C03), Panama: Chiriqui, Cerro La Galera, 8-Aug-1975, leg. Gordon B. Small; and 1♂ (NVG-19086C02), Panama: Panama Prov., Distrito de El Llano, Cordillera de San Blas, N of El Llano, elevation ca. 330 m, 10-May-1978, leg. Gordon B. Small. All paratypes are in USNM, except NVG-7701, which is in TAMU.

Type locality. Mexico: Veracruz, Huatusco, elevation ca. 4500 ft, GPS ca. 19.17, −96.97.

Etymology. This cryptic species is named in honor of John Burns, whose meticulous and insightful studies shed light on the speciation in the *Burnsius communis* species group and resolved the question in favor of species-level distinction between *Burnsius communis* and *B. albezens* sp. n., known as *Pyrgus albescens* at the time. The name is a noun in the genitive case.

Distribution. From Mexico to Panama.

Comments. In addition to DNA, the two species *B. communis* and *B. albezens* can be reliably separated only by male genitalia. Females of these two species cannot be told apart by phenotype, including genitalia. Here, we find an example of a species where even male genitalia fail confident identification, but suspect that future analyses of large series may be fruitful in finding phenotypic differences.

Burnsius adepta inepta Grishin, new subspecies

http://zoobank.org/D6F927E2-B298-4F80-B98E-BC733DDA044C

(Figs. 2p, 3 part)

Description and diagnosis. Populations from western Colombia and Ecuador that Evans (1953) attributed to taxa currently known as *B. adepta* or *B. orcynoides* show notable genetic differentiation from these species, in particular from *B. orcynoides*, and form a distinct clade in the tree (Fig. 3), indicating that they constitute a new taxon, which is sister to *B. adepta*. Fst/Gmin between this taxon and *B. adepta* computed on the Z chromosome are 0.22/0.08, and the COI barcodes differ between them by 0.6–0.8% (4–5 bp). These statistics do not support the differentiation at the species level, therefore the new taxon is proposed as a subspecies of *B. adepta* pending further research. This new subspecies mostly keys to G.1.10.(d). in Evans (1953), together with *B. orcynoides*, but some paler specimens from Colombia would key to G.1.10.(c)., together with *B. adepta*. Distinguished from the nominotypical subspecies by being darker on average, with generally smaller white spots. In particular, white streaks at the base of forewing cells M_1-M_2 and M_2-M_3 are smaller and less developed than in the nominotypical subspecies. Conversely, the submarginal white spot in forewing cell M_1-M_2 is usually larger compared to other spots. Distinguished from *B. orcynoides* by paler ventral forewing margins, which are overscaled with pale olive-brown up to, and partly fused with, white submarginal spots in cells M_1-M_2 and M_2-M_3. However, due to significant phenotypic variation (e.g., paratype NVG-15092E10 is boldly patterned), this new subspecies is largely delimited by its non-trivial genetic differentiation from the nominotypical one, and confident identification can be made through DNA sequences using the following DNA characters in the nuclear genome: aly35699.3.1:T159A, aly171.6.1:G5310A, aly171.6.1:G3873A, aly2582.35.2:A1227G, and aly1146.51.1:T897C, and in the COI barcode: C142T, T157T(not C), A217G, T367T(not C).

<u>Barcode sequence of the holotype</u>: Sample NVG-16108G09, GenBank ON255705, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCTTTAAGTTTATTAATTCGAACTGAATTAGGAAATCCCGGTTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTTACAGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGAAATTGATTAGTACCTTTAATACTAGGGGCTCCAGATATAGCATTCCCTCGTA
TAAATAACATAAGATTTTGATTATTACCCCCTTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTTTATCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCCTTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCAGGAGCTATTACTATATTATTAACAGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCTGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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Type material. Holotype: ♂ (Fig. 2p), deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), bears four rectangular printed labels: three white [ECUADOR Pichincha | Tandapi, 1500 m | 16 Sept. '90 | S. S. Nicolay], [DNA sample ID: | NVG-16108G09 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 00894451] and one red [HOLOTYPE ♂ | Burnsius adepta | inepta Grishin]. **Paratypes:** 1♂ (NVG-15092E10 in MGCL), Colombia, Valle, Cali, Pance, elevation 3000', 23-Jan-1987, leg. J. Bolling Sullivan; 1♂ (NVG-16108H07 in USNM), Ecuador, Pichincha, 4 km E of Tandapi, elevation 2050 m, 23-Sep-2002, leg. I. Aldas; and 1♀ (NVG-16108G08 in USNM), Ecuador, Pichincha, Tandapi, elevation 1700 m, 16-Nov-1992, leg. S. S. Nicolay.

Type locality. Ecuador: Pichincha, Tandapi.

Etymology. The name is an antonym of *adepta*, its sister subspecies, and refers to its "inability" to noticeably diverge phenotypically from the nominotypical subspecies, while exhibiting genetic diversification, and "inability" to be discovered and diagnosed without the genomic sequence analysis. The name is a noun in apposition, made into such to resolve gender (dis)agreement.

Distribution. western Colombia and Ecuador.

Comments. This is likely one of the first subspecies identified nearly exclusively by its genetic differentiation. Nevertheless, this differentiation confidently defines the clade from western Colombia and Ecuador, both in nuclear and mitochondrial genomes, including the COI barcode, thus strongly implying distinct evolutionary history of these populations. Therefore, these populations represent a distinct taxon that is rather advanced along its path to speciation, and it is possible that it is already distinct at the species level, something we were not able to support currently with our standard statistics.

Burnsius orcynus **Grishin, new species**

http://zoobank.org/9E8808A7-F6E1-4873-BE8A-6691B9085878

(Figs. 2j, o, 3 part)

Description and diagnosis. Sister to *B. orcynoides*, but genetically distinct from it at the level that suggests its species status (Fig. 3). Fst/Gmin between the new species and *B. orcynoides* computed on the Z chromosome are 0.29/0.04. The COI barcodes differ between them by about 1.7% (11 bp). This new species keys to G.1.10.(d). in Evans (1953), together with *B. orcynoides*, and is distinguished from it by broader discal white bands on both wings, and on average paler area along inner margin of ventral forewing, with discal spot edge at vein 1A+2A being defined weaker than in *B. orcynoides*. However, due to individual variation, can be confidently identified only by DNA sequences, in particular, by the following DNA characters in the nuclear genome: aly5294.24.2:C108T, aly728.49.1:T1263C, aly1849.9.6:C66A, aly3512.3.2:T90A, and aly318.4.2:T45C; and in the COI barcode T59C, C88T, C235C(not T), T340T(not C), T536T(not C), and T616T(not C).

<u>Barcode sequence of the holotype</u>: Sample NVG-19086D03, GenBank ON255706, 658 base pairs:

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AACTTTATATTTTATTTTTGGAATTTGAGCAGGAATAGTAGGTACTTCATTAAGTTTACTAATTCGAACTGAATTAGGAAATCCTGGTTCATTAATTGGAGATGATCAAATTTATAATACT
ATTGTCACAGCACATGCTTTTATTATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTCGGAAATTGATTAGTACCTTTAATATTAGGAGCTCCAGATATAGCATTCCCTCGTA
TAAATAATATAAGATTTTGATTATTACCCCCCTCATTAACATTACTTATTTCAAGAAGTATTGTAGAAAACGGTGCAGGAACTGGATGAACAGTATATCCCCCATTATCAGCTAATATTGC
TCATCAAGGTTCTTCTGTTGATTTAGCTATTTTTTCTTTACATTTAGCAGGAATTTCATCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGTATTAGAAATTTATCA
TTTGATCAAATACCTTTATTTGTTTGAGCAGTAGGTATTACAGCTTTATTATTATTATTATCATTACCTGTTTTAGCTGGAGCTATTACTATATTATTAACAGATCGAAACTTAAATACAT
CATTTTTTGATCCTGCCGGAGGAGGAGATCCTATTTTATATCAACATTTATTT
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Type material. Holotype: ♂ (Fig. 2o), deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM), bears four rectangular printed labels: three white [Curaçao | Hato Field | Nov. 27, 43 | W. H. Wagner], [DNA sample ID: | NVG-16108G09 | c/o Nick V. Grishin], [USNMENT | {QR Code} | 01588758] and one red [HOLOTYPE ♂ | Burnsius | orcynus Grishin]. **Paratypes:** 1♂ (NVG-16108H03) and 1♀ (NVG-16108H02) the same data as the holotype; 2♂♂ Venezuela, Margarita Island: La Sierra, elevation 600 m, GPS 11.017, −63.883, 13-18-Mar-1988, leg. R. K. Robbins (NVG-16108H08); and San Francisco, 24-Feb-1989, leg. J. F. G. Clarke & N. L. McIntyre (NVG-19086C10). All four paratypes are in USNM.

Type locality. Curaçao: Hato Field.

Etymology. The name is derived from its sister species *B. orcynoides*. The name is a masculine adjective.

Distribution. Currently known only from Margarita Island in Venezuela and Curaçao.

Comment. It is likely that this species was misidentified as *B. adepta* by Snellen (1887), who provided its description and illustration.

Burnsius titicaca (Reverdin, 1921) and *Burnsius chloe* (Evans, 1942) are confirmed as species-level taxa

Genomic comparison of *Burnsius titicaca* (Reverdin, 1921) (type locality Titicaca) and *Burnsius chloe* (Evans, 1942) (type locality Peru: Callao) reveals prominent genetic differentiation between them and even larger differences between either of them and *Burnsius communis* (Grote, 1872), a species they have been treated as subspecies of (Evans 1953) (Fig. 3): e.g., Fst/Gmin in the pairs *B. communis* vs. *B. titicaca* and *B. communis* vs. *B. chloe* are 0.70/0.00 and 0.65/0.00 respectively, suggesting nearly non-existent gene exchange between them; and for *B. titicaca* vs. *B. chloe* 0.39/0.02, revealing only 2% gene exchange, consistent with two closely related and yet distinct sister species.

Notably, COI barcodes did not diverge substantially and differ by 1.4% (9 bp) between *B. titicaca* and *B. chloe*. Comparing barcodes of *B. communis* with *B. titicaca* and *B. chloe*, we get 2.3% (15 bp) and 2.4% (16 bp) difference, respectively. To put these data in perspective, barcodes essentially do not differ between prominently distinct *B. communis* and *B. albezens* sp. n.: mostly 0.2% (1 bp), but their Z chromosome Fst/Gmin are well in the range of distinct species 0.50/0.03. Apparently, mitochondrial evolution experienced some irregularities in *Burnsius*, and the following three species possess nearly identical mitochondrial genomes: *B. communis*, *B. albezens* sp. n., and *B. burnsi* sp. n. Mitochondrial pool is shared between these three sympatric North American species, but differs from that in South America.

The data presented here offer additional support for the hypothesis (Li et al. 2019) that *Burnsius titicaca* (Reverdin, 1921) and *Burnsius chloe* (Evans, 1942) are species distinct from each other and from *Burnsius communis* (Grote, 1872). This distinction is also reflected in their wing patterns: *B. chloe* has greenish continuous and nearly straight ventral hindwing bands giving it a unique appearance; and in *B. titicaca*, the dark bands are jagged, outlined by darker lines and paler within, discal band almost broken into two or three spots as in most other *Burnsius* species (Evans 1953).

On the value of primary types

Primary type specimens are name bearers for taxa they represent. Specimens and populations that belong to the same taxon as the type get the name this type bears. Therefore, careful analysis of primary type specimens is essential for taxonomic research. Often, however, type specimens themselves have not been studied, so that (particularly in earlier works) name usage is based mostly on published descriptions and illustrations. Especially for taxa whose identification by facies is more challenging, this practice may involve mistakes. As a result, detailed analyses of primary types are often surprising and call for revision of previous taxonomic treatments. The dilemma in such cases is whether to change the name of a misnamed taxon to that of its primary type or to seek the ICZN ruling to preserve current but erroneous usage by designating a neotype. There are no definitive guidelines for what to do, but we can turn to a precedent of how a similar problem has been dealt with in the past (e.g., *Hesperia* discussion below).

The centerpiece of this work is the genomic analysis of primary type specimens that reveals their identity. For the two Plötz names where phenotypic identification is straightforward, genomic analysis of their types confirms the current usage of the names. For the other two Plötz names, where identification by facies is frequently impossible, we find that their lectotypes are not the taxa currently referred to by these names. While one of these names (*Pyrgus lycurgus*) has been consistently treated as a junior subjective synonym and would remain as such, just of a different taxon, the other (*Pyrgus albescens*) has long been misapplied. The issue with *Pyrgus albescens* is somewhat similar to that with *Hesperia colorado* (Scudder, 1874), a thoroughly researched case (MacNeill 1975; Scott 1998; Calhoun 2015b; Calhoun et al. 2020; Cong et al. 2021). For several decades, it has been assumed that the name *H. colorado* applied to a high elevation population (MacNeill 1975; Scott 1998), and as our studies revealed, one of the *H. colorado* paralectotypes indeed had a significant genetic component of this high elevation population (Cong et al. 2021). However, lectotype designation (Barnes and McDunnough 1916) fixed the application of the name to the Arkansas river valley population (Calhoun 2015b; Cong et al. 2021), which is inconsistent with the application of that name by most lepidopterists during the last several decades (Scott et al. 2018).

The only extant syntype of *P. albescens* (and maybe the only specimen available at the time of its original description) has been curated as the type of this taxon in the MFNB, previously investigated and dissected (dissection could not be located and the results were not published), and apparently accessible for research. Genomic comparisons reveal that this specimen, designated here as lectotype, defines *P. albescens* as a differentiate that we consider a southern subspecies of *B. communis* that is not conspecific with the species Burns called "*P. albescens*". Regarding *Hesperia colorado*, we have argued for the acceptance of the lectotype as the name bearer, and against designation of the neotype to preserve the widespread, but historically incorrect, usage of the name (Calhoun et al. 2020). Calhoun, who traced the provenance of the *H. colorado* lectotype through diligent research and discovery of historical documents, concluded that the high elevation populations, previously assumed to be *H. colorado*, lost this name to the Arkansas River valley populations, which already had a more recently proposed name, *Hesperia comma oroplata* J. Scott, 1981 (Calhoun 2015b; Calhoun 2015a). A new name for the high elevation populations was proposed (Warren and Calhoun 2015).

The situation with *Pyrgus albescens* is analogous. We found that according to its lectotype, it is not the species this name is currently used for, and this species loses its name to southern populations (southern Mexico, Central America) of *B. communis*. A new name for the species previously assumed to be *B. albescens* is proposed here. To soften the experience of the name change, the new name is chosen to be phonetically similar: *B. albezens* sp. n. However, in either case, be it *Hesperia colorado* or *Burnsius albescens*, one can argue that the lectotypes should be set aside and neotypes designated to preserve erroneous usage of these names. The erroneous usage is caused by mistakes of prior researchers who did not study the type material, although it was available and labeled appropriately in corresponding collections (Calhoun 2015b). We leave it to the community of lepidopterists to decide on the best solution, but chose to accept the lectotypes as the name bearers in both cases (*Hesperia colorado* and *Pyrgus albescens*).

Taxonomic history of the two *Burnsius* species in the US reveals evolving opinions. Skinner (1906) described new species *P. occidentalis* (subsequently, and as we show incorrectly, synonymized with *P. albescens*) but immediately changed his mind by stating that *occidentalis* "is not a species, but only a form or geographical race of *tessellata*" (currently *B. communis*). In so doing, he initiated the *communis*/*albescens* debate. Intrigued by the question of taxonomic rank, several workers soon found unmistakable differences in the male genitalia of these taxa but differed in their taxonomic conclusions (which were often equivocal) because of a lot of individual genitalic variation. Skinner and Williams (1923) clearly figured the typical genitalic differences between the two taxa. Lindsey et al. (1931), using the combination *Pyrgus communis* race *albescens*, reprinted those figures and stated that this taxon occurs "from California to Texas and Mexico" and that "this form is scarcely worthy of a name, but may be regarded as a pale southwestern geographic race." *Pyrgus communis albescens* has been used for decades to denote this subspecies (known in this century, first as *Pyrgus albescens* and then *Burnsius albescens*). Sequencing of the *P. albescens* lectotype shows that it is indeed closely related to *B. communis* but at no more than a subspecific level. The geographic distribution of this subspecies is far different from that of what, for a long time, has been erroneously called *P. c. albescens*, and constitutes the southernmost outskirts of its former vast range. As dictated by its lectotype, we now apply the name *B. c. albescens* to this subspecies and name its former owner, a distinct species, *Burnsius albezens* sp. n.

Nomenclature-wise, the situation with *Pyrgus albescens* is noteworthy because the name *albescens* has been applied to two subspecific taxa of *B. communis*. Lindsey et al. (1931) erroneously used it in their trinomial *Pyrgus communis albescens*, and now we correctly call a genomically and geographically distinct subspecies *Burnsius communis albescens*. Invalidating the previous use of *albescens* leaves its bearer without a name. We call it new species *Burnsius albezens*.

Species, subspecies, and genomics

Traditionally, species delimitation in Hesperiidae is often based on consistent differences in genitalia, and subspecies in butterflies are defined by geographic differences in wing patterns. Since the introduction of COI barcodes in 2003, they have been widely used to detect cryptic species (which often lack appreciable genitalic differences). However, any single locus, especially in mitochondrial DNA where the barcode is located, is subject to gene exchange between species, which is frequent within species complexes of close relatives. Due to gene exchange, significant barcode differences within a population do not necessarily indicate multiple species. On the other hand, the lack of differences in COI barcodes need not imply conspecificity, and closely related sympatric species may have identical barcodes.

One common way to define species is by a reproductive barrier that may not, however, be absolute. Genomic comparison enables direct assessment of this reproductive barrier through the analysis of genetic differentiation and gene exchange. Greater genetic differentiation between populations and lesser gene exchange between them suggest a higher reproductive barrier and a possible loss of conspecificity. Sex chromosomes, such as the Z chromosome in butterflies, are more instructive for these analyses than autosomes, because they encode a large fraction of genes important for mate recognition and are less susceptible to gene exchange due to a lower recombination rate. Recombination of Z chromosomes occurs only in the homogametic sex, which, in butterflies, is the male.

In traditional phylogenetic trees constructed from genomic alignment positions sampled from protein-coding genes in the Z chromosome, distinct species usually stand out as strongly supported clades with statistical support of 1 (Fig. 3b). To compute this statistical support, we draw 100 samples of positions and construct a tree from each sample. Statistical support for a node in the tree is the fraction of trees (out of 100) with this node present. Support of 1 means that all samples of different genomic regions result in the same grouping of specimens. With reproductive isolation, interspecific gene exchange that puts a specimen of one species within specimens of the other is rare. Most genomic regions group all specimens of the same species and away from specimens of a different species.

However, within species, phylogenetic trees are not expected to have clades with strong support. Indeed, due to free gene flow within each species, samples of various positions are not expected to group specimens the same way. Gene flow equilibrates gene frequencies within species and prevents a group of populations from diverging. Therefore, we see a lack of tree structure within species (Fig. 3b blue, red, or magenta clades) and species subtrees appear comb-like rather than the usual bifurcating trees (Fig. 3a).

Subspecies in butterflies have been defined by wing pattern differences. While some of these differences may be minor and might even be environmentally induced, others should reflect certain genetic differentiation between subspecies. Such genetically differentiated subspecies may be viewed as groups of populations on their way to allopatric speciation. Therefore, these subspecies may be delineated by genomic comparison as clades of specimens from different parts of the range. However, such subspecies clades would be less prominent than the clades corresponding to species, and with weaker statistical support due to gene flow between subspecies. This is what we observe with *Burnsius adepta inepta* ssp. n. (Fig. 3b, orange clade). The existence of this subspecies was first suggested by our genomic trees, and its wing pattern differences were only found afterwards.

While general concepts about genomic data, species, and subspecies presented here are reasonably well understood from a theoretical perspective, an exact numeric criterion for species vs. subspecies definition is unrealistic, remains uncertain in borderline cases, and should be investigated. Here, *B. adepta inepta* ssp. n. (Fig. 3b orange) is conservatively proposed as a subspecies due to its limited genetic differentiation from nominotypical *B. adepta* (Fig. 3b cyan). However, it is possible that it may be a species-level taxon. Genomic sequencing and analysis of a larger sample of specimens is necessary to shed further light on the situation. In particular, an analysis could be focused on Colombia, from which both taxa have been recorded.

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