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Two new species of *Hermeuptychia* from North America and three neotype designations (Nymphalidae: Satyrinae)

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ABSTRACT. Two new species of *Hermeuptychia* Forster, 1964 are described. *Hermeuptychia sinuosa* Grishin, **sp. n.** (type locality Guatemala: El Progreso, Morazán) is an isolated member of the genus that does not readily fit into known species groups, as suggested by its distinct male and female genitalia and COI DNA barcode sequences. It is distinguished from its congeners by prominently wavy submarginal lines, rounder wings and distinctive genitalia, and can typically be identified by a white dot, instead of an eyespot, near the ventral hindwing apex. *Hermeuptychia occidentalis* Grishin, **sp. n.** (type locality Mexico: Guerrero, Acapulco) belongs to the *Hermeuptychia sosybius* group as indicated by the presence of androconia on the dorsal surface of the wings, genitalia and COI DNA barcodes, and in addition to DNA characters, differs from its relatives in the shape of the uncus and female genitalia. Neotypes of *Oreas strigata canthe* Hübner, [1811] (type locality Suriname: Gelderland, Suriname River), *Megisto acmenis* Hübner, 1823 (type locality Argentina: Buenos Aires), and *Satyryx cantheus* Godart, [1824] (type locality USA: Florida, Pinellas Co., St. Petersburg) and lectotype of *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878 (type locality Argentina: Buenos Aires) are designated. These designations establish *Hermeuptychia canthe* as a valid species widely distributed in South America from Colombia to Bolivia and Southeast Brazil, *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878 as a junior objective synonym of *Ypthimoides acmenis*, and *S. cantheus* as a junior subjective synonym of *Hermeuptychia sosybius* (Fabricius, 1793). *Papilio camerta* Cramer, 1780 is treated as *nomen dubium* requiring further studies to determine an identity that is consistent with the original description, as it may be conspecific with *Parypthimoides poltys* (Prittwitz, 1865) instead of being a *Hermeuptychia* species as currently assumed.

Key words: biodiversity, cryptic species, Neotropical, Mesoamerica, satyrines, female genitalia.

RESUMEN. Se describe dos nuevas especies de *Hermeuptychia* Forster, 1964. *Hermeuptychia sinuosa* Grishin, **sp. n.** (localidad tipo Guatemala: El Progreso, Morazán), es un componente aislado del género que no encaja fácilmente en los grupos de especies conocidas, como lo indica su distintiva genitalia masculina y femenina y las secuencias de ADN del código de barras COI. Se distingue de sus congéneres por tener líneas submarginales prominentemente onduladas, alas más redondas y genitales diferentes, y se puede identificar típicamente por un punto blanco, en lugar de una mancha ocular, cerca del ápice ventral del ala anterior. *Hermeuptychia occidentalis* Grishin, **sp. n.** (localidad tipo México: Guerrero, Acapulco) pertenece al grupo de *Hermeuptychia sosybius* como lo indica la presencia de androconia en las alas anteriores, la estructura genital y secuencias de ADN de la región del código de barras COI, y además de caracteres del ADN, se diferencia de sus parientes en la forma del uncus y la genitalia femenina. Se designa neotipos para *Oreas strigata canthe* Hübner, [1811] (localidad tipo Surinam: Gelderland, Río Surinam), *Megisto acmenis* Hübner, 1823 (localidad tipo Argentina: Buenos Aires), y *Satyryx cantheus* Godart, [1824] (localidad tipo Estados Unidos: Florida, Pinellas Co., St. Petersburg), y el lectotipo de *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878 (localidad tipo Argentina: Buenos Aires). Estas designaciones establecen a *Hermeuptychia canthe* como una especie válida ampliamente distribuida en América del Sur desde Colombia hasta Bolivia y el sureste de Brasil, a *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878 como sinónimo objetivo más reciente de *Ypthimoides acmenis*, y a *S. cantheus* como sinónimo subjetivo más reciente de *Hermeuptychia sosybius* (Fabricius, 1793).

Papilio camerta Cramer, 1780 es tratado como un *nomen dubium* requiriendo más estudios para determinar una identidad que sea consistente con la descripción original, ya que puede ser coespecífica con *Paryphthimoides poltys* (Prittwitz, 1865) en lugar de ser una especie de *Hermeuptychia* como se asume actualmente.

Palabras clave: biodiversidad, especies crípticas, Neotrópico, Mesoamérica, satírinos, genitalia femenina.

ZooBank registration: <http://zoobank.org/58D9373E-D0C5-4D7D-860B-63BFDCFE85E0>

The Neotropical genus *Hermeuptychia* was erected by Forster (1964) on the basis of male genitalia characters to unite a group of relatives hardly identifiable by highly variable wing patterns, but distinct in male genitalia. Lamas (2004) recognized eight named species of *Hermeuptychia* and suggested the existence of several unnamed species in Colombia and Peru. One of these species has been described since (Nakahara et al. 2017). Subsequently, *Euptychia undulata* Butler, 1867 has been transferred to *Hermeuptychia* (Zacca et al. 2021).

DNA-based studies rationalized from the perspective of morphology revealed extensive cryptic species diversity in *Hermeuptychia* (Seraphim et al. 2014; Tan et al. 2021), with two new species named from the United States (Cong and Grishin 2014). The major challenge is to associate biological species delineated with a significant contribution from DNA sequences (Cong and Grishin 2014; Seraphim et al. 2014; Tan et al. 2021) with the names proposed on the basis of old type specimens (Cong et al. 2021) in agreement with the literature (Viloria 2021), and in a manner consistent with the International Code of Zoological Nomenclature (ICZN 1999). Furthermore, not all names placed in *Hermeuptychia* are currently associated with their primary type specimens, causing further confusion (Viloria 2021) and thus threatening the stability of nomenclature.

Here, to facilitate a future integrative revision of *Hermeuptychia* grounded in genome-based sequencing of primary type specimens, some of these challenges are addressed. Methods employed in this work are as those described previously (Cong and Grishin 2014). Collection acronyms are given in the Acknowledgments section below. New COI barcode sequences reported here were deposited in GenBank <<https://www.ncbi.nlm.nih.gov/genbank/>> with accession numbers OK641921–OK641923.

***Hermeuptychia sinuosa* Grishin, new species**

<http://zoobank.org/026F9922-541B-466C-B25E-34739C18C1BD>

(Figs. 1–10, 33a–d, j, k, 36 part)

Description and diagnosis. On average smaller than its congeners (forewing length 14–16 mm), wings rounder and of similar shape in both sexes, dorsally unspotted brown, ventrally with postmedian eyespots typically very small, nearly equal to each other in size, five on forewing and six on hindwing (some may be vestigial, especially on forewing), hindwing eyespots 2, 5 & 6 (counting from costa) developed best, usually black, yellow-ringed and pupillated with pale metallic blue. Recognized by a well-expressed and wavy (sinuous) submarginal line placed at some distance from the two thinner marginal lines, hindwing 6th eyespot on this line, 1st eyespot usually replaced by a white dot (sometimes a patch of cream-white scales overlays a small eyespot), making such specimens identifiable by this character. These cream-white scales forming the dot are different from iridescent scales that pupillate eyespots. Median lines are darker at veins in some specimens, which is another character atypical for *Hermeuptychia*. Male genitalia distinctive (Fig. 33a–d): uncus narrow, in dorsal view lanceolate, widest near the distal third, apex truncated, nearly straight (not strongly bent ventrad) in lateral view, without carina; saccus long and narrow, about as long as vinculum; valva nearly straight, only slightly concave ventrad in the middle, without a deep notch, dorsally narrows gradually towards cucullus, then more abruptly past the base of cucullus, which narrows further to a point, slightly upturned; aedeagus as long as valva, not expanded at its base. Female genitalia (Fig. 33j, k) with antrum small comparatively to other species, weakly sclerotized, obcordate in shape, widest near its distal third, in dorso-ventral dimension thin and appears flattened, not cup-like as in most congeners.

Barcode sequence of the holotype: Sample NVG-2307, GenBank accession OK641921, 658 base pairs:

```
AACTTTATATTTTATTTTGGTATTTGAGCAGGAATAATTGGAACATCATTAAAGTTAATTATTCGAATGGAATTAGGTAATCCAGGATTTTAAATGGGGATGATCAAATTTATAATACT  
ATTGTAACAGCTCAGCTTTTATATAATTTTATAGTAATACCTATTATAAATGGAGGATTTGGTAATTGACTATCCCTTAATATTAGGAGCTCCTGATATAGCCTCCACGTA  
TAAATAATATAAGATTTTGATTATTACCCCATCTTTAATTTTATTAATTTCTAGTAGTATTGTAGAAAATGGAAGTGGAACAGGATGAACAGTTTATCCCTCTTTCATCTAATATTGC  
TCATAGAGGATCATCGGTTGATTTAGCAATTTTCTCCTTCATTAGCTGGAATTTCTCAATTTAGGAGCTATTAATTTTATTACAACAATTAATAATACGAAATTAATAATATCT  
TATGATCAAATACCTTTATTTATCTGAGCTGTAGGAATCACAGCTCTCTTTACTTCTTCCCTTACCCGTTTGTAGCGGAGCTATTACTATACTTCTTACCACCGTAATTTAATACAT  
CATTTTTTGACCCCGCAGGAGGAGGTGATCTATTTTATACCAACATCTATTT
```

Type material. Holotype: ♂, has four rectangular printed labels: three white [GTM.ElProgreso.002 | Morazan | DurdenCJ 90010A07], [DNA sample ID: | NVG-2307 | c/o Nick V. Grishin], [NVG140403-35] and one red [HOLOTYPE ♂ | *Hermeuptychia* | *sinuosa* Grishin]. The locality label stands for Guatemala: El Progreso, Morazan, above k99, leg. C. J. Durden, 10-Jan-1990. NVG140403-35 is a genitalia preparation number, genitalia vial placed on the same pin with the specimen. The holotype is illustrated in Figs. 1–2 (genitalia Fig. 33a–d) and is currently in the University of Texas at Austin collection, Austin, TX, USA [TMMC]. **Paratypes:** 4 ♂♂ and 3 ♀♀, all from Mexico: ♀ Colima, Mar-1922, BMNH(E) #834698, ♂ Morelos, Cuernavaca, BMNH(E) #834699, ♂ Guerrero, Nov-1916, BMNH(E) #806416, ♀ Guerrero, Sierra de Guerrero, "Dec. 12" [probably 12-Dec-?], DNA sample NVG-2981, genitalia NVG141101-12 [USNM], ♂ Oaxaca, Chiltepec, 2-Nov-1969, RLR, DNA sample NVG-14112H06, ♀ Veracruz, Catemaco, Dos Amates, 23-Sep-1972, RLR, DNA sample NVG-14112H07, ♂ no data label [likely from one of the two "RLR" localities above], DNA sample NVG-14112H05.

Type locality. Guatemala: El Progreso, Morazán.

Etymology. The name refers to the sinuous submarginal dark line on wings beneath. The name is a feminine adjective.

Distribution. In addition to the type locality in Guatemala, this species is widely distributed in Mexico (Colima, Morelos, Guerrero, Oaxaca, Veracruz).

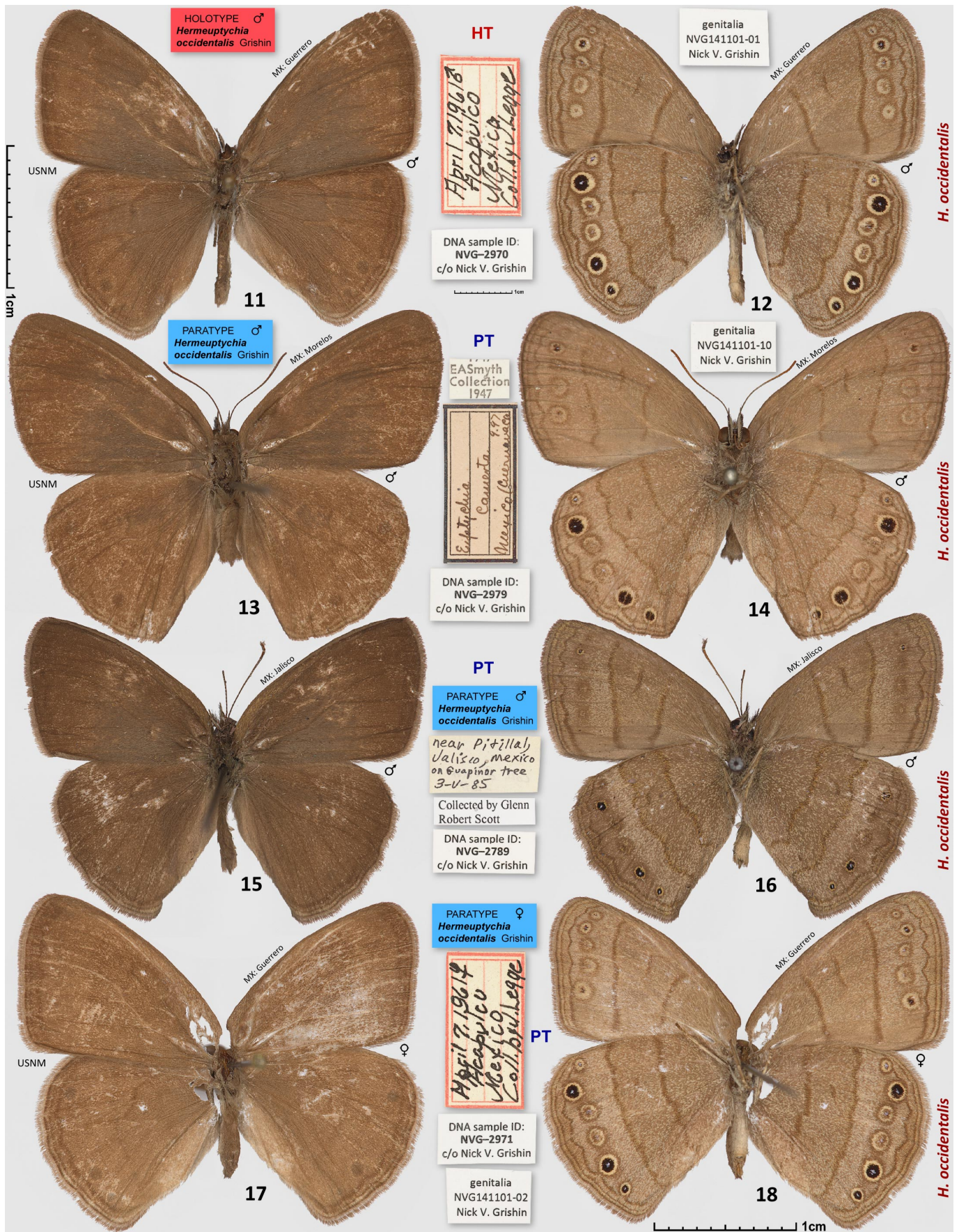
Comments. This species was at times identified as *Hermeuptychia lupita* (Reakirt, [1867]) (type locality Mexico: Veracruz) (Warren et al. 2016), which is incorrect, as also pointed out by Viloría (2021). Facies of *Hermeuptychia sinuosa* sp. n. do not agree with the original description of *Neonympha lupita*. In particular, the former species is smaller (wingspan <1.15 vs. 1.25 inches in *N. lupita*), and the wing pattern of the ventral side differs: the new species typically has more than 4 eyespots (1 forewing, 3 hindwing in *N. lupita*) and lacks additional (to the three median lines) "transverse lines" on the hindwing "towards the base" (Reakirt [1867]).

Hermeuptychia occidentalis Grishin, new species

<http://zoobank.org/7FB00257-D9A6-4C25-930B-78145BF3AFAC>

(Figs. 11–18, 33e–i, l, m, 36 part)

Description and diagnosis. Belongs to the same species group with *Hermeuptychia sosybius* (Fabricius, 1793) and *Hermeuptychia hermybius* Grishin, 2014 as judged by the presence of large areas on the dorsal surface of the wings covered with androconia, morphology of the male genitalia and COI DNA barcodes that place this species as sister to the two others (Fig. 36). Due to wing pattern variation, identification by facies is challenging. Characterized by a postmedian area on the ventral hindwings distad of the distal median line and to the eyespots (sometimes beyond them) paler than the rest of the wing, and markedly paler than the discal area forming a (somewhat) darker band bordered by the two median lines. The forewings in most specimens show the same, but weaker, tendency of being paler towards the outer margin from the distal median line. Veins not paler than the background, as they frequently are in *H. hermybius*. Diagnosed by genitalia and COI barcodes. In male genitalia (Fig. 33e–i), which are otherwise similar to *H. hermybius*, the uncus is narrower, lanceolate in dorsal view, being broadest near its basal third, rather than near or past its middle, not constricted before the truncated apex, the apex narrower as well. In the female genitalia (Fig. 33l, m), the antrum is broader, nearly round, broadest near its middle, nearly symmetrical. The following combination of characters in the COI DNA barcode is proposed as diagnostic: T5C, T247C, T484C, T580C, T583C, and T646C, where the number refers to the sequence



Figs. 11–18. *Hermeuptychia occidentalis* sp. n. type series. 11–12. holotype ♂, Mexico: Guerrero, Acapulco, 7-Apr-1961, leg. J. Legge, DNA sample NVG-2970, genitalia NVG141101-01 (Fig. 33e–h) [USNM]; paratypes: 13–14. ♂, Mexico: Morelos, Cuernavaca, Sep-1897, E. A. Smyth collection, DNA sample NVG-2979, genitalia NVG141101-10 (Fig. 33i) [USNM]; 15–16. ♂, Mexico: Jalisco, nr. Pitillal, 3-May-1985, leg. G. R. Scott, DNA sample NVG-2789; 17–18. ♀, Mexico: Guerrero, Acapulco, 7-Apr-1961, leg. J. Legge, DNA sample NVG-2971, genitalia NVG141101-02 (Fig. 33l, m) [USNM].



Figs. 19–32. *Hermeuptychia* specimens. *H. canthe*: 19–20. neotype ♂, designated herein, Suriname: Gelderland, Surinam River, genitalia slide W. D. F. #306 (Fig. 34), DNA sample NVG-14061C10 [USNM]; 21–22. ♂, Peru: Madre de Dios, Amazonia Lodge, Atalaya, 491 m, 25-Sep-2011, leg. Steve Kinyon, #1907, DNA sample NVG-2649, genitalia NVG140628-17 (Fig. 35i) [USNM]; 23–24. ♀, Guyana: Region 9, Kanuku Mts., Nappi Creek, 03°20.7'N 59°34.2'W, 500'-1000', 21-Feb-10-Mar-1999, leg. S. Fratello, R. Hanner, S. Hendricks & R. Williams, USNM ENT 00232265, DNA sample NVG-2675, genitalia NVG140628-43 (Fig. 35l-m) [USNM]; 25–26. ♂, Colombia: Cauqueta, Florencia, 6-Aug-1976, fairly wet hillside forest, leg. J. A. Scott, DNA voucher NVG-2798; 27–28. ♀, Suriname: Commewijne, De Nieuwe Grond, secondary forest, 2-Jun-1982, leg. Olle Pellmyr, DNA sample NVG-2644, genitalia NVG140628-12 (Fig. 35j-k) [USNM]; 29–30. illustrations of type specimens from the original description, not to scale (Hübner [1811]). 31–32. *H. cantheus* neotype ♂, designated herein, USA: Florida, St. Petersburg, 3-Nov-1938, leg. H. E. Wilford, DNA sample 11-BOA-15609E04 [USNM].

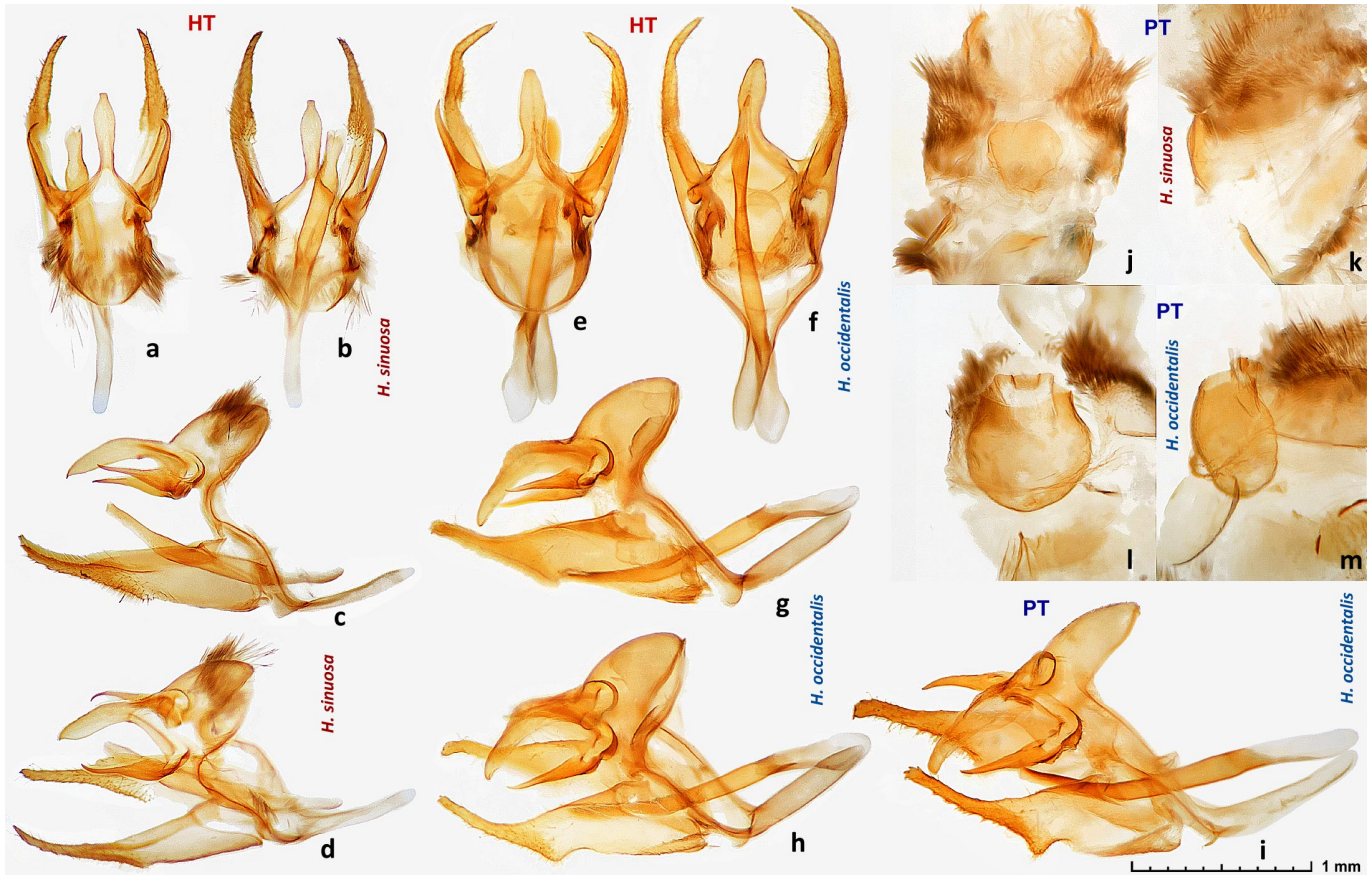


Fig. 33. Genitalia of *Hermeuptychia* type specimens. a–d. *H. sinuosa* holotype ♂, data in text and Figs. 1–2. e–h. *H. occidentalis* holotype ♂, data in text and Figs. 11–12. i. *H. occidentalis*, paratype ♂, Mexico: Morelos, Cuernavaca, Sep-1897, E. A. Smyth collection, DNA sample NVG-2979, genitalia NVG14101-10 [USNM] (specimen Figs. 13–14). j, k. *H. sinuosa* paratype ♀, Mexico: Sierra de Guerrero, Dec-1912, leg. R. Muller, #3670, DNA sample NVG-2981, genitalia NVG14101-12 [USNM] (specimen Figs. 9–10). l, m. *H. occidentalis* paratype ♀, Mexico: Guerrero, Acapulco, 7-Apr-1961, leg. J. Legge, DNA sample NVG-2971, genitalia NVG14101-02 [USNM] (specimen Figs. 17–18). Views: a, e, dorsal; b, f, j, l, ventral; c, g, k, m, lateral; d, h, i, dorsolateral. All images are to scale.

given below (from 1 to 658), the letter before the number is the expected ancestral base pair in this position and the letter after the number is the base pair in this new species.

Barcode sequence of the holotype: Sample NVG-2970, GenBank accession OK641922, 658 base pairs:

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AACTCTATATTTTATTTTGGTATCTGAGCAGGAATAATTGGTACATCATTAAAGTTTAAATTATCCGAATAGAATTAGGTAACCCAGGATTTTAAATGGAGATGATCAAATTTATAATACT
ATTGTTACAGCTCATGCTTTTATTATAATTTTATATAGTAATACCTATTATAAATGGAGGATTTGGTAATGACTTATTCCTTAAATATTAGGAGCTCCTGATATAGCTTTCCACGTA
TAAACAATATAAGATTTTGATTATTACCCCCATCTTAAATTTTATTAATTTCTAGTAGTATTGTAGAAAATGGAAGTGGAAACAGGATGAACAGTTTATCCCTTCTTTCATCTAATATTGC
TCATAGAGGTTCTCAGTAGATTTAGCAATTTTCTCTTCATTAGCTGGAATTTCTTCAATTTAGGAGCTAATTTTATTACAACAATTTAATATACGAATTAATAATATATCC
TATGATCAAATACCTTTATTATTGAGCTGTAGGAATTACAGCTCTCTTTACTTCTTTCATTACCTGTTTGTAGCAGGAGCTATCACTATACTCCTCACTGATCGAAATTTAAATACAT
CATTTTTTGATCCTGCAGGAGGAGGAGACCCCTATTTTATACCAACATTTATTT
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Type material. Holotype: ♂, has four rectangular labels: three white, one handwritten [April 7, 1961 ♂ | Acapulco | Mexico | Coll. by J. Legge], others printed [DNA sample ID: | NVG-2970 | c/o Nick V. Grishin], [genitalia | NVG141101-01 | Nick V. Grishin] and one red [HOLOTYPE ♂ | *Hermeuptychia* | *occidentalis* Grishin]. The holotype is illustrated in Figs. 11–12 (genitalia Fig. 33e–h) and is in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA [USNM].

Paratypes: 2 ♂♂ and 1 ♀, from Mexico: ♂ Jalisco, near Pitillal, 3-May-1985, leg. Glenn R. Scott, DNA sample NVG-2789; ♂ Morelos, Cuernavaca, Sep-1897, E. A. Smyth collection, DNA sample NVG-2979, genitalia NVG14101-10 [USNM]; ♀ Guerrero, Acapulco, 7-Apr-1961, leg. J. Legge, DNA sample NVG-2971, genitalia NVG14101-02 [USNM].

Type locality. Mexico: Guerrero, Acapulco.

Etymology. The name refers to the western distribution of this species. The name is a feminine adjective.

Distribution. This species is known from southwestern Mexico (Jalisco, Morelos, Guerrero).

Neotype designation for *Hermeuptychia canthe* (Hübner, [1811])

Meaningful integrative taxonomic revision of *Hermeuptychia*, a genus of many confusingly similar cryptic species, requires clarity about its nomenclature. Such clarity can only be achieved when all relevant names are objectively defined by their primary type specimens, and these specimens are sequenced to provide DNA datasets necessary for a more definitive identification and comparisons. No extant primary type specimens are known for *Hermeuptychia canthe* (Hübner, [1811]). Although, as documented in the literature, most of Hübner types were likely lost (Hemming 1937; Calhoun 2018), N.V.G. searched for possible *H. canthe* syntypes in the collections of the Muséum National d'Histoire Naturelle, Paris, France (MNHP), the Natural History Museum, London, UK (BMNH) and the Museum für Naturkunde, Berlin, Germany (ZMHB). These searches were unsuccessful, leading us to believe that the syntypes are no longer extant, and we proceed herein with a neotype designation. There is an exceptional need to designate the neotype of *H. canthe*. Kept as a junior subjective synonym for decades, *H. canthe* was resurrected by Vilorio (2021) who used the name as valid. To unambiguously establish the identity of this species necessary for further work on this very challenging genus, a neotype that facilitates DNA-based studies is required. We believe that it is not possible to discern the cryptic diversity of *Hermeuptychia* without DNA comparisons (Tan et al. 2021).

The original illustrations of *Oreas strigata canthe* Hübner, [1811] are identifiable as a *Hermeuptychia*, probably from Suriname (Hemming 1937), largely brown unspotted dorsally, and ventrally with 5 eyespots on the forewing (including the one near the apex) and 6 on the hindwing (Figs. 29, 30). All the eyespots on the illustrations are approximately the same size, e.g. those in hindwing cells R_5-M_1 and CuA_1-CuA_2 are not larger than others. The distance between the two brown lines on the ventral forewing increases towards the costa. We found a male specimen from Suriname that agrees with these distinctive features of the original illustrations and we hereby designate this specimen shown in Figs. 19, 20, genitalia Fig. 34, as the **neotype of *Oreas strigata canthe* Hübner, [1811]**. This species belongs to *Hermeuptychia*.

Our neotype of *H. canthe* satisfies all the requirements set forth by the ICZN Article 75.3. Namely: 75.3.1. It is designated to clarify the taxonomic identity of *O. canthe*, which remained hypothetical until now, impeding research on *Hermeuptychia*; 75.3.2. The characters that differentiate this taxon have been given above, as a description of the original illustrations, complemented here by the following features of male genitalia (Fig. 34, 35): saccus long, only somewhat shorter than tegumen with uncus; "truncated" at the end, uncus with thin, membranous carina in basal half; valva about 4 times longer than its height, ventrally with a broad notch, cucullus long and narrow, terminally without teeth, aedeagus slightly longer than valvae. The COI barcode sequence of the neotype (GenBank accession OK641923) is:

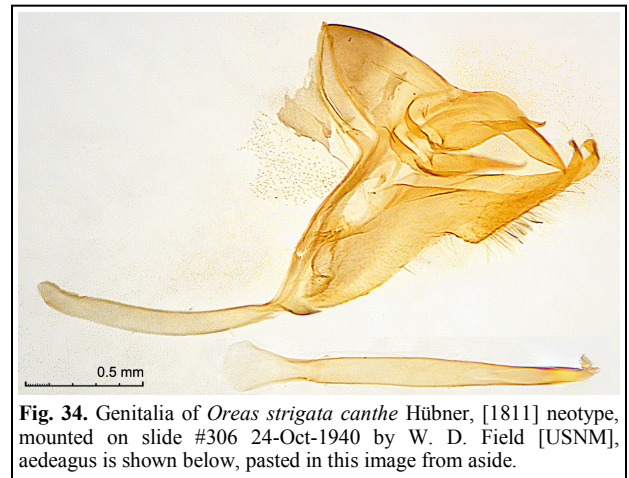


Fig. 34. Genitalia of *Oreas strigata canthe* Hübner, [1811] neotype, mounted on slide #306 24-Oct-1940 by W. D. Field [USNM], aedeagus is shown below, pasted in this image from aside.

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AACTTTATATTTTTATTTTTGGTATCTGAGCAGGAATAATTGGCACATCATTAAAGTTTAAATTATCCGAATAGAATTAGGTAATCCAGGATTTTTAATTGGAGATGACCAAAATTTATAATACT  
ATTGTTACAGCTCATGCTTTTATATAATTTTTTATAGTAATACCTATTATAATTGGTGGATTGGTAAATTGACTTATCCCTTAATATAGGAGCTCCTGATATAGCTTTCCACGTA  
TAAATAATATAAGATTTTGATTATACCTCCATCTTAATTTTAAATTTCTAGTAGCATGTAGAAAATGGAAGTGGAACTGGATGAACAGTTTATCCCTCTTTTCATCTAATATTGC  
TCATAGAGGTTCTTCTGTAGATTTGGCAATTTTTCTCTTCACTTAGCTGGAATTTCTTCAATTTTAGGAGCTATTAATTTTATTACAACAATTATTAATATACGAATTAATAATATATCT  
TATGATCAAATACCCCTATTTATTTGAGCCGTAGGAATTACAGCTCTCCTTACTTCTTTTACTTCTTTTACTTCTTACTGATCGAAATTTAAATACAT  
CATTTTTTGACCTGCGAGGAGGAGACCCCATTTTATATCAACATTTATTC
```

75.3.3. The neotype specimen is a male that bears the following five rectangular labels: [Gelderland, | Suriname River.], [Collection | Wm. Schaus], [genitalia | slide X-24-40 | W. D. F. #306], [DNA sample ID: | NVG-14061C10 | c/o Nick V. Grishin], and [NEOTYPE ♂ | *Oreas canthe* | Hübner, [1811] | designated by Grishin]; 75.3.4. Our search for the syntypes is described above, and it was unsuccessful, leading us to believe that they are no longer extant; 75.3.5. The neotype is consistent with what is known about this taxon, in particular with the original illustrations: e.g., on the ventral side, it has 5 eyespots on

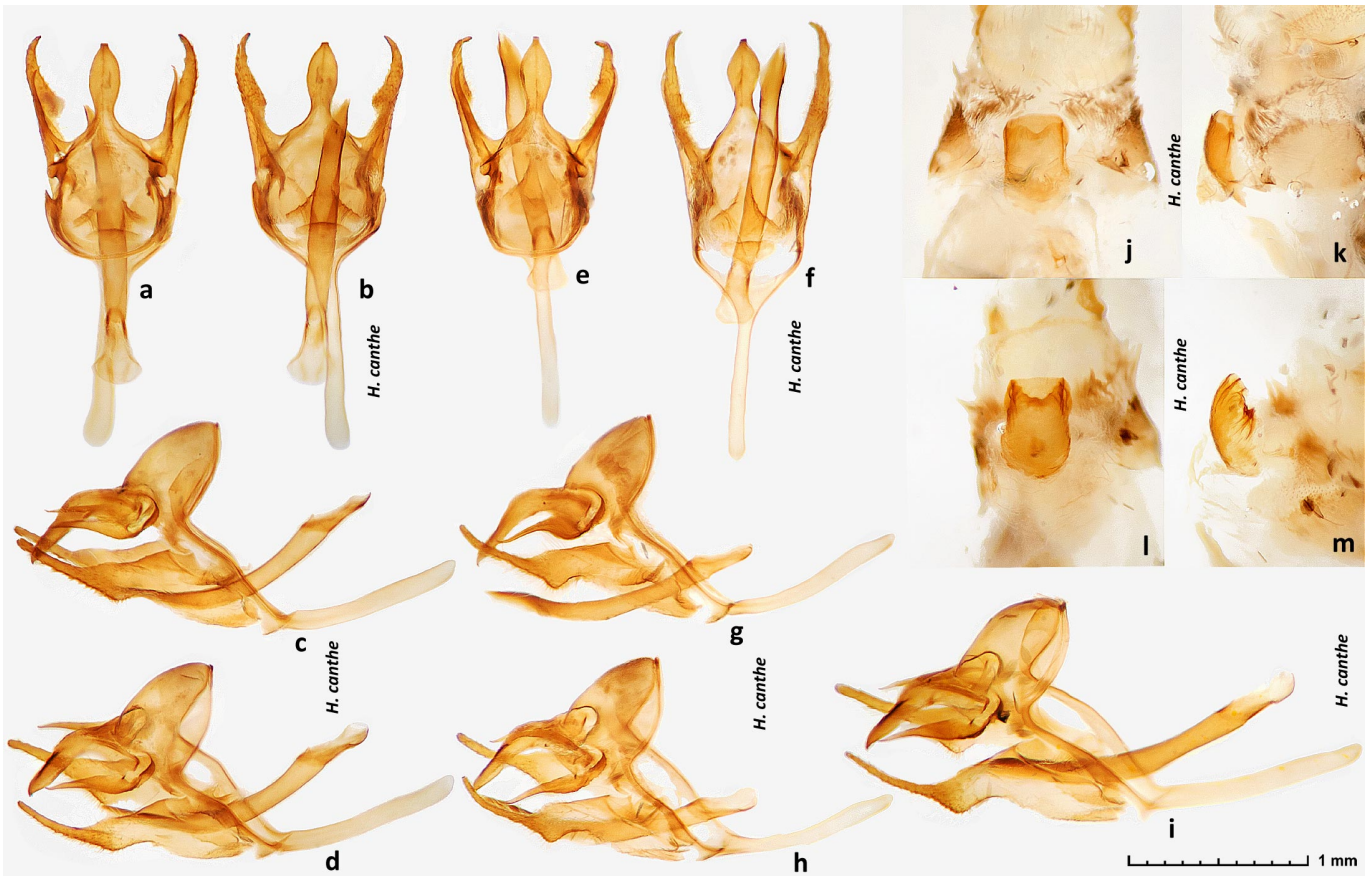


Fig. 35. Genitalia of *Hermeuptychia canthe*. a–d. ♂, Bolivia: Beni, 40 km E San Borja, Estacion Biologica Beni, Palm Camp at Rio Curiraba, 9-15-Sep-1987, malaise trap in inundation forest, leg. W. E. Steiner & M. G. Pogue, BIOLAT/LEPI 000002406, DNA sample NVG-2633, genitalia NVG140628-01; e–h. ♂, ibid, BIOLAT/LEPI 000002432, DNA sample NVG-2635, genitalia NVG140628-03 [USNM]; i. ♂, Peru: Madre de Dios, Amazonia Lodge, Atalaya, 491 m, 25-Sep-2011, leg. Steve Kinyon, #1907, DNA sample NVG-2649, genitalia NVG140628-17 (specimen Figs. 21–22); j, k. ♀, Suriname: Commewijne De Nieuwe Grond, secondary forest, 2-Jun-1982, leg. Olle Pellmyr, DNA sample NVG-2644, genitalia NVG140628-12 (specimen Figs. 27–28); l, m. ♀, Guyana: Region 9, Kanuku Mts., Nappi Creek, 03° 20.7'N 59° 34.2'W, 500'-1000', 21-Feb-10-Mar-1999, leg. S. Fratello, R. Hanner, S. Hendricks, R. Williams, USNM ENT 00232265, DNA sample NVG-2675, genitalia NVG140628-43 (specimen Figs. 24–25). All specimens are in USNM. Views: a, e. dorsal; b, f, j, l. ventral; c, g, k, m. lateral; d, h, i. dorsolateral. All images are to scale.

the forewing and 6 eyespots on the hindwing, all approximately the same size; 75.3.6. The neotype is from Suriname: Gelderland, Suriname River, and the syntypes were presumed to be from Suriname (Hemming 1937); 75.3.7. The neotype is in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

Distances between barcodes of species with confidently assigned names and those from morphogroups defined by Seraphim et al. (2014) are illustrated here as a dendrogram (Fig. 36). The neotype of *S. canthe* is a species from morphogroup 10 (Seraphim et al. 2014). In agreement with Vilorio (2021), we consider it to be a valid species, *Hermeuptychia canthe* (Hübner, [1811]). To facilitate recognition of this species, additional sequenced specimens from across its range are shown in Figs. 21–28, and their genitalia are shown in Fig. 35. In addition to its type locality in Suriname, this widely distributed species is recorded from Colombia, Guyana, French Guiana,

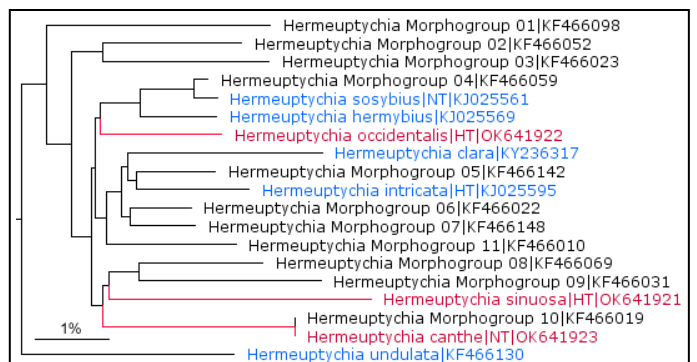


Fig. 36. COI barcode dendrogram constructed using BioNJ (Gascuel 1997) from Jukes-Cantor distances (Jukes and Cantor 1969) computed on the alignment after removal of all positions with gaps. Species names are given (and colored) only when they are determined with confidence. Species sequenced in Seraphim et al. (2014) are named by their morphogroup employed in that work. GenBank accessions are specified. Branches and species names for barcodes obtained in this work are shown in red. NT is neotype and HT is holotype. The dendrogram is rooted with the barcode of *Megisto cymela*|GU088434 (not shown). Due to insufficient phylogenetic signal in barcodes, the dendrogram may not reflect phylogeny and is only shown to illustrate divergence and similarity between barcodes.

Brazil (PA, MT, MG), Ecuador, Peru, and Bolivia, as evidenced by the specimens we studied (Fig. 19–28, 34, 35), the DNA sequence search of the BOLD database queried with the neotype barcode (Ratnasingham and Hebert 2007) and reports in the literature (Seraphim et al. 2014; Tan et al. 2021).

***Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878 is a junior objective synonym of *Ypthimoides acmenis* (Hübner, 1823)**

A number of Satyrini Boisduval, [1833] species have a dry season form, in which patterns of eyespots and stripes are much reduced to nearly absent, and the ventral side is paler, of mottled appearance (Freitas et al. 2010; Freitas et al. 2021). Similar to that, the original illustration of *Megisto acmenis* Hübner, 1823 (type locality "Baltimore") reveals "not the slightest trace of any eyespots" on the ventral side of its wings (Hübner 1823) (Fig. 37a). Type specimens of this species have not been located and its type locality is likely erroneous (Scudder 1875; Weymer 1910-1912) leading to confusion about this taxon. For instance, there is a *Hermeuptychia* specimen of unknown provenance in BMNH labeled "acmenis" and illustrated in D'Abrera (1988). This *Hermeuptychia* specimen, representing a rather extreme example of the dry season form or aberration, cannot be confidently identified to species without dissection or DNA sequencing, because many *Hermeuptychia* species are similar to this form. The status of *M. acmenis* and the *Hermeuptychia* "acmenis" specimen were discussed in detail by Vilorio (2021), who concluded that *M. acmenis* belongs to *Hermeuptychia* based on this specimen and wing shape similarity of the illustrated *M. acmenis* type(s) and *Hermeuptychia*. However, the progression of ventral wing pattern deterioration in *Hermeuptychia* is inconsistent with that of *M. acmenis*. *Hermeuptychia* possesses submarginal wavy lines that are similar in intensity to the two median lines. These lines tend to deteriorate similarly. I.e., if the median lines are expressed clearly (as in the *M. acmenis* illustration), then the submarginal lines are clear as well. If the submarginal lines are obsolete, then the median lines are obsolete too (as in the *Hermeuptychia* "acmenis" specimen).

A more detailed analysis of the *Hermeuptychia* "acmenis" specimen reveals that its wing patterns on the ventral side and size do not agree with the original description and illustration of *M. acmenis*. In particular, in this specimen: (1) both hindwings have clearly defined traces of eyespots: small brown spots in cells CuA₁-CuA₂ (larger) and RS-M₁ (smaller), but the description states: "von Augenpunkten nicht die geringste Spur", i.e., not the slightest trace of any eyespots (Hübner 1823: 11); (2) the hindwings are rather uniform in color and median lines are not visible: only a slightly paler diffuse postmedian band stands out from the brown background, vs. two prominent median lines outlining a darker area between them in the illustration of *M. acmenis*; (3) the forewing has a long dash along the distal end of discal cell, but the illustration shows a very short mark in that area; (4) the ventral side of the wings is of less mottled appearance than shown in the illustration; (5) the forewing length is <17 mm, but the illustration depicts a larger specimen, as extrapolated from the comparison with *Adelpha plesaura* Hübner, 1823 illustrated on the same plate (likely to scale): the forewing length is expected to be 18 mm or more. Moreover, the original description of *M. acmenis* states: "Mit *M. Euridice* hat sie viel ähnliches" (With *M. Euridice* has much in common), and *Lethe eurydice* (Linnaeus, 1763) is larger than most *Hermeuptychia*. Therefore, at the very least, this *Hermeuptychia* "acmenis" is not the specimen illustrated in the original description, not a syntype, and probably not *M. acmenis* at all.

To prepare for a more detailed genomic study of *Hermeuptychia*, we investigated *M. acmenis* further. If Baltimore was the correct locality, the only somewhat similar species that may reach this latitude is *Cyllopsis gemma* (Hübner, 1818). The similarity is in the placement and shape of lines and, in particular, in the degree of mottling and color gamut. However, if *M. acmenis* were *C. gemma*, it would have been an unusual aberration that totally lost the ventral hindwing submarginal patch of "spider-eye" spots. We have not seen such an aberration, although some of the more southern *Cyllopsis* R. Felder, 1869 species do experience deterioration of eyespots, e.g., *Cyllopsis pyracmon* (Butler, 1867).



Fig. 37. *Megisto acmenis*. a. Original illustration of *Megisto acmenis* from Hübner (1823) and individuals of *Ypthimoides celmis* that are similar to it: b. from Brazil: Paraná, Tapejara photographed by Tiago Barbosa in June 2019 ([CC BY-NC](#), Barbosa 2019); c, d. from Buenos Aires area in Argentina photographed by Holger Braun on 13 October 2019 ([CC BY](#), Braun 2019); d. shows its enlarged hindwing submarginal area that is essentially unspotted: "von Augenpunkten nicht die geringste Spur". The images are rotated, cropped, b. flipped, and c, d. color-corrected compared to the originals.

Weymer (1910-1912) likened *M. acmenis* to *Cissia phronius* (Godart, [1824]), which in size is more similar to *L. eurydice*, and larger than *Hermeuptychia*, in agreement with our *M. acmenis* size estimates from the original illustrations (Hübner 1823). As Weymer noted, darker dots in the median lines of *C. phronius* are absent in *M. acmenis*, therefore the two are distinct species and should be kept as such. Moreover, wingshape of *C. phronius* is different: the forewing is elongated and the hindwing has crenulate margins. Dry season forms of *Emeryus difficilis* (Forster, 1964) are known to possess similar hindwing pattern to that of *M. acmenis* and essentially lack the eyespots (Zacca et al. 2020). However, *E. difficilis* is larger (forewing ~21 mm), has well-expressed submarginal lines on the dorsal surface of the wings, and its hindwing outer margin is crenulate. These characters are not consistent with the original illustration of *M. acmenis*.

Out of all Satyrini worldwide, the only species known to us that may have the following combination of characters: mottled appearance of wings' ventral side, with two median lines, darker between them and paler just outside this darker median band framed by the two lines, with a small dash at the end of the forewing discal cell, and lacking essentially any spots in the postmedian areas of both wings, is *Ypthimoides celmis* (Godart, [1824]). Such dry season specimens look rather similar to the original illustration of *M. acmenis*. For instance, a butterfly photographed in Brazil: Paraná, Tapejara and shown on the iNaturalist website (Barbosa 2019) (Fig. 37b) comes particularly close to *M. acmenis*. Moreover, an individual from Argentina: Buenos Aires Province, Parque Pereyra (Braun 2019) (Fig. 37c, d) is entirely missing "a trace of any eyespots".

The only notable discrepancy is that the hindwing darker discal band is more strongly curved towards the anal margin in the *M. acmenis* illustrated by Hübner (1823) than in *Y. celmis*. However, the same discrepancy is also present in the *Hermeuptychia* "acmenis" specimen in BMNH: traces of median lines are not convex thus differing from the original illustration. This illustrated curvature, also mentioned by Weymer (1910-1912), is reminiscent of some species of *Erebia* Dalman, 1816 and *Oeneis* Hübner, [1819], but none of these species fits other features of the *M. acmenis* pattern. The closest might be *Erebia fasciata* A. Butler, 1868, but it has at least some red-toned areas on the forewing, and the submarginal dark area on both wings below is more clearly defined than the *M. acmenis* illustration shows. Thus, we hypothesize that the strongly curved band may have been an atypical feature of the illustrated specimen or an artistic interpretation, and agree with Lamas (2004) who placed *M. acmenis* in *Ypthimoides* Forster, 1964. One of the most commonly encountered species, *Ypthimoides celmis*, is found in southeastern South America. A number of species described in the same publication with *M. acmenis* come from South Brazil, and at least one from Argentina, so it is possible that *M. acmenis* was also collected in that region and mislabeled "Baltimore" at some point (Hübner 1823).

Although as documented in the literature, most of Hübner types were likely lost (Hemming 1937; Calhoun 2018), N.V.G. searched for possible *M. acmenis* syntypes in the collections of the Muséum National d'Histoire Naturelle, Paris, France (MNHP), the Natural History Museum, London, UK (BMNH) and the Museum für Naturkunde, Berlin, Germany (ZMHB). These searches were unsuccessful, leading us to believe that the syntypes are no longer extant, and we proceeded with the neotype designation. There is an exceptional need to designate the neotype of *M. acmenis*, because the identity of this species and its type locality have been unclear, and it was confused with *Hermeuptychia* in collections and publications (D'Abrera 1988; Vilorio 2021). To proceed with a meaningful integrative revision of *Hermeuptychia*, it is essential to have *M. acmenis* defined objectively and in agreement with the original description and original illustrations. Our investigations show that populations currently assigned to *Y. celmis* from around Buenos Aires (Argentina) agree with what is known about *M. acmenis* (Fig. 37). Therefore, we decided to select a specimen from these populations as the neotype of *M. acmenis*. The specimens with reduced or lacking eyespots from the region have been named *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878, which is characterized in the original description as "a remarkable variation ... almost without eyes" (Burmeister 1878). To simplify the synonymy, we hereby designate the specimen curated as the lectotype of *Euptychia celmis* var. *bonaërensis* Burmeister, 1878, illustrated in Warren et al. (2016), as the **neotype of *Megisto acmenis* Hübner, 1823**. Its forewing length is about 18 mm, which is in agreement with the size estimated from the original illustration of *M. acmenis*.

Our neotype of *M. acmenis* satisfies all the requirements set forth by the ICZN Article 75.3. Namely: 75.3.1. It is designated to clarify the taxonomic identity of *Megisto acmenis* Hübner, 1823, which remained undefined until now, impeding future research; 75.3.2. The characters that differentiate this taxon have been given in its original description by Hübner (1823: 11): "It has much in common with *M. Euridice* [sic!], but not the slightest trace of any eyespots" and can be further gleaned from the original illustration: brown unspotted wings above, and below paler yellow-brown, mottled in appearance, with a slightly darker broad discal band spanning both wings and outlined by even darker lines on both sides, paler just outside the band and devoid of eyespots; 75.3.3. The neotype specimen is a male, which is also a **lectotype of *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878** hereby designated by Gerardo Lamas, that bears the following 5 labels: [Buen. | Aires], [Typus.], [bonaërensis | Burm.], [Col. | Antigua], and [lectotype ♂ | *Euptychia celmis* var. | bonaerensis Burm. | 1878 | G. Lamas det. '92]. The following red rectangular label will be mailed to the curators of the collection to add to this specimen: [NEOTYPE ♂ | *Megisto acmenis* | Hübner, 1823 | designated by Barbosa | Freitas and Grishin]. This specimen was one of the two syntypes of *E. celmis* var. *bonaërensis*, both males with the same data in the same collection (see below), and is designated as the lectotype of that taxon to enhance the stability of nomenclature; 75.3.4. Our search for the syntypes is described above, and it was unsuccessful, leading us to believe that they are no longer extant; 75.3.5. The neotype is consistent with what is known about this taxon, in particular with the original illustration and description as detailed above; 75.3.6. The neotype is from Buenos Aires (Argentina), and the type material was stated to be from "Baltimore", which is likely erroneous, because no similar species have been found in eastern North America (Scudder 1875; Weymer 1910-1912), but both localities start with the letter B, suggesting a number of speculations. The specimen(s) on which Hübner based his description and illustrations of *M. acmenis* was/were given to him by a certain "Herr Berg", of whom nothing else appears to be known, except that other species forwarded by him to Hübner were supposedly obtained in Uruguay, Paraguay and Brazil, and only one other species (a crambid moth) was labeled "Baltimore" though it appears to be widespread, found from the USA south to at least Brazil; 75.3.7. The neotype is in the collection of the Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina [MACN].

Lamas (2004) lists *Ypthimoides acmenis* (Hübner, 1823) as a distinct species, and *Euptychia celmis* var. *bonaërensis* [sic] Burmeister, 1878 as a synonym of *Ypthimoides celmis* (Godart, [1824]). We have not investigated this synonymy, but if it holds, then due to objective synonymy established here by the neotype designation of *M. acmenis*, *Y. celmis* would become a junior subjective synonym of *Y. acmenis*. For now, we simply transfer *E. celmis* var. *bonaërensis* [sic] from *Y. celmis* to *Y. acmenis*,

keeping both *Ypthimoides* species as valid, to follow Lamas (2004). Furthermore, *Euptychia celmis* ab. "inocellata" Köhler, 1935 (an infrasubspecific name) and *Epinephele euptychioides* Köhler, 1939, both from Argentina, may also belong to *Y. acmenis* and/or *celmis*, but this possibility has not been investigated further.

***Satyrus cantheus* Godart, [1824] is a junior subjective synonym of *Hermeuptychia sosybius* (Fabricius, 1793)**

As detailed by Cardé et al. (1970) and further elaborated by Viloría (2021), Godart ([1824]) divided the Fabrician concept of *Papilio canthus* Linnaeus, 1767 into three species. Two of them are known today as *Lethe eurydice* (Linnaeus, 1763) (type locality USA: Pennsylvania) and *Emeryus argulus* (Godart, [1824]) (type locality Brazil: Pará, Santa Bárbara do Pará). The latter name was proposed in the same work that also coined the name for the third species: *Satyrus cantheus* Godart, [1824], which is a *nomen dubium* (Cardé et al. 1970). Viloría (2021) suggested that one of the two specimens in the Hunterian Collection in Glasgow pinned below the header label "Pap. Canthus / Fabr. pag 64 N^o 288" may have been used as a basis for the description of *S. cantheus*. Viloría discussed only the second specimen (GLAHM:127581, which is a female, not a male), without mentioning the first one (GLAHM: 127580, a male). These two specimens are of different species that are presently placed in different subtribes. The phenotype of this second specimen discussed by Viloría (GLAHM:127581) does not agree with the original description of *S. cantheus*. First, each of its forewings has five obvious eyespots instead of "three small eyespots not very pronounced" per the description. It is apparent, that Godart paid much attention to the number of eyespots and their structure. E. g., he separated *argulus* from *canthus* with *cantheus* (all of which Fabricius combined under *P. canthus* Linnaeus, 1767) by the number of ventral hindwing eyespots: 5 in the former versus 6 in the two latter species; and their structure: with two (not one) pupils in the former species. Second, the 5th eyespot (next to the 6th, which is stated to be at the anal angle [=tornus]) is not the largest: it is 1.2–1.3 times smaller than the 2nd eyespot, measured in longitudinal dimension. Third, the 6th eyespot (the one stated to be by the anal angle) is not the smallest: it is about 1.3 times larger than the 4th one. Fourth, the specimen is about 1.5 times smaller than a typical *L. eurydice*, but Godart's description states that *S. cantheus* [Godart species number 56] "is about the same in size as the previous one", which is the number 55 *P. canthus* Linnaeus, 1767 (a junior objective synonym of *L. eurydice*). For all these reasons, this specimen is not a syntype. Furthermore, this specimen would not define the name *S. cantheus* as intended in the original description to qualify as a neotype.

Fabricius did not propose a new name *canthus* homonymous with *Papilio canthus* Linnaeus, 1767 as suggested by Viloría (2021). This is because Fabricius gave the name *canthus* in the third line of his description and attributed it to the Linnaeus citation, in a manner he did for many other species when giving brief modified descriptions for previously proposed names (Fabricius 1775). Moreover, he repeated this treatment and attribution in subsequent publications, only adding an additional name and citation to it (*Papilio argante* Cramer, 1779) that he considered to refer to the same species (Fabricius 1781-[1782]; Fabricius 1793). No new name currently attributed to Fabricius that we know of referenced an identically spelled name citing a previous author and publication. Therefore, Fabricius either misidentified the Linnaean taxon completely, or expanded it to cover additional phenotypes, and Godart's work points to the latter (Godart [1824]). Moreover, all new names proposed by Fabricius have been thoroughly studied and catalogued in detail by a number of authors, and none mentions *canthus* as a new name. For instance, there is no mention of *canthus* with Fabricius as the author in the comprehensive catalogue by Zimsen (1964). There is no name *canthus* assigned to Fabricius in The Global Lepidoptera Names Index (Beccaloni et al. 2003). Furthermore, Godart ([1824]: 493) did not credit *canthus* to Fabricius, only to Linnaeus, mentioning that "Fabricius combined this butterfly [i.e. *canthus*] with the next [called *cantheus* by Godart]; but it appears to us to be a different species, at least judging from the description that follows" (interpretively translated and comments in brackets are added by us). Because

Fabricius did not propose a new name *canthus*, no name-bearing (i.e., type) specimens of the Fabrician concept of *canthus* are possible by definition: there was no new name to bear.

We agree with Cardé et al. (1970) and Vilorio (2021) that Godart's *S. cantheus* is not a misspelling of *P. canthus*, but is an available name. Our reading of Godart ([1824]) excludes the possibility of a misspelling, because Godart uses "*S. canthus*" for his species no. 55 and "*S. cantheus*" for his species no. 56: the two consecutively numbered species that are expected to have different names, as they do (not one being a misspelling of the other). Miller and Brown (1981) made a mistake in stating that Godart attributed the name *cantheus* to Linnaeus: only the name *canthus* [no. 55] was attributed to Linnaeus, not the name number 56, which cited only Fabricius. Therefore, the conclusion of Miller and Brown about the misspelling is erroneous. Furthermore, Godart used two sets of names throughout his work: French names that were not italicized, employed French words and had accents over letters when appropriate; and Latin names that were italicized, employed Latin or Latinized words and lacked accented letters. For instance, he used "Satyre" as a French name, which would be "Satyr" in English, not the Latin *Satyrus*, and therefore not a genus epithet. With this distinction, only Godart's Latin names would enter zoological nomenclature. For instance, for the species known today as *Neonympha areolatus* (J. E. Smith, 1797) (type locality USA: Georgia, Chatham Co.), Godart's species number 58, he used "Satyre aréolé" as a French name, and "*Satyrus areolatus*" as a Latin name (Godart [1824]). Even more striking an example is "Polyommate W-blanc" for "*Polyommatus W-album*" (Godart [1824]: 648). However, for the majority of species, the second word in the French name matched the species epithet more closely than in these cases. Because of that, the situation with two sets of names may be confusing to a casual reader, but Godart meticulously followed this distinction. Only French names were used in the section of the work giving brief diagnoses (e.g., pp. 460–476) (Godart [1824]). A French name was also used as the title for each species description (e.g., pp. 477–552), immediately following the species number. Latin names were given in the second line of these expanded descriptions, after the French names. Given this distinction between French and Latin names employed by Godart, a deviant spelling "cautheus" [3rd letter "u", not "n"] occurred only once and in the French name (Godart [1824]: 465), not in the Latin name, and therefore is irrelevant to zoological nomenclature. The correct (and only) spelling of this species epithet in Godart's work is "*cantheus*".

Furthermore, because there was no Fabrician name *canthus*, there could be no replacement name for it. Therefore, Godart did not propose a "replacement name", he proposed a new name: *Satyrus cantheus*, and this taxon must have had type specimen(s). Because Godart's description of *S. cantheus* ends with "(Translation of Fabricius)", it is possible that Godart did not inspect any specimens at all, as also suggested by Cardé et al. (1970): "type ... probably never existed", but based his new species entirely on the Fabrician texts. This hypothesis may not be entirely true, because Godart elaborated on the Fabrician description by mentioning the size of his *S. cantheus* (species number 56): "Its size is about the same as the previous one", which was species number 55 *P. canthus* Linnaeus, 1767 (a junior objective synonym of *L. eurydice*) (Godart [1824]). No reference to this size was given in any Fabrician works we studied, and it should have come from some additional knowledge Godart had about the type specimen(s). Whether Godart inspected the actual specimens or not, the name-bearing type currently encompasses a series of all specimens used to constitute Godart's description of *cantheus*, either directly examined by him, or described by Fabricius in those parts of his texts that were cited and translated by Godart as falling under Godart's concept of *cantheus*. Among these specimens, there should be at least one specimen possessing, as per its description, a combination of the following four characters: (1) size approximately as *L. eurydice*; (2) 3 small indistinct ventral forewing eyespots; (3) the 5th ventral hindwing eyespot (counting from the apex) being the largest of the six present, and (4) the 6th spot (by the anal angle) being the smallest. To define the taxon *S. cantheus*, we hereby designate the syntype that has all 4 characters stated above and was found first (with the earliest date and time) in the search for syntypes of *Satyrus cantheus* as the lectotype of *Satyrus cantheus* Godart, [1824]. This designation satisfies the ICZN Code (ICZN 1999). Our lectotype fulfills the definition of the term as a single specimen selected out of syntypes subsequently to the establishment of the name (ICZN Code Glossary). The designation is

individual: it is made for *cantheus* only (Art. 74.3.). We employ the term "lectotype" (Art. 74.7.1.). Our designation contains information sufficient to recognize this single specimen by the characters given as being the first syntype found in the search for syntypes that possesses all these characters (Art. 74.7.2.). The reason for the lectotype designation is to objectively define this taxon by selecting the specimen that actually agrees with the key characters given in the original description of *S. cantheus*, and thus represents this species as intended by Godart, promoting stability of nomenclature.

Next, we searched for the lectotype in collections and databases where the types of Fabricius and Godart could be. In particular, N.V.G. inspected the holdings of the Muséum National d'Histoire Naturelle, Paris, France (MNHP), which are known to have a number of Godart types, some with a characteristic "god." signature on their labels; and looked through the relevant parts of the collections of the Natural History Museum, London, UK (BMNH) and the Museum für Naturkunde, Berlin, Germany (ZMHB). We also extensively searched online databases, including the Natural History Museum of Denmark, University of Copenhagen, Denmark (2021), the Hunterian collections, University of Glasgow, Scotland, UK (2021) and the National Museums of Scotland, Edinburgh, UK (2021). Our searches failed to find the lectotype that also has not been found by previous workers, and therefore we believe it became lost. Hence, we proceed herein with a neotype designation. There is an exceptional need to designate the neotype of *S. cantheus*. Although this name has not been used as valid for over a century and some considered it a misspelling (Miller and Brown 1981), others a *nomen dubium* (Cardé et al. 1970), Viloría (2021) resurrected it and applied it in a manner inconsistent with the original description. To proceed with a meaningful integrative taxonomic revision of *Hermeuptychia*, it is essential to stabilize the identity of *S. cantheus* by a neotype that while being in a reasonable agreement with the original description, minimally disrupts currently used taxonomic arrangement and allows more detailed genomic studies of the neotype. DNA work plays a highly significant role in *Hermeuptychia* studies (Cong and Grishin 2014; Seraphim et al. 2014; Tan et al. 2021). Therefore, the neotype should facilitate DNA-based studies.

First, we agree with Viloría (2021) that *S. cantheus* is most likely a *Hermeuptychia*. Its description is rather similar to the descriptions of other *Hermeuptychia* species by these authors. Second, in agreement with the original type locality ("North America", which nevertheless could have been an error and simply carried by default from *P. canthus*, which is *L. eurydice*), we aim to select a neotype from North America. North American *Hermeuptychia* are typically decisively smaller than *L. eurydice*, and the largest populations are known from the southeastern USA, which is also a general area that contributed type specimens for many early butterfly names. Therefore, we looked for a southeastern USA *Hermeuptychia* specimen that matches best the original description of *S. cantheus*. The specimen that we hereby designate as the **neotype of *Satyris cantheus* Godart, [1824]** is the male pictured in Figs. 31, 32. It largely agrees with the original description: immaculate brown on dorsal side; ventral side paler, with 2 brownish lines on both wings, 3 not very large eyespots on the forewing, 6 on the hindwing, out of which the 5th is large and the 6th by the anal angle is smaller. The discrepancies with the original description are: the 5th eyespot is the same size as the 2nd eyespot (not larger); the 6th eyespot, while being small, is larger than the 1st (not the smallest); and this being large for a USA *Hermeuptychia* specimen (FW length 17 mm) is still smaller than a typical *L. eurydice*. However, due to significant variation in *Hermeuptychia* eyespots, we were satisfied with the reasonable match to the description, and did not invest additional effort into looking for a perfect match. Additional advantage of this specimen is the availability of DNA sequences.

Our neotype of *S. cantheus* satisfies all the requirements set forth by the ICZN Article 75.3. Namely: 75.3.1. It is designated to clarify the taxonomic identity of *Satyris cantheus* Godart, [1824], which remained undefined until now, impeding research on *Hermeuptychia*; 75.3.2. The characters that differentiate this taxon have been given in its original description by Godart ([1824]: 465, 493–494), i.e., wings brown on dorsal side, ventral side paler, with two ferruginous lines spanning both wings, forewing with three weakly defined eyespots and hindwing with six; 75.3.3. The neotype specimen is a male that bears the following six rectangular labels: [St. Petersburg, Fla. | XI-3-1938], [H. E. Wilford | collector], [96], [Ernest Shoemaker | Collection 1956], [DNA sample ID: | 11-BOA-15609E04 | c/o Nick V.

Grishin], and [NEOTYPE ♂ | *Satyrus cantheus* | Godart, [1824] | designated by Grishin] and its partial COI barcode sequence has been deposited in GenBank with accession KJ025563 (Cong and Grishin 2014); 75.3.4. Our search for the lectotype is described above, but it was unsuccessful, leading us to believe that the lectotype is no longer extant; 75.3.5. The neotype is consistent with what is known about this taxon, in particular with the original description: e.g. ventrally, it has 3 less prominent eyespots on the forewings and 6 eyespots on the hindwings, the 5th of which is large and the one by the anal angle is small; 75.3.6. The neotype is from USA: Florida: Pinellas Co., St. Petersburg, and the lectotype was stated to be from North America with no other details given about the locality; 75.3.7. The neotype is in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM).

The neotype of *S. cantheus* is the species known today as *Hermeuptychia sosybius* (Fabricius, 1793) (Cong and Grishin 2014): it has patches of darker androconia on the dorsal surface of the wings and its COI barcode sequence is identical to that of the *H. sosybius* neotype. Therefore, *Satyrus cantheus* Godart, [1824] is a junior subjective synonym of *Hermeuptychia sosybius* (Fabricius, 1793).

Papilio camerta* Cramer, 1780 is a *nomen dubium

Only the ventral side is illustrated in the original description of *Papilio camerta* Cramer, 1780 (type locality Suriname). The wings exhibit 2 median lines, 3 marginal lines, and small and similarly-sized submarginal dark eyespots: 4 on the forewing (no eyespot in cell R₅-M₁ by the apex) and 6 on the hindwing, each encircled with yellow and pupillated with silvery-blue. We also inspected and photographed the original drawing of *P. camerta* by G. W. Lambertz in the Library of the Natural History Museum, London, that served as a model for published engravings (Gilbert 2000). The Lambertz drawings, which are usually more accurate than stylized engravings, could help identify the species illustrated. Indeed, the Lambertz drawing of *P. camerta* reveals differences between the eyespots in this specimen: all forewing eyespots and the 4th eyespot on the hindwing (in cell M₃-CuA₁) are brown, others are black.

The ventral wing pattern combined with small size (forewing length 17 mm on the drawing) suggest that *P. camerta* may indeed be a *Hermeuptychia* species as currently placed (Lamas 2004). However, there is no dark dash at the end of the ventral forewing discal cell, and the description clearly mentions an eyespot (encircled yellow and pupillated with a silvery dot) on the dorsal forewing "extremities" (Cramer 1780). We know of no species worldwide that match the *P. camerta* description together with the Lambertz illustration. Similarly to Weymer (1910-1912), we cannot explain the dorsal forewing eyespot mentioned in the original description, and for this reason place ***Papilio camerta* Cramer, 1780** as a ***nomen dubium*** until a meaningful explanation can be found.

Assuming a number of inaccuracies, we can offer a hypothesis about the identity of *P. camerta*. Silver pupils in some eyespots on the Lambertz drawing are not round but irregular, and seemingly made by more than one stroke of a brush (they are rounder on the engraving though) (Fig. 38). It is unclear whether this is an imperfection of the drawing, or it meant to depict bipupillated eyespots. If the eyespots were bipupillated, then this species could have been *Paryphthimoides poltys* (Prittwitz, 1865) or a relative, and the dorsal eyespot might have been on the "extremities" of the hindwings (not forewings: a possible mistake in the description), as in *Paryphthimoides* Forster, 1964. In some specimens of *P. poltys*, the differences between eyespots agree with the Lambertz illustration: the forewing eyespots and the 4th hindwing eyespot are more brown than black, and the dashes at the end of the discal cells are vestigial on both wings. Thus, if "tippen" (Dutch) / "extrémités" (French) meant anal angle, forewing was a *lapsus calami* for hindwing, and with irregular silvery-blue dots in the eyespots Lambertz was depicting bipupillation, then *P. camerta* may be conspecific with *P. poltys*. Alternatively, is it conceivable that the dorsal eyespot mentioned in the description may have been on a specimen of a different species than the one illustrated by Lambertz, making the type series polytypic. These issues remain to be investigated and

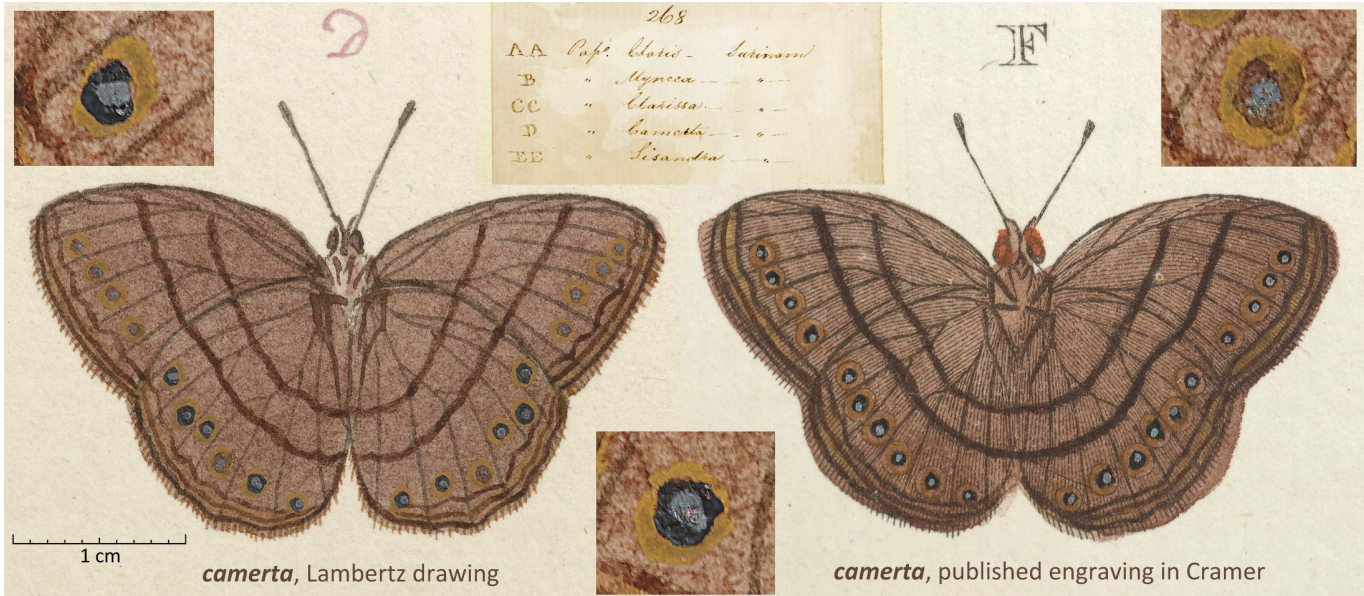


Image of the original description, pp. 10-11

Fig. F. *Camerta*. Is ook eene Surinaamsch Kapelletje, 't welk de bovenzijde der vleugelen effen bruin heeft. Aan de tippen der voorsten is een klein oogswys vlakje geplaatst in een geelen ring, in 't midden van 't zelve een zilverglanzig stipje. Met diergelyke stipjes zyn mede de twintig zogenaamde oogjes op de onderzijde gefiert.

Fig. G. H. *Lisandra*. Dit Kapelletje is uit China afkomstig, en beruist nevens alle op deze Plaat afgebeelde Kapellen in de Verzameling van den Heer C. Stoll.

Fig. F. *Camerta*. C'est aussi un petit Papillon de Suriname dont le dessus des ailes est d'un brun simple. Vers les extrémités des antérieures se trouve une petite tache ocellée dans un anneau jaune; & au milieu de cette tache se voit un petit point d'un lustre argenté. Les vingt petits yeux semblables, qui se trouvent sur la surface inférieure, sont ornés de pareils points.

Fig. G. H. *Lisandra*. Ce petit Papillon est de la Chine & se trouve avec tous les autres Papillons de cette Plaque, dans la Collection de Mr. C. Stoll.

Word-to-word translation from French

Fig. F. *Camerta*. This's also a small Butterfly from Suriname whose the dorsal of wings is of a brown plain. To the extremities of forewings is located a small spot eye-like in a ring yellow; & in the middle of this spot seen a small dot of a sheen silver. The twenty small eyes similar, which are located on the surface ventral, are decorated with such dots.

Fig. G. H. *Lisandra*. This small Butterfly is from the China & is located with all the other Butterflies from this Plate, in the Collection of Mr. C. Stoll.

Interpretation of the original text

Fig. F. *Camerta*. Is ook eene Surinaamsch Kapelletje, 't welk de bovenzijde der vleugelen effen bruin heeft. Aan de tippen der voorsten is een klein oogswys vlakje geplaatst in een geelen ring, in 't midden van 't zelve een zilverglanzig stipje. Met diergelyke stipjes zyn mede de twintig zogenaamde oogjes op de onderzijde gesiert.

Fig. G. H. *Lisandra*. Dit Kapelletje is uit China afkomstig, en beruist nevens alle op deze Plaat afgebeelde Kapellen in de Verzameling van den Heer C. Stoll.

Fig. F. *Camerta*. C'est aussi un petit Papillon de Suriname dont le dessus des ailes est d'un brun simple. Vers les extrémités des antérieures se trouve une petite tache ocellée dans un anneau jaune; & au milieu de cette tache se voit un petit point d'un lustre argenté. Les vingt petits yeux semblables, qui se trouvent sur la surface inférieure, sont ornés de pareils points.

Fig. G. H. *Lisandra*. Ce petit Papillon est de la Chine & se trouve avec tous les autres Papillons de cette Plaque, dans la Collection de Mr. C. Stoll.

Interpretive translation

Fig. F. *Camerta*. This is also a small butterfly from Suriname, its dorsal surface of wings is plain brown. At the tips of forewings [sic!] there is a small eyespot encircled with yellow; & in the middle of this spot there is a small gleaming silvery pupil. Twenty similar small eyespots, which are on the ventral surface, are decorated with such pupils.

Fig. G. H. *Lisandra*. This small butterfly is from China & like all the other butterflies on this plate, it is in the collection of Mr. C. Stoll.

Weymer 1911
p. 207

E. *camerta* Cr. Above brown. Forewing before the apex with a small eye-spot with yellow ring and silvery pupil. Under surface of the forewing with 4, of the hindwing with 6 similar ocelli of the same size, all with silver pupils, both wings with 2 brown, parallel median lines, curved on the hindwing, and with 3 marginal lines. From Surinam. GODMAN and SALVIN indeed unite this species with *hermes*, *sosybius* and *fallax*, but do not mention in their description the silver-pupilled eye-spot on the upper surface which STOLL distinctly describes in the 4th volume of CRAMER's work. Hence I regard *camerta* as a separate species.

Fig. 38. *Papilio camerta* Cramer, 1780. The original drawing (Lambertz, insets show enlarged right hindwing eyespots, © The Trustees of the Natural History Museum London, used with permission), published engraving and original description (Cramer 1780), its translation, and the text from Weymer (1911).

the best compromise reached. While we are not able to solve the problem of the *P. camerta* identity, to facilitate its eventual resolution, we illustrate the Lambertz drawing, the published engraving, and provide translations of the original description (Fig. 38).

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