

Plate 3. – Scale microstructure (upperside of forewing discal cell). – A: *M. hecuba*; B: *M. amathonte*; C: *M. anaxibia*; D: *M. sulkowskyi*; E: *M. granadensis*; F: *M. rhetenor*; G, H: *M. marcus*; I: *M. polyphemus*; J: *M. epistrophus catenaria*; K: *M. aega*; L: *M. absoloni*.

CONCLUSION

The monophyly of genus *Morpho* is confirmed, as found in the previous study of PENZ & DEVRIES (2002), but contrary to their results, eight of the nine subgenera were recovered as monophyletic. Only subgenus *Cytheritis* was not; it was divided into two well supported but widely separated clades, one of which (originally termed the “*marcus* species group”) we here describe as a new subgenus. The scale microstructure, which produces the iridescence phenomena, provided a stronger phylogenetic signal than the blue color simply coded as such.

Our study provides strong support for the subdivision of *Morpho* into subgenera, and underlines the quality of Le Moults & Réal’s approach, despite the confusion they engendered within subgenus *Iphimedeia* (BLANDIN, 1988). However, due to the great complexity of the wing structure (especially crossvein connections and assessing the concavity of the forewing discal cell apex and wing marginal edge) and to some difficulties in assessing homologies of some wing underside color pattern elements, we were unable to find sufficient characters to resolve deeper relationships among all subgenera. Moreover, relationships between species, and sometime subspecies, generally remained unclear. Therefore, further exploration of morphological, ecological, behavioral and molecular data is needed to strengthen our understanding of relationships among the subgenera.

No molecular phylogeny of *Morpho* has been published but work is in progress. It will probably lead to a better understanding of the evolution of *Morpho* butterflies. Fieldwork must also be undertaken to improve both our knowledge of the morphology, ecology and behavior of the immature stages of these butterflies and the flight behaviors of the adults (including the identification of homologous behavioral sequences). These data will be crucial to future phylogenetic studies.

 APPENDIX 1
 List of characters

Character number style explanations:

N. – used by PENZ & DEVRIES (2002), coding in the present study equivalent.

N. – used by PENZ & DEVRIES (2002), coding for at least one shared taxon changed in the present study.

N. – not used by PENZ & DEVRIES (2002).

IMMATURE STAGES

All characters taken from DEVRIES *et al.* (1985); not rechecked in the present study due to unavailability of material.

1. Egg: cartridge-shaped or spherical (0), hemispherical (1).
2. Vertex: setae erect or semi-erect (0), deflexed forward (1).
3. Labrum: distinctly wider than or longer than wide (0), approximately as long as wide (1).
4. Epipharyngeal setae 1: mesad to or under labral setae L3 (0), distinctly lateral to L3 (1).
5. Stipital and submental setae: smooth (0), barbed (1).

GENERAL MORPHOLOGY

HEAD

6. Eyes: bare (0), hairy (1).
7. Labial palpus: smooth (0), unkempt (1).
8. Labial palpus: mainly brown (0), white (1), orange (2), red scales present (3).
9. Labial palpus red or orange: entirely red or orange (0), with an even narrow white line on the internal edge (1). This white line does not exist on brown palpus.
10. Tuft of white scales on patagium: absent (0), present (1).
11. Tegula: entirely brown (0), with a white spot at base (1), nearly entirely white with brown edges (2).

THORAX

12. Thoracic dorsum: strongly iridescent blue scales absent (0) present (1).

LEGS

13. Male midleg, thin spines on dorsal surface of tarsus: absent (0), present (1).
 14. Male midleg, ventral spines on tarsomere 5: two rows (0), four rows (1).
 15. Male midleg, ventral pulvillar process: pointed (0), blunt (1).
 16. Female foreleg, pretarsal claws: absent or vestigial, single (0), well developed, paired (1). If vestigial, there is only one atrophied claw.
 17. Female foreleg, pulvillus: fused medially (0), not fused medially (1).

FOREWING SHAPE AND STRUCTURE

18. Apex: rounded (0), truncate (1).
 19. Virtual line direct from base to apex: passing over discal cell apical crossveins (0), not (1). The apex is taken as the distal end of vein Rs3. Pl. 2, fig. B.
 20. Crossvein m_{1-2} : conspicuously longer than m_{2-3} (0), shorter (1). The critical value for decision is m_{1-2}/m_{2-3} is 0.8. Pl. 2, fig. D.
 21. Curve of crossvein m_{1-2} : strong ($<130^\circ$) (0), weak ($130-170^\circ$) (1), absent ($>170^\circ$) (2). Pl. 2, fig. D
 22. Origin of vein Rs2: near the intersection of veins Rs3-Rs4 (0), halfway from discal cell (1). In other words, whether the origin is on the proximal or the distal half of the common stem of veins Rs3-Rs4. Pl. 2, fig. A.
 23. Stems of veins Rs3-Rs4 and M1: fused or almost fused (0), distinctly separated (1).

HINDWING SHAPE AND STRUCTURE

24. Discal cell: closed (0), open (1).
 25. Tail appendix on vein M3: present (0), absent (1).
 26. Small tail-like appendix on vein CuA1: absent (0), present (1).
 27. Small tail-like appendix on vein CuA2: absent (0), present (1).
 28. Small tail-like appendix on vein 1A: absent (0) or present (1).
 29. Small tail-like appendices on vein CuA1 and ACu2: rounded (0) or pointed (1).

FOREWING DORSAL COLOR PATTERN

30. Postmarginal spot row: absent (0), present (1). Pl. 2, fig. A, B.
 31. Marginal spot row: absent (0), present (1). Pl. 2, fig. A, B.
 32. Marginal and/or postmarginal spots: white (0), orange (1), blue (2).

FOREWING VENTRAL COLOR PATTERN

33. Color pattern : basal system (BS): absent (0), strongly blurred (1), very distinct (2). Pl. 2, fig. C,D.
 34. Eyespots: simple marks (0), true eyespots (1).

(In the following five characters, no distinction is made between “true eyespots” and simple marks. LEMOULT & RÉAL (1962) considered that the possible external blurred light ring is not included in the eyespot).

35. Eyespot in cell 8: absent (0), present (1).
 36. Eyespot in cell 5: entirely included within space 5 (0), extending into spaces 4 and 6 (1).
 37. Eyespot in cell 2: absent (0), present (1).
 38. Eyespot in cell 3: absent (0), present (1).
 39. Eyespot in cell 4: absent (0), present (1).

HINDWING VENTRAL COLOR PATTERN AND *EYESPOTS*

40. Color of areas in cellular and basal zones: brownish or cream (0), deep orange (1), green (2).
 Definitions of areas and zones follow BLANDIN (2007a), see Pl. 2, fig. H, I, J, L.
 41. Costal cell: brown or tan (0), white (1).
 42. Discal area (DA): absent (0), present (1). Pl. 2, fig. F.
 43. Discal area (DA): quite wide (0), thin (1). Pl. 2, fig. E, F, G.
 44. Discal area (DA): continuous (0), disrupted by veins (1). Pl. 2, fig. E, F, G, K.
 45. Discal Area (DA) external edge: nearly straight and far from edges of eyespots (0), undulating and very close to edges of eyespots (1). Pl. 2, fig. E, F, G.
 46. Subdiscal area (SDA): absent (0), connected to DA in cell 4 or on vein M_3 (1), separated out from DA (2). Pl. 2, fig. F, I, J, L.
 47. Eyespots: simple marks (0), true eyespots (1).
 (In the following five characters, no distinction is made between “true eyespots” and simple marks. LEMOULT & RÉAL (1962) considered that the possible external blurred light ring is not included in the eyespot).
 48. Eyespot in cell 3: present (0), absent (1).

49. Eyespot in cell 4: present (0), absent (1).
 50. Eyespot in cell 5: present (0), absent (1).
 51. Eyespot in cell 1c: absent (0), present (1).
 52. Eyespot in cell 6: entirely included (0), extending into spaces 5 and 7 (1).
 53. Eyespot shape: circular or nearly circular (0), very distorted or oblate (1).
 54. Eyespot in cell 1b: absent (0), present (1).
 55. Supernumerary eyespot in proximal half part of cell 1c: absent (0), present (1). Presence of a supernumerary eyespot results in a double eyespot in this cell.
 56. Eyespot between CuP and Sc: not aligned (0), aligned (1). The eyespot is considered aligned if $170^\circ < \alpha < 180^\circ$. The angle is figured by white lines on Pl. 2, fig. F, I.
 57. Eyespot external ring: absent (0), present even thin (1). Pl. 2, fig. G.
 58. Eyespot internal ring: yellow or yellowish-orange (0), deep orange (1) or red (2). Pl. 2, fig. G.
 59. Eyespot disk: well developed (0), reduced to a thin edging (1), absent (2). Pl. 2, fig. G.
 60. Claret shadow over eyespot disk: absent (0), present (1). Pl. 2, fig. J.
 61. Eyespot pupils: reduced (0), well developed (1), absent (2).
 62. Eyespot pupils: white only (0), white and blue (1). Pl. 2, fig. H.

FOREWING UPPERSIDE SCALES

63. Androconial scale comb on posterior edge of forewing ventral surface: present (0), absent (1).
 64. Androconial patch on vein A1: present (0), absent (1).

CENTRE OF DISCAL CELL

65. Cover scales: pigmented (0), not pigmented (1). Pl. 3, fig. B.
 66. Apex of cover scales: deeply indented (0), nearly smooth and straight (1), concave (2). Pl. 3, fig. L.
 67. Ground scales: pigmented (0), not pigmented (1). In terms of optics, white is not a pigment. The white wings of *Pessonia*, when immersed in a liquid of appropriate refractive index and observed with an optical microscope, appear devoid of pigment.
 68. Apex of ground scales: deeply indented (0), slightly indented (1), nearly smooth and straight (2).

APEX OF DISCAL CELL, JUST BASAL TO CROSSVEINS

69. Cover scales: normal size (0), atrophied (1), overdeveloped (2). Pl. 3, fig. C, L.
 70. Cover scales: not pigmented (0), pigmented (1).
 71. Cover scale shape: nearly rectangular (0), enlarged apically (1), folded (2), semicircular (3). Pl. 3, fig. B, C, H.
 72. Cover scales arrangement over the ground scales: a single-layered coat (0), a uniform multilayered coat (1).
 73. Ground scales: pigmented (0), not pigmented (1).
 74. Thin scales: present (0), absent (1). These scales superficially appear piliform but are actually flattened.

DISCAL CELL BASE

75. Thin scales: absent (0), present (1). Pl. 3, fig. E.

MICROSTRUCTURE OF COVER SCALES, CENTRE OF DISCAL CELL

76. Upperside *lamina*: absent (0), present, with small perforations between the cross-ridges (1), present, with large perforations (2). Pl. 3, fig. I, J.
 77. Ridge construction: comprising many *lamellae* per ridge (0), formed from a single *lamella* along the entire length of the scale (1). Pl. 3, fig. D, F, I.

MICROSTRUCTURE OF GROUND SCALES, CENTRE OF DISCAL CELL

78. Ridge density: low (0), high (1). When the ridge density is low, the underside *lamina* of the scale can be seen between the ridges. Pl. 3, fig. D, I.
 79. Upper *lamella* of ridges: not ending suddenly out-curved (0) ending suddenly curved outward (1). Pl. 3, fig. K.

SEXUAL DIMORPHISM

80. Size dimorphism: male and female equal in size (0), average male wingspan not more than 90% of female wingspan (1).
 81. Color dimorphism: weak (0), strong (1). [Weak dimorphism: blue coloration slightly more spread out on male wing or that one of the two sexes is slightly duller than the other. Strong dimorphism: males and females show major color pattern differences in ventral view, dorsal view or both].

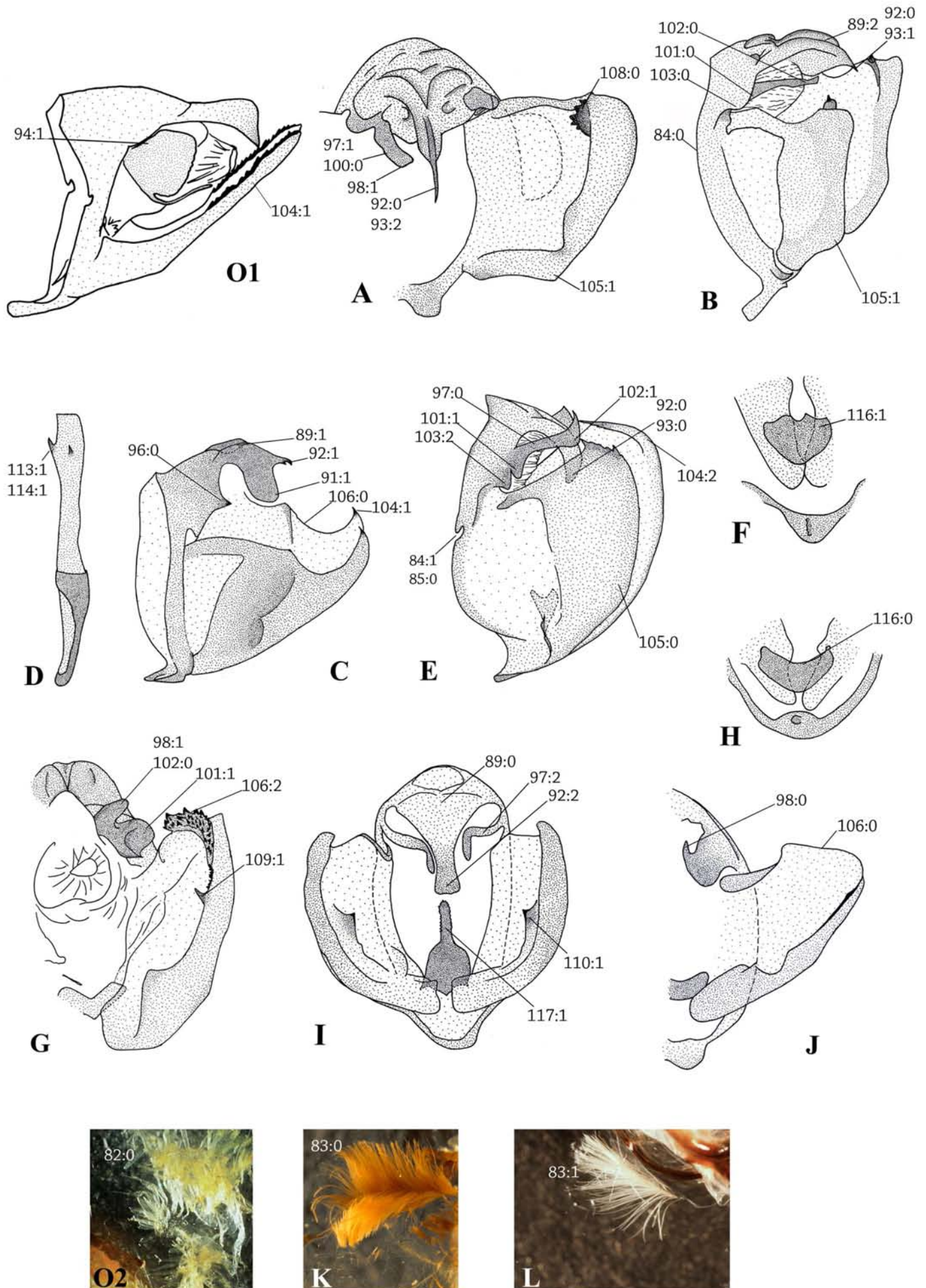


Plate 4. – Male genitalia. – O1, *Caligo ilioneus*, lateral view; – O2, *Antirrhea tomasia*, scale tufts; – A, *M. aurora*, posterior view; – B, *M. absolon*, lateral view; – C, *M. portis*, lateral view; – D, G, *M. polyphemus*, phallus and posterior view; – E, *M. helenor*, lateral view; – F, *M. granadensis*, juxta, anterior view; – H, *M. rhetenor*, juxta, anterior view; – I, *M. eugenia*, posterior view; – J, *M. sulkowskyi lympharis*, posterior view; – K, *M. telemachus*, scale tufts; – L, *M. helenor*, setae tufts.

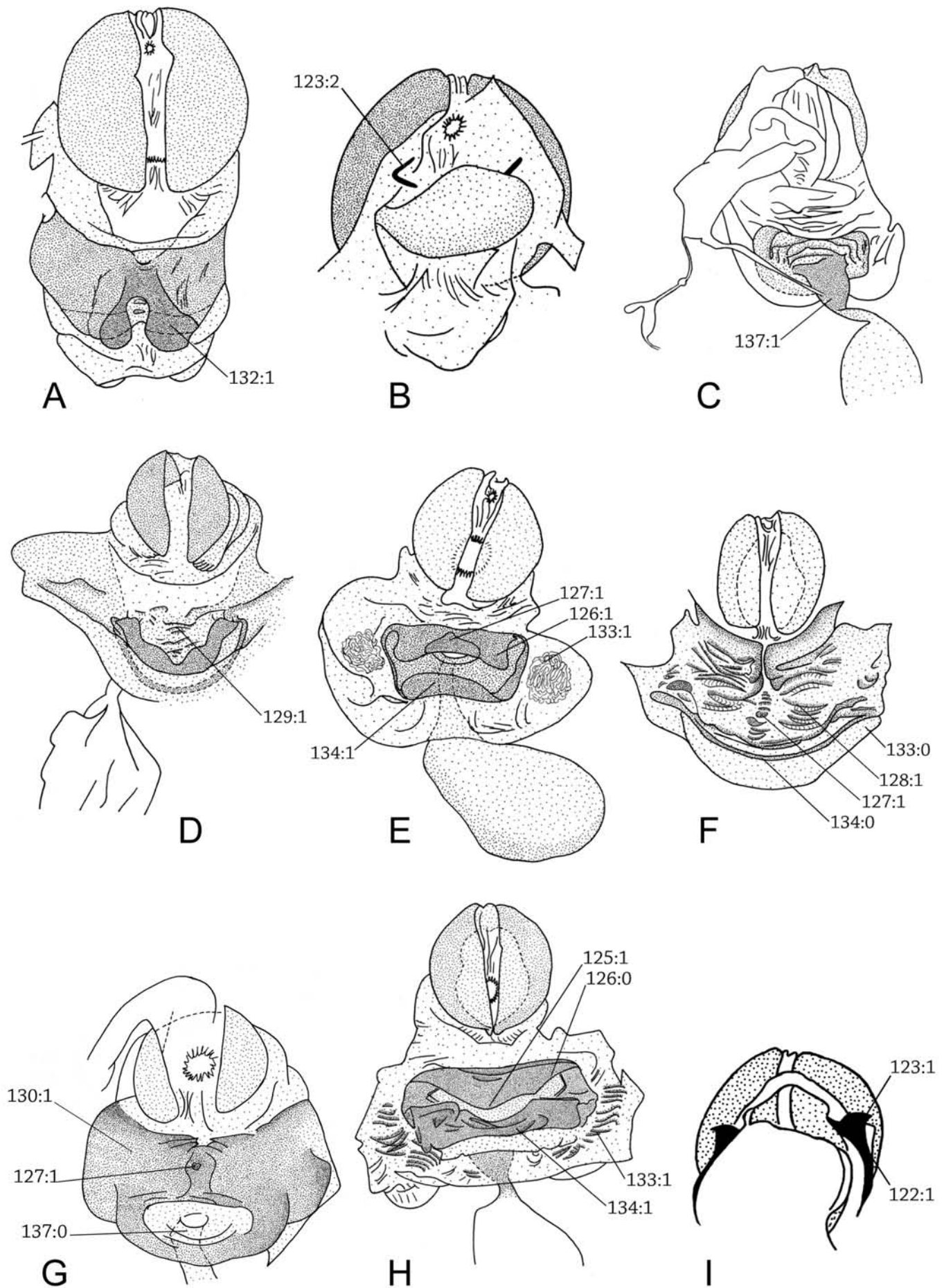


Plate 5. – Female genitalia. – A, B, *M. marcus*, posterior and anterior view respectively; – C, *M. cisseis*, anterior view; – D, *M. Hercules*, posterior view; – E, *M. Achilles*, posterior view; – F, *M. sulkowskyi*, posterior view; – G, *M. portis*, posterior view; – H, *M. deidamia*, posterior view; – I, *M. epistrophus*, anterior view.

MALE GENITALIA

ABDOMINAL SEGMENT IX

82. Vinculum tuft, composition: scales (0), setae (1). Pl. 4, fig. K, L.
 83. Vinculum tuft, scale/seta color: brown (0), white (1). Pl. 4, fig. L, M.
84. Joint between tegumen and vinculum: absent (0), rudimentary (1), well developed (2). Pl. 4, fig. B, E.
 85. Joint between tegumen and vinculum, if well developed: quite wide (0), very narrow (1). Pl. 4, fig. E.
 86. Tuft of setae/scales on tegumen midline: absent (0), present (1).
87. Small dimple on tegumen midline: absent (0), present (1).

UNCUS

88. Uncus length relative to tegumen: at least as long as (0), shorter (1).
 89. Dorsal fissure: absent (0), short (1), ending near the tip of uncus (2). Pl. 4, fig. G, C, I.
 90. Uncus ventral side distally: not expanded (0), expanded (1).
 91. Uncus flattened lateral processes: absent (0), present (1). Pl. 4, fig. C.
92. Tip of uncus: pointed (0), bifid (1), truncate (2). Pl. 4, fig. A, B, E, I.
 93. Uncus tip, if pointed: blunt (0), sharp (1), with a long spine (2). Pl. 4, fig. A, B, E.

GNATHOS

- 94.** Gnathos and tegumen: joined (0), separate (1). Pl. 4, fig. 1.
95. Suture between gnathos and tegumen: absent (0), distinct (1).
96. Gnathos: well developed (0), atrophied (1). Pl. 4, fig. C.
 97. Gnathos: slightly constricted (0), strongly flattened, even forming thin plate (1), stick-shaped (2).
 Pl. 4, fig. A, E, I.
 98. Gnathos: pointed and sharp (0), enlarged and blunt (1). Pl. 4, fig. A, G, J.
 99. Gnathos, in dorsal view: turned outward (0), straight or slightly turned inward (1), strongly curved upward (2).
 100. Small spines on gnathos: absent (0), present (1). Pl. 4, fig. A.
 101. Gnathos basal process: absent (0), present (1). Pl. 4, fig. B, E, G.
 102. Gnathos subterminal basal process: absent (0), present (1). Pl. 4, fig. B, E, G.

VALVA

103. *Appendices angulares*: absent (0), quite developed (1), overdeveloped (2). Pl. 4, fig. B, E.
 104. Apex of valva: pointed (0), very elongate (1), rounded (2). Pl. 4, fig. 01, C, E.
105. Base of valva, in dorsal view: rounded (0), angled (1). Pl. 4, fig. A, B, E.
 106. Ornaments on dorsal edge of valva: absent (0), numerous small, equally-sized spines (1), stronger, more differentiated spines (2). Pl. 4, fig. C, G, E.
 107. Posterior edge of valva: forming a bulge immediately before sclerotized rim (0), without a bulge (1).
108. Inner side of valva, just under dorsal edge: with a large bulge armed with strong spines (0), smooth (1). Pl. 4, fig. A.
109. Strong spine halfway along valva posterior edge: absent (0), present (1). Pl. 4, fig. G.
 110. Isolated strong spine on inner side of valva: absent (0), present (1). Pl. 4, fig. I.
 111. Costa of valva: projected at base (0), not projected (1).
 112. Valva: laterally flattened (0), conspicuously convex (1).

PHALLUS

113. *Carina penis*: absent (0), present (1). Pl. 4, fig. D.
 114. *Carina penis*: on proximal part of *rostellum* (0), near apex (1). This character was not used as such by PENZ & DEVRIES, 2002, but they included an equivalent character referring to the asymmetry of these spines (symmetrical spines are always distally placed). The taxa partition is the same in both studies. Pl. 4, fig. D.
 115. Distal part of *rostellum*: with small lateral processes (0), without (1).

JUXTA

116. Juxta, anterior view: U-shaped, even quite thin (0), large (1). From Pl. 4, fig. F, H.
 117. Juxta posterior margin: without a strong posteriorly directed process (0) with such a process (1).
 Pl. 4, fig. I.

FEMALE GENITALIA

118. *Papilla anales*: dorsally pointed (0), semicircular (1).
 119. *Lamella antevaginalis* and *lamella postvaginalis*: retracted, covered by sternite 8 (0); exposed (1).

120. *Papilla anales* setae: some as long as, or longer than, cross-section of one segment of the *papilla* (0), all setae shorter than cross section of one segment of *papilla* (1).
121. Setae on dorsal portion of *papilla anales*: inserted in long tubercles (0), inserted in short tubercles (1).
122. Sclerotized plate on abdominal segment 10, under *papilla anales*: narrow or atrophied (0), large (1). Pl. 5, fig. I.
123. Posterior apophysis: atrophied (0), small (1), overdeveloped (2). Pl. 5, fig. B, I.

LAMELLA POSTVAGINALIS (POSTERIOR GENITAL PLATE)

124. *Lamella postvaginalis*: smooth (0), bumpy (1), spinose (2).
125. *Lamella postvaginalis*: not developed (0), developed anteriorly (1). Pl. 5, fig. H.
126. *Lamella postvaginalis*: not developed laterally (0), laterally overdeveloped and curved inward (1). Pl. V, fig. E, H.
127. *Lamella postvaginalis* median bump: absent (0), present (1). Pl. 5, fig. E, F, G.
128. Integument of posterior area: not or only slightly wrinkled (0), very strongly wrinkled (1). Pl. 5, fig. F.
129. Supernumerary depression dorsal to *lamella postvaginalis*: absent (0), present (1). Pl. 5, fig. D.
130. Posterior area: at least partially membranous (0), entirely sclerotized (1). Pl. 5, fig. G.
131. Posterolateral area: not wrinkled (0), with widespread wrinkling (1).
132. Two flattened digit-like processes on *lamella postvaginalis*: absent (0), present (1). Pl. 5, fig. A.

LAMELLA ANTEVAGINALIS (ANTERIOR GENITAL PLATE)

133. Integument of anterolateral area: smooth (0), with strong wrinkles (1). Pl. 5, fig. E, F, H.
134. *Lamella antevaginalis*: not developed (0), developed backward (1). Pl. V, fig. E, F, H.
135. Sclerotized plate anterior to sterigma: absent (0), forming a continuous band (1), split at midline (2). In our preparations, these structures were mostly damaged so we used the states given by PENZ & DEVRIES (2002).
136. Separate units of sclerotized plate anterior to sterigma: far apart, not close to midline (0); close together, near midline (1). In our preparations, these structures were mostly damaged so we used the states given by PENZ & DEVRIES (2002).

DUCTUS BURSAE

137. *Antrum*: tubular (0), cone shaped (1). Pl. 5, fig. C, G.
138. *Antrum*: membranous (0), at least partially sclerotized (1). Sclerotization is correlated with integument thickness, so even though sclerotization is altered by heating, its presence can easily be detected.
139. Ductus bursae: long (0), short (1).

CORPUS BURSAE

140. Signa: long (0), short (1).

ECOLOGY AND BEHAVIOR

141. Adult flight: confined mostly to understorey (0), mid-storey (1), canopy (2). Coding of PENZ & DEVRIES, 2002, completed by personal observations.
142. Larval host plant: monocotyledonous (0), dicotyledonous (1).
143. Adult time of activity: crepuscular (0), diurnal (1).
144. Flight style: vigorous fluttering (0), mainly gliding (1).
145. Flight behavior: direct (0), twisting (1). In direct flight, the butterfly flies essentially in a straight line. In twisting flight, it twirls and often deviates up or down, left or right of the main general direction.

Characters of PENZ & DEVRIES, 2002, omitted in this analysis

Numbers are those given by PENZ & DEVRIES, 2002.

12. *Inner side of abdominal tergites 1 and 2, apodeme with longitudinal ribs in a loop: absent (0); present (1).* The abdominal terga were heavily damaged by the treatment with hot potassium hydroxide solution, and were often destroyed in the outgroup specimens, which were old and not very well preserved. Fortunately, the structure was present only in *Antirrhea* sp.
13. *Hairpencils: absent (0); present (1).* Penz & DeVries added that “*Surprisingly, hairpencils were absent in the two dissected M. sulkowskyi males. Both dissected specimens had intact, original abdomens [...]*”. In our *Morpho* sample, hairpencils are always present.

20. *Uncus ventral side: forming sharp lateral ridges (0); rounded (1)*. Adapted from FRUHSTORFER (1913) and LE MOULT & RÉAL (1962). We found we could not reliably distinguish these 2 states.
25. *Gnathos: absent (0); present (1)*. A gnathos is always present in our sample taxa. It was absent in one outgroup taxon used by Penz & DeVries.
34. *Small depressions at the dorsolateral edges of juxta: absent (0); present (1)*. Figure 14N. We noted nothing of note at this position.
40. *Setae on costal margin: absent or few (0); numerous (1)*. We were unable to code significant variation in setal number.
43. *Heavily sclerotized rim at posterior, internal edge of valva: absent (0); present (1)*. Figure 15A and B. This feature did not vary in our sample.
48. *Corpus bursae: elongated (0); nearly rounded (1)*. This is true for two of Penz & DeVries' outgroups, both of which were included in our sample but the states could not be observed because the specimens were heavily damaged during preparation.
49. *Signum: absent (0); present (1)*. This is true for two of Penz & DeVries' outgroups, both of which were included in our sample but the states could not be observed because the specimens were heavily damaged during preparation.
51. *Spines on signum: well developed (0); reduced (1)*. We define "well developed" as 36 μm or larger. It was hypothesized as an apomorphy of *Cytheritis* but we did not observe any difference.
64. *In ventral view, lobes between papilla anales and ostium bursa: membranous (0); sclerotized (1)*. We observed no such sclerotization but would note that most taxa were scored by Penz & DeVries as "?".
68. *FW R1 and R2: reduced at base, connection with radial system inconspicuous (0); not reduced, connection with radial system evident (1)*. We examined this region and could not discern the distinction claimed by Penz & DeVries.
70. *Recurrent vein on FW crossvein m1-m2: absent (0); present (1)*. This vein was present in all our samples, even in for *Antirrhea sp.*, in which genus it was noted as absent by Penz & DeVries.
71. *Recurrent vein at base of FW discal cell, off Cubital system: absent (0); present (1)*. This character did not vary in our samples.
72. *HW M2: with a basal bend (0); devoid of a basal bend (1)*. We did not observe any significant variation.
84. *Male FW dorsal surface, ephemeral androconial patch in cell Cu2: absent (0); present (1)*.
86. *Male HW dorsal androconial patches on R and M veins: absent (0); present (1)*.
87. *Male HW dorsal patch of elongated androconial scales in cell Cu2: absent (0); present (1)*. These characters concern either one or two of the outgroup taxa or are characters separating *Morpho* from the tribe Antirrheina. However, we did not observe these ephemeral androconial patches, nor any traces of them, neither on specimens nor in images.
92. *FW dorsal surface, basal to medial regions dark, contrasting with the rest of the wing at least in one sex (0); not dark (1)*. We could observe no potential phylogenetic signal above the species level and, even then, this character can be variable within species, especially in subgenus *Morpho*.
100. *Male HW ventral surface, ocellus in cell Cu1: basal (0); distal (1)*. Ocelli necessarily aligned if the ocellus in this cell is distal; coding both ocelli alignment and this ocellus position is equivalent to weighting.
108. *Male HW ventral surface, location of ocelli: near distal edge of medial brown band (0); near proximal edge of medial brown band (1)*. We found it difficult to determine what Penz & DeVries understood by the "medial brown band" because the discal and subdiscal areas (DA and SDA, Pl. 1) are absent in some taxa they coded as "1".
114. *Male HW ventral surface, light-colored medial band: straight across wing (0); angled (1)*. We had the same difficulty with this character as we had with #108.
117. *Male HW ventral surface, basal to submedial light-colored banding pattern: absent (0); two to three light bands, complete or incomplete (1); four or more light bands (2)*. After we had established homologies and counted the areas, we found many disagreements and ultimately the character did not appear relevant.

Matrix

	10	20	30	40	50	60	70	80
chorinaeus	11111000?0	000001001?	1?100001?0	100000000?	00?????00?0	0??000????	??00000001	000100????
ilioneus	00000000?0	001000?000	00101000?0	0?0110110?	00?????1010	0?0000?000	0011000001	0000000000
pterocephala	11111000?0	00??0??100	100000?0?0	100000111?	00?????0000	00?000????	??00000001	000000????
tomasia	11111000?0	00?0010000	1000011001	000000010?	00?????1000	000000????	??00000001	000000????
absoloni	10011001?1	1011001000	10111000?0	0?01001100	0110101011	1100001100	0011120200	0001000100
aureola	10011001?1	1011001000	11111000?0	0?21001100	0110121011	1100001000	0011120200	0001000100
aurora	10011001?1	1011001000	11111000?0	0?21001100	0110121011	1100001000	0011120200	0001000100
achillaena	1001110311	1011000000	01011000?1	0001001102	0110101011	1100001001	0011110120	110110????
achilles	1001110??1	1011000001	01111000?1	0001011102	0110101011	1100001001	0011110120	1101100000
anakreon	1001110311	1011000000	01011000?1	0001001102	0110101011	1100001001	0011110120	110110????
coelestis	1001110311	1011000000	?1011000?1	0001001102	0110101011	1100001001	0011110120	110110????
deidamia	10011001?1	1011000000	10011000?1	0021011102	?110021011	1100001001	0011110120	1101100000
electra	10011001?1	1011000000	10011000?1	0021011102	?110021011	1100001001	0011110120	110110????
granadensis	1001110311	1011000000	10111000?1	0001011102	?110021011	1100001101	0011110120	1101100000
helenor	1001110311	1011000000	00011000?1	0001011102	0110101011	1100001001	0011110120	11011000?0
jacki	10011001?1	1011000000	10111000?1	0021011102	?110021011	1100001001	0011110120	110110????
lycanor	1001110311	1011000000	10111000?1	0021011102	?110021011	1100001101	1011110120	110110????
macroptalm	1001110311	1011000000	?0011000?1	0001011102	0110101011	1100001001	0011110120	110110????
maculata	1001110311	1011000000	11011000?1	0001001102	0110101011	1100001001	0011110120	110110????
montezuma	1001110311	1011000000	11011000?1	0001011102	0110101011	1100001001	0011110120	110110????
peleides	1001110311	1011000000	1?011000?1	0001001102	0110101011	1100001001	0011110120	110110????
peleus	1001110311	1011000000	10011000?1	0001011102	0110101011	1100001001	0011110120	110110????
phokylides	1001110??1	1011000000	10011000?1	0001011102	0110101011	1100001001	0011110120	110110????
theodorus	1001110311	1011000000	01011000?1	0001001102	0110101011	1100001001	0011110120	110110????
vitrea	1001110??1	1011000000	11011000?1	0001001102	0110101011	1100001001	0011110120	110110????
anaxibia	10011001?1	1111001000	10111000?0	0?21001110	0100011000	1000001120	0011110200	3001000100
augustinae	1001100311	1011001000	11111000?1	1001001100	01001?1010	1001101100	2011??021?	?00100????
cacica	10011003?1	1011001000	11111000?0	1?01001100	01001?1010	1001101100	2011??021?	?00100????
cypris	1001100311	1011001000	?1111000?0	1?210011?0	?1000?1010	1001101100	1111??021?	?001000101
helena	1001100311	1011001000	?1111000?0	1?01001100	11001?1010	1001101100	2011??021?	?00100????
rhetenor	1001100311	1011001000	?1111000?0	0?01000100	01001?1010	1001101100	2011??021?	?001000101
cisseis	1001100201	101100100?	2011110001	1221011101	1100021011	1110101100	1011000001	0001000000
cisseistricta	1001100201	1011001000	2011110000	1221011101	1100021011	1110101100	1011000001	000100????
hecuba	1001100201	1011001000	2011110001	1121011101	1100021011	1100001100	1011000001	0001000000
obidona	1001100201	1011001001	2011110001	1121011101	1100021011	1100001100	1011000001	000100????
phanodemus	1001100201	1011001000	2011110000	1221011101	1100021011	1110001100	1011000001	000100????
coeruleus	1001110301	1011001010	?1111000?0	0?01001112	0111101011	1000001200	0011110200	000100????
didius	1001110300	1011001010	11111000?0	0?01001112	0111101011	?00001100	0011110100	00010001??
eberti	1001110301	1011001000	11111000?0	0?01001102	011110101?	1000001200	0011110200	000100????
amathonte	1001110301	101100101?	10111000?0	0?01001112	0111101010	1000001000	0011110200	0001000101
godartii	1001110301	1011001010	11111000?0	0?01001112	011110101?	?00001100	0011110200	000100????
julanthiscus	1001110301	1011001011	11111000?0	0?010011?2	0111101011	1000001200	0011110200	000100????
menelaus	1001110301	1011001000	11111000?0	0?01001102	0111101011	1000001200	0011110200	0001000100
occidentalis	1001110301	1011001000	11111000?0	0?01001112	0111101011	1000001200	0011110200	000100????
catenaria	1001100211	2011001000	10011000??	???100110?	1?????1000	100000?000	101101001	00011????1
epistrophus	1001100211	2011001000	10111000??	???100111?	1?????1000	101001?010	0011101001	0001120001
iphitus	1001100211	2011001000	10111000??	???100110?	1?????1000	101001?010	0011101001	0001120001
luna	10011002?1	2011001000	00111000??	???100110?	1?????1010	000000?010	1011101001	00011????1
nikolajevna	1001100??1	2011001000	10111000??	???100110?	1?????1000	100001?010	1011101001	00011????1
polyphemus	1001100211	2011001001	10?11000??	???10?110?	1?????1000	100000?010	1011101001	0001110001
titei	10011002?1	2011001000	00111000??	???100110?	1?????1000	101001?000	?011101001	00011????1
amphitryon	1001100201	1011001001	2011011001	1121001110	0100021011	1000000100	0011000001	0001000000
exsurarion	1001100201	1011001000	2011011001	1111001100	010002101?	100000?100	0011000001	000100????
hercules	1001100200	1011001000	2011011001	1121001110	0100021011	1100000100	0011000001	0001000000
jutama	1001100201	101100100?	2011011011	1111001100	0100021010	1000001100	0011000001	000100????
lilianae	1001100??1	1011001000	2011011001	1121001100	010002101?	100000?100	0011000001	000100????
martini	1001100??1	1011001000	2111011001	1121001100	0100021010	1000001100	0011000001	000100????
niepelti	1001100201	1011001001	2111011011	1111001100	0100021011	1000001100	0011000001	00010?????
oaxacensis	1001100201	1011001001	2111011011	1111001110	0100021010	100000?100	0011000001	000100????
pacificus	1001100201	1011001001	2111011011	1121001100	0100021010	1000000100	0011000001	000100????
telemachus	1001100??1	1011001000	2011011001	1121001110	010002101?	100000?100	0011000001	0001000000
theseus	1001100201	1011001001	2111011011	1121001100	0100021010	1000101100	0011000001	0001000000
aega	1001100201	1011001000	1001101000	0?11000100	0100011011	0000010020	00111?0100	0001000110
eros	1001101201	1011001001	1001101000	0?21001110	?100011001	1110011000	1011101000	0?1100????
eugenia	10011001?0	1011101010	1011101000	0?11001100	?1?0001111	1100011000	1011100100	2101001000
calderoni	1001101201	1011001001	10?1101000	0?21000110	?100011000	1110011000	1011101000	0?1100????
lympharis	1001101201	1011001001	10?1101000	0?21000110	110001100?	1110011000	1011101000	0?1100????
marcus	10011001?0	1011101000	1011101000	0?11001100	?1?0001111	1100011010	1011100100	210100100?
portis	1001101201	1011001001	1001111000	0?110001?0	0100011011	0100011000	1011100000	0001000100
rhodopteron	1001101201	1011001000	1001111000	0?21000100	1100011011	1100011000	10111?0200	0001000100
sulkowskyi	1001101201	1011001001	10?1101000	0?21001110	1100011000	1110011000	1011101000	0?11000100
thamyris	1001101201	1011001001	1001111000	0?21000100	0100011011	0100011000	1011100000	000100????
uraneis	10011001?0	10111010?0	10?1101000	0?11001100	?1?0001111	1100011000	1011100100	210100????
zephyritis	10011001?1	1011001000	1011101000	0?21000100	1100021011	0100011000	1011110200	0001000100

Matrix (continued)

	90	100	110	120	130	140	
chorinaeus	?000??0100	01?010?000	00?0100100	000?1100?1	1??20?????	?0?0??????	0000?
llioneus	00020?0100	001110????	??01110?00	000?100000	01100?1000	0000??100?	00000
pterocephala	1000??0000	00101011?0	0010?10000	000?0000?0	10100?0001	1000??0000	00001
tomasia	1000??0100	0010101?00	?011?10000	000?000???	???0?0????	?0????????	0000?
absoloni	11110??020	0020001100	000010?000	000?100111	11010?0000	0000??0010	?010?
aureola	1111??0020	0020001110	000010?000	000?100111	11010?0000	0000??0?10	?010?
aurora	1111?01020	0020001110	000010?000	000?100111	11010?0000	00001?0010	1010?
achillaena	0112000020	0010101110	1122020100	0010110111	1000111000	0011200010	0110?
Achilles	0112000020	00101011?0	1122020100	0010110111	1001111000	0011200010	0110?
anakreon	01120?0?20	0000101110	1122020100	0010110111	1?01111000	0011??0010	?110?
coelestis	01120??020	0010101110	1122020100	0010110111	1001111000	0011??0010	?110?
deidamia	011200??21	0010101110	1122020100	0010100111	1002100000	0001201110	0110?
electra	01120?0?21	0010101110	1122020100	0010100111	1002100000	00?1??1110	?110?
granadensis	0112000?20	0010101110	1122020100	0010110111	1001110000	0011200010	0110?
Helenor	01120?0020	0010101110	1122020100	0010110111	1001111000	0011??0010	0110?
jacki	01120?0?21	0010101110	1122020100	0010100111	10?2100000	00?1??1110	?110?
lycanor	01120?1?20	0010101110	1122020100	0010110111	1001110000	0011??0?10	?110?
macroptalm	01120?1?20	0000101110	1122020100	0010110111	1001111000	0011??0010	?110?
maculata	01120?1?20	0010101110	1122020100	0010110111	1001111000	0011??0??0	?110?
montezuma	01120?0?20	0000101110	1122020100	0010110111	1001111000	0011??0010	?110?
peleides	0112000?20	0000101110	1122020100	0010110111	1001111000	0011200010	0110?
peleus	01120??020	0000101110	1122020100	0010110111	1001111000	0011??0?10	?110?
phokylides	01120?1?20	0010101110	1122020100	0010110111	100?111000	0011??0010	01101
theodorus	01120?0?20	0010101110	1122020100	0010110111	1001111000	0011??0010	01101
vitrea	01120??020	0010101110	1122020100	0010110111	1000111000	0011??0010	?110?
anaxibia	1100?10?20	0010100120	0012001100	000?100111	10000?0000	0000?0010	211??
augustinae	1111??0111	001000111?	0?12021100	000?100111	1?010??000	0000??001?	?110?
cacica	1111??1111	000000111?	0012010100	000?100111	11010?1000	0000??001?	?110?
cypris	1111?11111	001000111?	0012021100	000?100111	1?010?1000	0000?0010	2110?
helena	1111??0?11	00100011??	001201?100	000?1?0111	11010?1000	0000??0010	2110?
rhetenor	1111?01111	001000110?	0012021100	000?1?0111	10010?0000	0000?0011	21100
cisseis	0102011010	0000000121	000201?100	0010100111	10020?0000	0000201110	2111?
cisseistricta	01020?0010	0000000121	0002010100	0010100111	10020?0000	0000??1110	?111?
hecuba	0102011010	0000000121	0002011100	0010100111	10020?0000	0000?1110	2111?
obidona	01020?1010	0000000121	0002010100	0010100111	10020?0000	0000??1110	?111?
phanodemus	01020??010	0000000121	0?0201?100	0010100111	10020?0000	0000?????0	21110
coeruleus	11020?1020	0010001111	0012011100	000?100111	10010?0000	0000??0010	?110?
didius	1102100120	0010001111	0012010100	000?100111	10010?0000	0000210010	0110?
eberti	1101??0020	0010001111	0012010100	000?100111	10010?0000	0000??0010	?110?
amathonte	1102100120	0010001111	0012010100	000?100111	10010?0000	0000210010	011??
Godartii	1102110120	0010001111	0012010100	000?100111	10010?0000	0000210010	?110?
julanthiscus	110??0?020	0010001111	0012010100	000?100111	10010?0000	0000??0010	11101
menelaus	1101?10020	0010001111	0012011100	000?100111	10010?0000	0000210010	0110?
occidentalis	11021??020	0010001111	0012011100	000?100111	10010?0000	0000??0010	?1101
catenaria	1112100120	0010101110	1?0202?100	0011110111	1001100000	0001201110	111??
epistrophus	0112100120	0010101110	1102021100	0011110111	1001100000	0001201110	?11??
iphitus	01121?0120	0010101110	1112021100	0011110111	1001100000	0001??1010	?11??
luna	11121?0020	0010101110	1102021110	0011100111	1001101000	0000??0110	?11??
nikolajevna	11121?0120	0010001110	1?12021100	0011110111	1001100000	0000??0110	?11??
polyphemus	1112100120	0010101110	1102021110	0011100111	1001101000	0000200110	111??
titei	01121?0120	0010101110	111202?100	0011110111	1001101000	0001??1110	?11??
amphitryon	0100?11011	0000000111	00?2010100	000?100111	10010?0010	0000??0010	211??
exsurarion	0100??1?11	0000000121	00?2010100	000?1?0111	10010?0010	0000??1110	?11??
hercules	0100?11011	0000000121	00?201?100	000?100111	10010?0010	0000?0011	211??
juturna	0100?0011	0000000121	00?2011100	000?110111	10010?0010	0000??010	21110
liliana	0100??0?11	0000000121	00?2010100	000?100111	1??10??010	0000??010	?11??
martini	0100??1?11	0000000121	00?2010100	000?100111	10010?0010	0000??0010	21110
niepelti	0100??1011	0000000121	00?2010100	000?110111	10010?0010	0000??0010	211??
oaxacensis	0100??0?11	0000000121	00?201?100	000?1?0111	10010?0010	0000??0010	?11??
pacificus	0100??1?11	0000000121	00?2011100	000?110111	1??10??010	0000??010	?11??
telemachus	0100?01011	0000000121	00?2010100	000?100111	10010?0010	0000210010	211??
Theseus	0100?01011	0000000121	00?2011100	000?110111	10010?0010	0000??0010	211??
aega	11?0?00011	10100010?0	0000?21100	110?100111	01000?1001	00001?00?0	?010?
eros	11?0??0010	0010001010	00120??100	000?100111	01?10?0100	0000??0010	?010?
eugenia	11??000000	02?0002100	000000?101	010?101111	10220?1000	0100210010	1010?
calderoni	11??0??010	0010?0?11?	00?0??0?100	000?1?0111	01010?0100	0000??0010	?010?
lympharis	11?0??0?10	0010?0?10?	00120??100	000?100111	01010?0100	0000??0010	?010?
marcus	11??000000	02?0002?00	000000?101	010?101111	?0220?1000	0100??1110	1010?
portis	11?0?00011	11?001?1?0	000102?100	010?100111	00100?1001	0000?0010	0010?
rhodopteron	11?0??0010	001000?110	000001?100	000?100111	01100?0000	0000??1110	?010?
sulkowskyi	11?0?10010	001010?110	00020??100	000?100111	01110?0100	0000?0010	?010?
thamyris	11?0??0?11	11?001??00	000102?100	010?100111	00100?1001	0000??0010	0010?
uraneis	11??0??1000	02?0102?00	00?000?101	010?101111	10220?1000	0100??010	?010?
zephyritis	11?0??1120	0010001110	0?0201?100	0?10110111	110010?000	0000??0010	?010?

APPENDIX 2

Description of *Deyrollia* Cassildé & Blandin, n. subgen.

Type species: *Morpho marcus* (Schaller, 1785); other included species: *Morpho eugenia* Deyrolle, 1860.

Diagnosis. – General ventral pulvillar process of male midleg blunt; distal edge of forewings slightly concave; distal edge of hindwings smooth (not even slightly scalloped) but with a small lobe at the end of vein Cu₂; 3 ocelli on ventral surface of forewings generally well developed; 3 ocelli on hindwing ventral surface, positioned on a brown band that is actually the fusion of several bands, from the cellular to the discal; no ocellus in cell 3, that in cell 1c reduced in size.

Scale microstructure on dorsal surface of wings: cover scales folded like an accordion and forming a multi-layered coat over the ground scale layer, each ridge made from a single *lamella* developed lengthwise and not disrupted. Sexual dimorphism very pronounced: male blue, smaller than the brown and very pale yellow female.

Genitalia ♂: valva with isolated strong spine on inner side, tip of uncus truncate, gnathos stick-shaped, juxta with a strong posteriorly projecting process.

Genitalia ♀: two flattened processes on *lamella postvaginalis*.

Etymology. – The subgenus is named in memory of Emile Deyrolle (1838-1917), a French entomologist who described several *Morpho* species in 1860, among which, *M. eugenia*.

Geographical distribution: eastern foothills of the Andes (from Colombia to Bolivia), Amazon Basin (Brazil, Venezuela, Colombia, Ecuador, Peru, Bolivia), the Guiana Shield.

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