

Phylogeny of the genus *Morpho* Fabricius, 1807, revisited (Lepidoptera, Nymphalidae)

by Catherine CASSILDÉ*, Patrick BLANDIN**, Jacques PIERRE*
& Thierry BOURGOIN*

*Muséum national d'Histoire naturelle, département Systématique et Évolution, UMR 7205
<cassilde@mnhn.fr> <jpierre@mnhn.fr> <bourgoin@mnhn.fr>

**Département Hommes-Natures-Sociétés, UMR CNRS/MNHN 7206 <blandin@mnhn.fr>

Summary. – Although the genus *Morpho* Fabricius, 1807, is an important component of the international butterfly trade, it is still poorly understood phylogenetically. The first phylogenetic analysis of the genus, based on morphological characters, was published in 2002, and its results contested the monophyly of three of the nine recognized subgenera, and suggested abandoning the subgeneric classification altogether. The present study re-evaluates the characters used previously, and adds new data derived from the microstructure of the wing scales. In contrast to previous studies, eight of the nine subgenera were recovered as monophyletic. *M. absoloni* was confirmed to be closely related to *M. aurora* within subgenus *Balachowskyna*. Subgenus *Cytheritis* was found to comprise two widely separated monophyletic groups centered on *M. portis* and *M. marcus*. The latter is described as a new subgenus. However, the evolutionary relationships among the subgenera remain poorly supported, except for two clades each composed of two subgenera: (*Morpho*, *Pessonia*) and (*Iphimedeia*, *Laurschwartzia*). We then use this new phylogeny to gain further understanding of the evolution of the famous blue wing coloration of certain *Morpho* species. In particular, we demonstrate that not all blue *Morpho* are blue in the same way.

Résumé. – Quoique les espèces du genre *Morpho* Fabricius, 1807, soient très recherchées par les collectionneurs et activement commercialisées, ce genre reste très mal connu sur le plan phylogénétique. La première analyse phylogénétique basée sur des caractères morphologiques a été publiée en 2002. Ses résultats contestent la monophylie de trois des neuf sous-genres reconnus et suggèrent d'abandonner l'ensemble de la classification subgénérique. La présente étude reprend l'analyse des caractères utilisés et en aborde de nouveaux concernant la microstructure des écailles alaires. Contrairement à la précédente analyse, ce nouveau travail montre que huit des neuf sous-genres sont monophylétiques. *Morpho absoloni* est confirmé comme étant proche parent de *M. aurora* dans le sous-genre *Balachowskyna*. Le sous-genre *Cytheritis* est révélé comme formé de deux groupes bien séparés centrés sur *Morpho portis* and *M. marcus*. Ce dernier est décrit comme un nouveau sous-genre. Cependant les relations évolutives entre les différents sous-genres sont peu soutenues, excepté pour deux clades, chacun composé de deux sous-genres: (*Morpho*, *Pessonia*) et (*Iphimedeia*, *Laurschwartzia*). Nous avons donc utilisé cette nouvelle phylogénie pour obtenir une meilleure compréhension de l'évolution de la fameuse coloration bleue des ailes de certaines espèces de *Morpho*. En particulier, nous démontrons que tous les *Morpho* bleus ne le sont pas de la même façon.

Keywords. – Lepidoptera, Nymphalidae, *Morpho*, phylogeny, subgenus *Balachowskyna*, *Deyrollia*.

For many people the name *Morpho* is immediately evocative of large blue butterflies encountered in Amazonian forests. But the genus *Morpho* Fabricius, 1807, also includes some very different species, such as the giant orange-brown *M. hecuba* (L., 1771) from the Guianas, the small *M. sulkowskyi* Kollar, 1850, with its brilliant transparent mother-of-pearl wings, which flies in the Andean cloud forests, the large white *M. polyphemus* Westwood, [1850], common in Mexican forests, or the black and blue *M. achilles* (L., 1758), the type species of the genus. Evidently, the genus *Morpho* is heterogeneous in colour pattern.

The first comprehensive study of the genus was published by FRUHSTORFER (1912-1913), who listed 30 species, and divided the genus into two species groups: *Iphimedeia* Fruhstorfer and *Morpho*. Fifty years later, LE MOULT & RÉAL (1962, 1963) distinguished 80 species. Using wing venation, male genitalia and wing color pattern, they divided the genus into

eight subgenera: *Iphimedeia* Fruhstorfer (10 species); *Iphixibia* Le Moult & Réal (1 sp.); *Cytheritis* Le Moult & Réal (16 sp.); *Balachowskyina* Le Moult & Réal (2 sp.: in Tome II, Le Moult & Réal indicated that *M. absoloni* is a distinct species belonging to *Balachowskyina*); *Cypritis* Le Moult & Réal, a junior synonym of *Megamede* Hübner, [1819] (6 sp.); *Pessonnia* Le Moult & Réal (5 sp.); *Grasseia* Le Moult & Réal (9 sp.) and *Morpho s. str.* (31 sp.). LE MOULT & RÉAL (1962) considered that subgenus *Cytheritis* was probably the group from which the other subgenera had emerged and they suggested it should be divided into new groups after further study. This represented the first attempt to suggest evolutionary relationships among members of *Morpho*.

Revisiting the systematics of *Morpho*, BLANDIN (1988) followed Le Moult & Réal's subgeneric classification, but created subgenus *Schwartzia*, later named *Laurschwartzia* (BLANDIN, 2007b), for two species previously included in subgenus *Iphimedeia*. BILOTTA (1992, 1994a, b) elevated all the subgenera to genus level, based on the marked morphological variation he observed among seven Brazilian *Morpho* species representing six subgenera.

No modern phylogenetic study of *Morpho* was published until that of PENZ & DEVRIES (2002). The aim of that work was to test explicitly the monophyly of the nine subgenera. They studied a sample of 27 *Morpho* species, used three *Antirrheina* species as outgroups, and defined 118 morphological and 2 ecological and behavioral characters. Although the monophyly of the genus *Morpho* was not challenged, they obtained a consensus tree in which subgenera *Iphimedeia*, *Schwartzia*, *Cypritis* and *Pessonnia* were monophyletic, but *Cytheritis*, *Grasseia* and *Morpho* were paraphyletic.

Based on these results, PENZ & DEVRIES (*l. c.*) rejected the subgeneric classification of *Morpho* butterflies, making all subgenera synonyms of *Morpho*. However, that work involved a relatively small sample of taxa. In this study, we revisit the phylogenetic relationships of genus *Morpho*, studying a more complete sample of species and including additional characters, especially from the genitalia and the microstructure of the scales on the upperside of wings, to bring new arguments to bear on the validity of the subgenera. We also aim to infer the evolution of wing color and certain biological traits within the genus.

MATERIAL AND METHODS

Increasing the support for and/or resolution of a phylogenetic hypothesis usually consists of increasing the number of characters analyzed, the number of taxa included, or both. We therefore added 43 ingroup taxa to the sample studied by PENZ & DEVRIES (2002) and an additional outgroup (Table I). Thus, all *Morpho* species, as recognized by BLANDIN (2007a, c), are included, several represented by more than one subspecies, to gain a better representation of their geographical range. The outgroups comprised three species of *Antirrheina*, the sister-subtribe of *Morphina* (DEVRIES *et al.*, 1985) within the tribe *Morphini*, and one species of *Brassolini*, the sister-tribe of *Morphini* within the subfamily *Morphinae*, according to the most recent higher classification (PEÑA *et al.*, 2006).

To increase objectivity in our search for phylogenetically informative characters, we initially coded characters without reference to PENZ & DEVRIES (2002). Wing characters were observed on males and we use a terminology based on BLANDIN (1988, 2007a; Appendix 1, plates 1 and 2). Scales were observed in discal cell of forewing upperside using a stereo magnifier (up to $\times 64$) for characters related to scale shape and organization, whereas their microstructure was examined with a scanning electronic microscope following gold metallization by cathodic plasma deposition (Appendix 1, plate 3). Presence or absence of pigments, and their density in scales, was determined by transmission photon microscopy. *Morpho* scale terminology and optics were described, richly explained and illustrated by BERTHIER (2007).

Table I. – Taxa sampled.

All specimens are deposited in the general collection and the Laurent Schwartz and Patrick Blandin collections at the Muséum national d'Histoire naturelle, Paris. Ingroup taxa marked with * were also studied by PENZ & DEVRIES (2002).

<u>Outgroups</u>	Subgenus <i>Cypritis</i> Le Moult & Réal, 1962
Brassolini, Brassolina	<i>M. cypris cypris</i> Westwood, 1851*
<i>Caligo ilioneus</i> (Cramer, 1775)	<i>M. rhetenor rhetenor</i> (Cramer, 1775)*
Morphini, Antirrheina	<i>M. rhetenor cacica</i> Staudinger, 1876
<i>Caerois chorinaeus</i> (Fabricius, 1775)	<i>M. rhetenor helena</i> Staudinger, 1890
<i>Antirrhea pterocopa</i> Salvin & Godman, 1868	<i>M. rhetenor augustinae</i> Le Cerf, 1925
<i>Antirrhea tomasia</i> (L., 1758)	Subgenus <i>Pessonnia</i> Le Moult & Réal, 1962
<u>Ingroup: Morphini, Morphina</u>	<i>M. polyphemus polyphemus</i> Westwood, [1850]*
Subgenus <i>Iphimedeia</i> Fruhstorfer, 1912	<i>M. polyphemus luna</i> Butler, 1869
<i>M. hercules hercules</i> (Dalman, 1823)*	<i>M. epistrophus epistrophus</i> (Fabricius, 1796)*
<i>M. theseus theseus</i> Deyrolle, 1860*	<i>M. epistrophus catenaria</i> (Perry, 1811)*
<i>M. theseus aquarius</i> Butler, 1872	<i>M. epistrophus nikolajevna</i> Weber, 1951
<i>M. theseus juturna</i> Butler, 1870	<i>M. iphitus iphitus</i> Felder & Felder, 1867
<i>M. theseus oaxacensis</i> Le Moult & Réal, 1962	<i>M. iphitus titei</i> Le Moult & Réal, 1962
<i>M. niepelti</i> Röber, 1927	Subgenus <i>Iphixibia</i> Le Moult & Réal, 1962
<i>M. telemachus telemachus</i> (L., 1758)*	<i>M. anaxibia</i> (Esper, [1801])*
<i>M. telemachus lilliana</i> Le Moult, 1927	Subgenus <i>Grasseia</i> Le Moult & Réal, 1962
<i>M. telemachus martini</i> Niepelt, 1933	<i>M. menelaus menelaus</i> (L., 1758)*
<i>M. telemachus exsusarion</i> Le Moult & Réal, 1962	<i>M. menelaus coeruleus</i> (Perry, 1810)
<i>M. amphitryon amphitryon</i> Staudinger, 1887*	<i>M. menelaus eberti</i> Fischer, 1962
Subgenus <i>Laurschwartzia</i> Blandin, 2007	<i>M. menelaus occidentalis</i> Felder & Felder, 1862
<i>M. hecuba hecuba</i> (L. 1771)*	<i>M. amathonte</i> Deyrolle, 1860*
<i>M. hecuba obidonus</i> Fruhstorfer, 1905	<i>M. godartii godartii</i> Guérin-Méneville, [1844]*
<i>M. cisseis cisseis</i> Felder & Felder, 1860*	<i>M. godartii didius</i> Hopffer, 1874*
<i>M. cisseis phanodemus</i> Hewitson, 1869	<i>M. godartii julanthiscus</i> Fruhstorfer, 1907
<i>M. cisseis cisseistricta</i> Le Moult & Réal, 1962	Subgenus <i>Morpho</i> Fabricius, 1807
Subgenus <i>Cytheritis</i> Le Moult & Réal, 1962	<i>M. achilles achilles</i> (L., 1758)*
<i>M. marcus marcus</i> (Schaller, 1785)*	<i>M. achilles phokylides</i> Fruhstorfer, 1912
<i>M. eugenia eugenia</i> Deyrolle, 1860*	<i>M. achilles vitrea</i> Butler, 1866
<i>M. eugenia uraneis</i> H. W. Bates, 1865	<i>M. helenor helenor</i> (Cramer, 1776)
<i>M. sulkowskyi sulkowskyi</i> Kollar, 1850*	<i>M. helenor achillaena</i> (Hübner, [1823])*
<i>M. sulkowskyi eros</i> Staudinger, 1892	<i>M. helenor peleides</i> Kollar, 1850*
<i>M. sulkowskyi lympharis</i> Butler, 1873	<i>M. helenor peleus</i> Röber, 1903
<i>M. sulkowskyi calderoni</i> Blandin & Lamas, 2007	<i>M. helenor theodorus</i> Fruhstorfer, 1907
<i>M. zephyritis</i> Butler, 1873	<i>M. helenor coelestis</i> Buttler, 1866
<i>M. portis portis</i> (Hübner, [1821])*	<i>M. helenor anakreon</i> Fruhstorfer, 1910
<i>M. portis thamyris</i> Felder & Felder, 1867	<i>M. helenor maculata</i> Röber, 1903
<i>M. aega aega</i> (Hübner, [1822])*	<i>M. helenor macrophtalmus</i> Fruhstorfer, 1913
<i>M. rhodopteron rhodopteron</i> Godman & Salvin, 1880	<i>M. helenor montezuma</i> Guenéé, 1859
Subgenus <i>Balachowskyina</i> Le Moult & Réal, 1962	<i>M. deidamia deidamia</i> (Hübner, [1819])*
<i>M. aurora aurora</i> Westwood, 1851*	<i>M. deidamia jacki</i> Nield, 2008
<i>M. aurora aureola</i> Fruhstorfer, 1913	<i>M. deidamia electra</i> Röber, 1903
<i>M. absoloni</i> May, 1924	<i>M. granadensis granadensis</i> Felder & Felder, 1867*
	<i>M. granadensis lycanor</i> Fruhstorfer, 1913

The abdomens of *Morpho* specimens are often removed just after the capture, to avoid “greasing” of the wings and unfortunately, they are often discarded or lost. Most specimens included in this analysis were intact but for some species, such specimens were not available. In those cases, we used specimens only when an unambiguous label was pinned with the abdomen, certifying its origin. We dissected at least one male (Appendix 1, plate 4) and one female (App. 1, plate 5) for each taxon. Only one female was available for *Antirrhoea tomasia* and *Caerois chorinaeus*. Both of these specimens were old, very fragile and were badly damaged during dissection. Nevertheless, we could still record most of the characters included in the analysis. We followed KRISTENSEN’S (2003) nomenclature for genitalia.

After our initial character search, we compared our morphological data matrix with that of PENZ & DEVRIES (2002). We evaluated how they treated and defined their characters, and how they were coded for all taxa. We then rechecked our characters and added several more. Among the characters coded by Penz & DeVries, we rejected most of those related to degree of sclerotization because we observed that it can be strongly affected by the length of time the preparations were heated in the aqueous potassium hydroxide solution used for maceration of soft tissues. Instead, we focused on the shapes of the same structures, which are never affected by such treatment. We omitted a further 23 characters that concerned structures we could not identify or recognize (Appendix 1). Our final matrix thus included 140 morphological characters (App. 1), of which 49 were new to this study. Of the remaining 91, which were also used by PENZ & DEVRIES (2002), 62 characters were either coded differently for some taxa (disagreement in observations) or treated differently: in case of conflicting observations, we favored our own character states as they were confirmed by many specimens; some characters were changed from binary to multistate characters and vice versa, depending on the number of states we could effectively observe on the structure (sometimes less, sometimes more than those indicated by Penz & DeVries). Moreover, we took care to code characters in such a way as to avoid redundancy and hence hidden weighting in the matrix. To avoid subjective assessments of color and differences caused by different viewing angles, color of wing upperside was coded only from the microstructure and not as it appears to the naked eye.

We also added the two ecological and behavioral characters used by PENZ & DEVRIES (2002) and three more following a field study of flight behavior using a watchtower in the río Shilcayo valley, near Tarapoto, department San Martín, Peru. Larval host plants are known with certainty for only a small number of *Morpho* butterflies and what is mostly reported is just whether the caterpillars feed on monocotyledonous or dicotyledonous plants. Five larval characters (Appendix 1) and as much data as possible about ecology and behavior were extracted from the literature (FRUHSTORFER, 1912-1913; OTERO, 1966; DEVRIES, 1987; ACKERY *et al.*, 1998; OTERO & MARIGO, 1990; TÁKÁCS & TELLO, 1993, 1994; DEVRIES & MARTINEZ, 1994; CONSTANTINO, 1997; BRÉVIGNON, 2003; MILLER *et al.*, 2007; NEILD, 2008; GUERRA-SERRUDO & LEDEZMA-ARIAS, 2008).

Most parsimonious cladograms (MPCs) and bootstraps values (FELSEINSTEIN, 1985) were found using TNT (GOLOBOFF *et al.*, 2003) by heuristic searching with tree bisection-reconnection (10 addition sequence replications and 10 rounds of branch swapping). As some replicates could overflow because of buffer capacity, many independent analyses were run, as recommended by GOLOBOFF *et al.* (2008), each with a different starting seed, until we found the most parsimonious score ten times. Strict consensus trees were generated from the results of these ten analyses. Two datasets were analyzed. The first comprised only the morphological characters, the second also included the ecological and behavioral characters. In each case, all characters were equally weighted and multistate characters were unordered. Values of Bremer’s Decay Index (BREMER, 1994) were calculated under *TreeRot.v2* (SORENSEN, 1999).

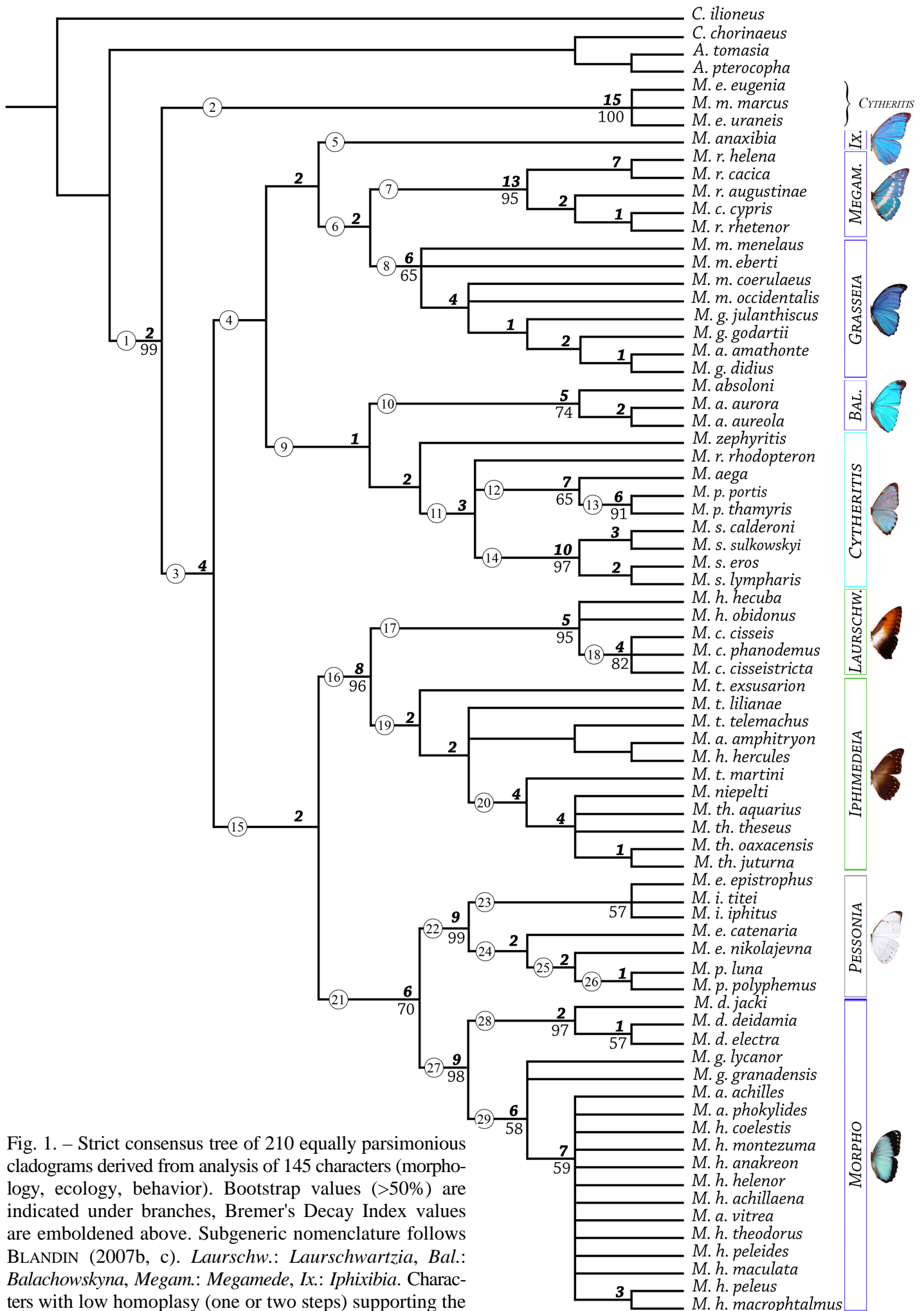


Fig. 1. – Strict consensus tree of 210 equally parsimonious cladograms derived from analysis of 145 characters (morphology, ecology, behavior). Bootstrap values (>50%) are indicated under branches, Bremer's Decay Index values are emboldened above. Subgeneric nomenclature follows BLANDIN (2007b, c). *Laurschw.*: *Laurschwartzia*, *Bal.*: *Balachowskyina*, *Megam.*: *Megamede*, *Ix.*: *Iphixibia*. Characters with low homoplasy (one or two steps) supporting the numbered clades are listed in Table II.

Table II. – List of synapomorphies with one to three steps. Clades are as numbered on fig. 1. Autapomorphies of the clades are emboldened. FW: forewing, HW: hindwing, SC: scales, ♂ and ♀: male and female genitalia.

Clade 1: Genus MORPHO	
8:1 Labial palpus white	6:1 Hairy eyes
10:1 Tuft of white scales on patagium present	40:2 HW: Areas over the cellular and basal zones greenish
11:1 Tegula with a white spot at base	43: 1 HW: Discal area thin
14:1 ♂: Midleg, four rows of ventral spines on tarsomere 5	44:1 HW: Discal area disrupted by veins
17:1 ♀: Foreleg, pulvillus not fused medially	100:1 ♂: Small spines on gnathos present
24:1 HW: Discal cell open	<i>M. didius</i>
42:1 HW: Discal area absent ♂	10:0 No white scales on patagium
65:1 SC: Discal cell cover scales not pigmented	Clade 9: (BALACHOWSKYNA, CYTHERITIS)
70:0 SC: Cover scales not pigmented near crossveins m ₁₋₂	142:0 Larva feeds on monocots
82:1 ♂: Scale tufts attached to vinculum	Clade 10: Subgenus BALACHOWSKYNA
105:0 ♂: Base of valva rounded	43:1 HW: Discal area thin
118:1 ♀: <i>Papilla anales</i> semicircular	66:2 SC: Apex of discal cell cover scales concave
139:1 ♀: Ductus bursae short	83:1 ♂: Tegumen scales white
143:1 Diurnal flight	105:1 ♂: Base of valva making an angle
	108:0 ♂: Valva inner side: spiny bulge present
	<i>M. zephyritis</i>
Clade 2: marcus species group	66:1 SC: Apex of discal cell cover scales nearly smooth and straight
15:1 ♂: Male midleg, ventral pulvillar process blunt	113:1 ♂: <i>Carina penis</i> present
48:1 HW: No eyespot in cell 3	125:1 ♀: <i>Lamella postvaginalis</i> developed forward
71:2 SC: Cover scale folded like an accordion	Clade 11
72:1 SC: Cover scales forming a uniform multi-layered coat	7:1 Labial palpus unkempt
77:1 SC: Each ridge a single <i>lamella</i> developed lengthwise	8:2 Labial palpus orange
92:2 ♂: Apex of uncus truncated	66:0 SC: Apex of cover scales deeply indented
97:2 ♂: Gnathos stick-shaped	89:1 ♂: Dorsal fissure short
110:1 ♂: Presence of one strong spine at inner side of valva	121:0 ♀: <i>Papilla anales</i> setae inserted in long tubercles
112:1 ♂: Valva conspicuously convex	Clade 12: (<i>M. aega</i>, <i>M. portis</i> ssp.)
117:1 ♂: Juxta developing a strong backward process	91:1 ♂: Uncus flattened lateral processes present
132:1 ♀: Flattened processes on <i>lamella postvaginalis</i>	112:1 ♂: Valva conspicuously convex
	130:1 ♂: Posterior area entirely sclerotized
Clade 3	<i>M. aega</i>
89:2 ♂: Dorsal fissure ending near the apex of uncus	7:0 Labial palpus smooth
142:1 Larval host plant: dicots	8:0 ♀: Foreleg, pulvillus fused medially
	79:1 SC: Upper <i>lamella</i> of ridges ending curved outward
Clade 4	98:0 ♂: Gnathos pointed and sharp
66:1 SC: Apex of cover scales nearly smooth and straight	111:1 ♂: Costa of valva projected at base
78:1 SC: Discal cell ground scales: high ridge density	Clade 13: <i>M. portis</i> ssp.
Clade 5: Subgenus IPHIXIBIA	92:1 ♂: Apex of uncus bifid
12:1 Strongly iridescent blue scales on thorax	96:1 ♂: Gnathos atrophied
71:3 SC: Semicircular cover scales	Clade 14: <i>M. sulkowskyi</i> ssp.
97:0 ♂: Gnathos slightly constricted	53:1 HW: Eyespots very distorted or oblate
Clade 6: (MEGAMEDE, GRASSEIA)	67:1 SC: Basal scales not pigmented in discal cell
8:3 Red scales on labial palpus	73:1 SC: Basal scales not pigmented around m ₁₋₂ , m ₂₋₃
Clade 7: Subgenus MEGAMEDE	121:0 ♀: <i>Papilla anales</i> setae inserted in long tubercles
9:1 Labial palpus red: a white line on the internal edge	128:1 ♀: Integument strongly wrinkled on posterior area
54:1 HW: Eyespot in cell 1b present	<i>M. eros</i>
69:1 SC: Atrophied cover scales	98:0 ♂: Gnathos pointed and sharp
83:1 ♂: Segment IX setae white	Clade 15
89:1 ♂: Dorsal fissure short	8:2 Labial palpus orange
<i>M. rhetenor</i>	70:1 SC: Cover scales pigmented around m ₁₋₂ , m ₂₋₃
140:1 ♀: <i>Signa</i> short	81:0 Color dimorphism weak
<i>M. cypris</i>	113:1 ♂: <i>Carina penis</i> present
62:1 HW: Eyespot pupils white and blue	Clade 16: (LAURSCHWARTZIA, IPHIMEDEIA)
Clade 8: Subgenus GRASSEIA	32:1 FW: Marginal and/or postmarginal spots orange

65:0 SC: Discal cell cover scales pigmented
 97:0 ♂: Gnathos slightly constricted
 100:1 ♂: Gnathos spinose
 144:1 Gliding flight

Clade 17: Subgenus LAURSCHWARTZIA
 40:1 HW: Cellular and basal areas: deep orange

Clade 18: *M. cisseis* ssp.
 32:2 FW: Marginal and/or postmarginal spots blue
 53:1 HW: Eyespots very distorted or oblate

Clade 19: Subgenus IPHIMEDEIA
 25:0 HW: Tail appendix on vein M3
 113:0 ♂: *Carina penis* absent
 129:1 ♀: Supernumerary depression dorsal to the *lamella postvaginalis* present

M. hercules
 10:0 No white scales on patagium
 140:1 ♀: Signa short

Clade 20: (*M. niepelti*, *M. theseus* ssp.)
 29:1 HW: Small tail-like appendices pointed

Clade 21: (*MORPHO*, *PESSONIA*)
 9:1 Labial palpus with a white line on the internal edge
 75:1 SC: Thin scales present at discal cell base
 83:1 ♂: Segment IX setae white
 101:1 ♂: Gnathos basal process present
 102:1 ♂: Gnathos subterminal basal process present
 125:1 ♀: *Lamella postvaginalis* developed forward
 134:1 ♀: *Lamella antevaginalis* developed backward

Clade 22: Subgenus PESSONIA
 11:2 Tegula nearly entirely white with brown edges
 67:1 SC: Basal scales not pigmented in discal cell
 114:1 ♂: *Carina penis* near apex of the *rostellum*

Clade 23
 53:1 HW: Eyespots very distorted or oblate
 76:2 SC: Upperside *lamina*: present with large perforations

Clade 24
 81:1 Color dimorphism strong

Clade 25
 134:0 *Lamella antevaginalis* not developed backward

Clade 26: *M. polyphemus* ssp.
 76:1 SC: Upperside *lamina*: present with small perforations

109:1 ♂: Strong spine halfway along valva posterior edge

Clade 27: Subgenus MORPHO
 17:0 Female foreleg, pulvillus fused medially
 40:2 HW: Areas over the cellular and basal zones greenish
 43:1 HW: Discal area thin
 60:1 HW: Claret shadow over the eyespot disk present
 66:1 SC: Apex of discal cell cover scales nearly smooth and straight
 69:2 SC: – At apex of discal cell, cover scales over developed
 70:0 SC: – *Idem*, not pigmented
 71:1 SC: – *Idem*, cover scale distal part enlarged
 72:1 SC: Cover scales forming a uniform multi-layered coat

Clade 28: *M. deidamia* ssp.
 8:1 Labial palpus white

Clade 29
 6:1 Hairy eyes
 8:3 Red scales on labial palpus
 126:1 ♀: *Lamella postvaginalis*: laterally overdeveloped
 133:1 ♀: Integument anterolateral area: strongly wrinkled

Table III. – Character consistency (ci) values of morphological, ecological and behavioral characters. Characters with ci values between 0.5 and 1 undergo at the most three state changes. The number of characters having a ci value equal to 1 is given in parentheses.

Character categories	Number of characters			
	per category	with ci < 0.5	with ci ≥ 0.5 (ci = 1)	novel characters ^a (with ci = 1)
Caterpillars	5	-	5 (5)	5 (5)
General morphology	12	1	11 (6)	1 ^b
Wing structure	12	7	5 (4)	6 (3)
Wing color pattern	33	21	12 (10)	12 ^b (3)
Scales	17	2	15 (10)	7 ^c (5)
Sexual dimorphism	2	2	-	1
Genitalia ♂	36	18	18 (11)	10 ^d (3)
Genitalia ♀	23	7	16 (9)	6 (2)
Ecology and behavior	5	3	2 (2)	3 (2)
Total for morphology only	140	58	82 (55)	48 (21)
Total for MEE	145	61	84 (57)	51 (23)

a: characters not previously used for phylogenetic studies of the genus; **b:** including one character with ci ≥ 0.5; **c:** including two characters with ci ≥ 0.5; **d:** including three characters with ci ≥ 0.5

RESULTS

Analyses with and without the ecological and behavioral characters produced respectively 210 MPCs ($L = 457$, $CI = 0.383$, $RI = 0.845$) and 140 trees ($L = 443$, $CI = 0.381$, $RI = 0.845$). However, the two strict consensus trees have the same topology (fig. 1). Forty-five characters are autapomorphies of subclades within the genus *Morpho* (*i.e.* characters having $ci = 1$; emboldened in Table II) and slightly more than half the characters have a character consistency index, $ci, \geq 0.5$. The morphological structures that generated characters with lower homoplasy were the scales of the forewing upperside and the female genitalia. A few other characters with high ci values came from general morphology and larvae (Table III).

Monophyly of the genus *Morpho* is confirmed, but contrary to the results of PENZ & DEVRIES (2002), only subgenus *Cytheritis* appears polyphyletic. Moreover, all the subgenera are quite well supported except *Iphimedeia*, and there are strongly supported sister-group relationships between *Laurschwartzia* and *Iphimedeia*, and *Morpho* and *Pessonia*. The deepest relationships between larger clades are not supported.

DISCUSSION

At the subgeneric level, the new phylogeny is better supported than that previously published (PENZ & DEVRIES, 2002), as at least one autapomorphy was found for eight of the nine subgenera. However, with regard to the deeper nodes, none receives improved support (with and without ecological and behavioral characters), and the most homoplastic characters in Penz & DeVries study remained homoplastic in the present study.

Phylogenetic relationships within the genus Morpho

Contrary to the results of the previous work of Penz & DeVries, subgenus *Morpho* is recovered as monophyletic, as it now includes *M. deidamia*. The topologies contradict Lamas' opinion (2004) that *M. granadensis* is a subspecies of *M. deidamia* but support a basal position of the latter. A sister-group relationship between subgenera *Morpho* and *Pessonia* was found. This pattern suggests interesting biogeographical questions, given that *Pessonia* is split into Mata Atlantica species-pair (*M. epistrophus*, *M. iphitus*) and a Mesoamerican species (*M. polyphemus*), and subgenus *Morpho* includes two strictly Amazonian species (*M. deidamia*, *M. achilles*), a trans-Andean species (*M. granadensis*) and the *Morpho* species with the largest range (from South-East Brazil to Mexico), *M. helenor*.

Also in contrast to the results of PENZ & DEVRIES (2002), subgenus *Grasseia* was also found to be monophyletic. Penz & DeVries did not study *M. absoloni*, which was considered to be a subspecies of *M. (Grasseia) amathonte* by LE MOULT & RÉAL (1962), but later placed by them in *Balachowskyina* (LE MOULT & RÉAL, 1963). This latter decision is strongly supported by our results, as the clade (*M. absoloni*, *M. aurora*) has good bootstrap and Bremer's Decay Index values.

Morpho hecuba and *M. cisseis* were originally included within subgenus *Iphimedeia* by FRUHSTORFER (1912), but when revisiting the subgenus taxonomy, BLANDIN (1988) placed these two species in a different subgenus (now called *Laurschwartzia* Blandin, 2007b). Unsurprisingly and as already demonstrated by PENZ & DEVRIES (2002), these two subgenera were distinct from each other in our phylogenetic analysis, yet they remained closely related.

LE MOULT & RÉAL (1962) included in subgenus *Cytheritis* those species they considered to be « among the most primitive » of genus *Morpho*. However, because these species have rather similar external appearance but markedly divergent genitalia, they believed that subgenus *Cytheritis* constituted a non-homogeneous group, a view supported by PENZ & DEVRIES (2002). On our cladogram, subgenus *Cytheritis* appeared as two widely separated groups. The first, which we term the *marcus* species group (*M. marcus* and *M. eugenia*), forms the most basal

Morpho clade. We refer to the second clade as *Cytheritis s. str.* It includes the type-species, *M. portis*, and this is placed as the sister clade of *Balachowskyna*. The distance between the *marcus* group and the *Cytheritis* group derives mainly from the very divergent male and female genital structures and wing upperside scales of the *marcus* species group. In all, we found seven striking autapomorphic traits for this group (Table II, clade 2), making it very different from *Cytheritis s. str.* but also very different from all other *Morpho* species. Therefore, we decided to erect a new subgenus, *Deyrollia*, n. subgen., which is described in Appendix 2 (p. 249).

Blues in blue: a phylogenetic test of the origin of blue coloration

Many *Morpho* butterflies are instantly recognizable by the dazzling blue color of males, which is due to optical phenomena produced by the upper lamina of the wing upperside scales. Consequently, we used scales organization characteristics, microscopic observations and the optical characteristics of *Morpho* wing upperside scales to test a hypothesis of color evolution within the genus. As the outgroup taxa are either not iridescent or iridescence is restricted to very small areas of hindwing, one would expect non-iridescent *Morpho* butterflies to constitute the more basal clades within the genus.

In *Morpho*, with the exception of the new subgenus *Deyrollia*, the iridescent blue coloration is produced by the Christmas tree-like structure of the ground scales (BERTHIER *et al.*, 2006). This characteristic structure is generated by a number of piled chitinous lamellae that form high ridges on the upper membrane of the scale. The ground scales also contain pigments and vary in size and shape. In general, the larger the ridge density, the number of lamellae per ridge and degree of melanization, the more dazzling is the resulting color. Although they do not produce color, the cover scales act to diffuse the light and thus reduce the spectral purity of the blue color (BERTHIER, 2007). They are therefore also important to our understanding of the structural colors. For example, *Morpho (Megamede) cypris* and *Morpho (Morpho) helenor* have ground scales that are similar in shape, size and pigment concentration. However, in *M. cypris* the structural color is intense and relatively pure because the cover scales are atrophied and cannot interact with the light reflected by the ground scales. In contrast, the spectral purity of the blue coloration on the wings of *M. helenor* is quite low because the enlarged and overlapping cover scales diffuse the light reflected by the ground scales in a large range of directions across the plane of the wing membrane.

Three main groups can be recognized within *Morpho* based on their color. The first is formed of the iridescent blue species of subgenera *Cytheritis* and *Deyrollia*, *Iphixibia*, *Grasseia*, *Megamede*, *Balachowskyna* and *Morpho*. The second includes the white species of subgenus *Pessonnia*. The last group comprises subgenera *Iphimedeia* and *Laurschwartzia*. This last group is a peculiar case in that it includes *M. cisseis*, which shows slightly iridescent blue areas, and species having dull colored areas that can be blue (some forms of *M. telemachus*, *M. niepelti*, *M. theseus schweizeri*), greenish and grayish-blue (*M. hercules*, *M. amphitryon*), white (*M. theseus juturna*), ocher-bronze or even yellow-orange (some forms of *M. telemachus*; *M. hecuba hecuba*).

The iridescent blue *Morpho* species do not form a monophyletic unit (fig. 2). With the naked eye, we could differentiate the deep blue species from the pale blue ones. In the first group are the subgenera *Iphixibia*, *Grasseia*, *Megamede*, *Balachowskyna* and *Morpho*. Their ground scales show a high ridge density, with 5 to 12 piled lamella, and strong melanin density (although not in some populations of *M. aurora*). Their cover scales are not pigmented and, depending on their size, they can modulate the spectral purity of the blue, as noted above. In the pale blue group, we could separate the new subgenus *Deyrollia* from *Cytheritis str.* The color difference between them is quite subtle when viewed with the naked eye but striking when the scale shape, organization and microstructure are considered. In the subgenus *Deyrollia*, the

Christmas tree-like structure does not exist. Each ridge is made from a single lamella, developed and not disrupted lengthwise, and having a circular cross-section. The piling of the lamellae, essential to produce iridescence, is replaced by a piling of the scales to form a multiple layer coat. Nonetheless, this piling is not sufficient to produce a very dazzling color. In contrast, *Cytheritis* str. species show the characteristic lamella piling of iridescent *Morpho*. The color difference between *Cytheritis* str. and the deep blue species does not come from differences in fundamental microstructure but from low melanin density or even, in the case of *M. sulkowskyi*, the complete absence of pigments in the scales of the wing upperside.

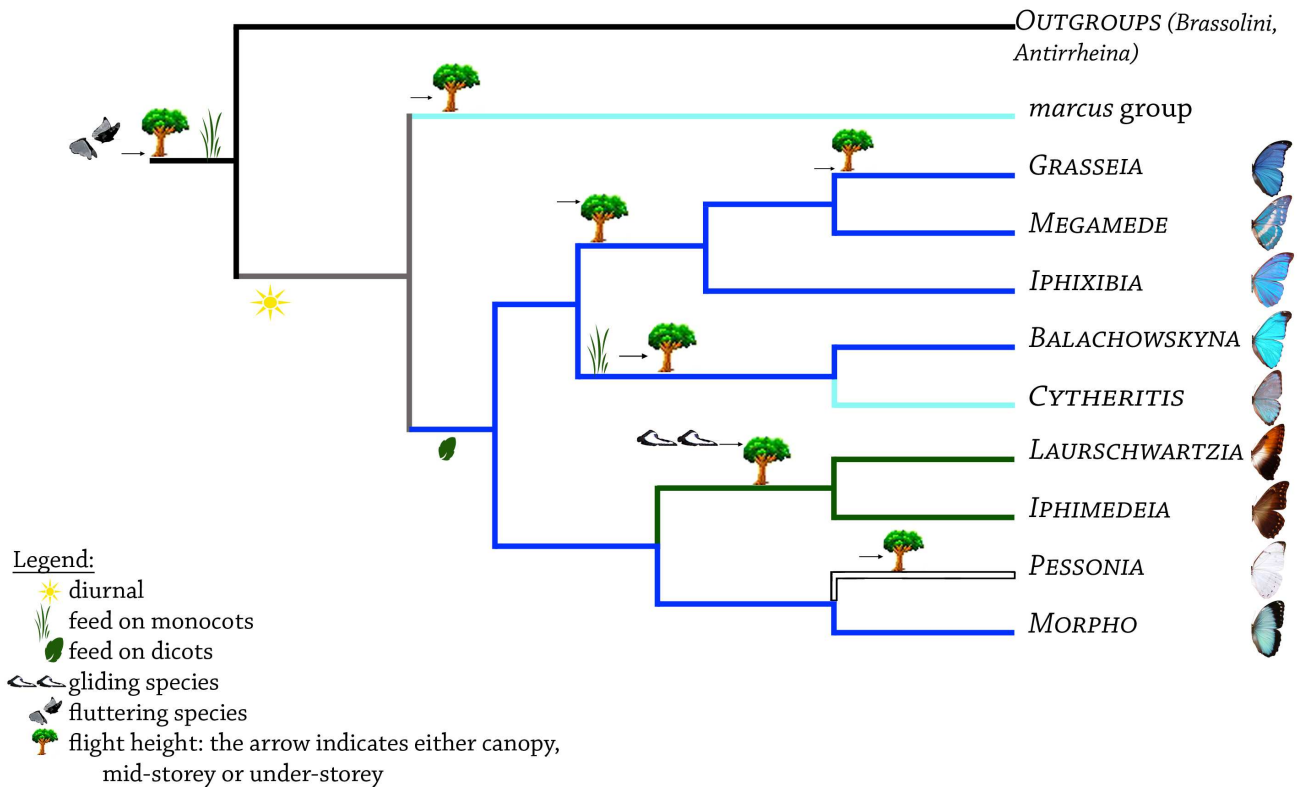


Fig. 2. – Evolution of the ecological and behavioral characters. Gregariousness data are really to scales to be included in character matrices.

Whiteness is the most notable characteristic of subgenus *Pessonnia* and supports the monophyly of the subgenus. This color results from absence of pigments, except for small black areas, and ability of the scales to reflect all wavelengths of visible light. At the microscopic level, we observed that they are the only *Morpho* butterflies having the upperside lamina developed between the ridges, but fenestrated at different degrees. Moreover, the ridges are only one lamella high, the lamella themselves being short compared with that observed in iridescent scales.

Our results also support the grouping of all the non-white/iridescent blue *Morpho*. In this clade (*Iphimedeia*, *Laurschwartzia*), scale microstructure cannot generate iridescence as each ridge is only one lamella high and both cover and ground scales are deeply pigmented. Greenish and grayish-blue could have different origins. Some of this type of coloration could come from optical phenomena that modify the wavelength reflected by underlying pigment grains. Alternatively, diverse tones of green, purple and blue can derive from biliary pigments, such as pterobilin, as in *Graphium weiskei* (Papilionidae). However a generally weak and localized iridescence in diverse colors, generated by both cover and ground scales, can be observed in few subspecies but it is a relatively unusual phenomenon and its microstructural origins remain unknown. Other candidates for iridescence include *M. theseus schweizeri* and some specimens of *M. hercules* but the occurrence and underlying physics of structural color in these taxa needs to be investigated. The only confirmed exception is *M. (Laurschwartzia) cisseis*, which is iridescent even though its ground scale ridges are only two lamellae high.

In conclusion, iridescence appears to be created by two different mechanisms – the subgenus *Deyrollia* and the *Morpho* type. Among the deep blue butterflies, optical and colorimetric differences occur (BERTHIER, 2007), which are the result of variations in ridge height and density, scale shape and organization. Considering this, all blue *Morpho* are differently blue. With the exception of the peculiar case of the subgenus *Deyrollia*, three major events could have generated much of the observed variation within the genus. In the clade (*Iphimedeia*, *Laurschwartzia*), species became drab and lost their blue coloration as the ridge density strongly decreased and ridge height reduced to one lamella. *Pessonia* species also lost their blue coloration and became white by losing the black pigment in ground scales. Finally, the blue color became pale within *Cytheritis* str. as the melanin concentration decreased.

Flight behavior of Morpho butterflies, host plants and larval behavior

Flight characteristics, derived from literature information and numerous oral communications, are much better known for males than for females. Inclusion of the male flight height character, coded following PENZ & DEVRIES (2002) and completed using personal observations in Peru, only brought further homoplasy to the results of our analysis (fig. 2). We observed that *Morpho* flying in the understorey never fly at canopy height but that the reverse is not true. For example, we observed *M. cisseis* flying quite high (i.e. 15 meters) in the canopy, but also at only a meter above a sandy river bank (see also NEILD, 2008). This behavior was also reported for *M. polyphemus* (D. Janzen, M. Balcazár-Lara, pers. comm.) and it certainly occurs in other taxa. Moreover, indications of species flying in “midstorey” are not precise as individuals can fly just under the lower branches of canopy, quite low over shrubs or throughout the entire space between – a space that can be very important in sites where trees are very tall. Furthermore, we noted some occasional, slight or marked variations in flight height between cloudy and sunny days, depending on the species group. Linking flight height to environmental parameters such as host plant stratification or weather/ microclimatic data should be investigated to determine the different parameters that influence this trait and then assess the part of it that is inherited. Now, it is more a locally useful diagnostic trait for recognizing species in the field than a phylogenetically significant character. Flight style – fluttering versus gliding – only distinguishes the clade (*Iphimedeia*, *Laurschwartzia*) (fig. 2). As we noticed in the field, perhaps more detailed and standardized observations would provide further significant characters.

Data related to larval host plants are scarce and exist only for about 20 *Morpho* taxa (data from various sources in CONSTANTINO, 1997; TÁKÁCS & TELLO, 1993; 1994; DEVRIES & MARTINEZ, 1994; BRÉVIGNON, 2003; MILLER *et al.*, 2007; NEILD, 2008; GUERRA-SERRUDO & LEDEZMA-ARIAS, 2008). According to our most parsimonious interpretation, evolution of larval host-plant type (monocots versus dicots, character 142) involves only two steps (Table II), a change from monocots to dicots in clade 3 followed by a reversal to monocot feeding again in clade 9. These data are very coarse-grained but they do suggest that the first host plant shift, to dicots, was associated with the diversification of the genus (fig. 2).

We did not include data about larval gregariousness in our analyses because it is too scarce, but this behavior should also be subjected to more intense scrutiny. For example, in subgenus *Iphimedeia*, *M. telemachus* and *M. hercules* larvae are gregarious throughout all instars, whereas *M. theseus* larvae are gregarious during the first four instars but solitary in the fifth (FRUHSTORFER, 1912-1913; OTERO, 1966; BRÉVIGNON, 2003; MILLER *et al.*, 2007). The same situation occurs in subgenus *Pessonia*: *M. epistrophus* and *M. iphitus* larvae are gregarious, (FRUHSTORFER, 1912-1913; OTERO, 1966; OTERO & MARIGO, 1990) but *M. polyphemus* larvae are not (YOUNG & MUYSHONDT, 1972; MILLER *et al.*, 2006). Within subgenus *Grasseia*, *M. amathonte* has solitary larvae (CONSTANTINO, 1997) but it has recently been observed that *M. godartii godartii* larvae in

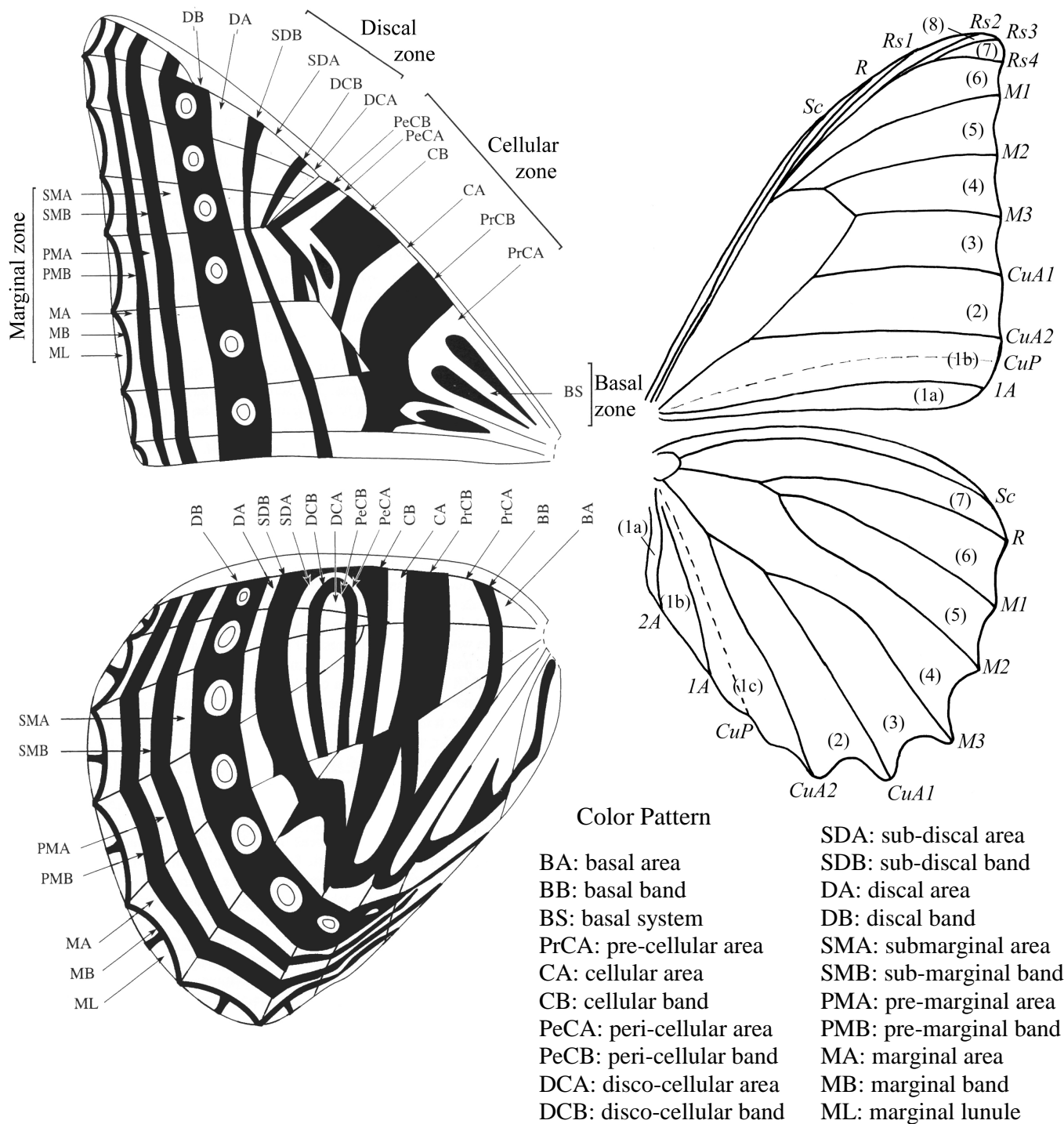


Plate 1. – *Morpho* butterfly wing color pattern of ventral surface (from BLANDIN, 2007a) and venation (*Sc*: subcostal; *R*: radius; *Rs*: radial sector; *M*: media; *CuA*: anterior cubitus; *CuP*: posterior cubitus; *A*: anal vein).

Bolivia (GUERRA-SERRUDO & LEDEZMA-ARIAS, 2008) and *M. godartii tingomariensis* larvae in Northern Peru, are gregarious (Douglas Cotrina Sánchez, pers. comm.). In contrast, *M. menelaus occidentalis* larvae are solitary (César Ramirez & Stéphanie Gallusser, pers. comm.). In subgenus *Morpho*, *M. helenor* (e.g. CONSTANTINO & CORREDOR, 2004) and *M. deidamia* (TÁKÁCS & TELLO, 1993) both have solitary larvae. According to the limited information available, larvae are also solitary in subgenus *Megamede* (TÁKÁCS & TELLO, 1994; DEVRIES & MARTINEZ, 1994). Even given our poor present knowledge, it is important to emphasize that gregariousness exists in several species in several different subgenera. Most gregarious larvae (*M. theseus* is an exception) share a common red and yellow pattern, whereas solitary larvae show a different but rather similar pattern characterized by large rhomboidal yellow or green patches. Presently, we cannot draw any definitive conclusions regarding the apomorphic or plesiomorphic status of larval behavior and pattern characters.

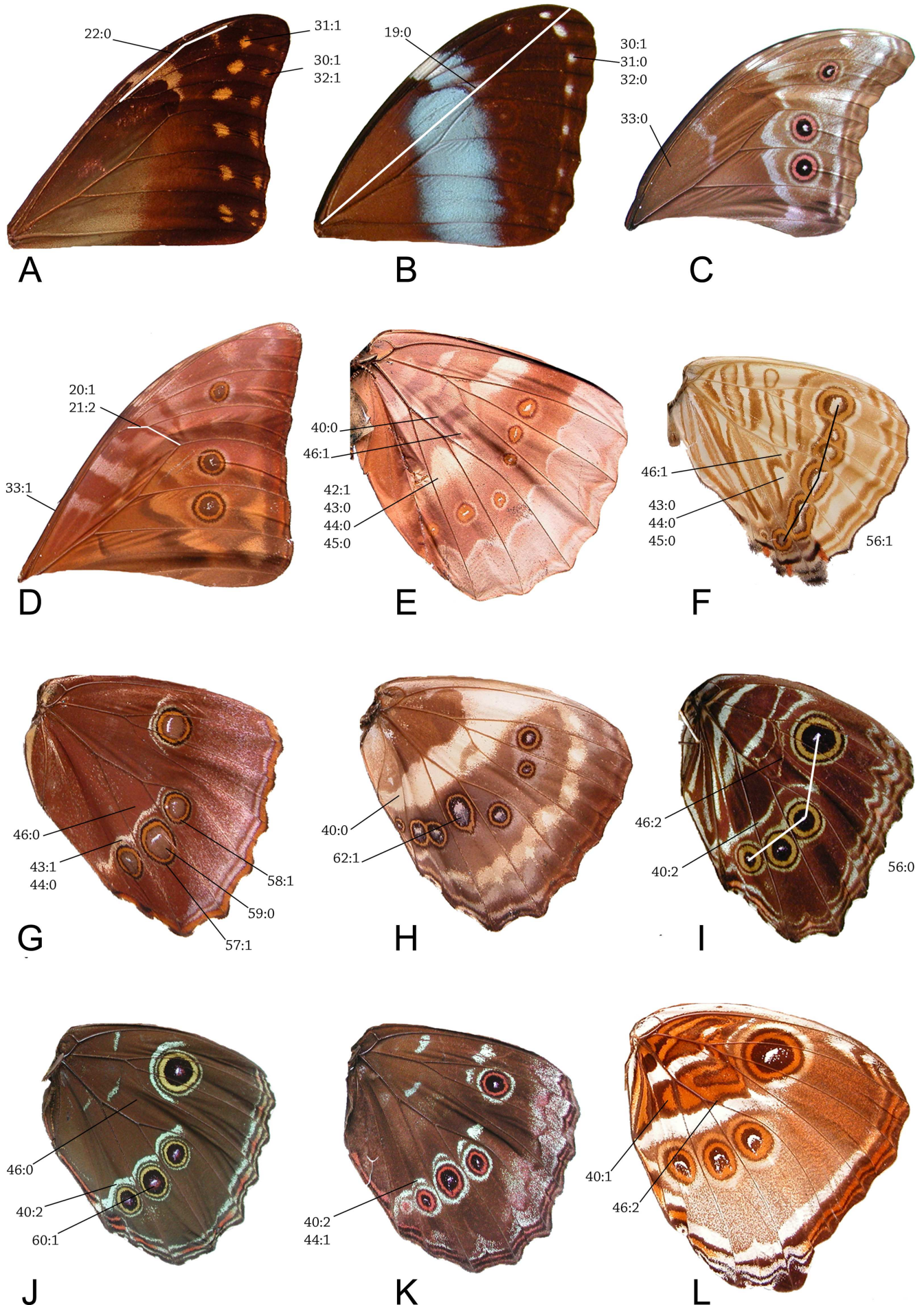


Plate 2. – Wing pattern. A-B, Forewing upperside – A: *M. hercules*; B: *M. helenor*. – C-D, Forewing underside – C: *M. godartii julanthiscus*; D: *M. theseus*. – E-L, Hindwing underside – E: *M. anaxibia*; F: *M. sulkowskyi*; G: *M. absoloni*; H: *M. cypris*; I: *M. deidamia*; J: *M. achilles phokylides*; K: *M. menelaus occidentalis*; L: *M. hecuba*.

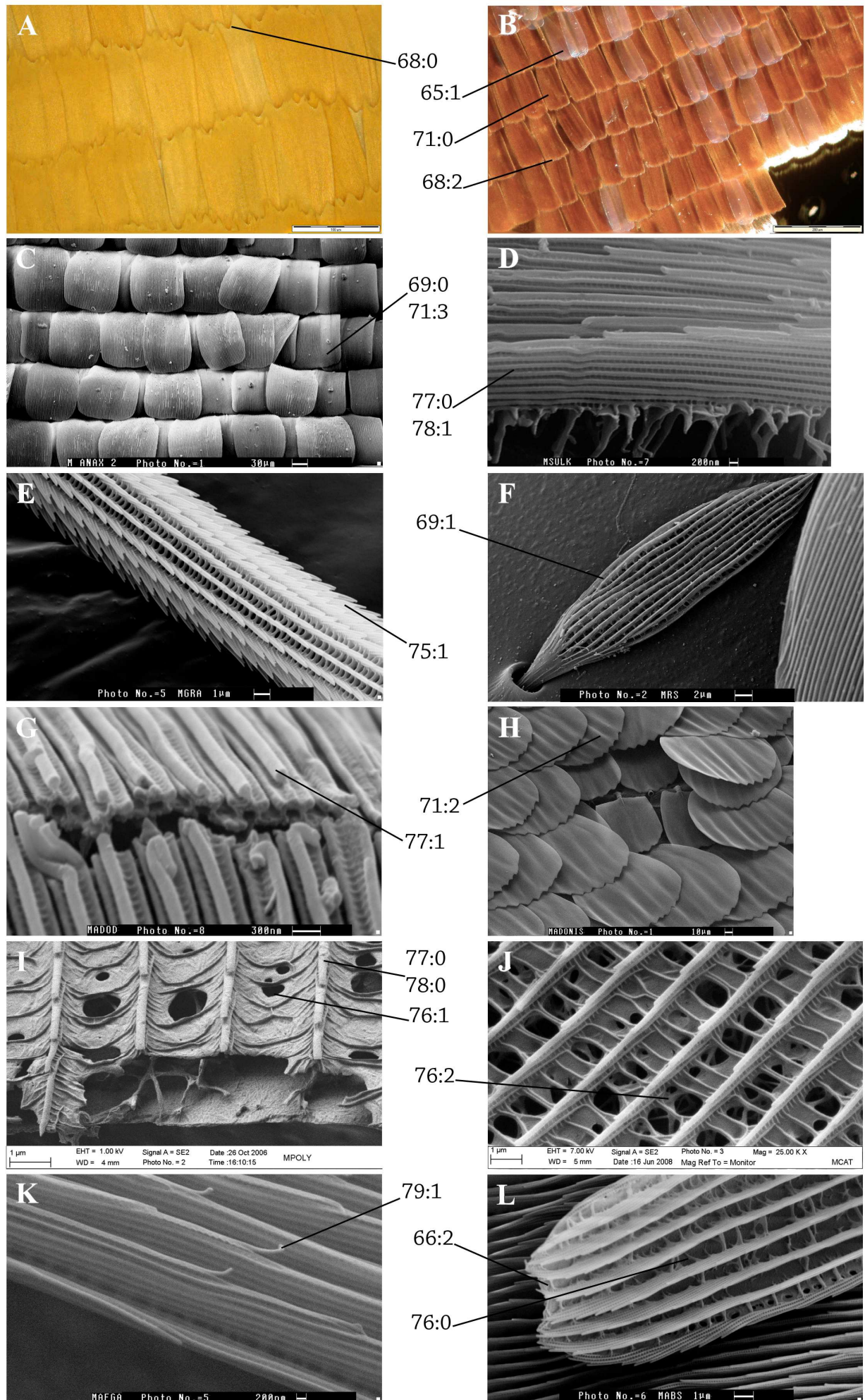


Plate 3. – Scale microstructure (upperside of forewing discal cell). – A: *M. hecuba*; B: *M. amathonte*; C: *M. anaxibia*; D: *M. sulkowskyi*; E: *M. granadensis*; F: *M. rhetenor*; G, H: *M. marcus*; I: *M. polyphemus*; J: *M. epistrophus catenaria*; K: *M. aega*; L: *M. absoloni*.

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].

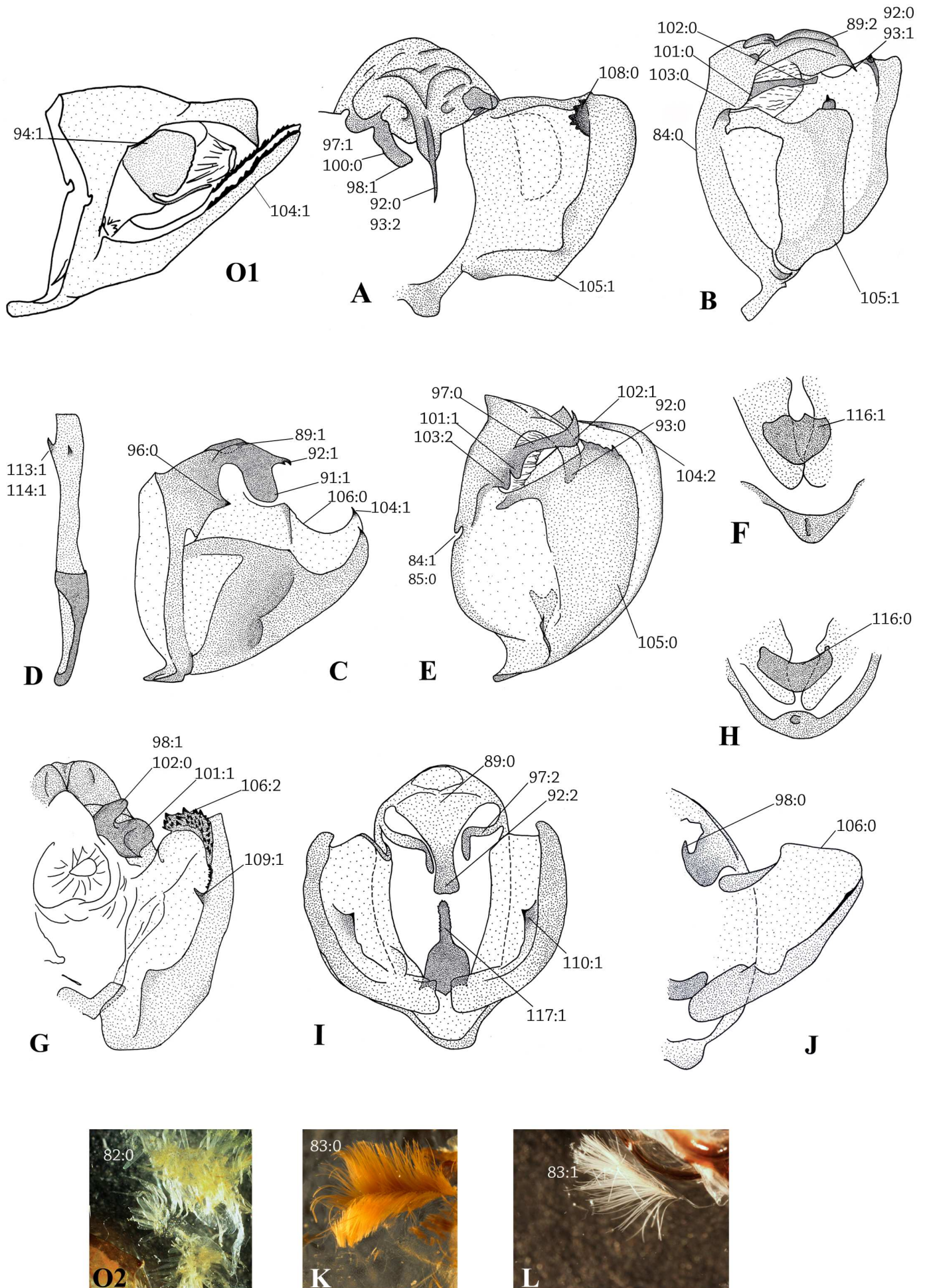


Plate 4. – Male genitalia. – O1, *Caligo ilioneus*, lateral view; – O2, *Antirrhea tomasia*, scale tufts; – A, *M. aurora*, posterior view; – B, *M. absolon*, lateral view; – C, *M. portis*, lateral view; – D, G, *M. polyphemus*, phallus and posterior view; – E, *M. helenor*, lateral view; – F, *M. granadensis*, 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.

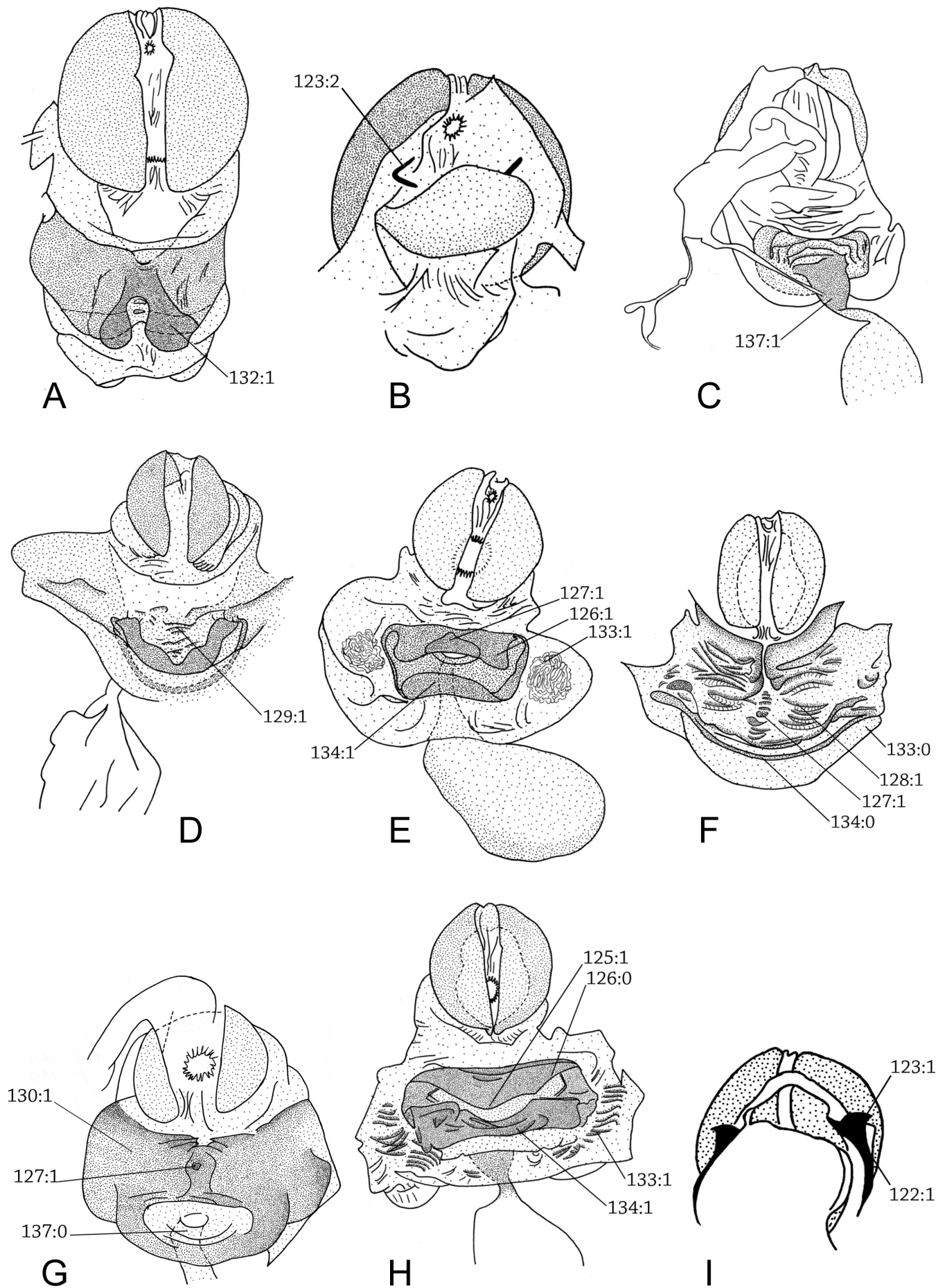


Plate 5. – Female genitalia. – A, B, *M. marcus*, posterior and anterior view respectively; – C, *M. cisseis*, anterior view; – D, *M. Hercules*, posterior view; – E, *M. Achilles*, posterior view; – F, *M. sulkowski*, posterior view; – G, *M. portis*, posterior view; – H, *M. deidamia*, posterior view; – 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	1?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?	1?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	1011101001	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?010	?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???20	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?010	?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???20	0000101110	1122020100	0010110111	1001111000	0011??0?010	?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???20	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?00111	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???0	000102?100	010?100111	00100?1001	0000??0010	0010?
uraneis	11????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.

ACKNOWLEDGEMENTS. – We thank the Conseil Régional de la Martinique. Our gratitude goes to J. Barbut for assistance in the laboratory, to S. Berthier and the Institut des Nanosciences de Paris for initiation to optics of butterfly scales, to A. Lévêque and G. Lachaume for information about flight behaviour. We also thank J. Minet, K. Plewack, P. Grandcolas, A. Soulier-Perkins and R. Robbins, A. Neild for advice and proofreading of previous version of this manuscript. Finally we are grateful to the referees for that valuable criticisms and comments on the study and manuscript, especially to K. Wilmott for interest he demonstrated for this work.

REFERENCES

- ACKERY P. R., DE JONG R. & VANE-WRIGHT R. I., 1998. – The Butterflies: Hedyloidea, Hesperioidea and Papilionoidea, p. 263-300 in Kristensen N. P. (ed.), *Lepidoptera, Moths and Butterflies*, Vol.1. (Handbuch der Zoologie [founded by Willy Kükenthal; ed. Fisher, M.], Band 4, Teilband35). Walter de Gruyter, Berlin.
- BERTHIER S., 2007. – *Iridescence – the physical colors of insects*. Paris: Springer, 160 p.
- BERTHIER S., CHARRON E. & BOULENGUEZ J., 2006. – Morphological structure and optical properties of the wings of Morphidae. *Insect Science*, **13**: 145-154.
- BILOTTA I., 1992. – Morfologia comparada da cabeça das espécies sulbrasileiras de Morphinae (Lepidoptera, Nymphalidae). *Revista Brasileira de Zoologia*, **9**: 261-271.
- 1994a. – Morfologia comparada do tórax das espécies sulbrasileiras de Morphinae (Lepidoptera, Nymphalidae). *Revista Brasileira de Zoologia*, **11**: 691-713.
- 1994b. – Biologia comparada do abdome das espécies sulbrasileiras de Morphinae (Lepidoptera Nymphalidae). *Revista Brasileira de Zoologia*, **11**: 737-748.
- BLANDIN P., 1988. – *The genus Morpho. Lepidoptera Nymphalidae. Part 1. The Sub-Genera Iphimedeia and Schwartzia*. Compiègne, France: Sciences Nat, 41 p + maps 1-6+ plates 1-20.
- 2007a. – *The systematics of the genus Morpho, Fabricius, 1807 (Lepidoptera Nymphalidae, Morphinae)*. Hillside Books, Canterbury, United Kingdom, 277 p.
- 2007b. – *The genus Morpho. Lepidoptera Nymphalidae. Part 3*. Hillside Books, Canterbury, United Kingdom, 237 p.
- 2007c. – *Laurschwartzia* nom. nov., nom de substitution pour le sous-genre *Schwartzia*, Blandin, 1988 (Lep., Nymphalidae, Morphinae). *Bulletin de la Société entomologique de France*, **112** (4): 510.
- BREMER K., 1994. – Branch support and tree stability. *Cladistics*, **10**: 295-304.
- BRÉVIGNON C., 2003. – *Les stades larvaires de Morpho telemachus* (L. 1758) en Guyane française (Lepidoptera, Nymphalidae, Morphinae), p. 30-32. In: Lacomme D. & Manil L. (eds), *Lépidoptères de Guyane. Bulletin des Lépidoptéristes parisiens*, numéro hors-série.

- CONSTANTINO L. M., 1997. – Natural history, immature stages and hostplants of *Morpho amathonte* from western Colombia (Lepidoptera: Nymphalidae: Morphinae). *Tropical Lepidoptera*, **8** (2): 75-80.
- CONSTANTINO L. M. & CORREDOR G., 2004. – The biology and morphology of the early stages of *Morpho macrophthalmus* and *Morpho peleides telamon* (Nymphalidae: Morphinae) from Western Colombia. *Boletín científico. Museo de Historia natural. Universidad de Caldas*, **8**: 201-209.
- DEVRIES P. J., 1987. – *The Butterflies of Costa Rica and their natural history*. Princeton University Press, 327 p.
- DEVRIES P. J., KITCHING I. J. & VANE-WRIGHT R. I., 1985. – The systematic position of *Antirrhea* and *Caerois*, with comments on the classification of the Nymphalidae (Lepidoptera). *Systematic Entomology*, **10**: 11-32.
- DEVRIES P. J. & MARTINEZ G. E., 1994. – The morphology, natural history, and behavior of the early stages of *Morpho cypris* (Nymphalidae Morphinae) – 140 years after formal recognition of the butterfly. *Journal of the New York Entomological Society* (1993), **101** (4): 515-530, 13 fig.
- FELSEINSTEIN J. F., 1985. – Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, **39**: 783-791.
- FRUHSTORFER H., 1912-1913. – *Familie: Morphidae* Westw., p. 333-356. In: Seitz A. (ed.), *Die Gross-Schmetterlinge der Erde*. Stuttgart, Alfred Kernen.
- GOLOBOFF P., FARRIS J. & NIXON K. 2003. – *T.N.T: Tree Analysis Using New Technology*. Program and documentation, available from the authors and at www.zmuc.dk/public/phylogeny.
- 2008. – TNT, a free program for phylogenetic analysis. *Cladistics*, **24**: 774-786.
- GUERRA-SERRUDO J. F. & LEDEZMA-ARIAS J., 2008. – Biología y Morfología de *Morpho menelaus godartii* (Lepidoptera: Nymphalidae: Morphinae) en el Parque Nacional Cotapata (Bolivia). *Ecología en Bolivia*, **43** (1): 40-52.
- KRISTENSEN N. P., 2003. – *Lepidoptera, Moths and Butterflies*. Vol. 2: Morphology, Physiology and Development. Handbook of Zoology: Vol. IV Arthropoda: Insecta, Issue 36, 564 p.
- LAMAS G., 2004. – *Tribe Morphini*, p. 192-201. In Lamas G. (ed.), *Checklist: Part 4A. Hesperoidea – Papilionoidea. Nymphalidae. Morphinae. Atlas of Neotropical Lepidoptera*. Vol. 5A. Gainesville: J.B. Heppner Ed., Association for Neotropical Lepidoptera, Scientific Publishers.
- LE MOULT E. & RÉAL P., 1962. – *Les Morpho d'Amérique du Sud et Centrale*. Tome I: Historique, Morphologie, Systématique. Paris: Cabinet Entomologique E. Le Moul, 296 p.
- 1963. – *Les Morpho d'Amérique du Sud et Centrale*. Tome II: Planches en couleurs et en noir. Paris: Cabinet Entomologique E. Le Moul, 16 p. + 92 plates.
- MILLER J. C., JANZEN D. H. & HALLWACHS W., 2006. – *100 Caterpillars. Portraits from the tropical forests of Costa Rica*. Cambridge, Massachusetts; London, England: The Belknap Press of Harvard University Press, 264 p.
- 2007. *100 Butterflies and Moths. Portraits from the tropical forests of Costa Rica*. The Belknap Press of Harvard University Press, Cambridge, Massachusetts; London, England, 256 p.
- NEILD A. F. E., 2008. – *The Butterflies of Venezuela. Part 2: Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae)*. A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae. London: Meridian Publications, 275 p.
- OTERO L. S., 1966. – *Biologie de sept Lépidoptères brésiliens du genre Morpho, Fabricius, 1807*. Thèse de Doctorat de l'Université de Paris, Faculté des Sciences, 73 p.
- OTERO L. S. & MARIGO L. C., 1990. – *Borboletas. Beleza e comportamento de espécies brasileiras*. Rio de Janeiro: Marigo Comunicação Visual, 123 p.
- PEÑA C., WAHLBERG N., WEINGARTNER E., KODANDARAMAIAH U., NYLIN S., FREITAS A. V. L. & BROWER A. V. Z., 2006. – Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular Phylogenetics and Evolution*, **40**: 29-49.
- PENZ C. & DEVRIES P. J., 2002. – Phylogenetic analysis of *Morpho* Butterflies (Nymphalidae, Morphinae): Implication for Classification and Natural History. *American Museum Novitates*, **3374**: 1-33.
- SORENSEN M. D., 1999. – *TreeRot.v2*. Boston University, Boston, Massachusetts.
- TÁKÁCS M. & TELLO C., 1993. – Notas sobre la biología de *Morpho deidamia* Hübner, 1819. *Revista peruana de Entomología* (1992), **35**: 37-40.
- 1994. – Notas sobre la biología de *Morpho rhetenor* f. *cacica* Staudinger, 1875. *Revista peruana de Entomología* (1993), **36**: 31-34.
- YOUNG A. M. & MUYSHONDT A., 1972. – Biology of *Morpho polyphemus* (Lepidoptera: Morphidae) in El Salvador. *Journal of the New York Entomological Society*, **80**: 18-42.