Phylogenetic Analysis of *Morpho* Butterflies (Nymphalidae, Morphinae): Implications for Classification and Natural History

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ABSTRACT

The classification of butterflies in the widely recognized genus *Morpho* previously used subgenera that were assumed to constitute natural species groups. Cladistic analysis of 120 characters provided a well-resolved tree showing that some subgenera do not constitute monophyletic groups. This study supported some traditional taxonomic species groupings, but rejected the concept of subgenera for *Morpho*. Therefore, we formally redefined the genus to be consonant with the assumptions of phylogenetic classification. Predictions about *Morpho* life histories, the correlation of color pattern and flight behavior with vertical flight height, and the evolution of sexual dimorphism are discussed in light of our phylogeny.

INTRODUCTION

In 1807, Fabricius erected the genus *Morpho* to embrace one of the most familiar groups of Neotropical insects. Not only the type species, *M. achilles* (Linnaeus, 1758), but many other species of *Morpho* have long been recognized by their large size and distinctive blue colors. Few people forget their first encounter with the big iridescent blue butterflies conspicuously flying through a forest, or simply preserved as specimens in a collection—even those who are generally oblivious to the natural world. Given their distinctness and allure to collectors of dazzling insects, one might expect the natural history and systematics of the big blues of

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Fabricius to be particularly well known. Surprisingly, this is not the case. Despite having been the subject of three monographic treatments (Fruhstorfer, 1913; Le Moult and Réal, 1962; Blandin, 1988, 1993), many fundamental aspects of *Morpho* systematics and biology remain uncertain. The general biology of some *Morpho* species is available in Fruhstorfer (1913), Young and Muyshondt (1972, 1973), and DeVries (1987), while Le Moult and Réal (1962) and D’Abrera (1984) include color illustrations of most species.

As a systematic and natural history synthesis, the work of Fruhstorfer (1913) provides the basis for all subsequent studies of scientific consequence. As one of the foremost butterfly biologists of his time, Fruhstorfer compiled information on internal and external morphology, geographic and altitudinal distribution, subspecies, behavior, and early stages to divide *Morpho* into two groups, or subgenera. At the time of publication, Fruhstorfer’s treatment probably summarized all known information on *Morpho*. It remains a valuable resource and makes for pleasurable reading.

Several characteristics have historically made *Morpho* butterflies a marketable commodity: their large size, variation in species abundance, sexual dimorphism, and exotic blues. In fact, a large proportion of all museum specimens and much of our taxonomic understanding of *Morpho* butterflies are inextricably linked to their collector market value. During the past 80 years the monetary value associated with the butterfly trade fueled an eagerness to name the world’s *Morpho* fauna, and impelled the description of a large number of species, subspecies, forms, and aberrations—all that could be considered commodity art to the enthusiastic collector. For example, Fruhstorfer (1913) listed 30 species plus 119 subspecies and forms of *Morpho*. In contrast, the monograph by the commercial insect dealers Le Moult and Réal (1962) recognized 75 species assigned to eight subgenera, and generated no less than 409 new names. Taken together, this tallied to more than 780 available taxonomic names applicable to *Morpho*—a generous offering to the potential collector’s dream catalog. However, if one disregards the immoderate naming of subspecies and varietal taxa, the service provided to *Morpho* systematics by Le Moult and Réal (1962) was a species-level classification, descriptions of subgeneric taxa, illustrations of adults and male genitalia for all species, and an account of type specimens.

The study by DeVries et al. (1985) focused on the relationships of the three Morphinae genera—*Morpho*, *Antirrhea* Hübnner, 1822 and *Caerois* Hübnner, 1819—and in doing so considered six species of *Morpho* in five subgenera. However, their limited taxon sampling precluded a detailed evaluation of relationships within *Morpho*. Furthermore, as their phylogeny was based almost entirely on early stage characters, its refinement depends on availability of preserved caterpillars for additional species.

Blandin (1988, 1993) acknowledged explicitly that his monographic reviews were not intended to be complete revisions of *Morpho*, or to address phylogenetic relationships among species. Rather, these works sought to improve the utility of Le Moult and Réal (1962) by offering revised definitions of selected subgenera and species. Although his treatment was comparatively conservative, Blandin (1988) also described a new subgenus, and he further suggested that the nine subgenera of *Morpho* might be regarded as full genera. Based on finding a high level of morphological variation among seven species in six *Morpho* subgenera, Bilotta (1992, 1994a, 1994b) elevated these subgenera to generic status. However, other researchers have not followed this action.

The works of Fruhstorfer (1913), Le Moult and Réal (1962), DeVries et al. (1985), Blandin (1988, 1993), and Bilotta (1992, 1994a, 1994b) all bear on how we perceive the diversification and evolution of *Morpho* butterflies. However, the variance in systematic approaches among these studies strongly implies that a better understanding of *Morpho* could be attained by application of modern phylogenetic analysis.

This paper presents a systematic overview of *Morpho* by sampling 27 species representing a wide range of taxonomic diversity within the genus as currently understood, and it explicitly tests the monophyly of the nine *Morpho* subgenera using phylogenetic methods. Analysis of 120 adult characters provid-
ed a well-resolved tree in which the subgenera *Iphimeidea* Fruhstorfer, 1913, *Schwartzia* Blandin, 1988, *Cypritis* Le Moult and Réal, 1962, and *Pessonia* Le Moult and Réal, 1962 were monophyletic, whereas *Cytheritis* Le Moult and Réal, 1962, *Grasseia* Le Moult and Réal, 1962, *Iphixibia* Le Moult and Réal, 1962 and *Morpho* Fabricius, 1807 were paraphyletic (*Balachowskyna* Le Moult and Réal, 1962 and *Iphixibia* Le Moult and Réal, 1962 are monotypic). The paraphyly and basal position of *Cytheritis* preclude dividing the genus *Morpho* into phylogenetically meaningful subunits. As a consequence, we propose abandoning the previous subgeneric classification, and redefine the genus *Morpho* based on our analysis. In light of our phylogeny, we then discuss ecological and phenotypic characteristics of *Morpho*.

**METHODS**

**SPECIES SAMPLED**

To avoid the excess taxonomic splitting of *Le Moult* and Réal (1962), our estimate of total species richness in *Morpho* followed the more conservative treatments of Fruhstorfer (1913) and Blandin (1988, 1993). We then assessed the monophyly of all *Morpho* subgenera by selecting 27 species representing the range of diversity within each subgenus (figs. 1–10). These included the monotypic *Balachowskyna* and *Iphixibia*, two species of each *Cypritis* and *Schwartzia*, three of *Pessonia*, four each of *Grasseia* and *Iphimeidea*, and five each of *Cytheritis* and *Morpho* (appendix 1). Males and females were dissected for all species, except for *M. adonis* (Cramer, 1775), *M. theseus* Deyrolle, 1860, and *M. amphitrion* Staudinger, 1887, for which female specimens with intact abdomens were unavailable.

Specimens of *Morpho* butterflies are typically abundant in most museums and theoretically represent a major source of study material. However, a widespread tradition has rendered many specimens of little use for systematic analysis. As this tradition bears upon the present and future studies of *Morpho* systematics, the reader may find some background useful.
Fig. 2. Ventral view of *Morpho* (*Balachowskyna*) aurora: A, male, B, female; *Morpho* (*Cytheritis*) sulkowskyi: C, male, D, female. See legend of figure 1 for locality data and FW lengths.

Fig. 3. Dorsal view of *Morpho* (*Cypritis*) cypris: A, male, Colombia, Boyacá, FW length of 59.3 mm (LACM); B, female, Colombia, FW length of 73.2 mm (USNM); *Morpho* (*Iphixibia*) anaxibia: C, male, Brazil, FW length of 75.5 mm (LACM); D, female, Brazil, Santa Catarina, FW length of 81.4 mm (MPM).
Fig. 4. Ventral view of *Morpho (Cypris) cypris*: **A**, male, **B**, female; *Morpho (Iphixibia) anaxibia*: **C**, male, **D**, female. See legend of figure 3 for locality data and FW lengths.

Fig. 5. Dorsal view of *Morpho (Grasseia) amathonte*: **A**, male, Costa Rica, FW length of 88.2 mm (MPM); **B**, female Colombia, Muzo, FW length of 99 mm (MPM); *Morpho (Schwartzia) hecuba*: **C**, male, Brazil, Obidos, Pará, FW length of 91.4 mm (MPM); **D**, female, Brazil, Obidos, Pará, FW length of 85 mm (MPM).
As in most insects, the abdomens of *Morpho* butterflies contain lipids. To prevent the lipids from greasing the iridescent wings and sullying so-called "perfect specimens", collectors often remove the abdomen of individuals immediately upon capture. Such procedures are particularly prevalent in the showy, iridescent blue species (e.g., *M. cypris* Westwood, 1851, *M. rhetenor* (Cramer, 1775), *M. adonis*, *M. eugenia* Deyrolle, 1860). For example, a cursory inspection of 16 showy species in the Milwaukee Public Museum collection revealed that 41% of the 293 specimens examined were without abdomens (table 1). This phenomenon is not peculiar to the Milwaukee Public Museum, but is general to most private and museum collections of *Morpho*.

To make specimens with excised abdomens appear cosmetically "perfect", they are often retrofitted with an abdominal prosthesis. During our study we not only found many *Morpho* specimens without abdomens, but some where the thorax and abdomen belonged to different species (e.g., one with a papilionid head, one with a danaine abdomen), and some specimens had the abdomi-
special preparation was performed on the head or any thoracic appendages. All structures were examined using an optical stereomicroscope.

General terminology for external morphology follows Scoble (1992). For male and female genitalia, we follow Klots (1970), and for wing scale, we follow Downey and Allyn (1975).

CHARACTERS

We examined 120 characters (105 binary and 15 multistate), of which 112 were phylogenetically informative (appendices 2 and 3). Some autapomorphic characters were included in our analysis because they represented departures from characteristic patterns of supraspecific taxa (e.g., the characteristic hairpencils of Morphinae were absent in *M. sulkowskyi* Kollar, 1850; character 13:0), and they may be useful in future analyses that include more species. Characters included flight behavior (1 character), general external morphology (11 characters), male and female genitalia (35 and 20 characters, respectively), wing venation (10 characters), scale morphology (11 characters), wing color pattern (31 characters), and larval host plant (1 character). To facilitate verification by future workers, we illustrated many of our characters and included explanatory notes where appropriate (appendix 2).

All characters were scored from direct observation, none from published descriptions. Nevertheless, comparative data published by other authors helped establish criteria for selecting characters for phylogenetic analyses. We examined all characters that Fruhstorfer (1913), Le Moult and Réal (1962), and Blandin (1988, 1993) used to define subgenera (see appendix 4). Those characters that could be defined and scored with confidence were used in our analyses, including some that were re-coded (see appendix 2). Our criteria for selecting characters were as follows.

HEAD: Bilotta (1992) reported subtle dif-
Fig. 8. Ventral view of *Morpho* (*Pessonia*) *catenarius*: A, male; B, female; *Morpho* (*Iphimedea*) *perseus*: C, male, D, female. See legend of figure 7 for locality data and FW lengths.

...ferences in the shape of the subgenal suture, size of the anterior tentorial pit, and the shape and size of the occipital foramen. We did not consider these characters because of the destructive nature of the preparations required for scoring them. We also did not include the distance between the paired scape and the size of labial palpus segments in our analyses since they seemed to vary continuously across taxa, thereby making it difficult to establish discrete character states.

**Thorax:** In addition to the open/closed hindwing cell (DeVries et al., 1985), we used several wing characters, including venation, scale morphology and pigmentation, and wing color pattern, some of which have been used previously to define *Morpho* subgenera (see appendix 4). Because of their ambiguous definitions, forewing shape characters used to define subgenera by Blandin (1988, 1993) were not included in the analysis (e.g., contrast definitions of forewing shapes for *Iphimedea*, *Schwartzia*, and *Iphixibia* in appendix 4). Although the continuous variation between a “more pointed” or “less pointed” forewing makes it difficult to define character states useful for systematic analyses, wing shape variation is likely important in the evolutionary history of *Morpho*. Therefore, these variations will form the topic of a future study on the evolution of wing morphology and flight behavior in light of the phylogeny proposed here (DeVries and Penz, in prep.). Characters for female leg 1 and male leg 2 are described here for the first time.

**Abdomen:** Although we found differences among species in size and shape of male abdominal tergite 8, and sternites 3 and 4, these variations could not be translated confidently into character states. Le Moul and Réal (1962) used several characters of male genitalia to characterize subgenera (see appendix 4), one of which was not used in our analyses because of difficulties in establishing discrete character states (uncus with extended wings, see “*Iphixibia*” in appendix 4). We re-coded the remaining genital characters to allow scoring across all species (appendix 2). Illustrations of genitalia for many species may be found in Le Moul and Réal (1962) and in Bilotta (1994b).
PHYLOGENETIC ANALYSIS

We employed parsimony analysis with the following settings: all characters were given equal weight, multistate characters were unordered, and polymorphic characters were treated as exhibiting both states. An heuristic search with 20 tree bisection reconnection (TBR) replicates was performed as implemented in PAUP 4.0b1 (Swofford, 1998). We used a successive approximation weighting procedure (SAW) of Farris (1969) to reduce the number of equally parsimonious trees and to preserve resolution. Decay indices (Bremer, 1994) and bootstrap values (Felsenstein, 1985) were provided as estimates of branch support. MacClade 4 (Maddison and Maddison, 2000) was used to assess the nature and number of character changes per branch, and to provide a comparison between topologies for a Wilcoxon rank sum test (WRS) (Templeton, 1983; Larson, 1994).

RESULTS

PHYLOGENETIC ANALYSIS

Analysis of 120 characters yielded nine equally parsimonious trees (tree length = 338, CI = 0.41, RI = 0.65), two of which are illustrated in figure 11A and B. Reduced resolution of the strict consensus of these nine trees (fig. 11C) was caused by ambiguities among equally parsimonious trees in the placement of two species: M. (Balachowskyna) aurora Westwood, 1851 (monotypic) and M. (Morpho) deidamia Hübner, 1816. Three trees favored a basal position of M. (Balachowskyna) aurora with respect to the subgenera Iphimedeia, Schwartzia, Iphixibia, Cypritis, Pessonia, and Morpho (e.g., fig. 11A), while in others this species appeared as a sister taxon to Pessonia (e.g., fig. 11B; see definition of Balachowskyna in appendix 4). Morpho (Morpho) deidamia appeared as a sister taxon to Pessonia in six trees (three of which contained the Balachowskyna).


**TABLE 1**

Sample of 16 Species of *Morpho* in the Milwaukee Public Museum Showing the Percentage of Individuals That Lacked Abdomens

| Species      | Total | With abdomens | Lacking abdomens | % lacking abdomens |
|--------------|-------|---------------|-------------------|--------------------|
| hercules     | 19    | 13            | 6                 | 31                 |
| theseus      | 15    | 13            | 2                 | 13                 |
| perseus      | 18    | 11            | 7                 | 39                 |
| neculae      | 16    | 11            | 5                 | 31                 |
| cisseis      | 3     | 0             | 3                 | 100                |
| portis       | 20    | 11            | 9                 | 45                 |
| sukowski     | 22    | 11            | 11                | 5                  |
| aega         | 48    | 31            | 17                | 35                 |
| aurora       | 11    | 6             | 5                 | 45                 |
| adonis       | 11    | 5             | 6                 | 54                 |
| eugenia      | 1     | 0             | 1                 | 100                |
| rhetenor     | 23    | 9             | 14                | 61                 |
| cypris       | 7     | 5             | 2                 | 29                 |
| anaxibia     | 18    | 8             | 5                 | 38                 |
| godarti      | 12    | 6             | 6                 | 5                  |
| menelaus     | 57    | 32            | 25                | 44                 |

Total 293 172 121 41

chowskyna + Pessonia grouping), and it moved to a more basal position in the remaining trees (e.g., fig. 11B).

Removing *M. aurora* and *M. deidamia* from the analysis resulted in three equally parsimonious trees (tree length = 310, CI = 0.45, RI = 0.68), and the strict consensus of these trees (fig. 11D) is congruent with the topology of the successive approximation weighting tree (see below), except for the relationships among *M. laertes* (Drury, 1782), *M. catenarius* Perry, 1811, and *M. polyphemus* Doubleday and Hewitson, 1851 (see figs. 11D and 12).

Successive approximation weighting selected three of the original nine equally parsimonious trees (fig. 11A being one of them). The strict consensus of these trees is presented in figure 12, and characters supporting each grouping are listed in table 2. Although all nine trees from the unweighted analysis are equally likely to be correct by principles of parsimony analysis, the remainder of our discussion is based on the consensus of the trees selected by SAW because (1) this procedure emphasizes the influence of robust characters for tree resolution, and (2) removal of problematic taxa (*M. aurora* and *M. deidamia*) produced a tree highly compatible with those selected by SAW.

The monophyly of some, but not all, subgenera is supported by our analysis using SAW (fig. 12). Herein, Iphimededia, Schwartzia, Cypritis, and Pessonia are monophyletic, and we corroborate the apparent monotypy of Balachowskyna and Iphixibia. On the other hand, Cytheritis, Grasseia, and Morpho did not constitute monophyletic groups. Although our results support several traditionally recognized subgenera, the paraphyly and basal position of Cytheritis argue that Morpho cannot be partitioned into monophyletic subgeneric units, because doing so violates a basic principle of phylogenetic classification. Enforcing the monophyly of Cytheritis significantly increased the number of steps of the tree in figure 12 (increase in 6 steps; WRS test: $T = 3.5$, $n = 7$, $\alpha = 0.047$), further weakening the validity of subgeneric classification. Based on our analysis (fig. 12), we therefore formally propose abandoning the subgeneric classification of Morpho and redefine the genus.

**THE GENUS MORPHO**

*Morpho* Fabricius, 1807

*Iphimededia* Fruhstorfer, 1913, NEW SYNONYM

*Iphixibia* Le Moul and Réal, 1962, NEW SYNONYM

*Cytheritis* Le Moul and Réal, 1962, NEW SYNONYM

*Balachowskyna* Le Moul and Réal, 1962, NEW SYNONYM

*Cypritis* Le Moul and Réal, 1962, NEW SYNONYM

*Pessonia* Le Moul and Réal, 1962, NEW SYNONYM

*Grasseia* Le Moul and Réal, 1962, NEW SYNONYM

*Schwartzia* Blandin, 1988, NEW SYNONYM

**DIAGNOSIS:** Within the Morphinae, *Morpho* is separated from *Antiirhea* and *Caerois* based on the following characters: male leg 2 with thin spines on dorsal side of tarsus (character 6:1); male leg 2 with four rows of ventral spines on tarsomere 5 (7:1); in dorsal view, pedunculi expanded laterally (23:1); dorsolateral edges of juxta with small depressions (34:1); lamella antea- and postvaginalis exposed (54:1); papilla anales hemispherical (65:1); recurrent vein present at the base of FW (forewing) discal cell, off Cubital system (71:1); HW (hindwing) cross-
Fig. 11. Trees yielded by the unweighted analysis of 120 characters (tree length = 338, CI = 0.41, RI = 0.65). A, B, Two of nine equally parsimonious trees that highlight the variation in position of M. aurora and M. deidamia; C, strict consensus of nine equally parsimonious trees for 30 taxa; D, strict consensus of three equally parsimonious trees from an analysis excluding M. aurora and M. deidamia (tree length = 310, CI = 0.45, RI = 0.68).
Fig. 12. Strict consensus of three equally parsimonious trees from the analysis of 120 characters for 30 taxa using SAW. Numbers above branches represent Bremer and bootstrap indices above 50% (e.g., 3/71). Characters supporting each numbered clade are listed in table 2. Subgeneric classification represented on the right is a synthesis of Fruhstorfer (1913), Le Moult and Réal (1962), and Blandin (1988).

vein m2–m3 absent (77:0), resulting in an open HW discal cell; males lack ventral patch of elongated androconial scales on FW cell Cu1 (85:0); males lack dorsal patch of elongated androconial scales on HW cell Cu2 (87:0); males lack dorsal androconial patch on HW cell A1 (88:0). Diagnostic larval characters given by DeVries et al. (1985)
### TABLE 2
Character Changes in Internal and Terminal Branches of the Strict Consensus Tree in Figure 12

Character changes were traced with MacClade 4 (Maddison and Maddison, 2000). Numbers in bold type represent unique and universal character changes. Abbreviations: a, homoplasy above; b, homoplasy below; c, changing above; u, unique and universal.

| Internal Branches |
|-------------------|
| **Clade 1: Genus Morphi** | **Clade 5** |
| 5:2 (a) | In dorsal view, gnathos broad |
| 6:1 (c) | Tegula with a diffuse light-colored marking at base |
| 7:1 (c) | Male leg 2, thin spines present on dorsal side of tarsus |
| 23:1 (u) | Male leg 2, ventral spines on tarsomere 5: four rows |
| 24:1 (u) | Appendices angularis well developed |
| 54:1 (c) | Lamella ante- and postvaginalis exposed, not covered by Stm 8 |
| 65:1 (c) | Papilla analis hemispherical |
| 71:1 (u) | Recurrent vein at base of FW discal cell, off Cubital system, present |
| 75:0 (a) | HW Cu2 produced to form a lobe at wing margin |
| 77:0 (u) | HW crossvein m2–m3 absent |
| 78:1 (a) | Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3 non-pigmented, transparent |
| 85:0 (u) | Male HW ventral patch of elongated androconial scales in cell Cu1 absent |
| 87:0 (u) | Male HW dorsal patch of elongated androconial scales in cell Cu2 absent |
| 88:0 (u) | Male HW dorsal androconial patch in cell A1 absent |
| **Clade 2** | **Clade 6** |
| 3:2 (b) | Ventral surface of labial palpus with white scales |
| 8:1 (u) | Male leg 2, ventral pulvillar process blunt |
| 19:0 (b) | Uncus dorsal ridges absent |
| 32:1 (u) | Juxta with a central prong |
| 43:0 (b) | Heavily sclerotized rim at posterior, internal edge of valva absent |
| 47:1 (u) | Spine at inner side of valva present |
| **Clade 3** | **Clade 7** |
| 18:0 (a) | Uncus tip more heavily sclerotized than base |
| 28:0 (a) | Gnathos with spines |
| 31:1 (a) | Distal end of gnathos blunt, more heavily sclerotized than base |
| 81:1 (a) | Male FW dorsal surface, cover scales at the apex of discal cell anterior to crossvein m2–m3, when similar to basal scales: rectangular |
| 21:0 (b) | Uncus ventral side expanded distally |
| 55:0 (u) | Sterigma smooth |
| 64:1 (b) | In ventral view, lobes between papilla analis and ostium bursa sclerotized |
| 101:0 (b) | Male HW ventral surface, ocellus in cell Cu2 absent |
| **Clade 4** | **Clade 8** |
| 50:0 (b) | Signum short |
| 51:1 (b) | Spines on signum reduced |
| 55:2 (b) | Sterigma with spines |
| 63:1 (b) | In ventral view, lobes in the region between papilla analis and ostium bursa well developed |
### TABLE 2
(Continued)

| Clade 11: Subgenus *Iphimelea* (continued) | Clade 18 |
|------------------------------------------|---------|
| 64:1 (b) In ventral view, lobes between papilla anales and ostium bursa sclerotized | 16:0 (b) Tuft of setae/scales on tegumen midline absent |
| 95:1 (ab) Male HW ventral surface, ocellus in cell Rs devoid of an outer whitish ring | 28:2 (ab) Gnathos smooth |
| | 31:0 (ab) Distal end of gnathos blunt, uniformly sclerotized to base |

| Clade 12 |
|------------------------------------------|
| 17:0 (b) Uncus elongated, dorsal ridges when present terminate well before tip of uncus |
| 18:1 (b) Uncus tip and base similarly sclerotized |
| 20:1 (b) Uncus ventral side rounded |
| 33:0 (b) Dorsal edge of juxta nearly straight |

| Clade 13 |
|------------------------------------------|
| 16:0 (b) Tuft of setae/scales on tegumen midline absent |
| 96:0 (b) Male HW ventral surface, ocellus in cell Rs smaller or same size as cell Rs |
| 113:1 (b) Male HW ventral surface, light-colored medial band: tan |

| Clade 14: Subgenus *Schwartzia* |
|------------------------------------------|
| 21:1 (b) Uncus ventral side not expanded |
| 53:1 (b) Antrum sclerotized |
| 74:0 (b) HW Cu1 produced to form a lobe at wing margin |
| 94:1 (b) Male HW ventral surface, costal cell white |
| 118:1 (b) Male HW ventral surface, longitudinal bands in cells 1A and 2A present |

| Clade 15: Subgenus *Cypritis* |
|------------------------------------------|
| 55:2 (b) Sterigma with spines |
| 94:1 (b) Male HW ventral surface, costal cell white |
| 102:1 (b) Male HW ventral surface, ocellus in cell Cu2 double |
| 103:1 (u) Male HW ventral surface, ocellus in cell 1A present |
| 117:0 (u) Male HW ventral surface, basal to submedial light-colored banding pattern absent |

| Clade 16 |
|------------------------------------------|
| 2:0 (a) Eyes hairy |
| 15:2 (ab) Hairpencil setae brown |
| 59:2 (b) Sclerotized plate anterior to sterigma split at midline |
| 69:1 (b) FW crossvein m1–m2 curved, conspicuously longer than m2–m3 |
| 93:0 (ab) FW ventral surface, longitudinal bands on discal cell absent |

| Clade 17 |
|------------------------------------------|
| 81:0 (ab) Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3, when similar to basal scales, fan-like or oval |
| 106:2 (ab) Male HW ventral surface, ocelli pupils white and purple |
| 109:2 (a) Ventral surface of wings devoid of distinguishable brown bands |
| 113:2 (a) Male HW ventral surface, light-colored medial band greenish |

| Clade 18 |
|------------------------------------------|
| 16:0 (b) Tuft of setae/scales on tegumen midline absent |
| 28:2 (ab) Gnathos smooth |
| 31:0 (ab) Distal end of gnathos blunt, uniformly sclerotized to base |

| Clade 19 |
|------------------------------------------|
| 46:0 (b) Size of spines at posterior edge of valva: small only |
| 55:2 (b) Sterigma with spines |
| 109:1 (b) Basal portion of wings darker than medial and apical portions |

| Clade 20 |
|------------------------------------------|
| 10:0 (ab) Female leg 1, pulvillus fused medially |
| 15:0 (b) Hairpencil setae white |
| 29:1 (u) Ventrolateral, basal process of gnathos present |
| 36:1 (b) Lateral spines of aedeagus present |
| 60:0 (b) Separate units of the sclerotized plate anterior to sterigma far apart, not close to midline |

| Clade 21 |
|------------------------------------------|
| 2:1 (b) Eyes bare |
| 21:0 (b) Uncus ventral side expanded distally |
| 53:1 (b) Antrum sclerotized |
| 56:1 (a) Anterolateral expansion of sterigma present |

| Clade 22: Subgenus *Pessionia* |
|------------------------------------------|
| 37:1 (u) Lateral spines of aedeagus symmetrical |
| 78:0 (b) Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3 pigmented |
| 89:1 (b) Wing main background pigmentation white |
| 90:1 (b) Male FW dorsal surface, dark band across apex of discal cell present |
| 97:1 (b) Male HW ventral surface, ocellus in cell M1 present |
| 98:1 (b) Male HW ventral surface, ocellus in cell M2 present |
| 106:1 (b) Male HW ventral surface, ocelli, pupils white only |

| Clade 23 |
|------------------------------------------|
| 5:2 (b) Tegula with a diffuse light colored marking at base |
| 10:1 (b) Female leg 1, pulvillus not fused medially |

| Clade 24 |
|------------------------------------------|
| 24:1 (b) Appendices angularis well developed |
| 27:0 (b) In dorsal view, gnathos curving inward |
| 31:2 (b) Distal end of gnathos pointed, uniformly sclerotized to base |
| 57:1 (b) Posterolateral projections of sterigma present |
| 58:0 (u) Anteromedial portion of sterigma expanded, forming a smooth lip curved posteriorly |

| Clade 25 |
|------------------------------------------|
| 18:1 (b) Uncus tip and base equally sclerotized |
| 107:1 (a) Male HW ventral surface, ocelli devoid of light brown ring around pupil |
are: stipes with 24–44 setae, and body with subdorsal tufts of barbed setae.

**DISCUSSION**

Ideally, the concept of subgenus should represent species groups that form monophyletic assemblages. In the particular case of *Morpho*, subsequent to the work of Le Moult and Réal (1962) subgenera were assumed to constitute natural groups, despite the ambiguities in defining them (appendix 4). Our study demonstrated a high level of morphological variation among and within *Morpho* subgenera, as suggested by both low Bremer indices and bootstrap values (fig. 12). This variation highlights the difficulty in providing characters that universally define these taxa (table 2). While our phylogenetic analyses do not support many aspects of previous *Morpho* subgeneric classifications, they do corroborate some traditional species groupings. For example, Fruhstorfer (1913) considered *M. hercules* Dalman, 1823, *M. theseus*, *M. perseus* (Cramer, 1779), and *M. hecuba* (Linnaeus, 1758) to be the most basal taxa within *Morpho*, and both Le Moult and Réal (1962) and Blandin (1988) maintained this view. Our results indicated that these species constitute a monophyletic group, but they occupy a more derived position within *Morpho* (fig. 12, clade 10). The grouping of *M. anaxibia* (Esper, 1798) with *M. hercules* and relatives (fig. 12, clade 9) agrees with Le Moult and Réal (1962), but the close relationships among these species and *M. hecuba* plus *M. cisseis* Felder, 1860 in our analyses have not been considered previously (fig. 12, clade 8). Our analyses also produced the novel hypothesis that *M. adonis* plus *M. euagena*, *M. aega* Hübner, 1819 plus *M. portis* Hübner, 1819, and *M. sulkowskyi* constitute basal clades within *Morpho*.

Although larval host plant records are

### TABLE 2 (Continued)

| **Terminal Branches** |
|-----------------------|
| **adonis**: 95:1 (b)  |
| **eugenia**: 72:1 (b) |
| **aega**: 31:3 (u), 39:0 (u), 59:1 (b), 93:0 (b), 95:1 (b), 96:0 (b), 100:1 (b), 105:1 (b), 113:1 (b), 114:0 (b) |
| **portis**: 5:1 (b), 44:1 (b), 45:0 (u), 74:0 (b), 76:0 (b), 117:2 (b) |
| **sulkowskyi**: 13:0 (u), 43:0 (b), 62:1 (b), 79:1 (u), 89:1 (b), 94:1 (b), 98:1 (b), 100:1 (b), 115:1 (b), 117:2 (b) |
| **hercules**: 4:0 (b), 31:0 (b), 46:1 (b) |
| **amphiadion**: 109:0 (b) |
| **perseus**: 3:1 (b), 97:1 (b), 98:1 (b) |
| **theseus**: 44:0 (b), 91:1 (b), 95:0 (b), 115:0 (b), 116:0 (b) |
| **hecuba**: 18:1 (b), 36:1 (b) |
| **cisseis**: 59:2 (b) |
| **anaxibia**: 11:1 (u), 57:1 (b), 62:1 (b), 83:1 (b), 97:1 (b), 105:1 (b), 113:1 (b) |
| **cypris**: 114:0 (b) |
| **rhetenor**: 16:0 (b), 31:0 (b), 44:1 (b), 78:0 (b), 97:1 (b), 98:1 (b), 105:2 (u), 113:1 (u) |
| **aurora**: 3:2 (b), 20:1 (b), 27:0 (b), 28:1 (b), 30:1 (b), 31:0 (b), 33:0 (b), 59:1 (b), 105:1 (b) |
| **godarti**: 5:0 (b), 55:2 (b) |
| **menelaus**: 61:0 (b), 115:1 (b) |
| **didius**: 4:0 (b), 4:2 (b), 21:0 (b), 28:1 (b), 81:1 (b) |
| **amathonte**: 92:0 (b), 97:1 (b), 101:0 (b), 112:1 (b), 115:1 (b) |
| **laertes**: 50:0 (b), 104:0 (b) |
| **caterinus**: 61:0 (b) |
| **polyphemus**: 27:2 (b), 56:0 (b) |
| **deidamia**: 27:2 (b), 55:2 (b), 92:0 (b), 93:1 (b), 118:1 (b) |
| **granadensis**: 30:1 (b), 93:1 (b), 110:1 (b), 118:1 (b) |
| **peleides**: 30:1 (b) |
| **achilaena**: 53:1 (b), 115:1 (b) |
| **achilles**: 92:0 (b) |
available for only 16 species of *Morpho* (Ackery, 1988; Lamas et al., 1995; Heredia and Alvarez-Lopes, 2002), our phylogeny provides a means for inferring the evolution of host plant associations (fig. 13). Caterpillars of *Antirrhea* and *Caeros* (sister genera of *Morpho*, DeVries et al., 1985) and many Brassolinae and Amathusiinae (putative sister groups to Morphinae, DeJong et al., 1996) feed predominantly on monocotyledons as larval host plants (see Ackery, 1988; Penz et al., 1999). Because species within *Morpho* known to use monocots as host plants (i.e., *M. aega*, *M. portis*, *M. sulkowskyi*) occupy a position basal to all other taxa (fig. 13), our phylogeny suggests that a host shift to dicotyledonous plants may have promoted species radiation and diversification within *Morpho*. Although the host plant of *M. aurora* is unknown, the position of this species in our phylogeny is particularly intriguing. Finding that *M. aurora* caterpillars feed on monocots would strengthen our placement of this species as a basal taxon within *Morpho*. On the other hand, a host shift to dicots may have occurred in the ancestor of *M. aurora* and its relatives. Thus, we think that documenting the life history of *M. aurora* should be a priority in future studies that attempt to reconstruct phylogenetic patterns of host plant use in *Morpho*.

Our field observations, in concert with Fruhstorfer (1913), DeVries and Martinez (1993), DeVries et al. (1997), DeVries et al. (1999b) and DeVries and Walla (2001), indicate that *M. hercules*, *M. amphitrition*, *M. theseus*, *M. perseus*, *M. anaxibia*, *M. hecuba*, *M. cisseis*, *M. cypris*, and *M. rhetenor* fly above or within the high forest canopy. Our phylogeny shows that canopy species form a monophyletic group (fig. 12, clade 8), suggesting a habitat shift from dark forest understory to an open environment pervaded by direct sunshine (fig. 13). As butterfly color patterns may be correlated with forest structure (e.g., Papageorgis, 1975; DeVries, 1988; DeVries et al., 1999a), this study raises the question as to whether a behavioral shift toward inhabiting the canopy influenced the evolution of color pattern in *M. hercules*, *M. hecuba*, and their relatives.

The basal placement of dull-colored *M. hercules* and relatives by Fruhstorfer (1913) implies that blue iridescence is derived. Compared to other nymphalids, the color of *Morpho* butterflies is exceptional in that blue iridescence is produced with basal scales, not cover scales (S. Berthier, personal commun.; CMP personal obs.), and this study is the first to suggest that blue iridescence is an ancestral trait that has been lost twice (fig. 13). We further note that some canopy species lack iridescence (i.e., *M. hercules*, *M. hecuba*, and their relatives; fig. 13), in addition to species known to fly in the subcanopy (*M. catenarius* and *M. polyphemus*). This implies a potential correlation among color pattern, flight behavior, and vertical stratification in *Morpho*, a topic that will be explored elsewhere (DeVries and Penz, in prep.).

Strong sexual dimorphism in *Morpho* may have evolved (or was lost) multiple times (fig. 13). Fruhstorfer (1913) noted that in species where males are exceptionally bright the females are normally dull-colored, and he hypothesized that in these instances females retained the coloration of their Brassolinae ancestors. This is consonant with Darwin's (1874) hypothesis that evolution of sexual dimorphism in butterflies is driven by female preference for brightly colored males. On the other hand, Wallace (1889) argued that sexual dimorphism could result from females acquiring defensive, cryptic coloration and diverging from male color patterns. Finally, inspired by observations that males often respond to visual stimuli, Silberglied (1988) proposed that sex-limited coloration in butterflies was driven by male-male interactions. An extension of Silberglied's hypothesis would be that iridescent, male-like *Morpho* females may increase their attractiveness by exploiting preexisting male-male antagonistic behaviors, thus representing an example of color pattern evolution via a male-biased sensory exploitation system (see Ryan et al., 1990), defined by Vane-Wright (1985) as “pseudosexual” selection.

Our phylogeny indicates that iridescence is an ancestral trait that has been lost twice, and historical literature and museum collections suggest that male-like, iridescent females occur at low frequencies in *M. aega*, *M. cypris*, and *M. rhetenor*. These observations imply that the genetic mechanisms determining sexual dimorphism are ancestral and univer-
Fig. 13. Morpho phylogeny where selected characters have been mapped.
sal in Morpho. That is to say, the same mechanisms determining female color pattern (either dull-colored or iridescent) may also be responsible for the complete loss of iridescence among separate lineages of Morpho.

CONCLUSIONS

For more than 200 years, big blue Morpho butterflies have captivated the imagination of natural historians, collectors, and the public. One result of this attention was the creation and use of a Morpho classification scheme based on recognition of taxonomic categories above the species level, without the benefit of modern systematic methods. Although this study supports some traditional taxonomic species groupings, our phylogenetic analysis argues against maintaining a subgeneric classification for Morpho. Accordingly we redefined Morpho and abandoned the use of subgenera to delimit species groups. Despite the paucity of natural history information, our phylogeny can serve to motivate studies on life histories, the correlation of color pattern and flight behavior with vertical flight height, and the evolution of sexual dimorphism in Morpho. We believe that studies focusing on these topics will not only provide a better understanding of species diversification within Morpho, but can provide an incentive for broader studies on the evolution of Neotropical butterflies in general.

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REFERENCES

Ackery, P. R. 1988. Host plants and classification: a review of nymphalid butterflies. Biological Journal of the Linnaean Society 33: 95–203.
Bilotta, I. 1992. Morfologia comparada da cabeça das espécies sulbrasileiras de Morphinae (Lepidoptera, Nymphalidae). Revista Brasileira de Zoologia 9: 261–271.
Bilotta, I. 1994a. Morfologia comparada do tórax das espécies sulbrasileiras de Morphinae (Lepidoptera, Nymphalidae). Revista Brasileira de Zoologia 11: 691–713.
Bilotta, I. 1994b. Morfologia 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 subgenera Iphime-deia and Schwartzia. Compiegne, France: Sciences Naturelles.
Blandin, P. 1993. The genus Morpho, Lepidoptera Nymphalidae. Part 2. The subgenera Iphixibia, Cytheritis, Balachowskyna, and Cypritis. Compiegne, France: Sciences Naturelles.
Bremer, K. 1994. Branch support and tree stability. Cladistics 10: 295–304.
D’Abrera, B. 1984. Butterflies of the Neotropical Region. Part II Danaidae, Ithomiidae, Heliconiidae & Morphidae. Victoria, Australia: Hill House.
Darwin, C. R. 1874. The descent of man and selection in relation to sex. London.
DeJong, R., R. I. Vane-Wright, and P. R. Ackery. 1996. The higher classification of butterflies (Lepidoptera): problems and prospects. Entomologica Scandinavica 27: 65–101.
DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton: Princeton University Press.
DeVries, P. J. 1988. Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. Journal of Research on the Lepidoptera 26: 98–108.
DeVries, P. J., I. J. Kitching, and R. I. Vane-Wright. 1985. The systematic position of Antirrhea and Caerolis, with comments on the higher classification of the Nymphalidae (Lepidoptera). Systematic Entomology 10: 11–32.
DeVries, P. J., R. Lande, and D. Murray. 1999. Associations of co-mimetic ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest. Biological Journal of the Linnaean Society 62: 343–364.
DeVries, F. J., and G. E. Martinez. 1993. The morphology, natural history, and behavior of the early stages of Morpho cypris (Nymphalidae: Lepidoptera: Nymphalidae).
Morphinae)—140 years after formal recognition of the butterfly. Journal of the New York Entomological Society 101: 515–530.

DeVries, P. J., D. Murray, and R. Lande. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. Biological Journal of the Linnaean Society 62: 343–364.

DeVries, P. J., and T. R. Walla. 2001. Species diversity and community structure in Neotropical fruit-feeding butterflies. Biological Journal of the Linnean Society 74: 1–15.

DeVries, P. J., T. R. Walla, and H. Greeney. 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. Biological Journal of the Linnaean Society 68: 333–353.

Downey, J. C., and A. C. Allyn. 1975. Wing-scale morphology and nomenclature. Bulletin of the Allyn Museum (31): 1–32.

Farris, J. A. 1969. A successive approximations approach to character weighting. Systematic Zoology 18: 374–385.

Felsenstein, J. F. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Fruhstorfer, H. 1913. Family: Morphidae. In A. Seitz (editor), Macrolepidoptera of the world, vol. 5: 333–356. Stuttgart: Alfred Kernen.

Heredia, M. D., and H. Alvarez-Lopes. 2002. Biología y conservación de Morpho sulkowskyi Kollar, 1850 (Nymphalidae: Morphinae) en Colombia. Tropical Lepidoptera (in press).

Klots, A. B. 1970. Lepidoptera. In S. L. Tuxen (editor), Macrolepidoptera of the world: 333–356. Stuttgart: Alfred Kernen.

Larson, A. 1994. The comparison of morphological and molecular data in phylogenetic systematics. In B. Schierwater, B. Streit, G. P. Wagner, and R. DeSalle (editors), Molecular ecology and evolution: approaches and applications: 371–390. Basel, Switzerland: Birkhäuser.

Le Moult, E., and P. Réal. 1962. Les Morpho D’Amérique du Sud et Centrale. Novitates Entomologicae (supplement). Paris, France: Éditions du Cabinet Entomologique, E. Le Moult.

Maddison, W. P., and D. R. Maddison. 2000. MacClade: version 4.0 PPC. Sunderland, MA: Sinauer.

Papageorgis, C. 1975. Mimicry in Neotropical butterflies. American Scientist 63: 522–532.

Penz, C. M., A. Aiello, and R. B. Srygley. 1999. Early stages of Caligo illioneus and C. idome neus (Nymphalidae, Brassolini) from Panama, with remarks on larval food plants for the subfamily. Journal of the Lepidopterists’ Society 53: 142–152.

Ryan, M. J., J. H. Fox, W. Wilczynski, and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog Physalaemus pustulosus. Nature 343: 66–67.

Scoble, M. 1992. The Lepidoptera: form, function and diversity. London: British Museum (Natural History).

Silberglied, R. 1988. Visual communication and sexual selection in butterflies. In R. I. Vane-Wright and P. R. Ackery (editors), The biology of butterflies: 207–223. Princeton: Princeton University Press.

Swofford, D. M. 1998. PAUP: phylogenetic analysis using parsimony, version 4.0b8. Sunderland, MA: Sinauer.

Templeton, A. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. Evolution 37: 221–244.

Vane-Wright, R. I. 1985. The role of pseudosexual selection in the evolution of butterfly colour patterns. In R. I. Vane-Wright and P. R. Ackery (editors), The biology of butterflies: 251–253. Princeton, NJ: Princeton University Press.

Wallace, A. R. 1889. Darwinism. London.

Young, A. M., and A. Muyschondt. 1972. Biology of Morpho polyphemus in El Salvador. Journal of the New York Entomological Society 80: 18–42.

Young, A. M., and A. Muyschondt. 1973. The biology of Morpho peleides in Central America. Caribbean Journal of Science 13: 1–49.
### Appendix 1

**Examined Material Used to Score Characters**

Specimens marked with an asterisk were dissected.

| Species                      | Location Details                                                                 |
|------------------------------|----------------------------------------------------------------------------------|
| **Antirrhea avernus**        | 1 male and 1 female: Peru, Satipo* (MPM); 1 female: Ecuador, Sucumbios Garza Cocha* (PJD) |
| **archaea**                  | 1 male: no data* (MPM); 1 female: Brazil, Santa Catarina* (MPM)                  |
| **Caerois gertrudus**        | 1 male: Ecuador, Esmeraldas, Tonchigue* (PJD); 1 female: no data* (PJD)           |
| **Morpho (Cytheritis) adonis**| 1 male: French Guiana* (LACM); 1 male: Guiana (GA); 1 male: Peru, Tingo Maria (GA); 1 male: Brazil, Rondônia, Ariquemas (GA); 1 female: Peru, Huanuco (LACM) |
| **eugenia**                  | 1 male: Newcomb (USNM); 1 male: French Guiana (LACM); 1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 female: no data* (LACM) |
| **aega**                     | 1 male: Brazil (LACM)*; 1 male: Brazil, Sta. Catarina (USNM); 1 female: Brazil, Sta. Catarina* (LACM); 1 female: no data* (MPM); 1 female: Brazil, Sta. Catarina (USNM); 1 female: Colombia (USNM) |
| **sulkowskyi**               | 1 male: Colombia, Muzo* (LACM); 1 male: Colombia, New Granada* (MPM); 1 male: Ecuador, Baños (USNM); 1 male: Ecuador, Macas (USNM); 1 female: Ecuador, Tungurahua* (LACM); 1 female: Ecuador, Rio Blanco (USNM); 1 female: Ecuador (USNM) |

*Balachowskyna aurora*

1 male: Bolivia* (LACM); 1 male: Bolivia (FMNH); 1 female: Bolivia, Coroico* (USNM); 1 female: Peru, Chanchamayo* (USNM); 1 female: Peru, La Merced (LACM)

*Balaclowskyna aurora*

1 male: Bolivia (LACM); 1 male: Bolivia (FMNH); 1 female: Bolivia, Coroico* (USNM); 1 female: Peru, Chanchamayo* (USNM); 1 female: Peru, La Merced (LACM)

*Cypritis cypris*

1 male: Colombia, Boyaca* (USNM); 1 male: no data* (MPM); 1 male: Colombia (LACM); 1 female: Colombia (USNM); 1 female: no data* (USNM)

*Cypritis rhetenor*

1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: Peru (LACM); 1 male: no data (GA); 1 female: no data (LACM); 1 female: Peru, Chanchamayo (USNM); 1 female: no data (GA)

*Iphixibia anaxibia*

1 male: Brazil, São Paulo* (LACM); 1 male: Brazil, Santa Catarina, Corupa* (GA); 1 female: Brazil, Santa Catarina, Taio* (MPM)

*Schwartzia hecuba*

1 male: Brazil, Manaus, Itacoatiara* (MPM); 1 male: Brazil, Para Obidos (MPM); 1 male: no data* (LACM); 1 female: Brazil, Amazonas, Itacoatiara* (MPM); 1 female: no data (LACM); 1 female: Brazil, Para Obidos (MPM)

*Cissellia cisellia*

1 male: Brazil, Pará* (LACM); 1 male: Brazil, Pará, Obidos (GA); 1 female: Brazil, Rondônia, Caucalândia* (GA); 1 female: Brazil, Pará (LACM)
### (Iphimeadeia)

| Species    | Collection Details                                                                 |
|------------|-----------------------------------------------------------------------------------|
| hercules   | 1 male: Brazil*; 1 male: no data (LACM); 1 male and 2 females: Brazil, Pará, Obidos (LACM); 1 female: Brazil, Rio de Janeiro, Nova Friburgo* (MPM) |
| amphitriton| 1 male: Peru, La Merced* (LACM); 1 female: no data (LACM)                         |
| perseus    | 1 male: Brazil, Pará, Obidos* (LACM); 1 male: Brazil, Amazonas (LACM); 1 male: Ecuador, Napo, Mishaualli (LACM); 1 male: Brazil, Pará, Obidos (GA); 1 female: Brazil, Pará, Santarém* (MPM) |
| theseus    | 1 male: Costa Rica* (PJD); 1 male: Costa Rica, Puntarenas (PJD); 1 female: Costa Rica, Puntarenas (PJD); 1 female: Colombia* (LACM) |

### (Grasseia)

| Species    | Collection Details                                                                 |
|------------|-----------------------------------------------------------------------------------|
| godarti    | 1 male: Bolivia, Buenavista, Ichino* (MPM); 1 male: Bolivia (LACM); 1 female: no data (MPM), 1 female: Bolivia (LACM) |
| menelaus   | 1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: Ecuador, Napo, Rio Pucuno (LACM); 1 male: Brazil, Rondonia, Ariquiamas; 1 female: Brazil, Pará, Obidos* (MPM); 1 female: Ecuador, Sucumbios, Garza Cocha (PJD) |
| didius     | 1 male: Peru* (USNM); 1 male Peru (USNM); 1 male: Peru, Tingo Maria (LACM); 1 female: Peru* (USNM); 1 female: Peru, La Merced (LACM) |
| amathonte  | 1 male: Costa Rica, Puntarenas, Osa* (PJD); 1 male: Costa Rica (MPM); 1 female: Ecuador, Pastaza* (USNM); 1 female: Colombia, Muzo* (MPM); 1 female: Napo, Mishaualli (LACM) |

### (Pessonia)

| Species    | Collection Details                                                                 |
|------------|-----------------------------------------------------------------------------------|
| laertes    | 1 male: no data* (LACM); 1 female: Brazil, Rio de Janeiro, Nova Friburgo* (MPM) |
| catenarius | 1 male: Brazil, Santa Catarina, Tayo* (LACM); 1 female: Brazil, Santa Catarina* (LACM) |
| polyphemus | 1 male: Mexico, Oaxaca, Palomas* (LACM); 1 male: Mexico, Chiapas (LACM); 1 female: Mexico, Oaxaca (LACM); 1 female: Mexico, Guerrero* (LACM); 1 female: no data (LACM) |

### (Morpho)

| Species    | Collection Details                                                                 |
|------------|-----------------------------------------------------------------------------------|
| deidamia   | 1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: French Guiana* (MPM); 1 male: Brazil, Pará, Obidos (MPM); 1 female: Brazil, Pará, Obidos* (MPM) |
| granadensis | 1 male: Costa Rica San Jose* (PJD); 1 male: Costa Rica, San Jose (MPM); 1 female: Colombia, Bogota (USNM); 1 female: no data* (MPM) |
| peleides    | 1 male: Costa Rica (MPM); 1 male: Colombia, Boyaca* (LACM); 1 female: Costa Rica, Puntarenas* (PJD); 1 male: Mexico, San Luis Potosi (MPM); 1 female: Honduras* (MPM); 1 female: Mexico, Chimalapapa (MPM) |
| achillaena  | 1 male: Brazil* (LACM); 1 female: Brazil, Santa Catarina, Joinville* (MPM); 1 female: Brazil (LACM) |
| achilles    | 1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: Brazil, Mato Grosso, Cuiabá (USNM); 1 male: Brazil, Pará, Obidos (USNM); 1 female: T.F.A. Isla del Esfuerzo* (USNM); 1 female: Ecuador, Sucumbios, Garza Cocha (PJD); 1 female: Brazil (USNM) |
APPENDIX 2

LIST OF CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

Characters are illustrated in figures 14–17.

FLIGHT HEIGHT

1. Adult flight confined mostly to: understory (0), midstory (1), canopy (2). Comments: Fruhstorfer (1913) used this as a defining character for the subgenus Iphi-medea. This character was coded based on our own observations, those published in the literature, and observations made available by colleagues.

GENERAL MORPHOLOGY

2. Eyes: hairy (0); bare (1).
3. Ventral surface of labial palpus with: bright orange scales (0); faint orange/cream scales (1); white scales (2).
4. Tuft of white scales on patagium: absent (0); present (1).
5. Tegula: solid color (0); with a discrete spot at base (1); with a diffuse light-colored marking at base (2).
6. Male leg 2, thin spines on dorsal side of tarsus: absent (0); present (1).
7. Male leg 2, ventral spines on tarsomere 5: two rows (0); four rows (1).
8. Male leg 2, ventral pulvilar process: pointed (0); blunt (1). Figure 14A and B.
9. Female leg 1, pretarsal claws: absent or vestigial, single (0); well developed, paired (1).
10. Female leg 1, pulvillus: fused medially (0); not fused medially (1). Figure 14C and D.
11. Iridescent scales on dorsum of thorax and abdomen: absent (0), present (1).
12. Inner side of abdominal tergites 1 and 2, apodeme with longitudinal ribs in a loop: absent (0); present (1). Figure 14E.

MALE GENITALIA

13. Hairpencils: absent (0); present (1). Surprisingly, hairpencils were absent in two dissected M. sulkowskyi males. Both dissected specimens had intact, original abdomens, unlike all other examined males of this species (including many specimens from MPM that have not been specifically used to score characters and therefore are not listed in appendix 1).
14. Hairpencil setae: thin (0); thick (1). Figure 14H and I.
15. Hairpencil setae: white (0); orange (1); brown (2).
16. Tuft of setae/scales on tegumen midline: absent (0); present (1).
17. Uncus: elongated, dorsal ridges when present terminate well before tip of uncus (0); short, dorsal ridges when present terminate near tip of uncus (1). Figures 14F and G, 15D and E. Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
18. Uncus tip: more heavily sclerotized than base (0); tip and base similarly sclerotized (1). Figure 15D and E.
19. Uncus dorsal ridges: absent (0); present (1). Figure 14F. Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
20. Uncus ventral side: forming sharp lateral ridges (0); rounded (1). Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
21. Uncus ventral side: expanded distally (0); not expanded (1). Figure 14F, G, and L. Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
22. Uncus: slightly expanded ventrally (0); strongly expanded (1). Figure 14L.
23. In dorsal view, pedunculi: flattened (0); expanded laterally (1).
24. Appendices angularis: reduced (0); well developed (1). Figure 15B.
25. Gnathos: absent (0); present (1).
26. In dorsal view, gnathos: narrow (0); broad (1). Figure 14F and L. Adapted from...
Fig. 15. Dissections showing characters used in the analysis. Male valva, internal view: A, *M. adonis*. Male genitalia in lateral view: B, *M. granadensis*. C, Dorsal view of the right gnathos of *M. granadensis*. Male genitalia in lateral view: D, *M. rhetenor*; E, *M. theseus*. Scale bars represent 0.5 mm.
Fig. 16. Dissections showing characters used in the analysis. Scale bars represent 0.5 mm. Female genitalia in ventral view: **A**, *M. deidamia*; **B**, *M. achillaena*; **C**, *M. catenarius*; **D**, *M. aega*. Corpus bursa: **E**, *M. achilles*, **F**, *M. aurora*. Scale bars represent 0.5 mm.
Fig. 17. Dissections showing characters used in the analysis. Hindwing in ventral view: A, *M. aega*; B, *M. peleides*. Scales from male specimens, dorsal surface of the forewing, distal portion of the discal cell; for each pair, cover scale on the left, basal scale on the right: C, *M. eugenia*; D, *M. aega*; E, *M. cypris*; F, *M. anaxibia*.

26. Character used in the analysis: A, *M. aega*; B, *M. peleides*. Scales from male specimens, dorsal surface of the forewing, distal portion of the discal cell; for each pair, cover scale on the left, basal scale on the right: C, *M. eugenia*; D, *M. aega*; E, *M. cypris*; F, *M. anaxibia*.

27. In dorsal view, gnathos: curving inward (0); straight (1); curving outward (2). Figure 14F and L.

28. Gnathos: with spines (0); with rounded protuberances (1); smooth (2). Figures 14L and 15E. Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).

29. Ventrolateral, basal process of gnathos: absent (0); present (1). Figure 15B.

30. In dorsal view, distal end of gnathos: a single process (0); with a subterminal, lateral process (1). Figure 15C.

31. Distal end of gnathos: blunt, uniformly sclerotized to base (0); blunt, more heavily sclerotized than base (1); pointed, uniformly sclerotized to base (2); pointed, more heavily sclerotized than base (3). Figure 14F and L.

32. Juxta: simple flat plate (0); with a central prong (1). Figure 14M.

33. Dorsal edge of juxta: nearly straight (0); arched (1). Figure 14N.

34. Small depressions at the dorsolateral edges of juxta: absent (0); present (1). Figure 14N.

35. Aedeagus: broadened at tip (0); not broadened (1).

36. Lateral spines of aedeagus: absent (0); present (1). Figure 14K. Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).

37. Lateral spines of aedeagus: asymmetrical (0); symmetrical (1). Figure 14J and K.

38. Valva: laterally flattened (0); conspicuous (1).
ously convex (1). Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
39. Costa of valva: projected at base (0); not projected (1).
40. Setae on costal margin: absent or few (0); numerous (1).
41. Posterior edge of valva: rounded (0); pointed (1). Figure 15A and E.
42. Pointed posterior edge of valva: elongated, forming a thin rod-like process (0); short (1).
43. Heavily sclerotized rim at posterior, internal edge of valva: absent (0); present (1). Figure 15A and B.
44. Posterior edge of valva: forming a bulge immediately before sclerotized rim (0); without a bulge (1). Figure 15B and D.
45. Spines at posterior edge of valva: absent (0); present (1). Figure 15B. Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
46. Size of spines at posterior edge of valva: small only (0); small and large (1).
47. Spine at inner side of valva: absent (0), present (1). Figure 15A.

FEMALE GENITALIA
48. Corpus bursa: elongated (0); nearly rounded (1).
49. Signum: absent (0); present (1).
50. Signum: short (0); long (1). Figure 16E and F.
51. Spines on signum: well developed (0); reduced (1). Comments: We define well developed as 36 μm or larger.
52. Ductus bursa: short (0); long (1).
53. Antrum: membranous (0); sclerotized (1).
54. Lamella ante and postvaginalis: retracted, covered by Stn 8 (0); exposed (1).
55. Sterigma: smooth (0); with nubs (1); with spines (2).
56. Anterolateral expansion of sterigma: absent (0); present (1). Figure 16C and D.
57. Posterolateral projections of sterigma: absent (0); present (1). Figure 16A and B.
58. Anteromedial portion of sterigma: expanded, forming a smooth lip curved posteriorly (0); not expanded (1). Figure 16A and B.
59. Sclerotized plate anterior to sterigma: absent (0); forming a continuous band (1); split at midline (2). Figure 16A and D.
60. Separate units of sclerotized plate anterior to sterigma: far apart, not close to midline (0); close together, near midline (1). Figure 16A.
61. Cuticular pleating on lateral edges of sterigma: absent (0); present (1).
62. Protruding cuticular pleating posterior to sterigma: absent (0); present (1).
63. In ventral view, lobes between papilla anales and ostium bursa: reduced (0); well developed (1). Figure 16D.
64. In ventral view, lobes between papilla anales and ostium bursa: membranous (0); sclerotized (1).
65. Papilla anales: triangular (0); hemispherical (1). Figure 16A. Adapted from DeVries et al. (1985).
66. Some setae as long as, or longer than, cross section of one segment of papilla anales (0); all setae shorter than cross section of one segment of papilla anales (1).
67. Setae on dorsal portion of papilla anales: inserted in long tubercles (0); inserted in short tubercles (1).

WING VENATION
68. FW R1 and R2: reduced at base, connection with Radial system inconspicuous (0); not reduced, connection with Radial system evident (1).
69. FW crossvein m1–m2: straight, similar in length to m2–m3 (0); curved, conspicuously longer than m2–m3 (1).
70. Recurrent vein on FW crossvein m1–m2: absent (0); present (1).
71. Recurrent vein at base of FW discal cell, off Cubital system: absent (0); present (1).
72. HW M2: with a basal bend (0); devoid of a basal bend (1).
73. HW M3: produced to form a lobe at wing margin (0); similar to other veins, wing margin devoid of a lobe (1). Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
74. HW Cu1: produced to form a lobe at wing margin (0); similar to other veins, wing margin devoid of a lobe (1). Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
75. HW Cu2: produced to form a lobe at wing margin (0); similar to other veins, wing margin devoid of a lobe (1). Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
76. HW edge around tornus: scalloped (0); smooth (1). Adapted from Fruhstorfer (1913) and Le Moult and Réal (1962).
77. HW crossvein m2–m3: absent (0); present (1). Adapted from Fruhstorfer (1913), Le Moult and Réal (1962), and DeVries et al. (1985).
WING SCALES

78. Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3: pigmented (0); non-pigmented, transparent (1).
79. Male FW dorsal surface, basal scales at apex of discal cell anterior to crossvein m2–m3: pigmented (0); non-pigmented, transparent (1).
80. Male FW dorsal surface, size of cover scales at apex of discal cell anterior to crossvein m2–m3: similar to basal scales (0); smaller than basal scales (1). Figure 17C–F.
81. Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3, when similar to basal scales: fan-like or oval (0); rectangular (1). Figure 17C and F.
82. Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3, when smaller than basal scales: similar length to basal scales (0); conspicuously shorter than basal scales (1). Figure 17D and E.
83. Male FW dorsal surface, edge of cover scales at apex of discal cell anterior to crossvein m2–m3: denticulated (0); smooth (1).
84. Male FW dorsal surface, ephemeral androconial patch in cell Cu2: absent (0); present (1).
85. Male FW ventral patch of elongated androconial scales 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).
88. Male HW dorsal androconial patch in cell A1: absent (0); present (1).

WING COLOR PATTERN

89. Wing main background pigmentation: brown (0); white (1). Adapted from Fruhstorfer (1913), and Le Moult and Réal (1962).
90. Male FW dorsal surface, dark band across apex of discal cell: absent (0); present (1).
91. FW dorsal surface, discal cell nearly completely dark, contrasting with the rest of the wing at least in one sex (0); not dark (1).
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).
93. FW ventral surface, longitudinal bands in discal cell: absent (0); present (1).
94. Male HW ventral surface, costal cell: brown (0); white (1).
95. Male HW ventral surface, ocellus in cell Rs: with an outer whitish ring, complete or incomplete (0); devoid of an outer whitish ring (1).
96. Male HW ventral surface, ocellus in cell Rs: smaller or same size as cell Rs (0); larger than cell Rs, expanding over veins Rs and M1 (1).
97. Male HW ventral surface, ocellus in cell M1: absent (0); present (1).
98. Male HW ventral surface, ocellus in cell M2: absent (0); present (1).
99. Male HW ventral surface, ocellus in cell M3: absent (0); present (1).
100. Male HW ventral surface, ocellus in cell Cu1: basal (0); distal (1). Figure 17A and B.
101. Male HW ventral surface, ocellus in cell Cu2: absent (0); present (1).
102. Male HW ventral surface, ocellus in cell Cu2: single (0); double (1).
103. Male HW ventral surface, ocellus in cell 1A: absent (0); present (1).
104. Male HW ventral surface, alignment angle between ocellus in cell Rs and ocelli in cells M3, Cu1, and Cu2 (measured toward base of HW): nearly 180° (0); larger than 90° but smaller than 180° (1). Figure 17A and B. Adapted from Le Moult and Réal (1962).
105. Male HW ventral surface, ocelli rings: outer brown ring followed by an orange ring and inner brown ring (0); outer brown ring followed by an orange ring, inner brown ring absent (1); outer brown ring absent, orange ring and inner brown ring present (2). Adapted from Le Moult and Réal (1962) and Blandin (1993).
106. Male HW ventral surface, ocelli, pupils: absent (0); white only (1); white and purple (2).
107. Male HW ventral surface, ocelli: with light brown ring around pupil (0); devoid of light brown ring (1).
108. Male HW ventral surface, location of ocelli: near distal edge of medial brown band (0); near proximal edge of medial brown band (1).
109. Ventral surface of wings with distinguishable brown bands uniform in coloration (or nearly so) across the length of wings (0); basal portion of wings darker than medial and apical portions (1); wings devoid of brown bands (2).
10. Orange or yellow bands on ventral surface of wings: absent (0); present (1).
11. Male HW ventral surface, light-colored medial band: absent (0); present (1).
12. Male HW ventral surface, light-colored medial band: similar in width or narrower than cell Sc+Rs is tall (0); broader than cell Sc+Rs is tall (1).
13. Male HW ventral surface, light-colored medial band: white (0); tan (1); greenish (2).
14. Male HW ventral surface, light-colored medial band: straight across wing (0); angled (1).
15. Male HW ventral surface, light-colored medial band: continuous (0); interrupted (1).
16. Male HW ventral surface, light-colored medial band: undulating to follow the ocelli edges (0); straight, not undulating to follow the ocelli edges (1).
17. Male HW ventral surface, basal to sub- medial light-colored banding pattern: absent (0); two to three light bands, complete or incomplete (1); four or more light bands (2).
18. Male HW ventral surface, longitudinal bands in cells 1A and 2A: absent (0); present (1).
19. Sexual dimorphism: strong to moderate (0); weak (1). Comments: Species with strong sexual dimorphism are those in which females are not iridescent (i.e., *M. adonis, M. eugenia, M. aega, M. cypris*, and *M. rhetenor*). When males and females differed somewhat, but are both iridescent (i.e., *M. anaxibia, M. godarti, M. didius, M. amathonte*, and *M. deidamia*), such species were classified as showing moderate sexual dimorphism.

**Larval Host Plant**

20. Larval host plants: monocotyledonous (0); dicotyledonous (1).
Species of *Morpho* have been classified in the following subgenera: 1–5, *Cytheritis*; 6–9, *Iphimedea*; 10–11, *Cypritis*; 12–13, *Schwartzia*; 14, *Balachowskyna*; 15, *Iphixibia*; 16–19, *Grasseia*; 20–22, *Pessonia*; 23–27, *Morpho*.

### APPENDIX 3

#### DATA MATRIX

| 10  | 20  | 30  | 40  |
|-----|-----|-----|-----|
|     |     |     |     |

#### OUTGROUPS

**Antirhea**  

|      |      |      |
|------|------|------|
| avernas |      |      |
| archaea |      |      |
| Caeoroides | geradrudus |      |

#### INGROUP

|      |      |      |      |
|------|------|------|------|
| 1. adonis | 11202111? | ?10000100 | 1710101200 | 01?1107?111 |
| 2. eugenia | 1121211101 | 010000100 | 1710101200 | 01?1107?111 |
| 3. aega | 7?11211001 | 010000010 | 0110102000 | 301110701 |
| 4. sulkowski | 0101211001 | 000?10010 | 1710111000 | 1011107110 |
| 5. portis | 011717??01 | 01?000010 | 0110000000 | 1011107010 |
| 6. hercules | 2100011001 | 0102111010 | 0710111000 | 0011107110 |
| 7. amphitiron | 21011110?? | 0?10211110 | 0011011000 | 1011107110 |
| 8. perseus | 2111111001 | 0102011110 | 0011110000 | 1011107110 |
| 9. thesesus | 21011110?? | 0102011110 | 0011110000 | 1011107110 |
| 10. cypris | 2101111001 | 0100111010 | 0011110000 | 1011107110 |
| 11. rhetenor | 2110111100 | 0100010100 | 0011110000 | 1011107110 |
| 12. hecuba | 2111111000 | 0102111110 | 1711111000 | 1011107110 |
| 13. cissis | 211111??77 | 0?10211101 | 1711101100 | 1011107110 |
| 14. aurora | 1121111100 | 010000011 | 1710110101 | 0011107110 |
| 15. anaxibia | 2111111101 | 1010111010 | 0011011000 | 1011107110 |
| 16. menelambus | 0011111001 | 0102111101 | 1711101100 | 1011107110 |
| 17. godarti | 701107??01 | 0102111010 | 1711111000 | 1011107110 |
| 18. didius | 000027??01 | 0102010100 | 0011011000 | 001107110 |
| 19. anamonti | 000111107 | 0102010100 | 1711112000 | 001107110 |
| 20. laertes | 7?71111000 | 0100001010 | 0011011110 | 0011111110 |
| 21. catenarius | 11(3,2)1210001 | 0010001010 | 0011112110 | 0011111110 |
| 22. polyphemus | 1121211100 | 0010001010 | 0011211010 | 001111110 |
| 23. deidamia | 0111111000 | 0010010100 | 0011121210 | 0011111010 |
| 24. granadensis | 0001111000 | 0010001010 | 1711110211 | 2001110110 |
| 25. peleides | 0001111000 | 0010011110 | 0111012110 | 2001111010 |
| 26. achilaena | 0001111000 | 0010001110 | 1711110210 | 2001110110 |
| 27. achilles | 0001111000 | 0010011110 | 1711110210 | 2001110110 |

| 50  | 60  | 70  | 80  |
|-----|-----|-----|-----|
| 1001110111 | 11070700?? | 010001111 | 001111100 |
| 11071001?? | ?00700??7 | 007501011 | 0011110100 |
| 1107???1?7 | ????????? | ????????? | 1011101010 |
| 1107??1111 | 0100110121 | 007??11110 | 1111010100 |
| 1107111011 | 0010001010 | 0011111100 | 1011000110 |
| 1107???111 | 0011010101 | 0011111100 | 1011000110 |
| 0711101110 | 1000121010 | 0100111100 | 1111100000 |
| 0711100117 | ????????? | ????????? | 1111100000 |
| 0711100110 | 1001201121 | 0111111000 | 1111100000 |
## APPENDIX 3
(Continued)

| 9  | theseus  | 0?10100?1?1? | ??????????? | ??????????? | 11111000000 |
| 10 | cypris    | 0?11110111    | 001120010? | 100?11110000 | 101110010 | 101110010 |
| 11 | rhetenor  | 0?11110011    | 000120010? | 100?11100000 | 101110010 | 101110010 |
| 12 | hecuba    | 0?11100011    | 001110010? | 100?11100000 | 1110110000 | 1110110000 |
| 13 | cisseis   | 0?10100111    | 0011100120 | 10001100000 | 1110110100 | 1110110100 |
| 14 | aurora    | 0?10101011    | 000110011? | 00101011000 | 101110010 | 101110010 |
| 15 | anaxibia  | 0?10100011    | 0001101010 | 110?11110000 | 101110010 | 101110010 |
| 16 | menelaus  | 0?10110011    | 0001100121 | 000?11111000 | 101110010 | 101110010 |
| 17 | godarti   | 0?10100111    | 0001200121 | 100?11111000 | 101110010 | 101110010 |
| 18 | didus     | 0?10100111    | 0001200121 | 100?11111000 | 101110010 | 101110010 |
| 19 | amathonte | 0?10100011    | 0001200121 | 100?11111000 | 101110010 | 101110010 |
| 20 | laerates  | 0?10110111    | 0011110120 | 100?11011000 | 101110010 | 101110010 |
| 21 | catenarius| 0?10101111    | 0011110120 | 000?11011000 | 101110010 | 101110010 |
| 22 | polyphemus| 0?10110111    | 00111100120| 100?11111000 | 101110010 | 101110010 |
| 23 | deidamia  | 0?10110111    | 0011210120 | 100?11111000 | 101110010 | 101110010 |
| 24 | granadensis| 0?10110111 | 0001101020 | 100?11111000 | 101110010 | 101110010 |
| 25 | peleides  | 0?10110111?   | 0?01101020 | 100?11111000 | 101110010 | 101110010 |
| 26 | achillaena| 0?10110111    | 0011110120 | 100?11111000 | 101110010 | 101110010 |
| 27 | achilles  | 0?10110111    | 0001101020 | 100?111111? | 1?11101000 | 101110010 | 101110010 |

### OUTGROUPS

- Antirhea
  - avernus 0?10111100? ??????????? ??????????? ??????????? 0 ?????110?
  - archaea 0?10111110? ??????????? ??????????? ??????????? ?????????0

- Caeloris
  - gerdrudius 0?0011010? ??????????? ??????????? ????????? ?????????0

### INGROUP

1. adonis 0?00000000 0011010000 100010000 0????110?
2. eugenia 0?00000000 0011010000 100010000 0????110?
3. asea 0?00000000 1101000111 0?01101000 10110111000
4. suikowskij 0?00000000 1101101011 100010000 1001112110
5. portis 0?00000000 1101100100 1001101010 1001112110
6. hercules 0?00000000 0110110100 1001101010 1101111101
7. amphitriton 0?00000000 0110110100 1001101010 1101111111
8. perseus 0?00000000 0110110110 1001101010 1111111101
9. theseus 0?00000000 1110000010 1001101011 1111010000
10. cypris 0?00000000 011000010 1110201000 1010000100
11. rhetenor 0?00000000 0111000110 111200010 1111000001
12. hecuba 0?00000000 0111001000 1001101010 1110111101
13. cisseis 0?00000000 0111001000 1001101011 1101111111
14. aurora 0?00000000 1100000100 1001101000 1001000101
15. anaxibia 0?10000000 110000100 1001101000 1111111111
16. menelaus 0?10000000 110000010 1001202020 1021101011
17. godarti 0?10000000 1100000010 1001020101 1010100100
18. didus 0?10000000 1100000010 1001020101 1021001001
19. amathonte 0?10000000 100000010 1000120100 1021001001
20. laerates 0?00000000 1000001110 1000010000 0????????11
21. catenarius 0?00000000 1107011010 1001101000 0????????11
22. polyphemus 0?00000000 1107011010 1001101000 0????????11
23. deidamia 0?00000000 1010010010 1001202070 1021101101
24. granadensis 0?00000000 111000100 1001202072 1021011111
25. peleides 0?00000000 1000010010 1001021212 10012101011
26. achillaena 0?00000000 1100010010 1001202120 1021001011
27. achilles 0?00000000 1000010010 1001020120 1021101011
Definitions of *Morpho* subgenera by Fruhstorfer (1913), Le Moult and Réal (1962), and Blandin (1988, 1993) are provided.

**Subgenus *Iphimedeia* Fruhstorfer, 1913**

*Fruhstorfer (1913):* Lacking metallic gloss, color varies from greenish blue to whitish in all gradations. Upper discocellular long, middle only inappreciably concave (i.e., proximally curved), the lower straight and placed at right angles to the anterior median. Forewing cell very narrow at the apex. Uncus broad, lateral clasps strikingly flat, valves lack distal spines.

*Le Moult and Réal (1962):* Quoted verbatim from Fruhstorfer (1913).

*Blandin (1988):* Distal edge of the forewing sometimes almost straight, but more often with at least a slight concavity between the ends of M1 and Cu1. Forewing apex always more pointed than in *Schwartzia*, often clearly protruding. Hindwing edge forming clear undulations at the ends of the veins, particularly M3, Cu2, and Cu1, with small true caudal appendages in some species. Pattern of the ventral surface little contrasted: background tint varies from light to dark through a range of ochre with yellowish gray or reddish brown nuances. Generally, the tone is lighter in females than in males. Silver areas less bright than in *Schwartzia*, and silver scales reduced or absent. On the hindwings, the dark edge of the basal area forms, depending on the individual, an obtuse, straight or acute angle between M2 and M3; it goes towards the anal edge in an almost perpendicular direction at A1 and reaches it near the end of A2.

**Subgenus *Schwartzia* Blandin, 1988**

*Blandin (1988):* Distal edge of the forewing more or less straight (very weak concavity or convexity). Forewing apex always more rounded than *Iphimedeia*, never protruding. Pattern on the ventral surface very contrasted with black and silver markings on a brown, more or less reddish background. Silvery areas more developed in females than in males. Hindwing costal edge, base of the wing, and proximal portion of the anal edge silvery white. Basal area totally bounded by a black distal border, with some black twisted patterns and two silvery white marks forming a discontinuous transversal band. Wide silvery patch outside the black border. The black border forms an acute or (rarely) a right angle between M2 and M3, it goes towards the anal edge of the wing in an almost perpendicular direction at A1 and reaches it more or less at the end of A2.

**Subgenus *Ipixibia* Le Moult and Réal, 1962**

*Le Moult and Réal (1962):* Discal area broad and little contrasted with respect to the background. Ocelli faded, but well defined in the proximal area. Uncus in dorsal view broadly sub-triangular with two broad, extended wings, more or less erect or sub-horizontal, where six nerves can be seen.

*Blandin (1993):* Forewing distal edge slightly concave. Forewing apex slightly protruding and rounded. Hindwing distal edge weakly undulate, lacking protrusions at the ends of the veins and lacking a wide lobe at the point of the cubital veins. Underside pattern with the same structure as that of the subgenus *Iphimedeia* but the line of hindwing ocelli curves inward less strongly. Ocelli structure modified by the disappearance of the black pupil, the ochre circle coming into contact with the silver center which can sometimes be absent.

**Subgenus *Cytheritis* Le Moult and Réal, 1962**

*Le Moult and Réal (1962):* Subuncus sometimes straight, when it is inserted vertically it expands horizontally, simuate-dentate but more often spiny or with rods.

*Blandin (1993):* Forewing distal edge from slightly concave to weakly convex. Distal edge of the hindwing from weakly to strongly undulate with a small lobe at the point of the cubital veins in some species. Pattern of the ventral surface variable but always characterized by having the line of ocelli on the hindwing nearly straight or weakly curved inward and forming a very acute angle with the anal edge.

**Subgenus *Balachowskyna* Le Moult and Réal, 1962**

*Le Moult and Réal (1962):* Distinct from *Morpho* by wings shape and color, ocelli arrangement and constitution, dorsal wing pattern, and other less obvious characters. Although the uncus resembles the less accentuated characteristic of the *portis-aega* group of *Cytheritis*, the subuncus (gnathos in this study) has a distorted form that resembles certain *Pessonia*. Apex of the valva with teeth similar to *Morpho* sensu strictu, although displaying a general shape similar to the *rhodopteron* group.

*Blandin (1988):* Forewing distal edge some-
times mildly undulate, slightly concave. Forewing apex sometimes clearly projecting. Hindwing distal edge weakly to moderately undulate, with no lobe formed at the point of the cubital veins. Coloration of the ventral surface similar to Grasseia although rather pale and uniform. The genitalia shows affinities with Cytheritis, while wing morphology (shape, underside pattern) is similar to Grasseia and Morpho.

Subgenus Cypritis Le Moul and Réal, 1962

Le Moul and Réal (1962): Uncus shape intermediate between that of Iphixibia plus Iphimedeia and Grasseia: in lateral view it resembles the former two, although smaller; it lacks the well developed wings present in Grasseia.

Blandin (1988): Forewing distal edge concave; apex relatively protruding, or even strongly elongated. Hindwing with a regular contour and slight undulations, but lacking protrusions at the ends of veins Cu1 and Cu2. Hindwing ocelli form a line broken nearly at a right angle. Ocelli M3–Cu1, Cu1–Cu2, Cu2–PCu, PCu–A1 and A1–A2 form a line making a very obtuse angle with the basal part of the anal edge of the wing. Hindwing ventral, basal area practically uniform, without any patterns—its brown coloring lighter on the anal region. Pronounced sexual dimorphism: males very brilliant metallic blue, possibly with white markings and bands, females yellow ochre with very dark brown, almost black patterns (except for M. cypris female form cyanides). Female ventral surface distinguished from that of males by the large extension of the yellow ochre colored discal areas.

Subgenus Pessonia Le Moul and Réal, 1962

Le Moul and Réal (1962): Wings pale. Genitalia similar to that of subgenus Morpho, distal portion of subuncus (gnathos in this study) inserted in the vertical plan but extending in the horizontal plan and with a rounded outline. Uncus as tall as broad, and almost equally long. Aedeagus with small spines.

Subgenus Grasseia Le Moul and Réal, 1962

Le Moul and Réal (1962): Disal band often the same thickness as the diameter of the ocelli, or strongly irregular, reduced or interrupted at the wing veins to produce contiguous markings. In dorsal view, uncus strongly sub-triangular with two large longitudinal wings more or less erect or sub-horizontal. Subuncus tip (gnathos in this study) oval, more or less elongated, spiny. Valvae similar to Iphimedeia and Iphixibia.

Subgenus Morpho Fabricius, 1807

Le Moul and Réal (1962): Subuncus tip (gnathos in this study) inserted and developed in the vertical plan, thus allowing for the development of a basal, ventral expansion (similar to Pessonia). Subuncus tip (gnathos in this study) may be curved distally in an oblique plan, but never rounded. Uncus always longer than tall or broad. Aedeagus spines well developed.

Note added in proof: After going to press it came to our attention that M. sulkowskyi males from Colombia have vestigial hairpencils. These are composed of sparse “hairs” that are easily detached during KOH treatment (M. D. Heredia, personal comm.). Although this finding does not alter the topology of the tree (fig. 12), for completeness’ sake we note that the hairpencils of M. sulkowskyi can be either absent or greatly reduced.
