



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

Authors: PENZ, CARLA M., and DeVRIES, P. J.

Source: American Museum Novitates, 2002(3374) : 1-33

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2002\)374<0001:PAOMBN>2.0.CO;2](https://doi.org/10.1206/0003-0082(2002)374<0001:PAOMBN>2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3374, 33 pp., 17 figures, 2 tables

July 25, 2002

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

CARLA M. PENZ¹ AND P. J. DEVRIES²

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

¹ Department of Invertebrate Zoology, Milwaukee Public Museum, 800 West Wells Street, Milwaukee, WI 53233, and Programa de Pós-Graduação em Biociências, Pontifícia Universidade Católica do Rio Grande do Sul, Av. Ipiranga 6681, Porto Alegre, RS, 90619-900, Brazil. e-mail: flea@mpm.edu

² Research Associate, Division of Invertebrate Zoology, American Museum of Natural History; Center for Biodiversity Studies, Milwaukee Public Museum, 800 West Wells Street, Milwaukee, WI 53233. e-mail: pjd@mpm.edu

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 Muysshondt (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*, *Antirrhoea* Hübner, 1822 and *Caerois* Hübner, 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 Real (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-

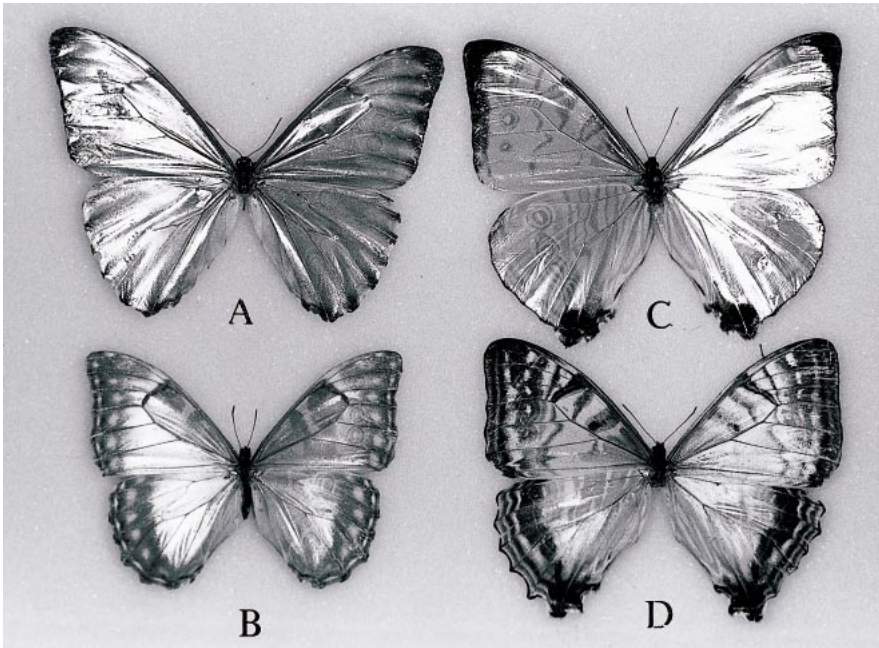


Fig. 1. Dorsal view of *Morpho (Balachowskyina) aurora*: **A**, male, Bolivia, FW length of 56.2 mm (FMNH); **B**, female, Peru, La Merced, FW length of 47.5 mm (LACM); *Morpho (Cytheritis) sulkowskyi*: **C**, male, Colombia, Muzo, FW length of 56.4 mm (LACM); **D**, female, Ecuador, Tungurahua, FW length of 52.7 mm (LACM).

ed a well-resolved tree in which the subgenera *Iphimedeia* 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 and *Morpho* Fabricius, 1807 were paraphyletic (*Balachowskyina* 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 *Balachowskyina* and *Iphixibia*, two species of each *Cypritis* and *Schwartzia*, three of *Pessonia*, four each of *Grasseia* and *Iphimedeia*, 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. amphitriton* 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.

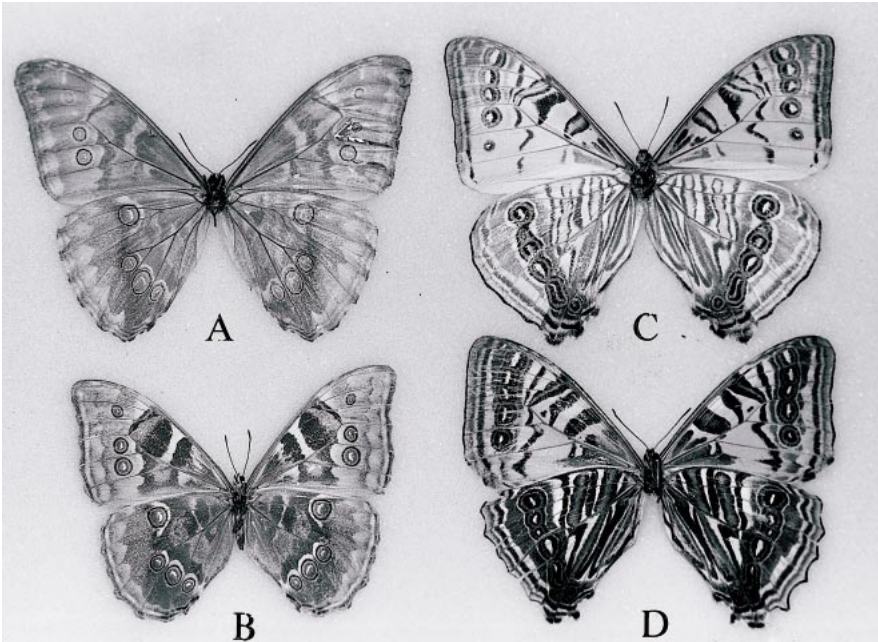


Fig. 2. Ventral view of *Morpho (Balachowskyna) aurora*: A, male, B, female; *Morpho (Cytheritis) sulkowskyi*: C, male, D, female. See legend of figure 1 for locality data and FW lengths.

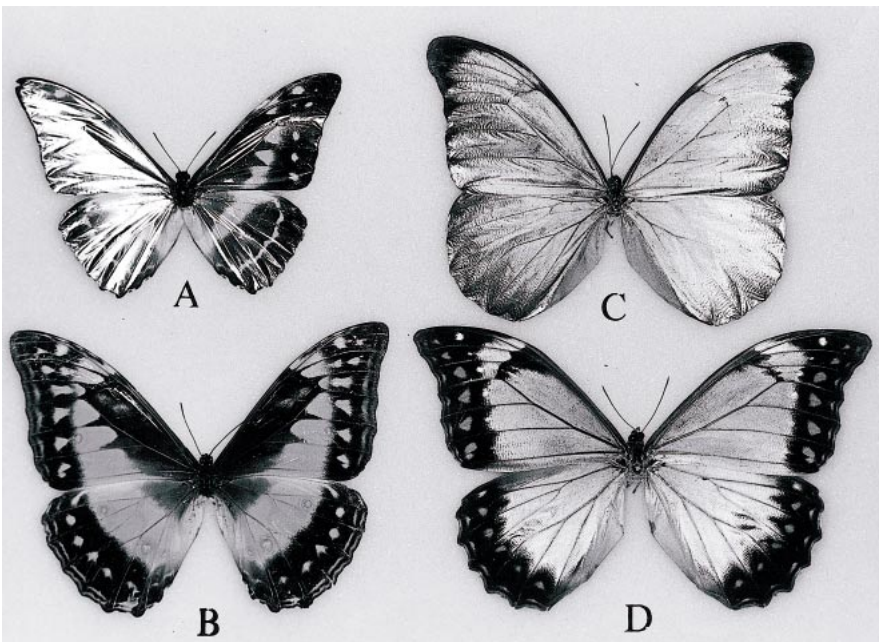


Fig. 3. Dorsal view of *Morpho (Cypritis) cypris*: A, male, Colombia, Boyacá, FW length of 59.3 mm (LACM); B, female, Colombia, FW length of 73.2 mm (USNM); *Morpho (Iphixibia) anaxibia*: C, male, Brazil, FW length of 75.5 mm (LACM); D, female, Brazil, Santa Catarina, FW length of 81.4 mm (MPM).

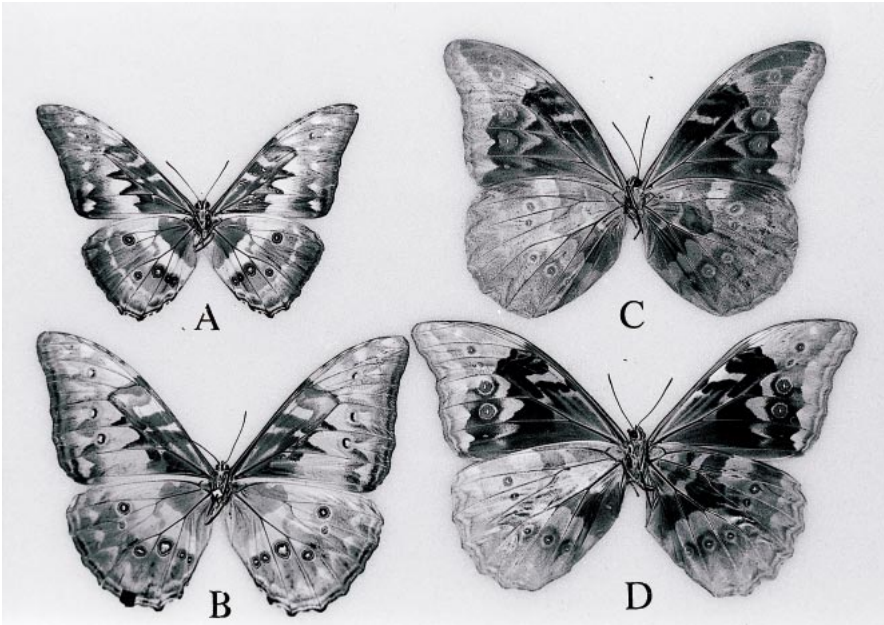


Fig. 4. Ventral view of *Morpho (Cypritis) cypris*: **A**, male, **B**, female; *Morpho (Iphixibia) anaxibia*: **C**, male, **D**, female. See legend of figure 3 for locality data and FW lengths.

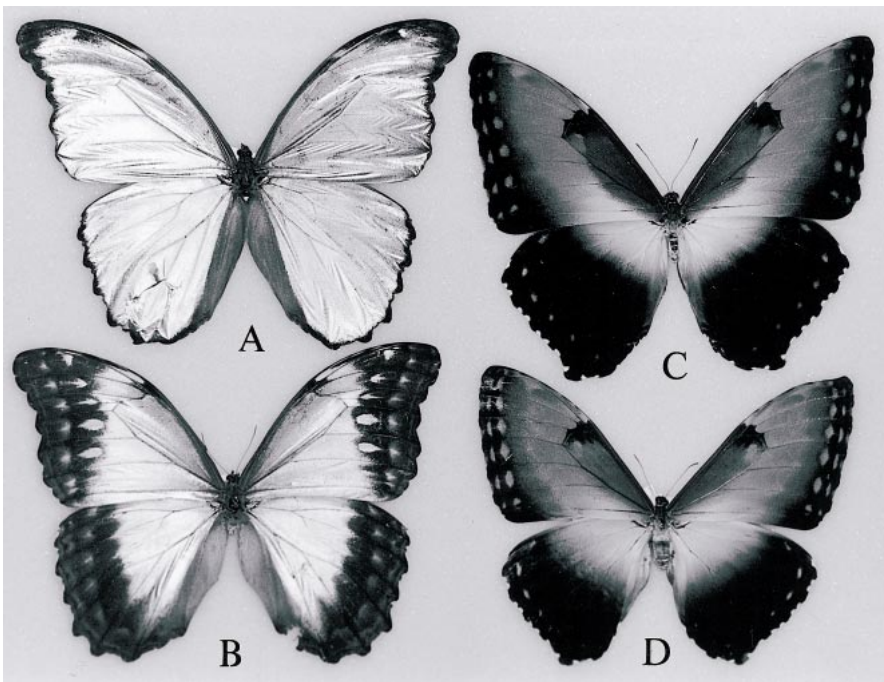


Fig. 5. Dorsal view of *Morpho (Grasseia) amathonte*: **A**, male, Costa Rica, FW length of 88.2 mm (MPM); **B**, female Colombia, Muzo, FW length of 99 mm (MPM); *Morpho (Schwartzia) hecuba*: **C**, male, Brazil, Obidos, Pará, FW length of 91.4 mm (MPM); **D**, female, Brazil, Obidos, Pará, FW length of 85 mm (MPM).

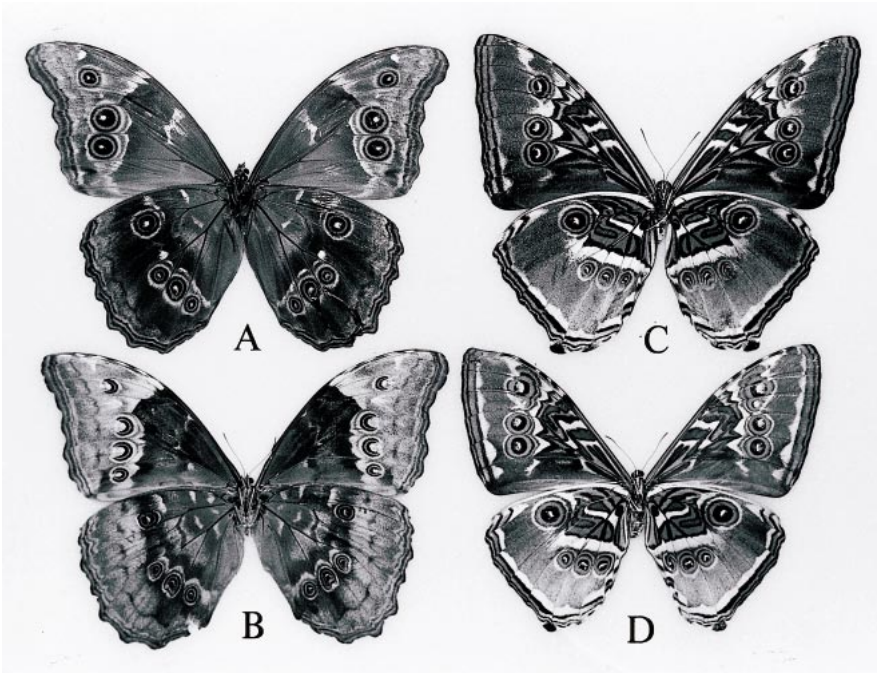


Fig. 6. Ventral view of *Morpho (Grasseia) amathonte*: **A**, male; **B**, female; *Morpho (Schwartzia) hecuba*: **C**, male; **D**, female. See legend of figure 5 for locality data and FW lengths.

As in most insects, the abdomens of *Morpho* butterflies contain lipids. To prevent the lipids from greasing the iridescent wings and sullyng 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-

nal contents microsurgically removed and carefully replaced with cotton wool, miraculously leaving the genitalia intact. The practice of excising and/or changing *Morpho* abdomens illustrates how potential scientific utility is sacrificed on the altar of cosmetic traditionalism.

In sum, availability of useful material played a peculiar and important role in taxon sampling for this study. We utilized only species for which preserved material included specimens that had intact, original abdomens.

Examined specimens (appendix 1) were obtained from: Natural History Museum of Los Angeles County (LACM), National Museum of Natural History (USNM), The Field Museum (FMNH), Milwaukee Public Museum (MPM), and private collections of P. DeVries (PJD), and G. Austin (GA).

PREPARATION OF MATERIAL AND TERMINOLOGY

Female forelegs, male mesolegs, and male and female abdomens were prepared using a standard 10% solution of potassium hydroxide, and subsequently stored in glycerol. No

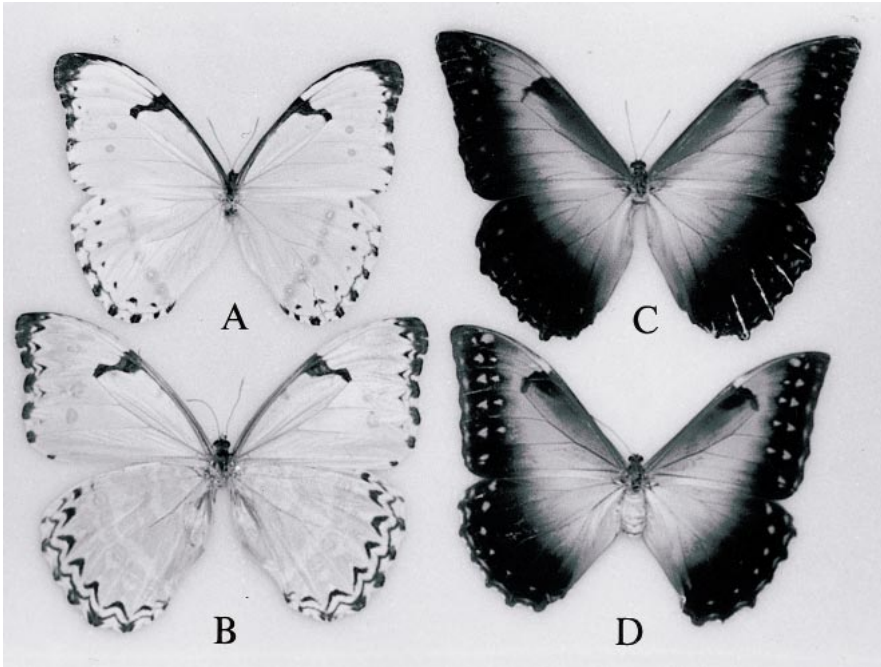


Fig. 7. Dorsal view of *Morpho (Pessonia) catenarius*: **A**, male, Brazil, Santa Catarina, FW length of 66.8 mm (LACM); **B**, female, Brazil, Santa Catarina, FW length of 77 mm (LACM); *Morpho (Iphimedeia) perseus*: **C**, male, Brazil, lower Amazon, FW length of 79 mm (LACM); **D**, female, Brazil, Pará, FW length of 75.5 mm (LACM).

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-

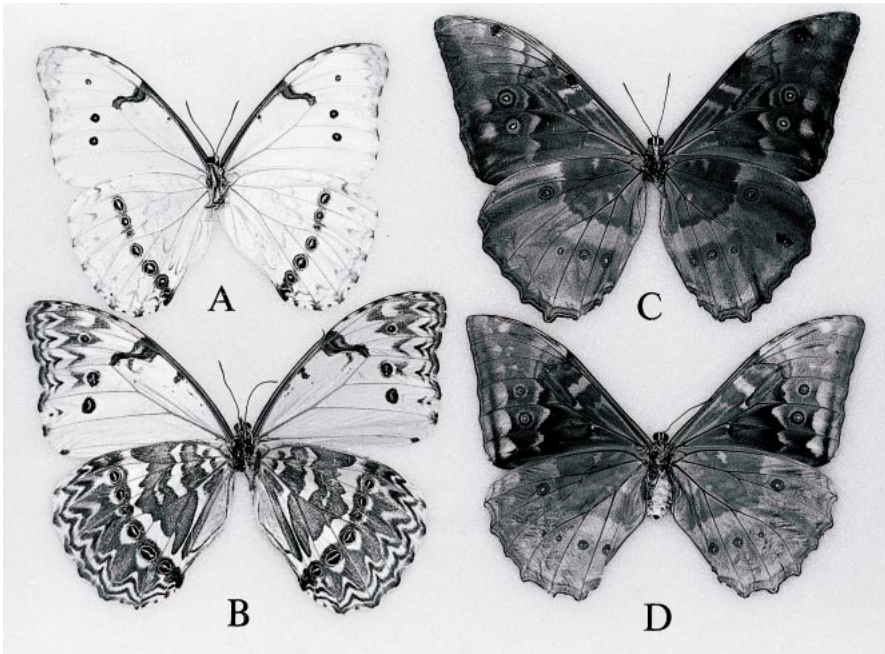


Fig. 8. Ventral view of *Morpho (Pessonia) catenarius*: **A**, male, **B**, female; *Morpho (Iphimedeia) perseus*: **C**, male, **D**, female. See legend of figure 7 for locality data and FW lengths.

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 *Iphimedeia*, *Schwartzia*, and *Iphixibia* in appendix 4). Although the continuous variation between a “more pointed” or “less pointed” forewing makes it difficult to define charac-

ter 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 Moult 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 Moult and Réal (1962) and in Bilotta (1994b).

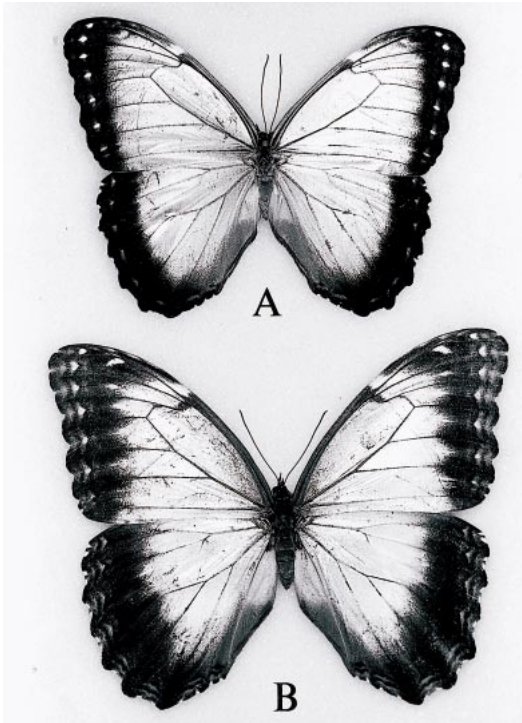


Fig. 9. Dorsal view of *Morpho (Morpho) peleides*: **A**, male, Mexico, San Luis Potosi, FW length of 56.7 mm (MPM); **B**, female, Chimalapa, FW length of 72.3 mm (MPM).

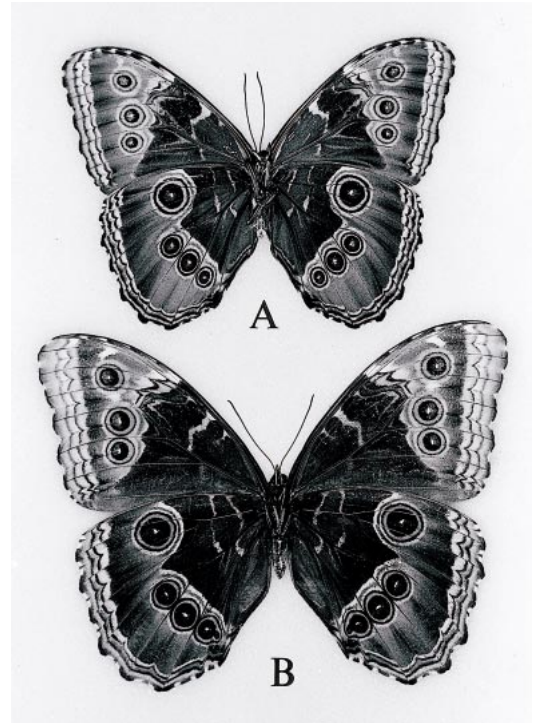


Fig. 10. Ventral view of *Morpho (Morpho) peleides*: **A**, male, **B**, female. See legend of figure 9 for locality data and FW lengths.

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. (Balachowskyina) aurora* Westwood, 1851 (monotypic) and *M. (Morpho) deidamia* Hübner, 1816. Three trees favored a basal position of *M. (Balachowskyina) 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 *Balachowskyina* in appendix 4). *Morpho (Morpho) deidamia* appeared as a sister taxon to *Pessonia* in six trees (three of which contained the *Bala-*

TABLE 1
Sample of 16 Species of *Morpho* in the Milwaukee Public Museum Showing the Percentage of Individuals That Lacked Abdomens

Sexes are not discriminated.

Species	Total	With abdomens	Lacking abdomens	% lacking abdomens
<i>hercules</i>	19	13	6	31
<i>theseus</i>	15	13	2	13
<i>perseus</i>	18	11	7	39
<i>hecuba</i>	16	11	5	31
<i>cisseis</i>	3	0	3	100
<i>portis</i>	20	11	9	45
<i>sulkowskyi</i>	22	11	11	5
<i>aega</i>	48	31	17	35
<i>aurora</i>	11	6	5	45
<i>adonis</i>	11	5	6	54
<i>eugenia</i>	1	0	1	100
<i>rhetenor</i>	23	9	14	61
<i>cypris</i>	7	5	2	29
<i>anaxibia</i>	13	8	5	38
<i>godarti</i>	12	6	6	5
<i>menelaus</i>	57	32	25	44
Total	293	172	121	41

chowskyina + *Pessonnia* 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. polyphe-mus* 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, *Iphimedeia*, *Schwartzia*, *Cypritis*, and *Pessonnia* are monophyletic, and we corroborate the apparent monotypy of *Balachowskyina* 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

Iphimedeia Fruhstorfer, 1913, NEW SYNONYM

Iphixibia Le Moult and Réal, 1962, NEW SYNONYM

Cytheritis Le Moult and Réal, 1962, NEW SYNONYM

Balachowskyina Le Moult and Réal, 1962, NEW SYNONYM

Cypritis Le Moult and Réal, 1962, NEW SYNONYM

Pessonnia Le Moult and Réal, 1962, NEW SYNONYM

Grasseia Le Moult and Réal, 1962, NEW SYNONYM

Schwartzia Blandin, 1988, NEW SYNONYM

DIAGNOSIS: Within the Morphinae, *Morpho* is separated from *Antirrhoea* 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 ante- 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-

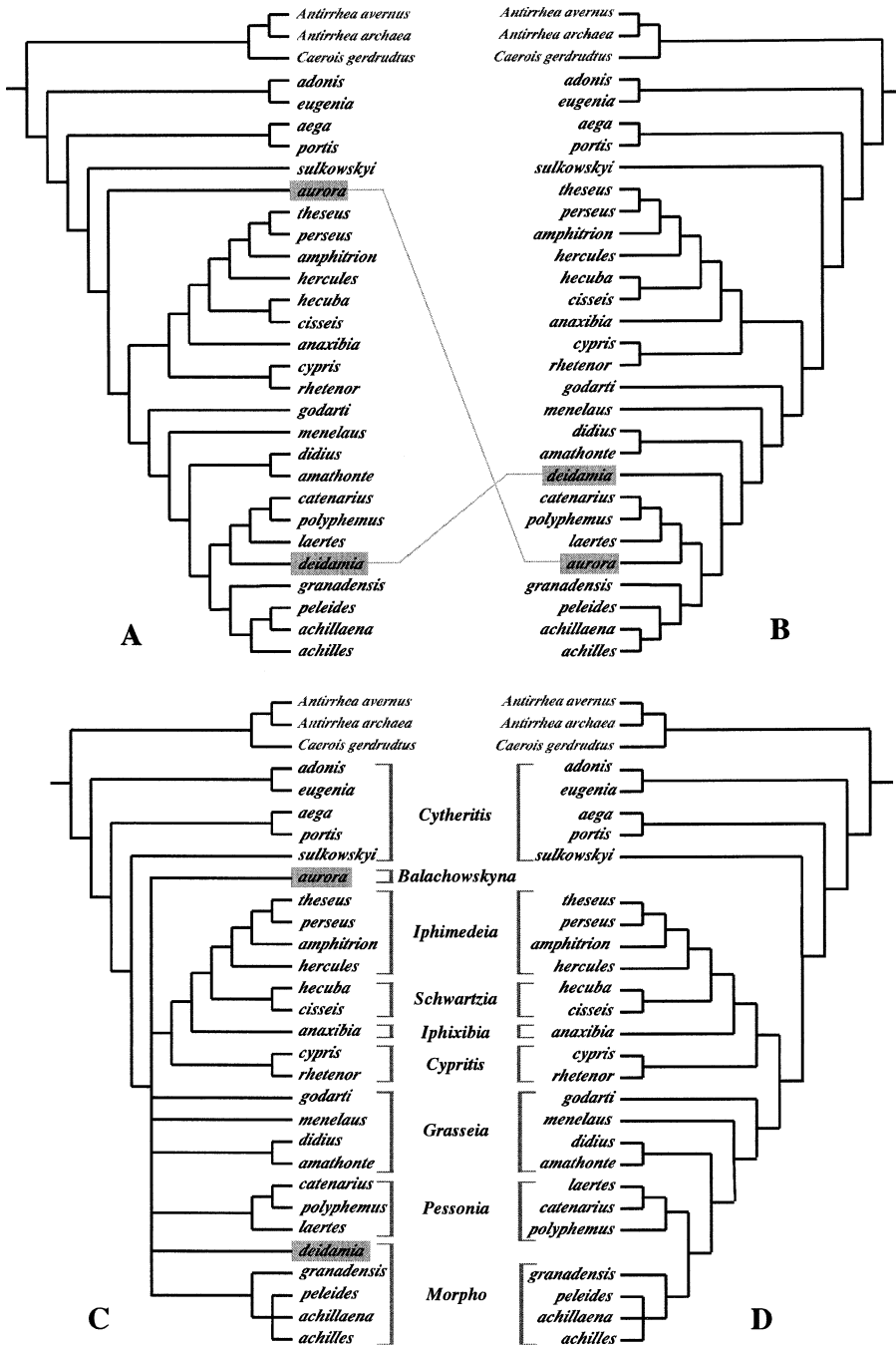


Fig. 11. Trees yielded by the unweighted analysis of 120 characters (tree length = 338, CI = 0.41, RI = 0.65). **A**, **B**, Two of nine equally parsimonious trees that highlight the variation in position of *M. aurora* and *M. deidamia*; **C**, strict consensus of nine equally parsimonious trees for 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).

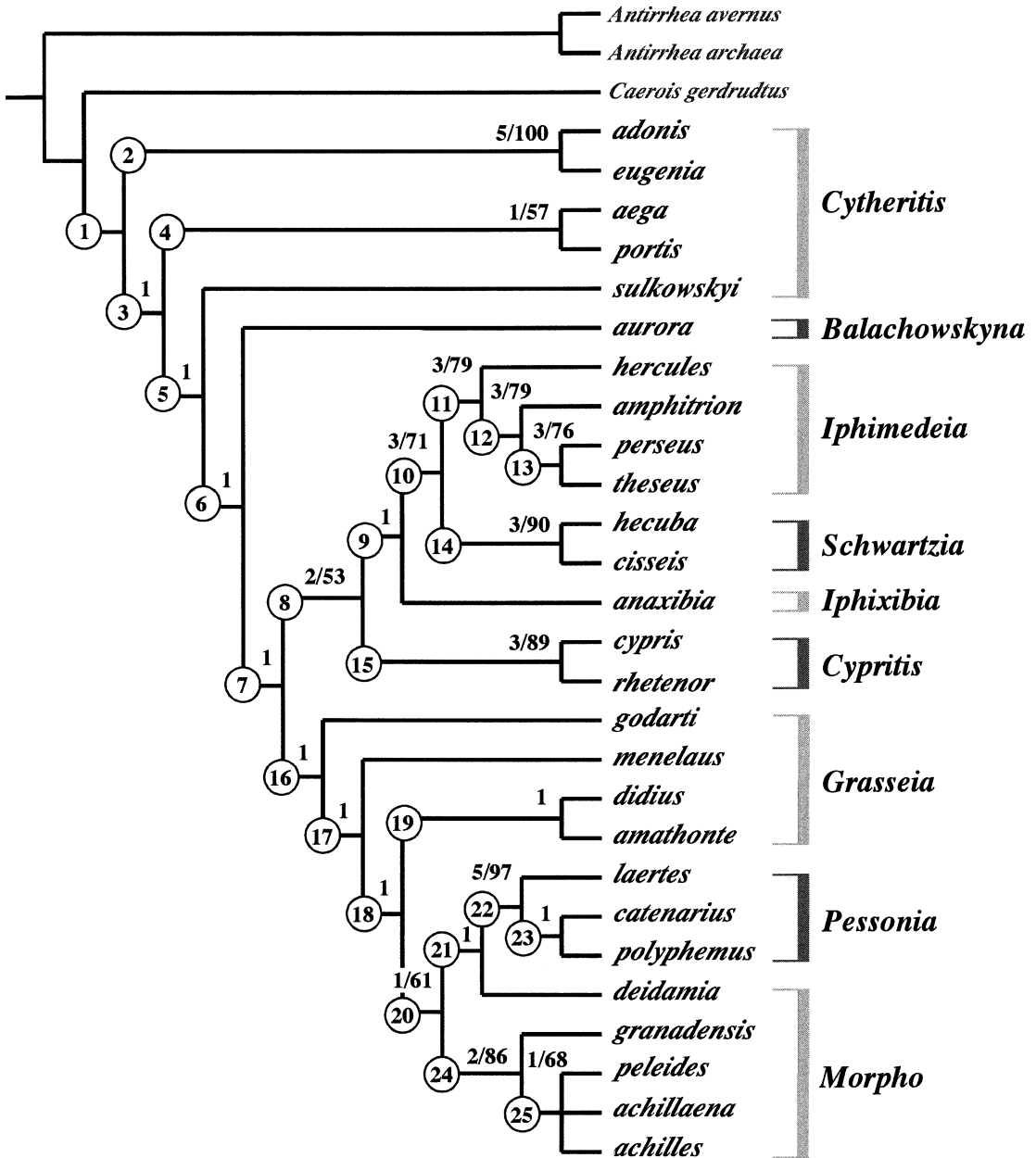


Fig. 12. Strict consensus of three equally parsimonious trees from the analysis of 120 characters for 30 taxa using SAW. Numbers above branches represent Bremer and bootstrap indices above 50% (e.g., 3/71). Characters supporting each numbered clade are listed in table 2. Subgeneric classification represented on the right is a synthesis of Fruhstorfer (1913), Le Moutl 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 <i>Morpho</i>	
5:2 (a)	Tegula with a diffuse light-colored marking at base
6:1 (c)	Male leg 2, thin spines present on dorsal side of tarsus
7:1 (c)	Male leg 2, ventral spines on tarsomere 5: four rows
23:1 (u)	In dorsal view, pedunculi expanded laterally
24:1 (u)	Appendices angularis well developed
54:1 (c)	Lamella ante- and postvaginalis exposed, not covered by Stn 8
65:1 (c)	Papilla anales 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 FW 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	
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	
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
Clade 4	
21:0 (b)	Uncus ventral side expanded distally
55:0 (u)	Sterigma smooth
64:1 (b)	In ventral view, lobes between papilla anales and ostium bursa sclerotized
101:0 (b)	Male HW ventral surface, ocellus in cell Cu2 absent
Clade 5	
26:1 (u)	In dorsal view, gnathos broad
Clade 6	
5:1 (ab)	Tegula with a discrete spot at base
41:0 (u)	Posterior edge of valva rounded
75:1 (b)	HW Cu2 similar to other veins, wing margin devoid of a lobe
76:0 (ab)	HW edge around tornus scalloped
104:1 (a)	Male HW ventral surface, alignment angle between ocellus in cell Rs and ocelli on cells M3, Cu1, and Cu2 (measured toward base of HW) larger than 90° but smaller than 180°
118:0 (a)	Male HW ventral surface, longitudinal bands in cells 1A and 2A absent
Clade 7	
17:1 (a)	Uncus short, dorsal ridges when present terminate near tip of uncus
96:0 (ab)	Male HW ventral surface, ocellus in cell Rs smaller or same size as cell Rs
120:1 (u)	Larvae feed on dicotyledonous plants
Clade 8	
21:0 (ab)	Uncus ventral side expanded distally
109:1 (ab)	Basal portion of wings darker than medial and apical portions
112:1 (u)	Male HW ventral surface, light-colored medial band broader than cell Sc+Rs is tall
Clade 9	
46:0 (ab)	Size of spines at posterior edge of valva: small only
115:1 (ab)	Male HW ventral surface, light-colored medial band interrupted
Clade 10	
15:2 (b)	Hairpencil setae brown
72:1 (b)	HW M2 devoid of a basal bend
90:1 (b)	Male FW dorsal surface, dark band across apex of discal cell present
96:1 (ab)	Male HW ventral surface, ocellus in cell Rs larger than cell Rs, expanding over veins Rs and M1
110:1 (b)	Orange or yellow bands on ventral surface of wings present
Clade 11: Subgenus <i>Iphimedeia</i>	
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 anales and ostium bursa well developed

TABLE 2
(Continued)

Clade 11: Subgenus <i>Iphimedeia</i> (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
Clade 12		31:0 (ab)	Distal end of gnathos blunt, uniformly sclerotized to base
17:0 (b)	Uncus elongated, dorsal ridges when present terminate well before tip of uncus	Clade 19	
18:1 (b)	Uncus tip and base similarly sclerotized	46:0 (b)	Size of spines at posterior edge of valva: small only
20:1 (b)	Uncus ventral side rounded	55:2 (b)	Sterigma with spines
33:0 (b)	Dorsal edge of juxta nearly straight	109:1 (b)	Basal portion of wings darker than medial and apical portions
Clade 13		Clade 20	
16:0 (b)	Tuft of setae/scales on tegumen midline absent	10:0 (ab)	Female leg 1, pulvillus fused medially
96:0 (b)	Male HW ventral surface, ocellus in cell Rs smaller or same size as cell Rs	15:0 (b)	Hairpencil setae white
113:1 (b)	Male HW ventral surface, light-colored medial band: tan	29:1 (u)	Ventrolateral, basal process of gnathos present
Clade 14: Subgenus <i>Schwartzia</i>		36:1 (b)	Lateral spines of aedeagus present
21:1 (b)	Uncus ventral side not expanded	60:0 (b)	Separate units of the sclerotized plate anterior to sterigma far apart, not close to midline
53:1 (b)	Antrum sclerotized	Clade 21	
74:0 (b)	HW Cu1 produced to form a lobe at wing margin	2:1 (b)	Eyes bare
94:1 (b)	Male HW ventral surface, costal cell white	21:0 (b)	Uncus ventral side expanded distally
118:1 (b)	Male HW ventral surface, longitudinal bands in cells 1A and 2A present	53:1 (b)	Antrum sclerotized
Clade 15: Subgenus <i>Cypritis</i>		56:1 (a)	Anterolateral expansion of sterigma present
55:2 (b)	Sterigma with spines	Clade 22: Subgenus <i>Pessonia</i>	
94:1 (b)	Male HW ventral surface, costal cell white	37:1 (u)	Lateral spines of aedeagus symmetrical
102:1 (b)	Male HW ventral surface, ocellus in cell Cu2 double	78:0 (b)	Male FW dorsal surface, cover scales at apex of discal cell anterior to crossvein m2–m3 pigmented
103:1 (u)	Male HW ventral surface, ocellus in cell 1A present	89:1 (b)	Wing main background pigmentation white
117:0 (u)	Male HW ventral surface, basal to submedial light-colored banding pattern absent	90:1 (b)	Male FW dorsal surface, dark band across apex of discal cell present
Clade 16		97:1 (b)	Male HW ventral surface, ocellus in cell M1 present
2:0 (a)	Eyes hairy	98:1 (b)	Male HW ventral surface, ocellus in cell M2 present
15:2 (ab)	Hairpencil setae brown	106:1 (b)	Male HW ventral surface, ocelli, pupils white only
59:2 (b)	Sclerotized plate anterior to sterigma split at midline	Clade 23	
69:1 (b)	FW crossvein m1–m2 curved, conspicuously longer than m2–m3	5:2 (b)	Tegula with a diffuse light colored marking at base
93:0 (ab)	FW ventral surface, longitudinal bands on discal cell absent	10:1 (b)	Female leg 1, pulvillus not fused medially
Clade 17		Clade 24	
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	24:1 (b)	Appendices angularis well developed
106:2 (ab)	Male HW ventral surface, ocelli pupils white and purple	27:0 (b)	In dorsal view, gnathos curving inward
109:2 (a)	Ventral surface of wings devoid of distinguishable brown bands	31:2 (b)	Distal end of gnathos pointed, uniformly sclerotized to base
113:2 (a)	Male HW ventral surface, light-colored medial band greenish	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

TABLE 2
(Continued)

Terminal Branches	
<i>adonis</i> : 95:1 (b)	<i>rhetenor</i> : 16:0 (b), 31:0 (b), 44:1 (b), 78:0 (b), 97:1 (b), 98:1 (b), 105:2 (u) , 113:1 (u)
<i>eugenia</i> : 72:1 (b)	<i>aurora</i> : 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)
<i>aega</i> : 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)	<i>godarti</i> : 5:0 (b), 55:2 (b)
<i>portis</i> : 5:1 (b), 44:1 (b), 45:0 (u) , 74:0 (b), 76:0 (b), 117:2 (b)	<i>menelaus</i> : 61:0 (b), 115:1 (b)
<i>sulkowskyi</i> : 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)	<i>didius</i> : 4:0 (b), 4:2 (b), 21:0 (b), 28:1 (b), 81:1 (b)
<i>hercules</i> : 4:0 (b), 31:0 (b), 46:1 (b)	<i>amathonte</i> : 92:0 (b), 97:1 (b), 101:0 (b), 112:1 (b), 115:1 (b)
<i>amphitron</i> : 109:0 (b)	<i>laertes</i> : 50:0 (b), 104:0 (b)
<i>perseus</i> : 3:1 (b), 97:1 (b), 98:1 (b)	<i>catenarius</i> : 61:0 (b)
<i>theseus</i> : 44:0 (b), 91:1 (b), 95:0 (b), 115:0 (b), 116:0 (b)	<i>polyphemus</i> : 27:2 (b), 56:0 (b)
<i>hecuba</i> : 18:1 (b), 36:1 (b)	<i>deidamia</i> : 27:2 (b), 55:2 (b), 92:0 (b), 93:1 (b), 118:1 (b)
<i>cisseis</i> : 59:2 (b)	<i>granadensis</i> : 30:1 (b), 93:1 (b), 110:1 (b), 118:1 (b)
<i>anaxibia</i> : 11:1 (u) , 57:1 (b), 62:1 (b), 83:1 (b), 97:1 (b), 105:1 (b), 113:1 (b)	<i>peleides</i> : 30:1 (b)
<i>cypris</i> : 114:0 (b)	<i>achillaena</i> : 53:1 (b), 115:1 (b)
	<i>achilles</i> : 92:0 (b)

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). Although recognition of high variation led Bilotta (1992, 1994a, 1994b) to elevate subgenera to generic status, we think that her limited sampling and lack of a phylogeny make this action unjustified. Our analysis also demonstrated that three of nine *Morpho* subgenera are not monophyletic, and we therefore reject subgenera as valid taxa in *Morpho*. Based on our proposed phylogeny (fig. 12), maintaining *Morpho* subgeneric classification would require description of five new subgenera—an unjustifiable proliferation of names given the evident taxonomic confusion within this genus. Abandoning

Morpho subgenera is a first step toward reorganizing species within a modern systematic framework. What accounts for the high levels of character variation within *Morpho* remains to be explained.

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. eugenia*, *M. aega* Hübner, 1819 plus *M. portis* Hübner, 1819, and *M. sulkowskyi* constitute basal clades within *Morpho*.

Although larval host plant records are

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 *Antirrhoea* and *Caerois* (sister genera of *Morpho*, DeVries et al., 1985) and many Brassoliniinae 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. amphitrion*, *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 understorey 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 Brassoliniinae 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-

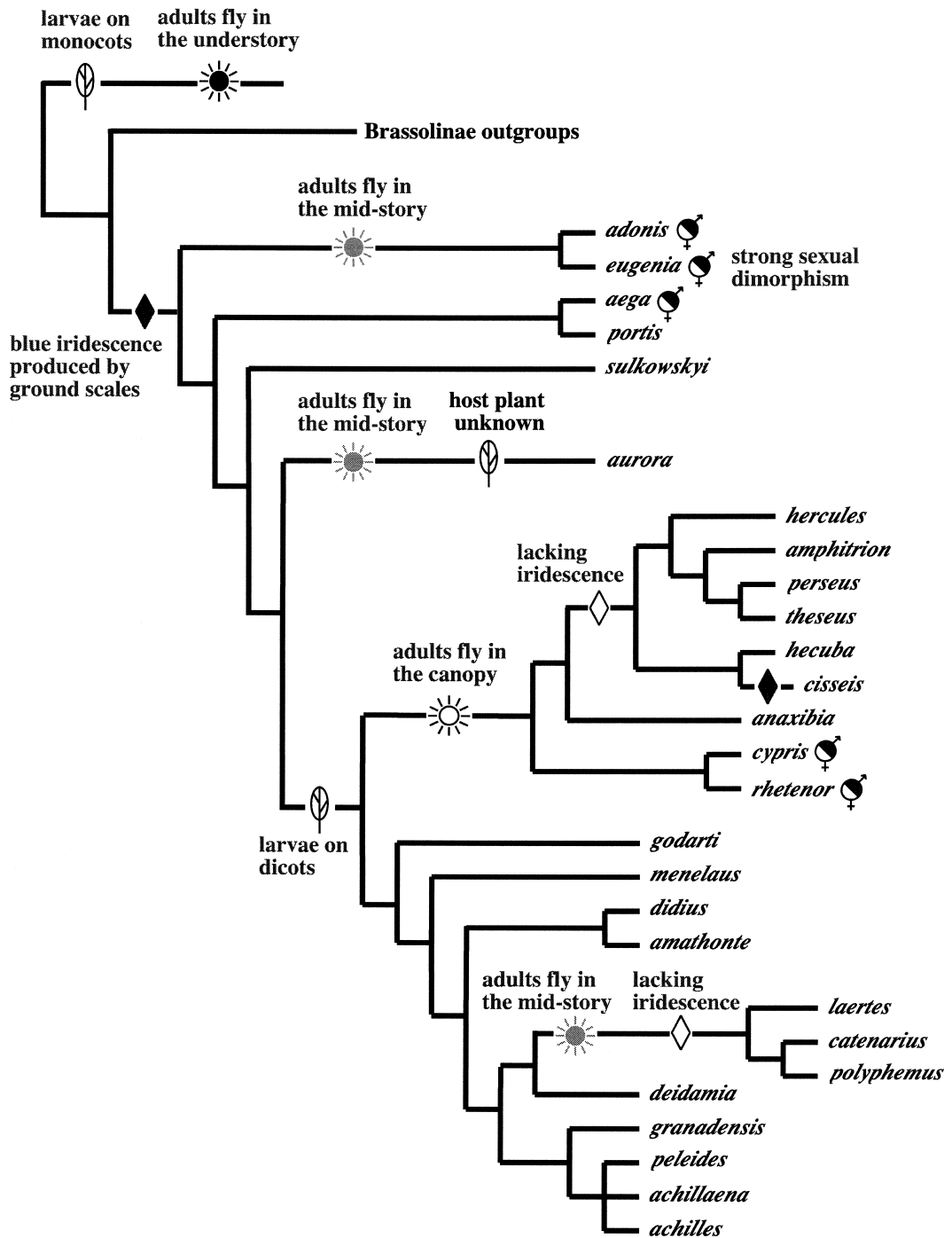


Fig. 13. *Morpho* phylogeny where selected characters have been mapped.

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.

ACKNOWLEDGMENTS

For lending specimens, we thank G. Austin (Nevada State Museum), B. Brown (LACM), P. Goldstein (FMNH), B. Harris (LACM), and R. Robbins (USNM). For sharing field observations, we thank K.S. Brown, Jr., A.V.L. Freitas, M.D. Heredia, K. Roze-ma, J.A. Testón, and A. Young. Phil Ackery, Sasha Gimelfarb, N. "Duke" Martin, and R.D. Mooi provided useful suggestions and comments on earlier drafts of this manuscript. Support for this study was provided by the National Science Foundation (DEB 00-96241). We dedicate this paper to the memory of H. Fruhstorfer, butterfly systematist and natural historian extraordinaire, and Billy Higgins, master of time.

REFERENCES

- Ackery, P. R. 1988. Host plants and classification: a review of nymphalid butterflies. *Biological Journal of the Linnean 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 *Iphimedeia* and *Schwartzia*. Compiègne, France: Sciences Naturelles.
- Blandin, P. 1993. The genus *Morpho*, Lepidoptera Nymphalidae. Part 2. The subgenera *Iphixibia*, *Cytheritis*, *Balachowskyna*, and *Cypritis*. Compiègne, 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, Heliconidae & 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 *Antirrhoea* and *Caerois*, 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 Linnean Society* 62: 343–364.
- DeVries, P. J., and G. E. Martinez. 1993. 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* 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 Linnean 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 Linnean 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), *Taxonomist's glossary of genitalia in insects*: 115–130. Copenhagen: Munksgaard.
- Lamas, G., R. G. Robbins, and W. D. Field. 1995. Bibliography of butterflies. An annotated bibliography of the Neotropical butterflies and skippers (Lepidoptera: Papilionoidea and Hesperioidea). In J.B. Heppner (editor), *Atlas of Neotropical Lepidoptera*: 1–428. Gainesville, FL: Association for Tropical Lepidoptera Scientific Publishers.
- 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 Moul, E., and P. Réal. 1962. *Les Morpho D'Amérique du Sud et Centrale*. *Novitates Entomologicae* (supplement). Paris, France: Éditions du Cabinet Entomologique, E. Le Moul.
- 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. idomeus* (Nymphalidae, Brassoliniinae) 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. Muysshondt. 1972. Biology of *Morpho polyphemus* in El Salvador. *Journal of the New York Entomological Society* 80: 18–42.
- Young, A. M., and A. Muysshondt. 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.		<i>portis</i>	1 male: Brazil, Paraná, Guarapuava* (MPM); 1 male: Brazil* (LACM); 1 female: Brazil, Santa Catarina, São Bento* (LACM)
<i>Antirrhoea</i>		(<i>Balachowskyina</i>)	
<i>avernus</i>	1 male and 1 female: Peru, Satipo* (MPM); 1 female: Ecuador, Sucumbios Garza Cocha* (PJD)	<i>aurora</i>	1 male: Bolivia* (LACM); 1 male: Bolivia (FMNH); 1 female: Bolivia, Coroico* (USNM); 1 female: Peru, Chanchamayo* (USNM); 1 female: Peru, La Merced (LACM)
<i>archaea</i>	1 male: no data* (MPM); 1 female: Brazil, Santa Catarina* (MPM)		
<i>Caerolis</i>		(<i>Cypritis</i>)	
<i>gertrudtus</i>	1 male: Ecuador, Esmeraldas, Tonchigue* (PJD); 1 female: no data* (PJD)	<i>cypris</i>	1 male: Colombia, Boyaca* (USNM); 1 male: no data* (MPM); 1 male: Colombia (LACM); 1 female: Colombia* (USNM); 1 female: no data* (USNM)
<i>Morpho</i>		<i>rhetenor</i>	1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: Peru (LACM); 1 male: no data (GA); 1 male: no data (LACM); 1 female: Peru, Chanchamayo* (USNM); 1 female: Peru, Chanchamayo (USNM); 1 female: no data (GA)
(<i>Cytheritis</i>)			
<i>adonis</i>	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)	(<i>Iphixibia</i>)	
<i>eugenia</i>	1 male: Newcomb (USNM); 1 male: French Guiana (LACM); 1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 female: Ecuador, Sucumbios, Garza Cocha (PJD); 1 female: French Guiana (USNM)	<i>anaxibia</i>	1 male: Brazil, São Paulo* (LACM); 1 male: Brazil, Santa Catarina, Corupa* (GA); 1 female: Brazil, Santa Catarina, Taio* (MPM)
<i>aega</i>	1 male: Brazil (LACM)*; 1 male: Brazil, Sta. Catarina (USNM); 1 female: Brazil (LACM); 1 female: Brazil, Sta. Catarina* (LACM); 1 female: no data* (MPM); 1 female: Brazil, Sta. Catarina (USNM); 1 female: Colombia (USNM)	(<i>Schwartzia</i>)	
<i>sulkowskyi</i>	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)	<i>hecuba</i>	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)
		<i>cisseis</i>	1 male: Brazil, Pará* (LACM); 1 male: Brazil, Pará, Obidos (GA); 1 female: Brazil, Rondônia, Caucaândia* (GA); 1 female: Brazil, Pará (LACM)

<i>(Iphimedeia)</i> <i>hercules</i>	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); 1 female: Brazil (MPM)	<i>(Pessonia)</i> <i>laertes</i>	1 male: no data* (LACM); 1 female: Brazil, Rio de Janeiro, Nova Friburgo* (MPM)
<i>amphitrion</i>	1 male: Peru, La Merced* (LACM); 1 female: no data (LACM)	<i>catenarius</i>	1 male: Brazil, Santa Catarina, Tayo* (LACM); 1 female: Brazil, Santa Catarina* (LACM)
<i>perseus</i>	1 male: Brazil, Pará, Obidos* (LACM); 1 male: Brazil, Amazonas (LACM); 1 male: Ecuador, Napo, Misahualli (LACM); 1 male: Brazil, Pará, Obidos (GA); 1 female: Brazil, Pará, Santarém* (MPM); 1 female: Brazil, Para, Obidos (LACM); 1 female: Obidos, Pará Brazil (GA)	<i>polyphemus</i>	1 male: Mexico, Oaxaca, Palomas* (LACM); 1 male: Mexico, Chiapas (LACM); 1 male: Mexico, Oaxaca (LACM); 1 female: Mexico, Guerrero* (LACM); 1 female: no data (LACM)
<i>theseus</i>	1 male: Costa Rica* (PJD); 1 male: no data* (MPM); 1 female: Costa Rica, Puntarenas (PJD); 1 female: Colombia* (LACM)	<i>(Morpho)</i> <i>deidamia</i>	1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: French Guiana* (MPM); 1 male: Brazil, Pará, Obidos (MPM); 1 male: Surinam (USNM); 1 female: Brazil, Pará, Obidos* (MPM)
<i>(Grasseia)</i> <i>godarti</i>	1 male: Bolivia, Buenavista, Ichino* (MPM); 1 male: Bolivia (LACM); 1 female: no data* (MPM), 1 female: Bolivia (LACM)	<i>granadensis</i>	1 male: Costa Rica San Jose* (PJD); 1 male: Costa Rica, San Jose (MPM); 1 female: Colombia, Bogota (USNM); 1 female: no data* (MPM)
<i>menelaus</i>	1 male: Ecuador, Sucumbios, Garza Cocha* (PJD); 1 male: Ecuador, Napo, Rio Pucuno (LACM); 1 male: Brazil, Rondonia, Arique-mas; 1 female: Brazil, Pará, Obidos* (MPM); 1 female: Ecuador, Sucumbios, Garza Cocha (PJD)	<i>peleides</i>	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, Chimalapa (MPM)
<i>didius</i>	1 male: Peru* (USNM); 1 male Peru (USNM); 1 male: Peru, Tingo Maria (LACM); 1 female: Peru* (USNM); 1 female: Peru, La Merced (LACM)	<i>achillaena</i>	1 male: Brazil* (LACM); 1 female: Brazil, Santa Catarina, Joinville* (MPM); 1 female: Brazil (LACM)
<i>amathonte</i>	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, Misahualli (LACM)	<i>achilles</i>	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 *Iphimedea*. 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 pulvillar 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

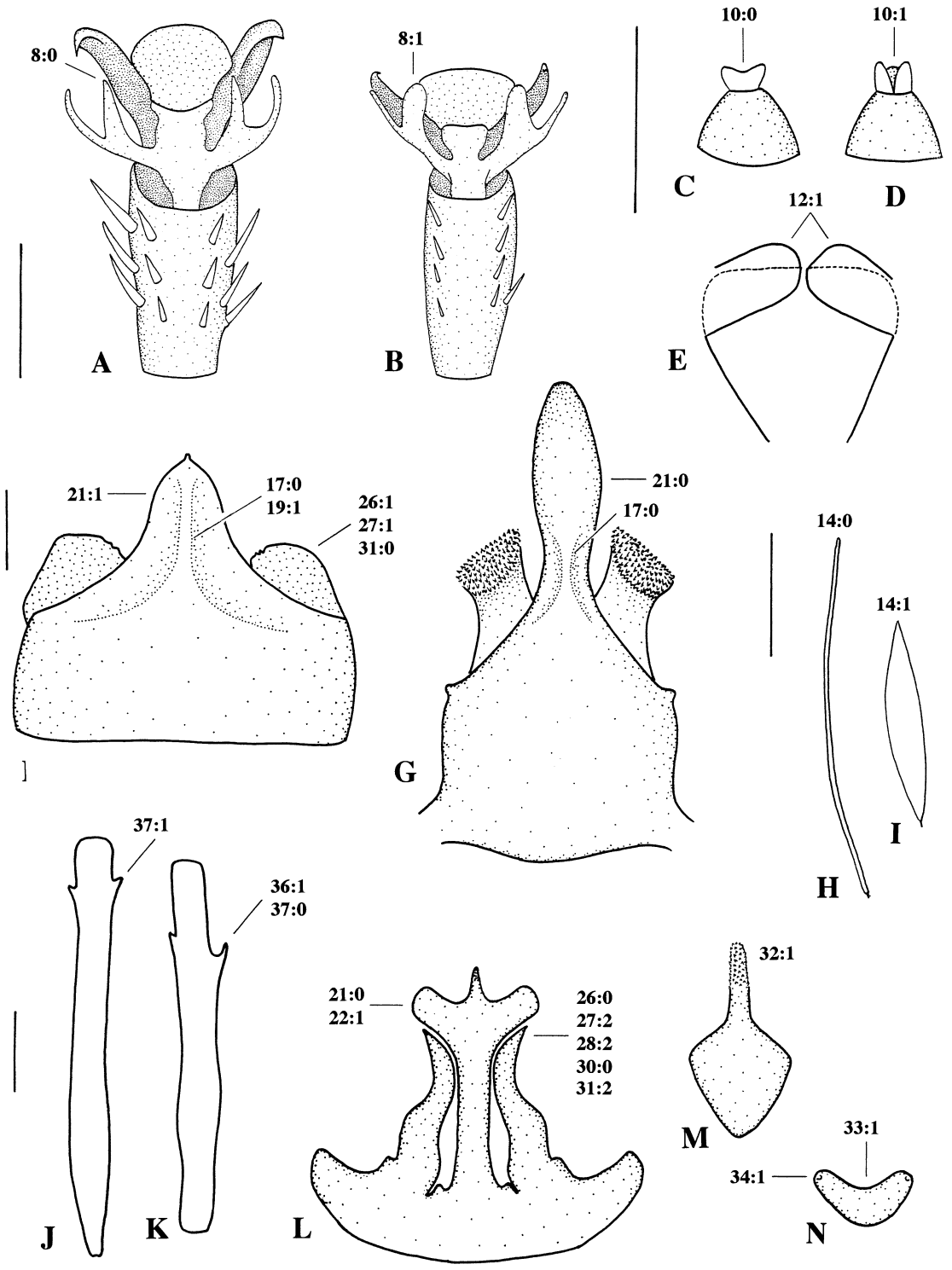
13. Hairpencils: absent (0); present (1). Surprisingly, hairpencils were absent in two

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 Moul et 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 Moul et Réal (1962).
20. Uncus ventral side: forming sharp lateral ridges (0); rounded (1). Adapted from Fruhstorfer (1913) and Le Moul et Réal (1962).
21. Uncus ventral side: expanded distally (0); not expanded (1). Figure 14F, G, and L. Adapted from Fruhstorfer (1913) and Le Moul et 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. 14. Dissections showing characters used in the analysis. Male meso tarsus in ventral view: **A**, *M. catenarius*; **B**, *M. eugenia*. Female fore tarsus in ventral view: **C**, *M. achillaena*; **D**, *M. sulkowskyi*. **E**, Schematic drawing of the internal portion of the first male abdominal tergite of *A. avernus*. Tegumen, uncus, and gnathos is dorsal view: **F**, *M. rhetenor*; **G**, *M. hercules*. Hairpencil setae: **H**, *M. achilles*; **I**, *A. avernus*. Silhouette of the aedeagus in dorsal view: **J**, *M. polyphemus*; **K**, *M. achilles*. Tegumen, uncus, and gnathos is dorsal view: **L**, *M. aega*. Juxta in ventral view: **M**, *M. eugenia*; **N**, *M. portis*.



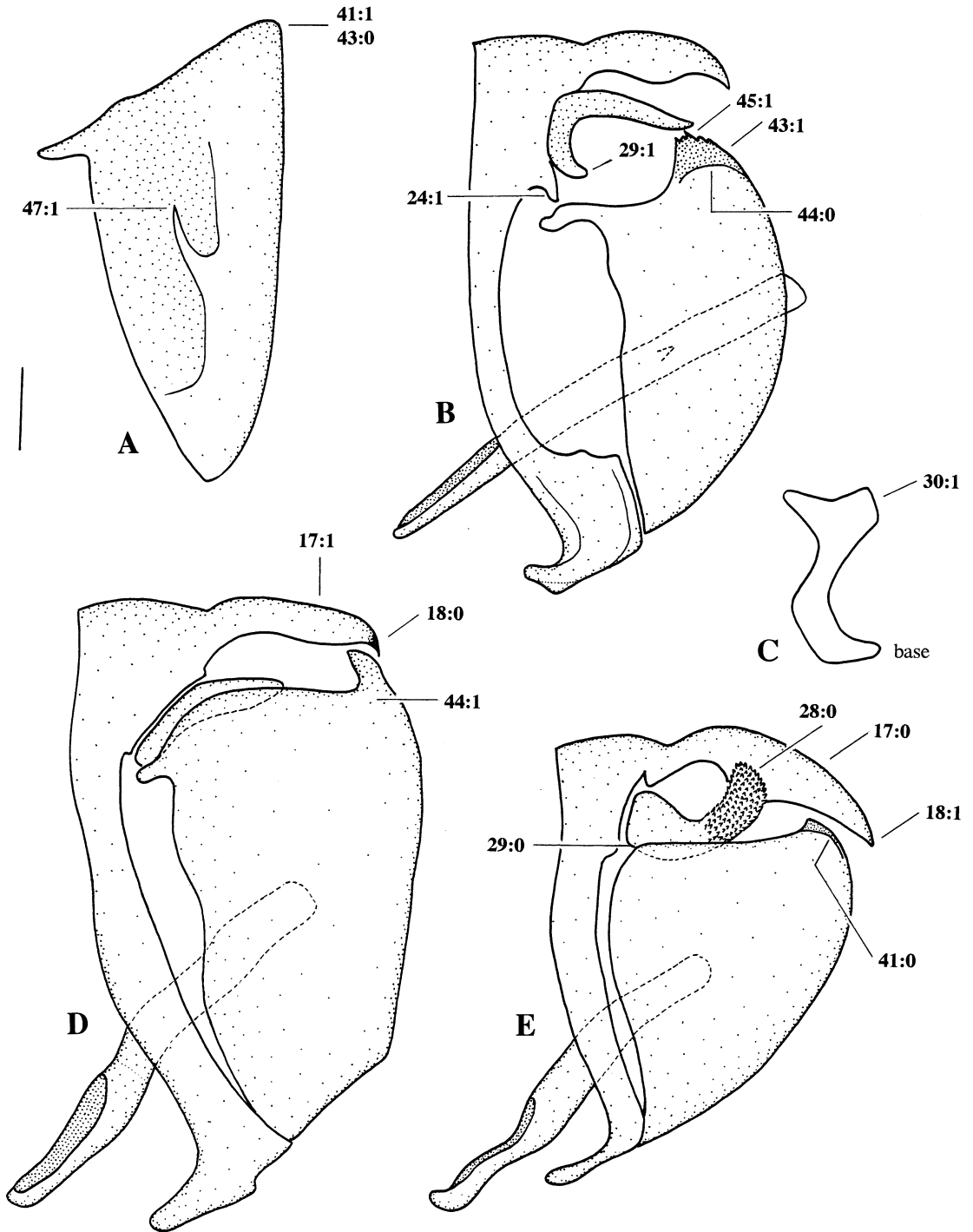


Fig. 15. Dissections showing characters used in the analysis. Male valva, internal view: **A**, *M. adonis*. Male genitalia in lateral view: **B**, *M. granadensis*. **C**, Dorsal view of the right gnathos of *M. granadensis*. Male genitalia in lateral view: **D**, *M. rhetenor*; **E**, *M. theseus*. Scale bars represent 0.5 mm.

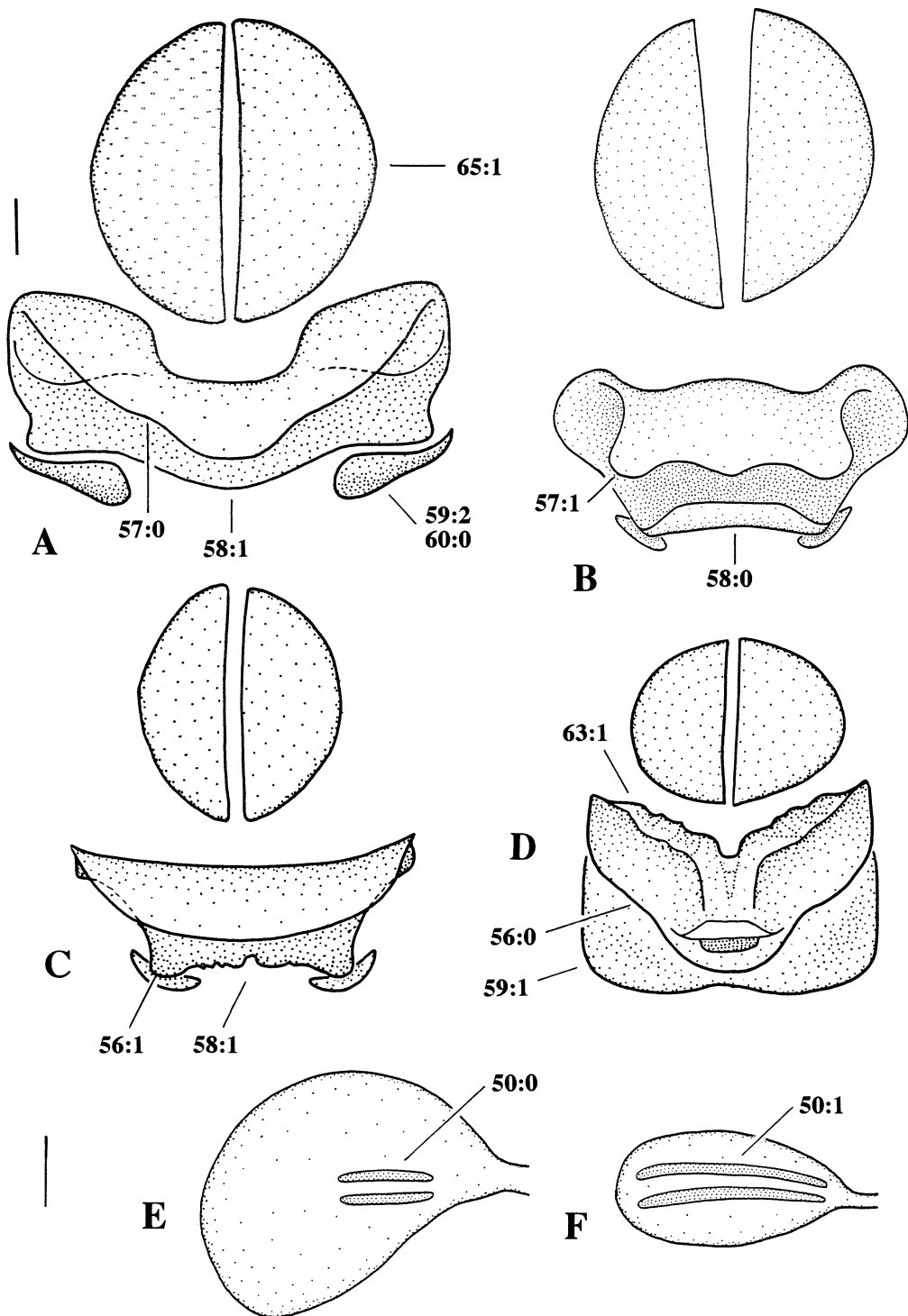


Fig. 16. Dissections showing characters used in the analysis. Scale bars represent 0.5 mm. Female genitalia in ventral view: **A**, *M. deidamia*; **B**, *M. achillaena*; **C**, *M. catenarius*; **D**, *M. aega*. Corpus bursae: **E**, *M. achilles*, **F**, *M. aurora*. Scale bars represent 0.5 mm.

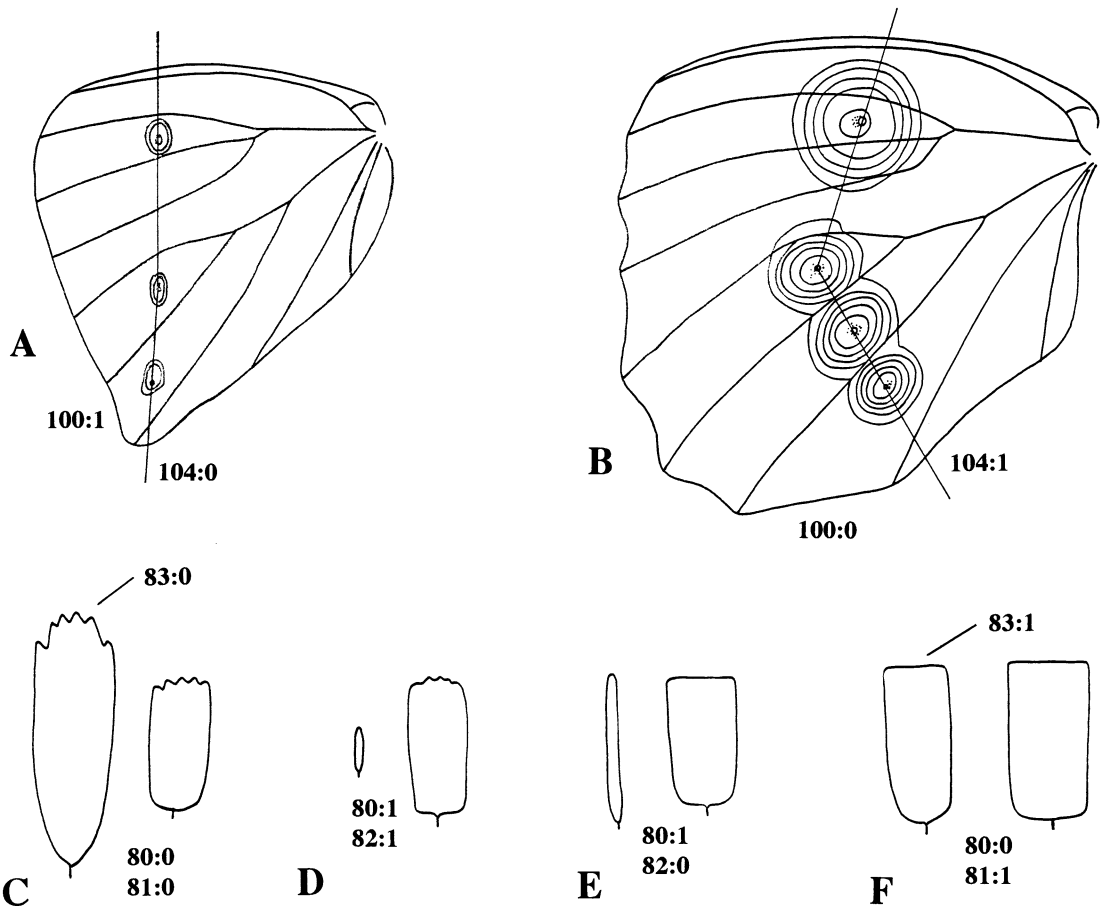


Fig. 17. Dissections showing characters used in the analysis. Hindwing in ventral view: **A**, *M. aega*; **B**, *M. peleides*. Scales from male specimens, dorsal surface of the forewing, distal portion of the discal cell; for each pair, cover scale on the left, basal scale on the right: **C**, *M. eugenia*; **D**, *M. aega*; **E**, *M. cypris*; **F**, *M.anaxibia*.

- Fruhstorfer (1913) and Le Moulton and Réal (1962).
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 Moulton 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 Moulton and Réal (1962).
 37. Lateral spines of aedeagus: asymmetrical (0); symmetrical (1). Figure 14J and K.
 38. Valva: laterally flattened (0); conspicu-

- ously convex (1). Adapted from Fruhstorfer (1913) and Le Moulton 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 Moulton 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 Moulton 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 Moulton 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 Moulton and Réal (1962).
76. HW edge around tornus: scalloped (0); smooth (1). Adapted from Fruhstorfer (1913) and Le Moulton and Réal (1962).
77. HW crossvein m2–m3: absent (0); present (1). Adapted from Fruhstorfer (1913), Le Moulton 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 Cu1: 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).
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).

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).

110. Orange or yellow bands on ventral surface of wings: absent (0); present (1).
 111. Male HW ventral surface, light-colored medial band: absent (0); present (1).
 112. 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).
 113. Male HW ventral surface, light-colored medial band: white (0); tan (1); greenish (2).
 114. Male HW ventral surface, light-colored medial band: straight across wing (0); angled (1).
 115. Male HW ventral surface, light-colored medial band: continuous (0); interrupted (1).
 116. Male HW ventral surface, light-colored medial band: undulating to follow the ocelli edges (0); straight, not undulating to follow the ocelli edges (1).
 117. 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).
 118. Male HW ventral surface, longitudinal bands in cells 1A and 2A: absent (0); present (1).
 119. 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
120. Larval host plants: monocotyledonous (0); dicotyledonous (1).

APPENDIX 3

DATA MATRIX

Species of *Morpho* have been classified in the following subgenera: 1–5, *Cytheritis*; 6–9, *Iphimedeia*; 10–11, *Cypritis*; 12–13, *Schwartzia*; 14, *Balachowskyna*; 15, *Iphixibia*; 16–19, *Grasseia*; 20–22, *Pessonia*; 23–27, *Morpho*.

	10	20	30	40
OUTGROUPS				
<i>Antirrhea</i>				
<i>avernus</i>	0110000011	?111000100	1?01102200	201000?111
<i>archaea</i>	011000001?	?110200110	1?010?????	?00000?111
<i>Caerois</i>				
<i>gerdrudtus</i>	0100000000	?010100111	1?00102200	000010?111
INGROUP				
1. <i>adonis</i>	11202111??	0?10000100	1?10101200	01?110?011
2. <i>eugenia</i>	1121211101	0010000100	1?10101200	01?110?011
3. <i>aega</i>	?111211001	0010000010	0110102000	301110?001
4. <i>sulkowskyi</i>	0101211001	000??10010	1?10111000	101110?110
5. <i>portis</i>	011?1???01	0010000010	0110100000	101110?010
6. <i>hercules</i>	2100111001	0010211010	0?10111000	001110?110
7. <i>amphitriion</i>	21011110??	0?10210111	0010111000	100110?110
8. <i>perseus</i>	2111111001	0010200111	0010111000	100110?110
9. <i>theseus</i>	21011110??	0?10200111	0010111000	100110?110
10. <i>cypris</i>	2101111001	0010011010	0010111000	101110?110
11. <i>rhetenor</i>	2101111001	0010001010	0010111000	001110?110
12. <i>hecuba</i>	2111111000	0010211110	1?10111000	1011110110
13. <i>cisseis</i>	21111?????	0?10211010	1?10111000	101110?110
14. <i>aurora</i>	112111100?	0010000011	1?10110101	000110?110
15. <i>anaxibia</i>	2111111001	1010011010	0010111000	101110?110
16. <i>menelaus</i>	0001111001	0010211010	1?10111000	101110?110
17. <i>godarti</i>	?0110???01	0010211010	1?10111000	101110?110
18. <i>didius</i>	00002???01	0010201010	0010111100	000110?110
19. <i>amathonte</i>	000111100?	0010201010	1?10111200	001110?110
20. <i>laertes</i>	?1?1111000	0010001010	0010111110	0001111110
21. <i>catenarius</i>	11(1,2)1210001	0010001010	0010111210	0001111110
22. <i>polyphemus</i>	1121211001	0010001010	0010112110	0001111110
23. <i>deidamia</i>	0111111000	0010001010	0010112210	0001110110
24. <i>granadensis</i>	0001111000	0010001010	1?11110211	2001110110
25. <i>peleides</i>	0001111000	0010001110	1?11110211	2001110110
26. <i>achillaena</i>	0001111000	0010001110	1?11110210	2001110110
27. <i>achilles</i>	0001111000	0010001110	1?11110210	2001110110
	50	60	70	80
OUTGROUPS				
<i>Antirrhea</i>				
<i>avernus</i>	1011110011	1100?00???	1010010111	0001101000
<i>archaea</i>	110?10010?	?000?00???	000?010111	0011101000
<i>Caerois</i>				
<i>gerdrudtus</i>	101011000?	?000?00???	1010011100	0001111000
INGROUP				
1. <i>adonis</i>	110????1?1?	???????????	???????100	1011010100
2. <i>eugenia</i>	110????1111	0001101121	000?111100	1111010100
3. <i>aega</i>	1110110111	000100011?	0011111100	1011010101
4. <i>sulkowskyi</i>	110???0111	000110010?	110?101100	1011010111
5. <i>portis</i>	11110?0111	000100010?	0011101100	1010000100
6. <i>hercules</i>	0?11110110	100120010?	1011111100	1111100000
7. <i>amphitriion</i>	0?11100?1?	???????????	???????000	1111100000
8. <i>perseus</i>	0?11100110	1001200121	1011111000	1111100000

APPENDIX 3
(Continued)

	50	60	70	80
9. <i>theseus</i>	0?10100?1?	???????????	????????000	1111100000
10. <i>cypris</i>	0?10110111	000120010?	100?111100	1011100101
11. <i>rhetenor</i>	0?11110111	000120010?	100?111100	10111(0,1)0001
12. <i>hecuba</i>	0?11100111	001110010?	100?111000	1110110000
13. <i>cisseis</i>	0?10100111	0011100120	1000111000	1110110100
14. <i>aurora</i>	0?10110111	000110011?	0010101100	1011100101
15. <i>anaxibia</i>	0?10100111	000110110?	110?111100	1011110100
16. <i>menelaus</i>	0?10110111	0001100121	000?111110	1011100100
17. <i>godarti</i>	0?10110111	0001200121	100?111110	1011100100
18. <i>didius</i>	0?10100111	0001200121	100?111110	1011100100
19. <i>amathonte</i>	0?10100111	0001200121	100?111110	1011100100
20. <i>laertes</i>	0?10110110	0011110120	100?101110	10111(0,1)0000
21. <i>catenarius</i>	0?10110111	0011110120	000?101110	1011100000
22. <i>polyphemus</i>	0?10110111	0011100120	100?111110	1011100000
23. <i>deidamia</i>	0?10110111	0011210120	100?111110	1011100100
24. <i>granadensis</i>	0?10110111	0001101020	100?111110	1011100100
25. <i>peleides</i>	0?1011011?	?001101020	100?111110	1011100100
26. <i>achillaena</i>	0?10110111	0011101020	100?111110	1011100100
27. <i>achilles</i>	0?10110111	0001101020	100?11111?	1?111?0100
	90	100	110	120
OUTGROUPS				
<i>Antirrhea</i>				
<i>avernus</i>	0?0111110?	???????????	???????????	???????????
<i>archaea</i>	0?0111110?	???????????	???????????	???????????
<i>Caerois</i>				
<i>gerdrudtus</i>	0?0010110?	???????????	???????????	???????????
INGROUP				
1. <i>adonis</i>	0?00000000	0010110000	1000010000	0?????110?
2. <i>eugenia</i>	0?00000000	0010010000	1000010000	0?????110?
3. <i>aega</i>	?1?0000000	1100100011	0?00110100	1010011100
4. <i>sulkowskyi</i>	?0?0000010	1111010111	1000010100	1001112110
5. <i>portis</i>	1?00000000	1110010010	0000010100	1001012110
6. <i>hercules</i>	1?00000001	0110110010	1001010111	1101111011
7. <i>amphitriion</i>	1?00000001	0110110010	1001010101	110111101?
8. <i>perseus</i>	1?00000001	0110101110	1001010111	111111101?
9. <i>theseus</i>	1?00000001	1110000010	1001010111	111100101?
10. <i>cypris</i>	?1?0000000	0111000010	1111020110	1100010001
11. <i>rhetenor</i>	?1?0000000	0111001110	1111200110	1111000001
12. <i>hecuba</i>	1?00000001	0111010010	1001010111	1101111111
13. <i>cisseis</i>	1?00000001	0111010010	1001010111	1101111111
14. <i>aurora</i>	?0?0000000	1110010010	1001110100	100100101?
15. <i>anaxibia</i>	1?10000000	1110001010	1001110110	1111111001
16. <i>menelaus</i>	0?10000000	1100000010	1001020?20	1021101011
17. <i>godarti</i>	1?00000000	110?00(0,1)010	1001010100	100100100?
18. <i>didius</i>	1?10000000	1100000010	1(0,1)01020110	1021001001
19. <i>amathonte</i>	0?10000000	1000001010	0001020110	1021101001
20. <i>laertes</i>	0?00000011	110??01110	1000010?00	?????????11
21. <i>catenarius</i>	0?00000011	110??01110	1001010?00	?????????11
22. <i>polyphemus</i>	0?00000011	110??01110	1001010100	?????????011
23. <i>deidamia</i>	0?00000000	1010010010	1001020?20	102101110?
24. <i>granadensis</i>	0?00000000	1110010010	1001020?21	1021011111
25. <i>peleides</i>	0?00000000	1(0,1)00010010	1001021120	10(0,2)1001011
26. <i>achillaena</i>	0?00000000	1100010010	1001021120	1021101011
27. <i>achilles</i>	0?00000000	1000010010	100102(0,1)120	1021(0,1)01011

APPENDIX 4

DEFINITIONS OF *MORPHO* SUBGENERA

Definitions of *Morpho* subgenera by Fruhstorfer (1913), Le Moulton 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 Moulton 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 to 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 al-

most perpendicular direction at A1 and reaches it more or less at the end of A2.

SUBGENUS *IPHIXIBIA* LE MOULT AND RÉAL, 1962

Le Moulton 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 nervures 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 Moulton and Réal (1962): Subuncus sometimes straight, when it is inserted vertically it expands horizontally, sinuate-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 Moulton 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 *Pessonina*. 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 MOULT AND RÉAL, 1962

Le Moulton 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 MOULT AND RÉAL, 1962

Le Moulton 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 MOULT AND RÉAL, 1962

Le Moulton and Réal (1962): Discal 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 Moulton 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 *Pessonnia*). 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 commun.). 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.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site <http://library.amnh.org>. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org

Ⓢ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).