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PHYLOGENY AND BIOGEOGRAPHY OF *EUPHYES* SCUDDER (HESPERIIDAE)

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ABSTRACT. The 20 species of *Euphyes* were analyzed phylogenetically and were found to fall into four monophyletic species groups, each of which is defined by one or more apomorphic characters. The *peneia* group contains *Euphyes peneia* (Godman), *E. eberti* Mielke, *E. leptosema* (Mabille), *E. fumata* Mielke, *E. singularis* (Herrich-Schäffer), and *E. cornelius* (Latreille). The *subferruginea* group contains *E. subferruginea* Mielke, *E. antra* Evans, and *E. cherra* Evans. The *dion* group contains *E. dion* (Edwards), *E. dukei* (Lindsey), *E. bayensis* Shuey, *E. pilatka* (Edwards), *E. berryi* (Bell), and *E. conspiciua* (Edwards). The *vestris* group contains *E. vestris* (Boisduval), *E. chamuli* Freeman, *E. bimacula* (Grote and Robinson), and *E. arpa* (Boisduval and Leconte). *Euphyes ampa* Evans could not be placed confidently within this framework.

Geographic distribution of each species group suggests that exchange between South America and North America took place at least twice. The two Caribbean Basin species (*E. singularis*, *E. cornelius*) share a common ancestor with *E. peneia*, a species found in Central and South America. This suggests a vicariant event involving Central America and the Greater Antilles. The *dion* and *vestris* groups show strong patterns of allopatric differentiation, suggesting that the isolation and subsequent differentiation of peripheral populations has played an important role in the development of the extant species.

Additional key words: evolution, cladistics, wetlands, vicariance biogeography, population differentiation.

The genus *Euphyes* Scudder as previously defined included a heterogeneous assemblage of skippers distributed throughout the New World (Evans 1955, Mielke 1972). I recently demonstrated that *Euphyes* was paraphyletic with respect to *Problema* Skinner and Williams and I redefined the two genera monophyletically, resurrecting the genus *Arotis* Mabille in the process (Shuey 1987). *Arotis* and *Problema* appear to represent sister genera defined by the unique shape of the female eighth abdominal tergite and the heavy armature of the aedeagus. The resurrection of *Arotis* removed seven species from *Euphyes* [*Arotis sirene* Mabille, *A. derasa* (Herrich-Schäffer), *A. kayei* (Bell), *A. mapirica* (Bell), *A. pandora* (Lindsey), *A. bryna* (Evans), and *A. evansi* (Mielke)].

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Arotis and *Problema* together form the probable sister group of *Euphyes*.

As redefined, *Euphyes* consists of 20 species with 3 centers of endemism: central South America, the northern Antilles, and eastern North America. In this paper I construct a detailed phylogenetic hypothesis for *Euphyes* and relate species distributions to it.

MATERIALS AND METHODS

I examined material of all available species. Because some of the South American species are rare, several species were not available in North American museums for examination. However, Mielke (1972, 1973) figures these species allowing me to tentatively assign some character states without examining specimens. Unless otherwise indicated, I critically examined 20 or more specimens of each sex, chosen to encompass most of the range of each species. Material which was less critically examined generally exceeded 100 specimens or more per species. Species examined include: *E. arpa* (Boisduval and Leconte), *E. pilatka* (Edwards), *E. dion* (Edwards), *E. dukesi* (Lindsey), *E. conspicua* (Edwards), *E. berryi* (Bell), *E. bayensis* Shuey, *E. bimacula* (Grote and Robinson), *E. singularis* (Herrich-Schäffer), *E. vestris* (Boisduval), *E. cornelius* (Latreille), *E. peneia* (Godman), *E. chamuli* Freeman, and *E. subferruginea* Mielke.

I identified 29 morphological characters, including structures of the female and male genitalia, male stigma, and wing pattern. Characters were polarized using the genera *Problema* and *Arotis* as out-groups. This choice was based on a prior analysis which indicated that these two genera together comprised the sister group to *Euphyes*. The data set of 29 characters and 18 operational taxonomic units (OTUs) was analyzed using the "Penny" program from the PHYLIP 2.7 Metro package (Felsenstein 1984), which uses Wagner parsimony. The data set was analyzed five times using different random seed numbers as recommended by Felsenstein.

CHARACTER ANALYSIS

The morphological characters employed in the analysis include 9 characters of the female genitalia, 14 male secondary sexual characters, and 6 characters of the wings. Table 1 summarizes the character state distributions for each species. The figures emphasize North American, Caribbean, and common South American species. Comparative figures of South American species can be found in Mielke (1972, 1973).

Female Genitalia Characters

In the underived condition the ductus bursae is a completely sclerotized, short, straight tube and the corpus bursae is a short, blunt sac.

TABLE 1. Character matrix for *Euphyes* species. Character numbers refer to character numbers in text. 0 = plesiomorphic character state. 1 = derived character state. ? = unknown character states.

| OTU's | CHARACTER NUMBERS | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|----------------------|-------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 |
| out-group | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>bayensis</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| <i>dion</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| <i>dukesi</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| <i>berryi</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>pilatka</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 |
| <i>conspicua</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>vestris</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>chamuli</i> | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>arpa</i> | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>bimacula</i> | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| <i>peneia</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>singularis</i> | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>comelius</i> | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>fumata</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>eberti</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>leptosema</i> | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>subferruginea</i> | 0 | 1 | ? | 0 | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

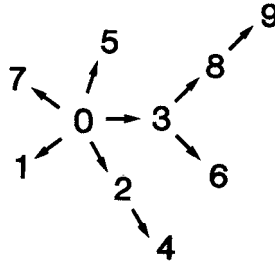


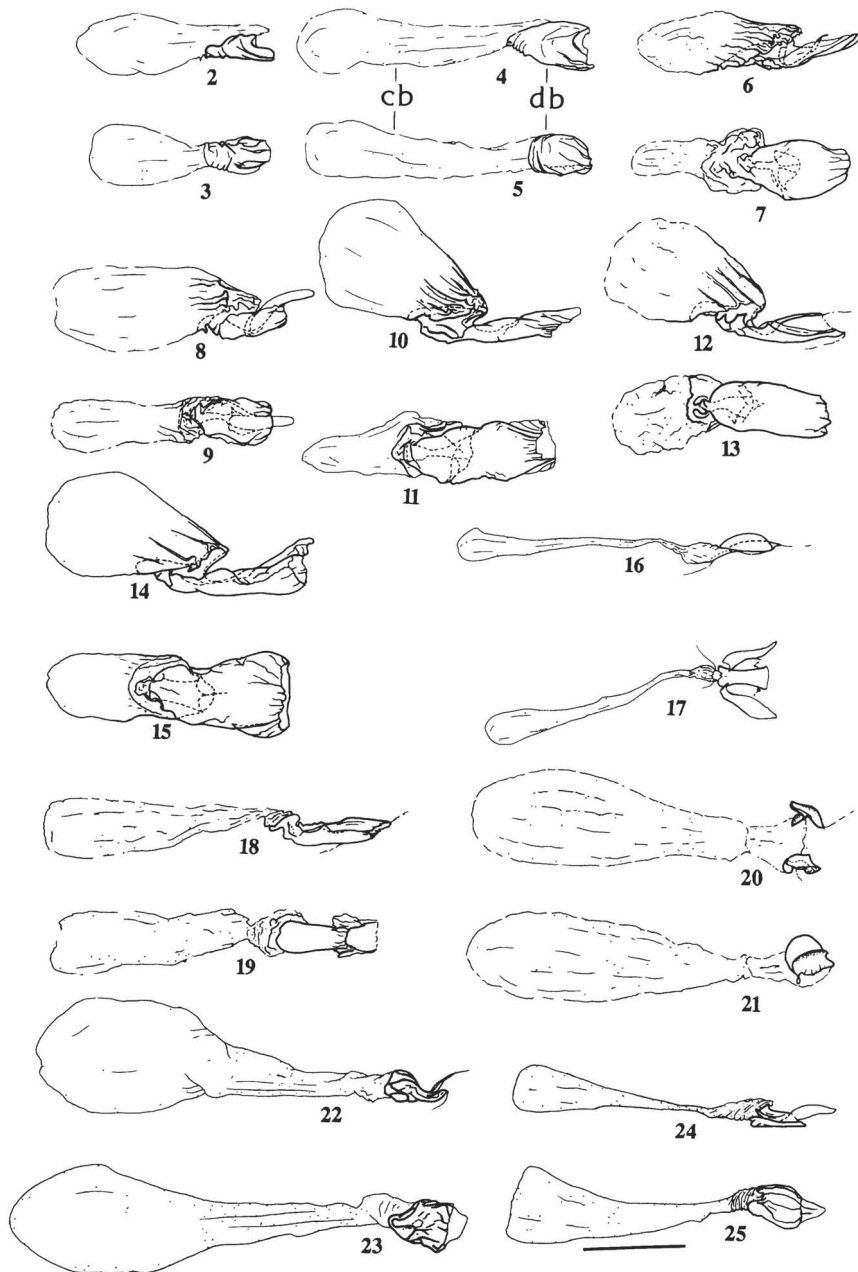
FIG. 1. Hypothesized transformation of female genitalic characters. 0 is plesiomorphic condition. All other numbers are derived and refer to character numbers in text.

The hypothetical derivations of the following apomorphies are shown in Fig. 1.

1. Ductus bursae unsclerotized dorsally (Figs. 2–5). This condition is found in *E. vestris* and *E. chamuli*.
2. Corpus bursae elongate (Figs. 4–25). This character is found in all *Euphyes* except *E. vestris*.
3. Ductus bursae elongate (Figs. 6–21). This character is found in the *dion* and *peneia* groups. Based on Mielke's (1972) figures, this character state may be present in the *subferruginea* group.
4. Corpus bursae very elongate (Figs. 22–25). This condition is found in *E. arpa* and *E. bimaacula*.
5. Ductus bursae with lateral projections (Figs. 16–21). This condition characterizes the *peneia* group. Based upon Mielke's (1972) figures, this character state may be present in the *subferruginea* group, but has been coded as “?” for this group in the data set.
6. Ductus bursae with a slight bend posteriorly (Figs. 18 & 19). This condition is an autapomorphy for *E. singularis*.
7. Ductus bursae unsclerotized (Figs. 20 & 21). This character is interpreted as a autapomorphy for *E. cornelius* where the only sclerotized regions of female genitalia are lateral extensions of the ductus bursae (character 5).
8. Ductus bursae doubled back upon itself (Figs. 6–15). This condition characterizes the *dion* group.
9. Corpus bursae erect (Figs. 10–15). This character state defines a clade within *dion* group composed of *E. conspicua*, *E. pilatka*, and *E. berryi*. Because neither this character state nor the alternative character state (corpus bursae not erect) occur in the out-group, the polarization of this and the alternate state (Figs. 6–9) is tentative.

Male Secondary Sexual Characters

Aedeagus. The underived condition is assumed to be a short, blunt, open-ended tube, with large, curved, lateral spines. The out-group lacks



FIGS. 2-25. *Euphyes* female genitalia (even numbers—lateral view, odd numbers—ventral view; 2-3, *vestris*; 4-5, *chamuli*; 6-7, *dion*; 8-9, *dukesi*; 10-11, *berryi*; 12-13, *conspicua*; 14-15, *pilatka*; 16-17, *peneia*; 18-19, *singularis*; 20-21, *cornelius*; 22-23, *arpa*; 24-25, *bimacula*. db = ductus bursae, cb = corpus bursae. Scale line = 2 mm.

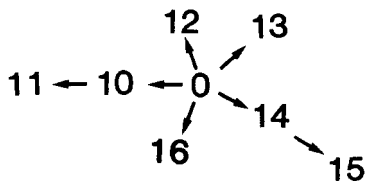


FIG. 26. Hypothesized transformation of male genitalic characters. 0 is plesiomorphic condition. All other numbers are derived and refer to character numbers in text.

cornuti. Figure 26 represents the hypothesized derivation of the following characters:

10. Lateral spines reduced and straight (Figs. 27–29). This condition characterizes the *peneia* group.

11. Lateral spines very small (Fig. 28). This autapomorphy is found in *E. singularis*.

12. Lateral spines absent (Figs. 30–35). This condition is found in the *subferruginea* and *dion* groups. The most parsimonious solution suggests that it has arisen independently in *E. cornelius*.

13. Lateral portion of the aedeagus recurved inward to form a lateral slit-like opening at the posterior end (Figs. 27–29). This condition represents a synapomorphy for the *peneia* group.

14. Cornuti present on the membranous end of the aedeagus (Figs. 30–35). This condition is found in the *subferruginea* and *dion* groups.

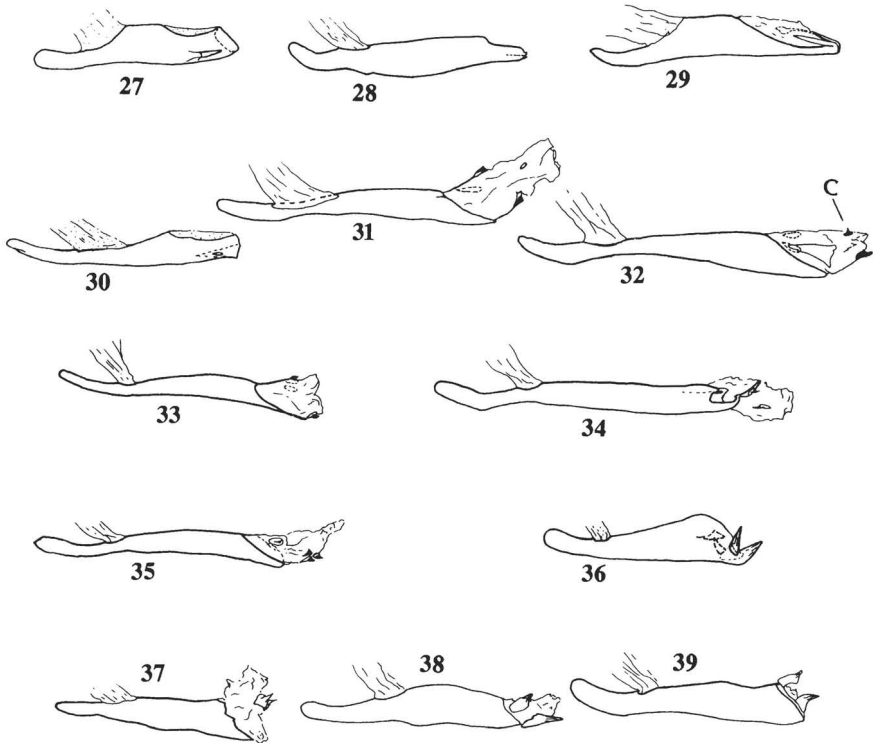
15. Dorsal median cornuti present (Figs. 36–37). This condition is found in *E. vestris* and *E. chamuli*.

16. Lateral spines hinged and flexible (Figs. 36–39). This condition is found in the *vestris* group.

Male stigma. In *Problema* the stigma is absent; in *Arotis* a highly modified stigma is present (Shuey 1987). Consequently, simple out-group comparison does not help determine polarity of this character. The most parsimonious explanation from the phylogenetic analysis indicates that the presence of a stigma represents the plesiomorphic state. Based on other genera in Evans' (1955) group M, the typical hesperiine stigma is relatively slender, the ratio of width to length usually near 1:5 (Figs. 40–45). Burns (1964) speculates that the presence of scent organs in the Hesperiiidae may be controlled by a single gene, whereas their development is polygenic. This is consistent with the pattern observed in *Euphyes*.

17. Stigma absent. This condition characterizes the *subferruginea* group.

18. Stigma wide, approximately $\frac{1}{3}$ as wide as it is long (Figs. 46–48). This condition is found in *E. singularis* + *E. cornelius* and *E. conspiciua*, and apparently developed independently twice.



FIGS. 27–39. *Euphyes* male genitalia—aedeagus (lateral view): 27, *peneia*; 28, *singularis*; 29, *cornelius*; 30, *subferruginea*; 31, *dion*; 32, *dukest*; 33, *berryi*; 34, *conspicua*; 35, *pilatka*; 36, *vestris*; 37, *chamuli*; 38, *arpa*; 39, *bimacula*. c = cornuti (the scale of these figures is variable).

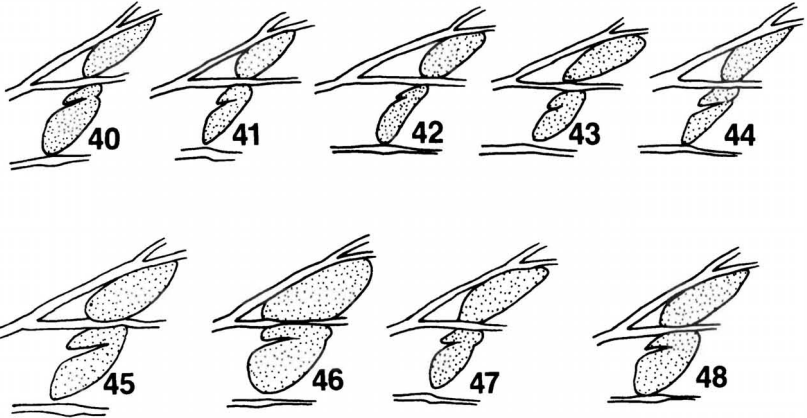
Uncus. In the plesiomorphic condition the two prongs of the uncus are widely separated (Figs. 49–56) and each prong ends posteriorly in a point (Figs. 61–63). The following characters are derived from this condition.

19. Uncus prongs closely spaced (Figs. 57–60). This condition probably arose independently in two lineages, once in *E. arpa*, and again in *E. singularis* + *E. cornelius* + *E. peneia*.

20. Uncus prongs with a small lateral posterior suture (Figs. 61–73). This condition defines *Euphyes*.

21. Uncus prongs posteriorly blunt (Figs. 64–73). This condition is found in the *dion*, *subferruginea* and *vestris* groups.

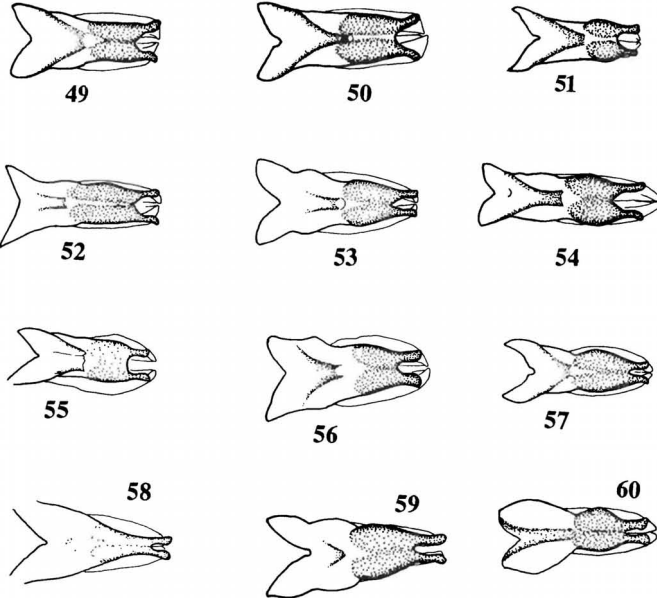
Valva. In the plesiomorphic condition, the valva is short and cup-shaped (Figs. 64–73). This condition is found in the majority of *Euphyes* except for the following two apomorphic conditions.



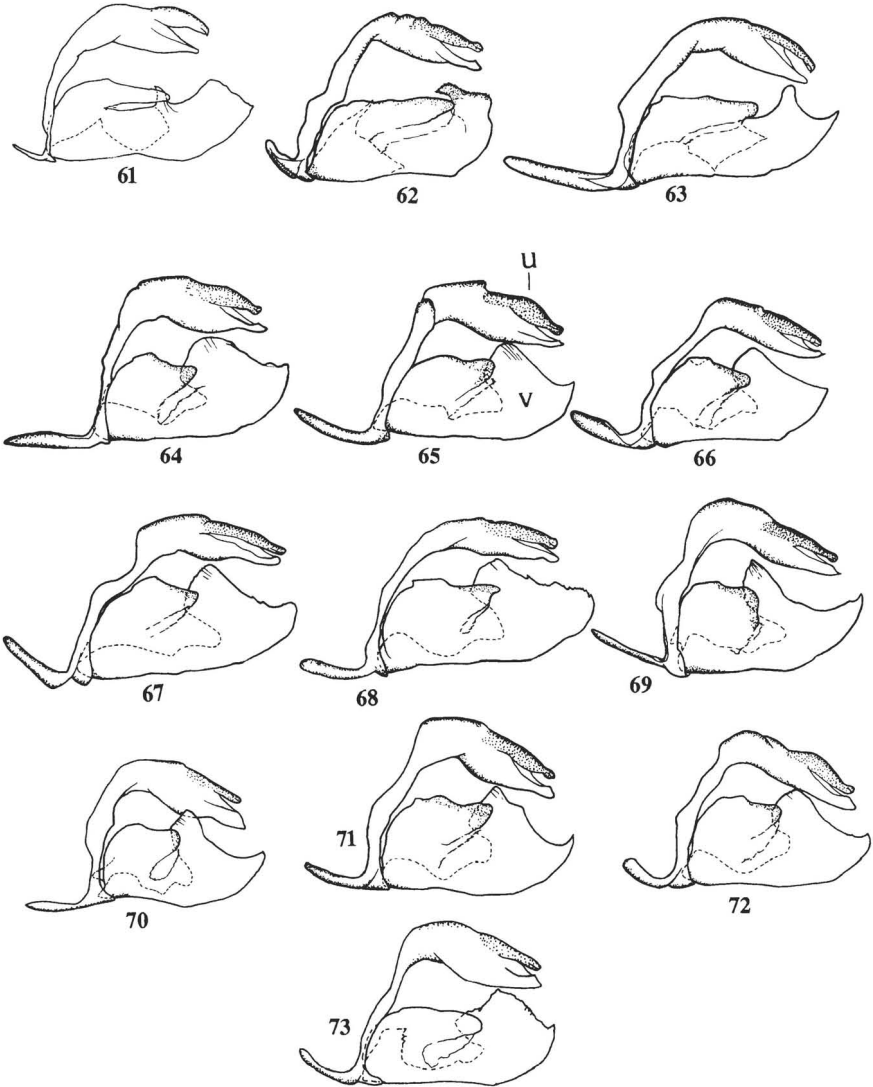
FIGS. 40–48. *Euphyes* male stigmata (dorsal view); 40, *dion*; 41, *berryi*; 42, *bimacula*; 43, *vestris*; 44, *arpa*; 45, *pilatka*; 46, *singularis*; 47, *cornelius*; 48, *conspicua* (the scale of these figures is variable).

22. Valvae basally elongate (Figs. 61–63). This condition is found in *E. peneia*, *E. singularis* and *E. cornelius*.

23. Valvae recurved posteriorly into a hook-shaped spine (Fig. 62). This is an autapomorphy for *E. singularis*.



FIGS. 49–60. *Euphyes* male genitalia—uncus (dorsal view): 49, *dion*; 50, *dukesi*; 51, *conspicua*; 52, *berryi*; 53, *pilatka*; 54, *vestris*; 55, *chamuli*; 56, *bimacula*; 57, *arpa*; 58, *peneia*; 59, *cornelius*; 60, *singularis* (the scale of these figures is variable).



FIGS. 61-73. *Euphyes* male genitalia—valva and uncus (lateral view): **61**, *peneia*; **62**, *singularis*; **63**, *cornelius*; **64**, *dion*; **65**, *dukest*; **66**, *conspicua*; **67**, *pilatka*; **68**, *berryi*; **69**, *vestris*; **70**, *chamuli*; **71**, *bimacula*; **72**, *arpa*; **73**, *subferruginea*. v = valva, u = uncus (the scale of these figures is variable).

Wing Pattern Characters

Two conditions occur in both the in- and out-groups. The species of *Arotis* are basally black, a condition shared by the *peneia* and *subferruginea* groups and by *E. vestris* and *E. chamuli*. The species of *Prob-*

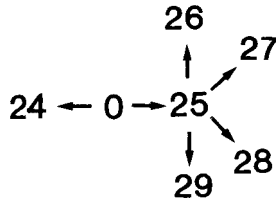


FIG. 74. Hypothesized transformation of wing pattern characters. 0 is plesiomorphic condition. All other numbers are derived and refer to character numbers in text.

lema are tawny with dark wing margins. The ventral hind wings have a light orange medial patch and light orange veins. This pattern is found in the *dion* group and in slightly modified form in *E. bimacula* and *E. arpa*. I originally considered the tawny pattern to be plesiomorphic because of the similarity in pattern between *Problema* and certain members of the *dion* group, especially *E. conspicua*. However, based on the distribution of other characters, the most parsimonious solution suggests that the ancestral wing pattern was black. I hypothesize that the original ancestor of *Euphyes* had black wings; however, it seems likely that this melanic pattern is controlled by one or a few genes which suppress the more complex and presumably polygenically controlled tawny pattern. This could explain why both basic character states of wing pattern of the out-group are found almost unchanged in the in-group. The following conditions are considered apomorphic and the hypothetical derivation of these states is illustrated in Fig. 74. Illustrations of *Euphyes* species can be found in Mielke (1972, 1973), Howe (1975) and Shuey (1988).

24. Tan scales suffused dorsally over otherwise black wing surfaces. This is an autapomorphy for *E. singularis*.

25. Tawny wing pattern. The most parsimonious conclusion is that this condition arose independently twice, once in the *dion* group, and again in *E. bimacula* + *E. arpa*.

26. Orange ray on ventral hind wing. This condition is found in *E. dion*, *E. dukei*, and *E. bayensis*.

27. Ventral hind wing without an orange patch. This condition apparently arose independently in two lineages, once in *E. pilatka* + *E. berryi* and once in *E. bimacula* + *E. arpa*.

28. Ventral hind wing veins the same color as the wings. This is an autapomorphy for *E. pilatka*.

29. Dorsal tawny areas brown. This is an autapomorphy for *E. dukei*. The net result of this condition is strikingly similar to that of character 24 when viewed dorsally, but ventral examination reveals that the two conditions occur over the two basic color patterns.

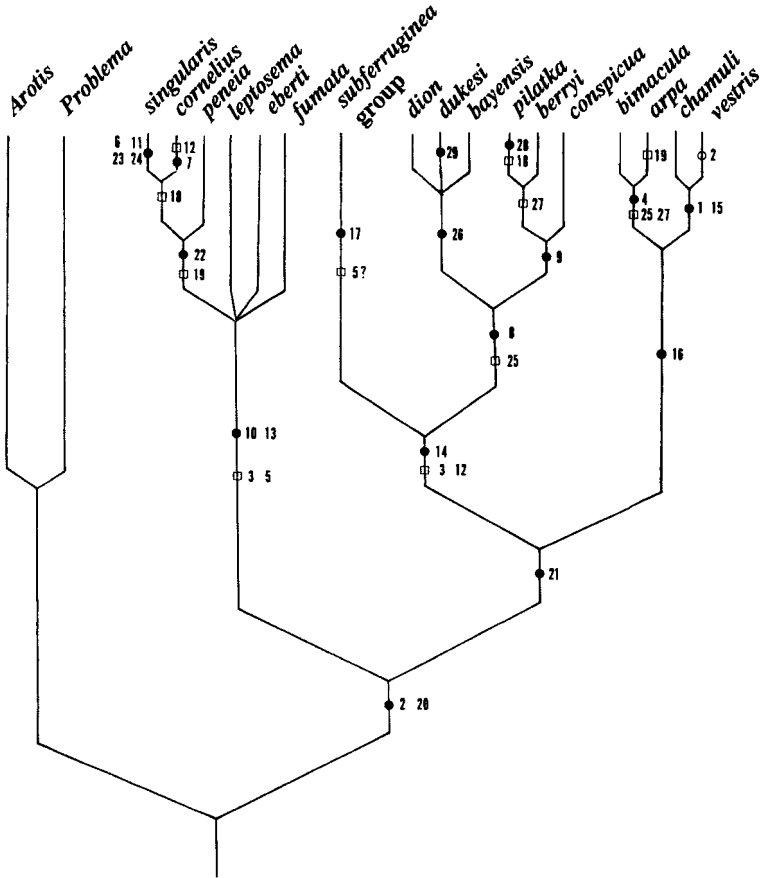


FIG. 75. Hypothesized phylogeny of *Euphyes*. Closed circles are apomorphic characters defining single lineages. Open squares are homoplasic apomorphic characters. Open circle is a reversal. Character numbers refer to character numbers in text. The relationship of *Euphyes* to the out-group genera, *Problema* and *Arotis*, is detailed in Shuey (1987).

PHYLOGENETIC ANALYSIS

The five independent analyses using random seed numbers generated identical cladograms (Fig. 75), which lead me to recognize four monophyletic species groups in *Euphyes*, each characterized by several synapomorphies.

***Peneia* group.** Originally proposed by Mielke (1972), the *peneia* group is defined by lateral fixed spines on the aedeagus (character 10), lateral extensions of the dorsal portion of the ductus bursae (character 5), and black wing pattern. Mielke included four species, *E. peneia*, *E.*

eberti Mielke, *E. leptosema* (Mabille), and *E. fumata* Mielke. I add the two Caribbean species, *E. singularis* and *E. cornelius*, to this group.

Hypothesized relationships within the group are tentative. *Euphyes singularis* and *E. cornelius* are sister species (character 18), which form a monophyletic group with *peneia* (characters 19 and 22). The remaining relations within this clade are unresolved.

Subferruginea group. Mielke (1972) included three species in this group, all of which lack a stigma (character 17): *E. subferruginea*, *E. antra* Evans, and *E. cherra* Evans. Although I examined only one of these species (a male *subferruginea*), Mielke's figures of the male genitalia provided some character states for this analysis. His figures of the female genitalia are more difficult to interpret, but I was able to assign some character states while leaving several states questionable (coded as "?" in data set). The *subferruginea* group shares with the *dion* group the development of cornuti on the aedeagus (character 14), and they are tentatively considered sister groups. If this relationship is correct, the absence of a stigma is a reversal (character 17). *Euphyes ampa* Evans probably belongs in this species group, but Mielke (1972, 1973) did not attempt to place it. Because Mielke's figures are difficult to interpret, *Euphyes ampa* was not included in the phylogenetic analysis.

Dion group. This group is characterized by the doubled-back course of ductus bursae (character 8), thornlike cornuti on the aedeagus (character 14), and tawny wing pattern (character 25). There are two distinct lineages within this group. The first is an unresolved trichotomy defined by presence of an orange ray on the ventral hind wing (character 26) (*E. dion*, *E. dukesi*, and *E. bayensis*). The second lineage is defined by erect corpus bursae (character 9). Within the latter lineage, *E. pilatka* and *E. berryi* are sister species defined by the unmarked ventral hind wing (character 27), and together form the sister group to *E. conspicua*.

Vestris group. This group is characterized by cone-shaped cornuti on the aedeagus (character 16). There are two very distinct group lineages. The first has tawny wings (character 25) and a straight, very elongate corpus bursae (character 4), and includes *E. bimacula* and *E. arpa*. The second lineage includes *E. vestris* and *E. chamuli* and is characterized by black wings, a ductus bursae that lacks sclerotization dorsally (character 1), and by an additional dorsal hinged cone on the aedeagus (character 15).

BIOGEOGRAPHY OF *EUPHYES*

Each species group in *Euphyes* is limited primarily to either tropical America (*subferruginea* and *peneia* groups) or temperate North America (*dion* and *vestris* groups), suggesting that the initial splitting of these

Fontenela & Cruz 1986). This model assumes that Caribbean species represent dispersers from the mainland into previously unoccupied areas. As it applies to the Caribbean basin, all species are presumed to have colonized the islands via over-water dispersal or via land bridges presumably present during the Pleistocene. The most parsimonious dispersal explanation for *Euphyes* distributions is based entirely upon the known current distributions of each species. The first event would have been the immigration of the common ancestor of *E. singularis* + *E. cornelius* onto one of the Greater Antilles, probably Cuba since both species occur there. From there, *E. singularis* apparently immigrated to either Jamaica or Hispaniola, where it differentiated into subspecies *insolata*, and subsequently spread to unoccupied islands. *Euphyes cornelius* may have immigrated from Cuba to the Bahamas where it differentiated into subspecies *agra*.

The **vicariant model** assumes allopatric speciation after barriers separate parts of formerly continuous populations (Rosen 1975, Savage 1982). In the case of the Caribbean Basin, the movement of the Greater Antilles (via plate tectonics) probably provided the vicariance event that transported the common ancestor of *E. singularis* + *E. cornelius* into the area. The islands of Cuba, Puerto Rico, and most of Hispaniola presumably were part of a plate that at one time was either in contact or very near Central America (Buskirk 1985). An additional vicariance event separated Cuba and Hispaniola, and today recognizably different subspecies of *E. singularis* are found on these islands. Because Puerto Rico is on the same plate as is Hispaniola, this model predicts that *E. singularis* may be present but undetected on Puerto Rico. Jamaica and southern Hispaniola have drifted somewhat independently from the other Greater Antilles, and only recently (i.e. within the last 10 million years) has Jamaica approached the other islands. Thus, the vicariant model alone cannot explain the presence of *E. singularis* on Jamaica. Likewise, the presence of *E. cornelius* on the Bahamas is not explained by the model.

A more compelling and realistic explanation combines both models (Fig. 77). The *Euphyes* ancestral species probably arrived in the Caribbean via vicariance (Event 1) where it differentiated into two species lineages. The presence of recognizably different populations of *E. singularis* on Cuba and Hispaniola indicates another vicariant event following the development of that species (Event 2). This is consistent with the geologic history of the area (Buskirk 1985); congruent distribution patterns are found in reptiles (Savage 1982) and fishes (Rosen 1975). Since neither Jamaica (*E. singularis*) or the Bahamas (*E. cornelius*) have contacted either Cuba or Hispaniola respectively, over-water dispersal is probably the most likely explanation for the occur-

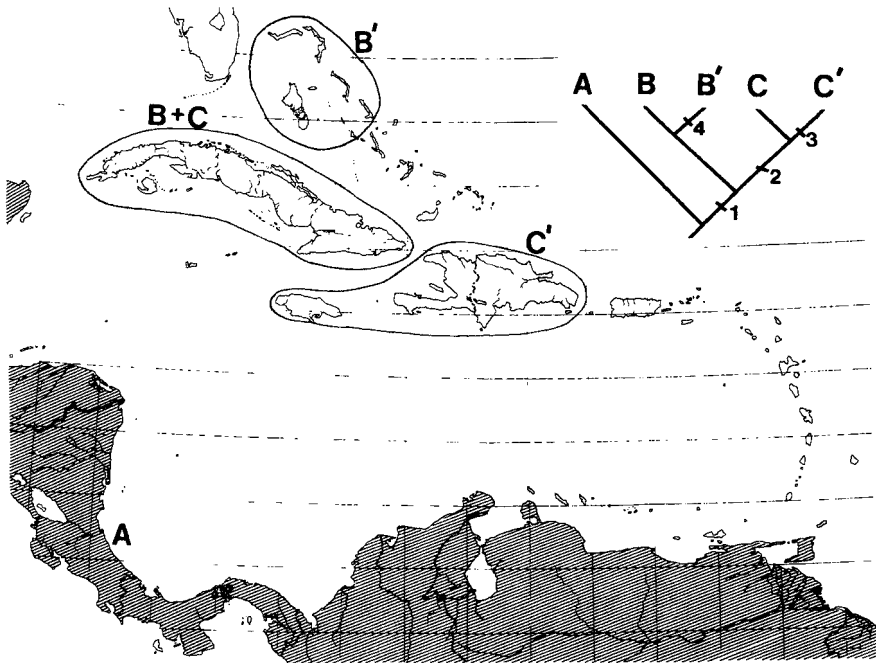


FIG. 77. Area cladogram of the proposed model of *Euphyes* distribution in the Caribbean Basin based on *Euphyes* phylogeny and the tectonic history of the northern Caribbean. See text for explanation of Event numbers on cladogram. A = generalized range of the ancestral species to the *peneia* + *singularis* + *cornelius* lineage. B = range tract of *E. cornelius cornelius*. B' = range tract of *E. cornelius agra*. C = range tract of *E. singularis singularis*. C' = range tract of *E. singularis insolata*.

rence of *Euphyes* on Jamaica and the Bahamas (Events 3 and 4, respectively).

This model for the Caribbean distribution of *Euphyes* is consistent with Miller and Miller's (1990) model for the reconstruction of the West Indian butterfly fauna. They recognize that neither vicariance nor dispersal alone can fully explain the current distribution of butterflies in the Caribbean Basin. Based on their model the initial vicariant event in the Caribbean Basin (Event 1) probably dates to the formation of the proto-Greater Antilles during the late Cretaceous to Eocene periods. The vicariant event which led to differentiation of *E. singularis* on Cuba and Hispaniola (Event 2) may date to the Oligocene to Pliocene period. The dispersal events cannot be dated (Events 3 and 4).

The biogeography of the *subferruginea* group is less complex. All of the known species occur in South America (Mielke 1972).

The *dion* group is restricted to eastern North America. The species are mostly associated with wetlands, and the distribution of these fea-

tures along the Atlantic and Gulf coasts, the Mississippi River drainage, and in glaciated regions may account for the limited ranges of the species in this group. Shapiro (1971) suggested that the present distribution of many wetland butterflies in the eastern U.S. is the result of the happenstance location of refugia during periods of glacial maxima. This may have severely limited the available routes for dispersal into newly formed habitats as they become available behind retreating glaciers.

In addition, several species in the *dion* group have undergone differentiation at the periphery of their ranges. Populations of *E. pilatka* in the Florida Keys have recently been recognized as subspecies *klotsi* (Miller et al. 1985). These populations may have colonized the Keys during a glacial maximum period, when sea levels were lower providing an overland dispersal route into the Keys. Current sea level isolates the Keys as islands, limiting the potential for gene flow with mainland populations. Likewise, *E. conspicua* has recognizable subspecies at the northern and western edges of its range [*orono* (Scudder) and *bucholzi* (Ehrlich & Gillham), respectively]. *Euphyes bayensis* is a subtly differentiated species inhabiting the extreme southern edge of its probable sister species, *E. dion* (Shuey 1988). Although the total range of *E. bayensis* is unknown, its apparent restriction to tidally influenced freshwater marshes (*sensu* Mitsch & Gosselink 1986) suggests that it will be limited to the southern edge of the North American Coastal Plain. Populations of *E. dukesi* from Florida represent an undescribed subspecies (Shuey, unpubl.). This taxon is ecologically similar to mainland *E. dukesi* populations but is morphologically distinct.

This general trend of differentiation at the edge of species ranges in the *dion* group is consistent with allopatric divergence. In these cases, this process may be enhanced by glacial cycling, which results in the expansion and contraction of coastal and inland wetlands on a regular basis (Pielou 1992). This rearrangement of wetland habitat during each glacial cycle presumably fragmented and relocated (via dispersal) populations of wetland butterflies, possibly to small refugia where they may have been more susceptible to environmentally induced or somewhat random genetic changes (Shuey 1985).

Distributions of the two clades of the *vestris* group also suggest allopatric speciation. *Euphyes vestris* is widely distributed throughout North America and northern Mexico. *Euphyes chamuli* occurs to the south of *E. vestris*. Known from less than 10 specimens, *E. chamuli* appears to be confined to the highland region along the Mexican-Guatemalan border. These two species are morphologically very similar and it seems likely that *E. chamuli* is directly derived from a peripheral *E. vestris* population. In addition, isolated populations of *E. vestris* in

southern California (subspecies *harbisoni* Brown & McGuire) are amply distinct from the remaining populations (Brown & McGuire 1983), possibly indicating that *E. vestris harbisoni* represents a relict series of populations with a long history of isolation.

The remaining clade demonstrates a similar pattern. *Euphyes bimacula* occurs in the Great Lakes region of North America and along the Atlantic Coastal Plain south to Georgia. *Euphyes arpa* has been reported from southern Georgia through peninsular Florida (Opler & Krizek 1984). This allopatry could be interpreted as the result of competitive interactions between the sister species. However, *E. arpa* and *E. bimacula* have very dissimilar ecologies, and *E. arpa* is the only *Euphyes* known to use a non-sedge larval food plant: *Serenoa repens* (Bartram) (Palmae), a common plant of xeric habitats in Florida, is the only documented host for *E. arpa* (Opler & Krizek 1984). *Euphyes bimacula* is more typical of the genus and uses wetland species of *Carex* (Cyperaceae) as the larval food plant. Thus, competition for larval resources is not apparent, and this pattern suggests an ancient allopatric divergence of a formerly widespread ancestral species.

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LITERATURE CITED

- BURNS, J. M. 1964. Evolution in skipper butterflies of the genus *Erynnis*. Univ. Calif. Publ. Entomol. 37: 217 pp.
- BROWN, F. M. 1978. The origins of the West Indian butterfly fauna, pp. 5-30. In Gill, F. B. (ed.), Zoogeography in the Caribbean. Acad. Natur. Sci. Phila. Spec. Publ.
- BROWN, J. W. & W. W. MCGUIRE. 1983. A new subspecies of *Euphyes vestris* (Boisduval) from southern California (Lepidoptera: Hesperidae). Trans. San Diego Soc. Nat. Hist. 20:57-68.
- BUSKIRK, R. E. 1985. Zoogeographic patterns and tectonic history of Jamaica and the northern Caribbean. J. Biogeogr. 12:445-461.
- EVANS, W. H. 1955. A catalogue of the American Hesperidae indicating the classification and nomenclature adopted in the British Museum (Natural History). Part IV: Groups H-P, Hesperinae and Megathyminae. British Museum (Natural History), London. 588 pp.
- FELSENSTEIN, J. 1984. The statistical approach to inferring evolutionary trees and what it tells us about parsimony and compatibility, pp. 169-191. In Duncan, T. & T. F. Stuessy (eds.), Cladistics: perspectives in the reconstruction of evolutionary history. Columbia Univ. Press, New York.
- FONTENELA, J. L. & J. DE LA CRUZ. 1986. Análisis zoogeográfico de las mariposas

- antillanas (Lepidoptera: Rhopalocera) a nival subespecífico. *Ciencias Biol.* 15:107-122.
- HENNIG, W. 1966. Phylogenetic systematics. Univ. Ill. Press, Urbana. 263 pp.
- HOWE, W. H. 1975. The butterflies of North America. Doubleday, New York. 633 pp.
- MIELKE, O. H. 1972. As espécies Sul-Americanas do gênero *Euphyes* Scudder, 1872. (Lepidoptera: Hesperiiidae). *Bol. Univ. Paraná, Zool.* 5:175-222.
- 1973. Sobre *Euphyes ampa* Evans, 1955 (Lepidoptera: Hesperiiidae). *Atas Soc. Biol. Rio de Janeiro.* 17:1-3.
- MILLER, L. D., D. J. HARVEY & J. Y. MILLER. 1985. Notes on the genus *Euphyes*, with description of a new subspecies (Lepidoptera: Hesperiiidae). *Florida Entomol.* 68: 323-335.
- MILLER, L. D. & J. Y. MILLER. 1990. The biogeography of West Indian butterflies (Lepidoptera: Papilionoidea, Hesperioidea): A vicariance model, pp. 229-262. *In* Woods, C. W. (ed.), *Biogeography of the West Indies: Past, present and future.* Sandhill Crane Press, Florida.
- MITSCHE, W. J. & J. G. GOSSELINK. 1986. *Wetlands.* Van Nostrand Reinhold, New York. 539 pp.
- OPLER, P. A. & G. KRIZEK. 1984. *Butterflies east of the Great Plains.* Johns Hopkins Univ. Press, Baltimore. 249 pp.
- PIELOU, E. C. 1992. After the ice age: The return of life to glaciated North America. Univ. Chicago Press. 366 pp.
- ROSEN, D. E. 1975. The vicariance model of Caribbean biogeography. *Syst. Zool.* 24: 431-464.
- SAVAGE, J. M. 1982. The enigma of the Central American herpetofauna; dispersals or vicariance. *Ann. Missouri Bot. Gard.* 69:464-547.
- SCOTT, J. A. 1972. Biogeography of Antillean butterflies. *Biotropica* 4:32-45.
- SHAPIRO, A. M. 1971. Post glacial biogeography and the distribution of *Poanes viator* (Hesperiiidae) and other marsh butterflies. *J. Res. Lepid.* 9:125-155.
- SHUEY, J. A. 1985. Habitat association of wetland butterflies near the glacial maxima in Ohio, Indiana, and Michigan. *J. Res. Lepid.* 24:176-186.
- 1987. Phylogenetic position of *Arotis*. *Ann Entomol. Soc. Amer.* 80:584-589.
- 1988. The morpho-species concept of *Euphyes dion* with the description of a new species (Hesperiiidae). *J. Res. Lepid.* 27:160-172.

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