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New Data on Miocene Butterflies in Dominican Amber (Lepidoptera: Riodinidae and Nymphalidae) with the Description of a New Nymphalid

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ABSTRACT

A new, virtually complete and well-preserved female specimen of *Voltinia dramba* Hall, Robbins, and Harvey, 2004 (Lepidoptera: Riodinidae) provides new data on this fossil species, and a new fossil species of the Recent genus of Nymphalidae *Dynamine* Hübner, 1819 (Lepidoptera: Nymphalidae) is described as *Dynamine alexae* n.sp., on the basis of a male specimen. The two species are preserved in Miocene amber from the Dominican Republic. *Dynamine alexae* n.sp. represents the first adult nymphalid butterfly found as a fossil in amber. The four taxa of butterflies found up to the present in Dominican amber indicate post-Miocene extinctions in Hispaniola, probably caused by insularization. The butterflies found in Dominican amber do not support a hypothesis of a Gondwanan origin for many butterfly tribes and subfamilies as previously proposed; we conclude that this hypothesis is implausible based on the age of the butterflies as inferred from the fossil record. Some palaeoecologic and taphonomic questions are discussed.

INTRODUCTION

Amber preserves delicate arthropods, mainly insects, with high fidelity, including microscopic features like setae and sensilla on the external cuticle as well as wing and other color patterns (Grimaldi, 1996). In some cases

amber preserves soft internal tissues, including cells, organelles, and even endosymbiotic spirochetes and protists (Grimaldi, 1996; Grimaldi et al., 1994; Henwood 1992a, 1992b; Wier et al., 2002).

The most diverse organisms in amber are insects, particularly of the orders Diptera,

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Hymenoptera, and Coleoptera. Lepidoptera specimens tend to be less common and even rare in amber, the principal record being adult moths. The fossil record of adult butterflies in the world, from the Paleocene to Miocene, contains approximately 50 specimens known, comprising about 33 named species in all living families, but only seven of the specimens have been found in amber, all of them in Dominican amber (Grimaldi and Engel, 2005). For Miocene Dominican amber, the list of fossilized Lepidoptera includes other families: Blastobasidae, Cosmopterygidae, Gelechiidae, Noctuidae, Tineidae and Tortricidae (Poinar [1992]), Tortricidae (Poinar and Brown [1993]), and Oecophoridae (Kristensen and Skalski [1999]). Grimaldi and Engel (2005) figured a caterpillar and two adults of the family Geometridae, an adult of the genus *Acrolophus* (Acrolophidae), and other adults of Tortricidae and Gelechioidea; an interesting tineoid moth figured by these authors is a case with the caterpillar inside. The scarce butterflies found in Dominican amber have been studied in detail, and are represented as caterpillars of the families Nymphalidae and Riodinidae (DeVries and Poinar, 1997; Hammond and Poinar, 1998) and adults of Riodinidae (Poinar, 1992; Grimaldi, 1996; DeVries, 1997; Hall et al., 2004). Here, we report two additional adult butterfly specimens of the families Riodinidae and Nymphalidae as inclusions in Miocene Dominican amber; the nymphalid specimen is the first adult known of this family preserved in amber.

The family Riodinidae contains about a thousand species, most of which occur in the American tropics and are partly characterized by the greatly reduced male forelegs and the silver or leaden spots in the wings, which is why these butterflies are commonly named metalmarks (see DeVries, 1997). Riodinid caterpillars and pupae resemble those of lycaenids, which is why some authors classify them into a single family (Kristensen, 1976; De Jong et al., 1996), though the families are usually considered sister groups (Ackery et al., 1999). The family Riodinidae contains three subfamilies (Nemeobiinae, Euselasiinae and Riodininae). Riodininae, the largest subfamily, is divided into eight

tribal groupings; two of them—Mesosemiini and Eurybiini—possessing five forewing radial veins; the other six possess four forewing radial veins (Hall, 2003). The Riodinidae fossil record is comprised only of a caterpillar specimen (DeVries and Poinar, 1997; see the discussion about other putative riodinid fossils in Hall et al., 2004) and the recently described species *Voltinia dramba* based on five adult females (Hall et al., 2004), both preserved in Miocene Dominican amber. A new female specimen of *Voltinia dramba* in the collection of the American Museum of Natural History (AMNH) provides an opportunity to complete some details in the description of this interesting species. The most recent investigations on the phylogeny of Riodinidae are Harvey (1987) in Hall (2003), plus the subsequent contributions by Hall (1998, 1999) and Hall and Harvey (2002). The most recent study on the phylogeny of the subfamily Riodininae, by Hall (2003), is a cladistic analysis of the 16 genera that have five forewing radial veins; this study coded data on the adult ecology, wing venation and pattern, the adult head and body, male and female genitalia, and early-stage ecology and morphology. That analysis confirmed the monophyly of the tribes Mesosemiini and Eurybiini, and established two subtribes for Mesosemiini (Mesosemiina and the new subtribe Napaeina). The fossil species *Voltinia dramba* belongs to the subtribe Napaeina. For Hall (2003), the best hypothesis about the relationships among the four- and five-radial-vein groups of Riodininae is Mesosemiini + (Eurybiini + all four-radial-vein tribes).

The Nymphalidae is the most diverse family of butterflies, with more than 6,000 described species worldwide. The nymphalid butterflies are found in virtually every terrestrial habitat except Antarctica, and have their greatest diversity in the Neotropics (DeVries, 1987). The nymphalids are characterized by very short forelegs in males and females, on which the males of many species carry a “brush” of long scales. The family contains many colorful, large species, and most of the mimicry complexes in butterflies. Nymphalid larvae feed on dicotyledonous plants, very often toxic ones, and they are also generally adorned with a variety of spines and tubercles (DeVries, 1987; Smith et

al., 1994). The species of Nymphalidae have been placed into more than 500 genera classified into 12 subfamilies. The oldest nymphalid fossil is an undescribed form from the Early Eocene of Green River (Colorado), but its classification within the family is unclear, and other Eocene records are several species described from Florissant (reviewed in Grimaldi and Engel, 2005). The systematic relationships among the subfamilies and tribes of Nymphalidae are still poorly known and thus the phylogeny of the family has been frequently discussed. There is some evidence of a sister-group relationship between Lycaenidae and Nymphalidae, and Pieridae is possibly the sister group of the Lycaenidae + Nymphalidae (De Jong et al., 1996). Freitas and Brown (2004) presented a historical overview of Nymphalidae phylogeny. Two recent studies, using the *wingless* gene (Brower, 2000) and mitochondrial and nuclear genes (Wahlberg et al., 2003), concluded that many of the traditional subgroups are monophyletic. The latest and most complete cladistic analysis to date, using 234 characters from all life stages of 95 nymphalid species, has been published by Freitas and Brown (2004), concluding that the taxa can be grouped into six main lineages and it supports the monophyly and relationships of most presently recognized subgroups. That study also supported the position of the subfamily Libytheinae as the basal group of Nymphalidae.

Due to the poor fossil record of butterflies, they have rarely been used in phylogenetic studies. For this reason it is very important to study all remains found in the fossil record, like the two specimens embedded in Dominican amber described here.

MATERIAL AND METHODS

Dominican amber is fossil resin that was formed by an extinct species of *Hymenaea* tree (Leguminosae: Caesalpinioidea), and is mid-Miocene in age (Iturralde-Vinent and MacPhee, 1996; see the discussion in Grimaldi, 1995, about the erroneous dating of this amber as Eocene-Oligocene by some authors). This amber derives mainly from outcrops in the mountains in the north and northeast of Santiago. The material studied here was acquired through purchase, and as such its exact

provenance within the outcrops of Dominican amber mines is unknown, but its authenticity is certain, based on physical characteristics and typical preservation of the inclusions.

The pieces were polished and some parts of the specimens were studied using sugar gel applied between the amber surface and a slide, which reduces the optical distortion caused by the curvature and imperfections of the amber surface. Photomicrography used the Infinity® K-2 long distance microscope and the MicroOptics® fiber optic flash unit (www.microoptics.com). The specimens were drawn using a drawing tube attached to a Zeiss Stemi SV8 stereoscope. Specimens are housed in the amber fossil collection, Department of Invertebrate Zoology, AMNH.

SYSTEMATIC PALEONTOLOGY

CLASS INSECTA LINNAEUS, 1758

ORDER LEPIDOPTERA LINNAEUS, 1758

SUPERFAMILY PAPILIONOIDEA
LATREILLE, 1802

FAMILY RIODINIDAE GROTE, 1895

SUBFAMILY RIODININAE GROTE, 1895

TRIBE MESOSEMIINI BATES, 1859

SUBTRIBE NAPAEINA HALL, 2003

GENUS *VOLTINIA* STICHEL, 1910

Voltinia dramba Hall, Robbins,
and Harvey, 2004
Figures 1, 2a-c

MATERIAL: AMNH DR-18-1 (female) in a large clear piece of amber measuring 83 mm length × 44 mm width × 24 mm thickness. The piece also contains small specimens (syninclusions) of three dipterans, two beetles, one moth (of the superfamily Gelechioidea), one hymenopteran of undetermined family and one Chalcidoidea, one mite, and one seed.

This butterfly is virtually complete and well preserved, lacking only the antennae, the proboscis and small portions of the posterior area of the hind wings. The wings are overlapping. The venation and color pattern of the left wings are very well preserved. The

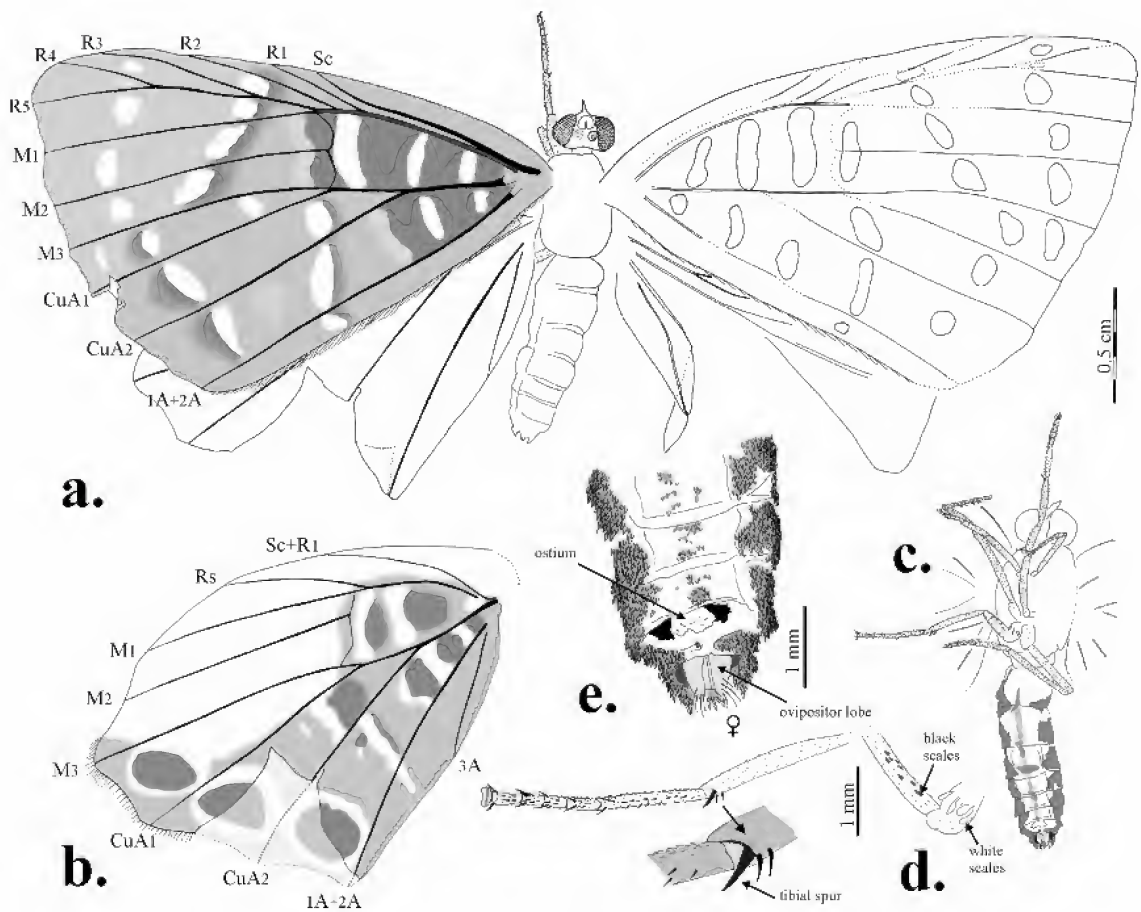


Fig. 1. Camera lucida drawings of the new specimen of *Voltinia dramba* (AMNH DR-18-1) in Miocene amber from the Dominican Republic. a. Complete dorsal view of body with the color forewing pattern. b. Hind wing with the color pattern preserved. c. Ventral view of body. d. Hind leg. e. Female genitalia. a-c to same scale.

specimen occurs in a piece that, prior to purchase, was broken into several portions, which were then fused with adhesive.

DESCRIPTION: **Head** with eyes bare, having entirely brown margins. **Thorax** brown, length 5.08 mm. **Forewing** shape triangular; length 23.6 mm, greatest width 14.9 mm. Five radial veins (fig. 1a). Underside with three narrow, straight white bars at base of CuA₂ cell, the distal one is faint, and other three in discal cell, all separated by darker brown areas. A faint bar present at the base of M₁ and M₂ cells, separated from the discal cell by a darker brown area. Three lines of white spots in cells R₂ to M₂ (straight diagonal line), in cells CuA₁ to A₁ + A₂ at level of middle disco-cellular

vein (straight line), and in cells R₃ to CuA₂ (submarginal line comprised of eight spots, including a very small spot at base of cell R₄). Two additional white spots present in cell M₃, one closest to the base and another in the distal part. Faint spot in cell CuA₂ present between the two lines that cross this cell. **Hind wing** length 19.9 mm, greatest width 13.9 mm. Underside with three narrow, straight white bars at base of CuA₂; distal one is curved, and other three in discal cell, all separated by darker brown surfaces (fig. 1b). Narrow, straight white bars in middle of CuA₁, CuA₂, and A₁ + A₂ cells (only the distal color pattern of cell M₃ is visible); the bars of CuA₁ and CuA₂ have a darker brown basal margin and

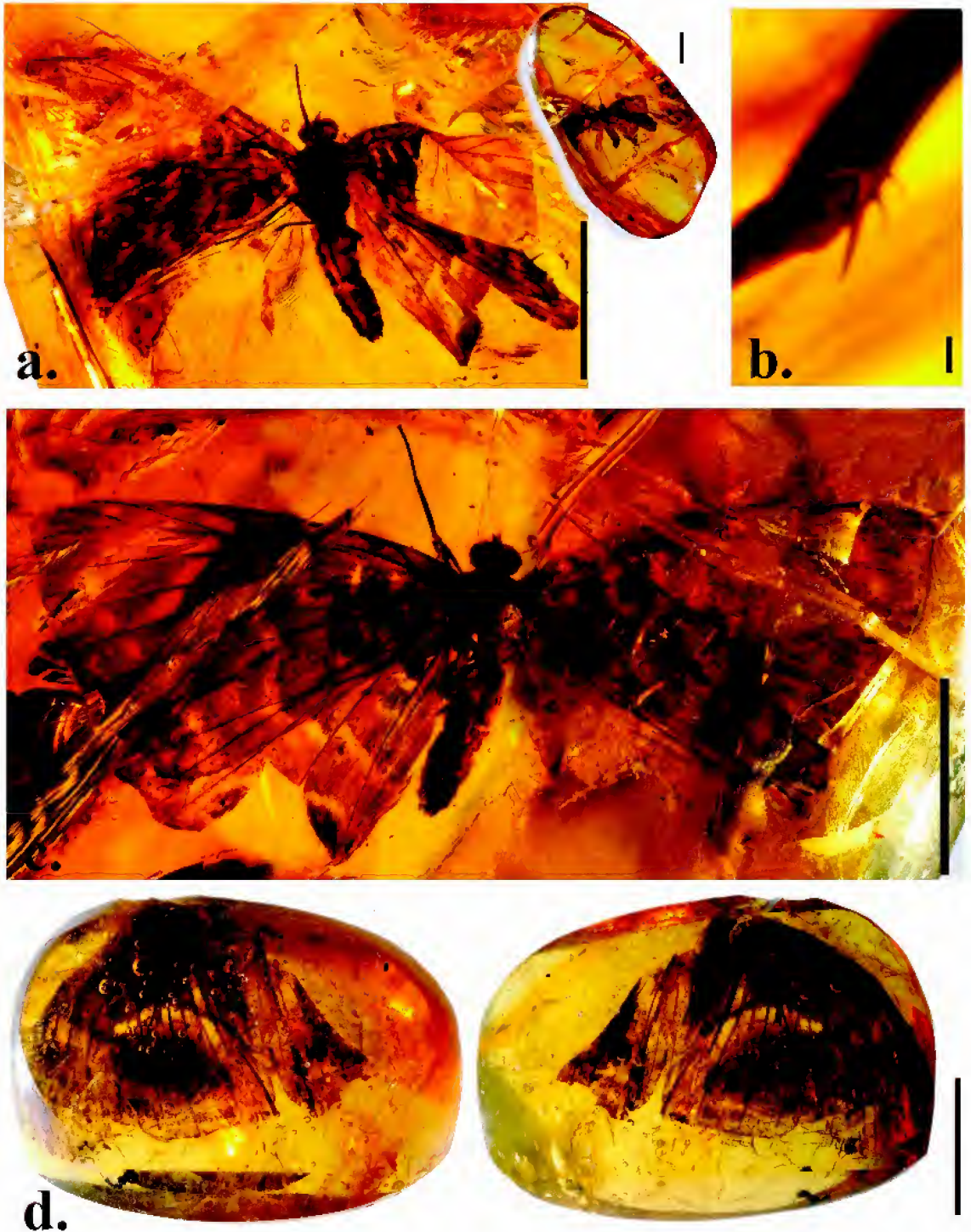


Fig. 2. Photomicrographs of Miocene butterflies in Dominican amber. **a.** Female of *Voltinia dramba* (AMNH DR-18-1) in ventral view, and complete view of the amber piece. **b.** Apical tibial spur in the hind leg of the same specimen. **c.** Dorsal view of the new *Voltinia dramba* specimen; this butterfly is fossilized with the wings at an angle and so this image was made with six consecutive pictures of the specimen taken at successive focal planes. **d.** Male of *Dynamine alexae* n.sp. holotype (AMNH DR-18-2) in dorsal (left) and ventral view (right). Scale bars = 1 cm in panels a, c, d; = 0.1 mm in panel b.

a closer small white spot on the distal margin. Submarginal, darker brown spots at least in cells M_3 , CuA_1 , and CuA_2 (the last two are not complete). These spots large, semicircular in shape, with narrow pale border. Wing pattern in cells $Sc + R_1$ to M_2 not visible. **Legs** brown; hind leg with distal tibial spur (length 0.28 mm) and white scales on coxa (fig. 1d). Length of femora, tibiae, basitarsi, and tarsi II + III + IV + V in mm: foreleg 2.15, 1.31, 0.69 and 0.92; midleg 3.54, 2.31, 1.38 and 1.15; hind leg 2.69, 3.15, 1.46 and 1.62. Claws unforked. **Abdomen** brown dorsally, ventral surface laterally brown and with a longitudinal band of pale brown scales (fig. 1c). Length 8.15 mm, greatest width 2.31 mm. **Female genitalia** preserves the ostium of the bursa in segment VIII and the ovipositor lobes, which are of moderate size (fig. 1e).

NEW CHARACTERISTICS FOR *V. DRAMBA*: The new specimen has practically the same wing color pattern as previously described specimens of the species, but shows some slight differences. The new specimen has a very small white spot at the base of cell R_4 and a faint spot in cell CuA_2 between the two lines that cross this cell, both in the forewing. Also, the new specimen has two spots not present in the original description of the species, one distal faint spot in cell M_3 and a white spot, in line, on cell $A_1 + A_2$. In addition, the new specimen lacks the extra faint spot at the base of cell CuA_1 in the hind wing.

The most important difference observed in our specimen is the presence of a distal spur in the hind tibia. In addition, the ventral surface of the abdomen is laterally brown and has a longitudinal band of pale brown scales (vs. the ventral surface of the abdomen being completely brown in the original description).

COMMENTS: This specimen was erroneously referred to as a nymphalid by Grimaldi and Engel (2005: fig. 13.68). Ironically, this identification was based on study of the specimen by several experienced lepidopterists. The male for this fossil species is as yet unknown. The fracture surfaces of the amber piece hinder observation of the right wings, but their venation and color pattern have been drawn and compare well with those of the left wings. The color pattern of the anterior middle area of

the hind wings has not been observable due to the overlapping of the wings.

Hall et al. (2004) placed *V. dramba* in the tribe Mesosemiini because it apparently lacked a hind tibial spur, in addition to other characters. However, in the new specimen an apical spur on the hind tibia is clearly present (figs. 1d, 2b). It is not easy to observe this structure, and surely it is present in the fossil specimens studied by Hall et al., though probably obscured. The presence of a spur does not preclude placement of the fossil riodinids in the tribe Mesosemiini and in the genus *Voltinia*, since this character is present in the extant species *V. radiata* and *V. theata* and in some other genera of Mesosemiini (Hall, 2003; Hall et al., 2004). However, this is an important character for understanding relationships in the genus.

The differences observed in the color pattern of the new specimen are not indicative of a distinct species. These differences may be a consequence of intraspecific variation and/or distinct preservation. It is well documented that butterfly wing patterns frequently show spectacular differences among individuals of the same species (e.g., Brakefield and French, 1999). Some additional spots observed in the new specimen are faint, and possibly not evident in all the fossils. Hall et al. (2004) even indicated that the wing pattern reconstruction was adapted from the sister species *V. danforthi*, and presumably is a combination of the wing patterns of the five specimens. We describe the differences observed because variation for this species is presumably significant.

The riodinid caterpillar found previously in Dominican amber was identified as a member of the genus *Theope* (DeVries and Poinar, 1997), which belongs to the tribe Nymphidiini.

FAMILY NYMPHALIDAE SWAINSON, 1827

SUBFAMILY BIBLIDINAE BOISDUVAL, 1833

TRIBE DYNAMININI BURMEISTER, 1878

Genus *Dynamine* Hübner, 1819

TYPE SPECIES: *Papilio mylitta* Cramer, 1780: 107. By subsequent designation (Scudder, 1875: 160).

Dynamine alexae, new species

Figures 2d, 3, 4, 5

MATERIAL: AMNH DR-18-2 (male), holotype, in an amber piece 32 mm length \times 22 mm width \times 8 mm thickness.

The holotype is incomplete, having lost the anterior part of the body at the surface of the amber (figs. 2d, 3), specifically the head, the anterior part of the thorax, most of the right wings and proximal portions of the left fore- and hind wings. Preserved are only the distal part of the mid- and hind legs, most of the left wings, and abdomen with genitalia. The wings partly preserve the color pattern as tones of brown and are overlapping. The wing surfaces have small to medium gas bubbles trapped during immersion in the resin.

ETYMOLOGY: Patronym in honor of Mrs. Alex Goelet, wife of Mr. Robert G. Goelet, Chairman Emeritus and trustee of the AMNH; for their generous sponsorship of research at the AMNH.

TYPE LOCALITY: Mid-Miocene amber from mines in the Cordillera Septentrional, north and northeast of Santiago, Dominican Republic (Hispaniola).

DIAGNOSIS: According to wing size this new *Dynamine* species was large. Greatest width of the hind wing larger than greatest width of the fore wing (HW/FW = 1.19). White median band under both fore and hind wings; costal white subband on fore wing covers M_3 - CuA_1 cell and ends in CuA_1 - CuA_2 . Two identical ocelli under hind wing. Continuous, broad, brown postmedial band under hind wing connects the two ocelli, and has a broad, pale brown proximal margin. Two strong, short apical spines at apex of each male valve, one dorsal and one ventral.

DESCRIPTION: Large body size. **Forewing** (figs. 3a, 4): the preserved portion of forewing indicates a triangular shape (fig. 4), inferred length is 25.80 mm, and the greatest width is 16.11 mm; L/W inferred = 1.60. White median band on underside broken at level of CuA_1 in two subbands, the apical part of the costal subband covers M_3 - CuA_1 cell and ends in CuA_1 - CuA_2 ; apical part of anal subband ending in vein CuA_1 . **Hind wing** (figs. 3b, 4): equal in length and width (inferred length is 18.75 mm and greatest width 19.17 mm); L/W inferred = 0.98. White underside with ocelli

and brown bands: underside with paired submarginal ocelli in M_1 - M_2 and CuA_1 - CuA_2 , identical and very circular in shape; ocelli connected by broad, brown, continuous postmedial band (this band has a broad pale brown proximal margin); one wide medial brown band preserved has a pale area in the anal region; distal marginal brown band has a longitudinal, pale band for entire length. Proximal part of wing is not preserved. Margin without expansions or tails. **Legs:** Tibiae with white scales ventrally and two large apical spurs. Mid and hind tarsomeres with four rows of strong setae (two ventral and two ventrolateral), except for tarsomere V, which has two rows of ventral setae (fig. 3d). Length of tarsomeres of midleg: I, ? mm; II, 0.73 mm; III, 0.43 mm; IV, 0.29 mm; and V, 0.52 mm. Length of tarsomeres of hind leg: I, 2.29 mm; II, 0.51 mm; III, 0.23 mm; IV, 0.26 mm; and V, 0.46 mm. White scales present on tibiae. Claws unforked. **Abdomen** dorsally and laterally dark brown and white ventrally. **Male genitalia** with valves exposed, which are long, flattened, and narrow, and a narrow tubular structure that possibly corresponds to the uncus (figs. 3c, 5); the apex of each valve has two strong, short spines, one dorsal and one ventral.

COMMENTS: The female for this new fossil species is as yet unknown. The reconstruction of the wing color pattern of the preserved areas was partial (fig. 4) because the wings are incomplete, overlapping, and touching.

This specimen belongs to the genus *Dynamine* due to the combination of the following characters: presence of a white median band on fore- and hind wings, absence of ocelli on the forewing, two ocelli under the hind wing restricted to M_1 - M_2 and CuA_1 - CuA_2 and connected by a broad brown band, hind wing margin without expansions or tails, and a dark brown abdomen that is white ventrally. Some species of *Dynamine* do not have ocelli, but the two extant species present in the Antilles have ocelli. We include the genus *Dynamine* in the subfamily Biblidinae and tribe Dynamini, sensu Oppler and Warren (2003) and Freitas and Brown (2004). The subfamily Biblidinae is one of six groups that have been established by the cladistic analysis of Freitas and Brown (2004).

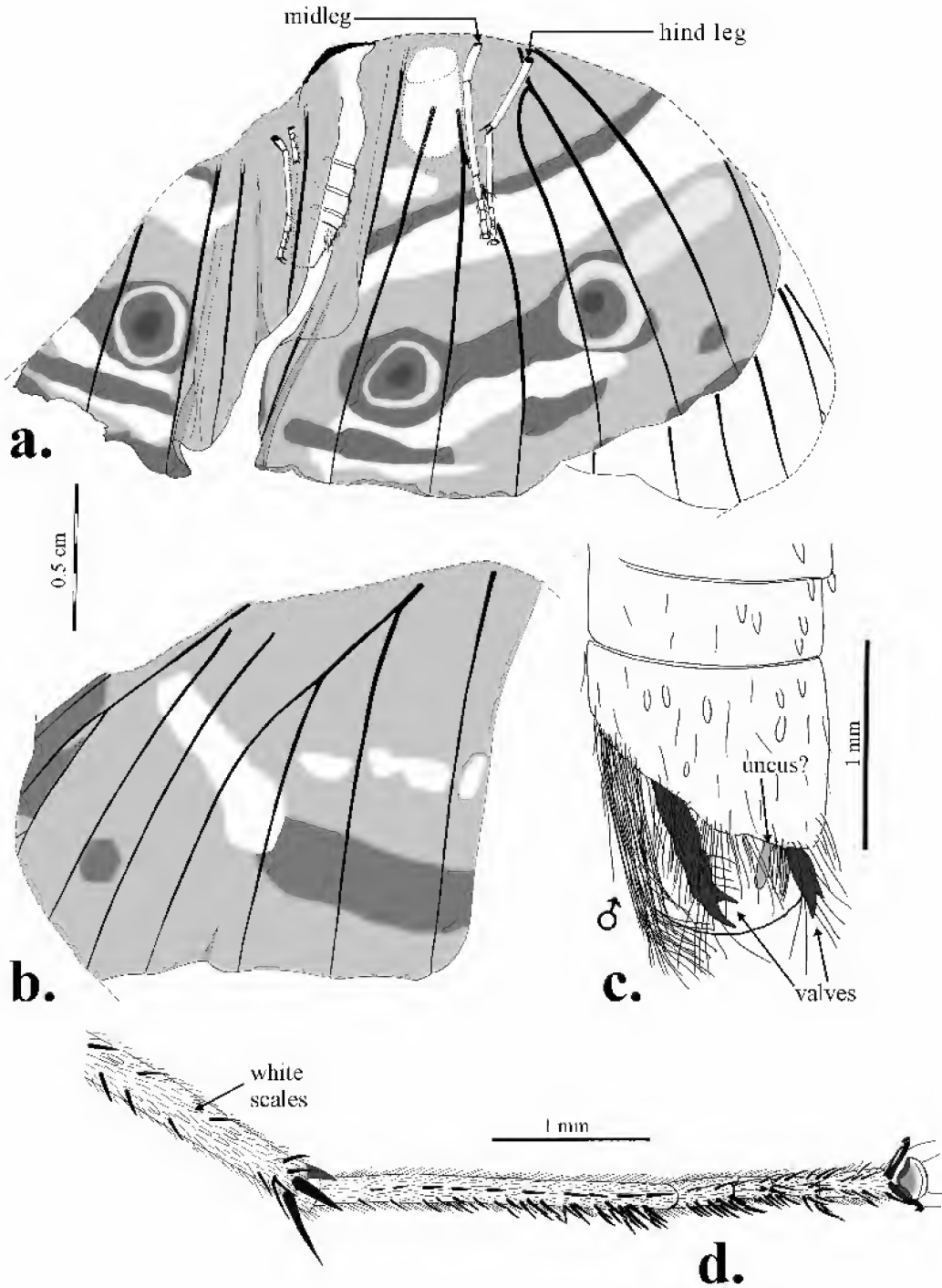


Fig. 3. Camera lucida drawings of *Dynamine alexae* n.sp. (AMNH DR-18-2) in Miocene amber from the Dominican Republic, holotype. **a.** Body ventral view with the hind-wing color pattern preserved. **b.** View of the upper side of the forewing, showing the preserved color pattern. **c.** Male genitalia. **d.** Hind leg. **a–b** to same scale.

The family Nymphalidae has been found previously in Dominican amber, represented by a caterpillar placed near the genus *Smyrna* of the subfamily Nymphalinae (Hammond and Poinar, 1998), and thus without any relationship to the new fossil nymphalid specimen.

COMPARISON WITH EXTANT *DYNAMINE*: The genus *Dynamine* has very characteristic wing color patterns, especially that of the underside, and for this reason it can be confused only with the genus *Lucinia*. However, *Lucinia* has two larger wing ocelli, with each covering more of one cell and not connected by any continuous or broken brown band; and the hind wing margin is not rounded. Röber (1916) superficially segregated the species of *Dynamine* into three groups: 1) those with little difference in wing pattern between males and females; 2) those with appreciable difference in the patterning of the sexes and without wing ocelli on the underside; and 3) those that differ in the wing pattern of the sexes and which have wing ocelli.

The genus *Dynamine* is represented in the West Indies by only two species (*D. egea* Fabricius, 1775 and *D. mylitta* Cramer, 1780), both belonging to group 3. *Dynamine alexae* new species has wing ocelli, but it is unknown whether the sexes were dimorphic and whether the wing uppersides had white spots or bands. *Dynamine mylitta* has a range from Mexico to Argentina including Cuba, and has a wing pattern very different from that of *D. alexae* (the former has a white median band under the forewing divided in three small parts and the anterior ocellus on the hind wing is present in $\text{CuA}_1\text{-CuA}_3$). *Dynamine egea* has a range from Mexico to Colombia, including Cuba, Hispaniola, and Jamaica, where it purportedly occurs as three subspecies (*D.e.calais*, *D.e.zetes* and *D.e.egea*, respectively). *Dynamine alexae* is much larger than all the West Indies forms (25.80 mm estimated forewing length vs. 21–22 mm; and 18.75 mm greatest hind wing width vs. 12.46 mm; see fig. 4). The broad continuous band that connects the two hind wing ocelli is similar to the band in the extant subspecies *D. egea calais* from Cuba and *D. e. egea* from Jamaica, and different from the subspecies on Hispaniola that has a narrow, occasionally broken, brown band (fig. 4). In general, the

wing color pattern of *D. alexae* is similar to that of *D. egea* on the continent and the West Indies.

The species of *Dynamine* possessing two ocelli that are not present in the West Indies are: *D. ate*, *D. artemisia*, *D. onias*, *D. glauce*, *D. meridionalis*, *D. agatha*, *D. pebana*, *D. aerata*, *D. paulina*, *D. perpetua*, *D. gisella*, and *D. zenobia* (for wing pattern and other characteristics of these species, see D'Abbrera, 1987). *Dynamine alexae* differs from all of these species in some characters, most obviously in a size significantly larger than that of the first seven species listed. Butterflies in the genus *Dynamine* are all small-sized (FW length from 13 to 28 mm approx.) and, for this range *D. alexae* (FW length = 25.80 mm) equals in size the largest specimens of the largest continental species (e.g., *D. hoppi gillotti* with a range of FW length from 26 to 28 mm, or *D. hecuba* from 22 to 24 mm). Furthermore, *D. alexae* n.sp. has a very broad hind wing compared to the greatest width of its forewing. In extant *Dynamine* species the greatest width is identical in both wings or even larger in the forewing. In addition, *Dynamine aerata* has the posterior wing ocellus larger than the anterior one. *Dynamine paulina* has a very large anterior ocellus that extends over three cells, and the white median band on the underside of the forewing is divided into three small parts (fig. 4). *Dynamine perpetua*, *D. gisella*, and *D. zenobia* have a very small, costal, white subband on the fore wing in comparison with *D. alexae*.

The male valves in extant *Dynamine* vary greatly in form. We have compared the valves of *D. alexae* n.sp. with four species (fig. 5), which differ most in the structure of the apex. The two "subspecies" of *D. egea* that were studied from the West Indies have a broad, granulate apex without spines. The continental "subspecies" *D. paulina thalassina* has three strong, short spines (one dorsal and two ventral) in the apex. Lastly, the continental *D. glauce* and *D. artemisia* have two small apical spines.

TAPHONOMY

Amber in general preserves insects and other organisms that are uncommon in the

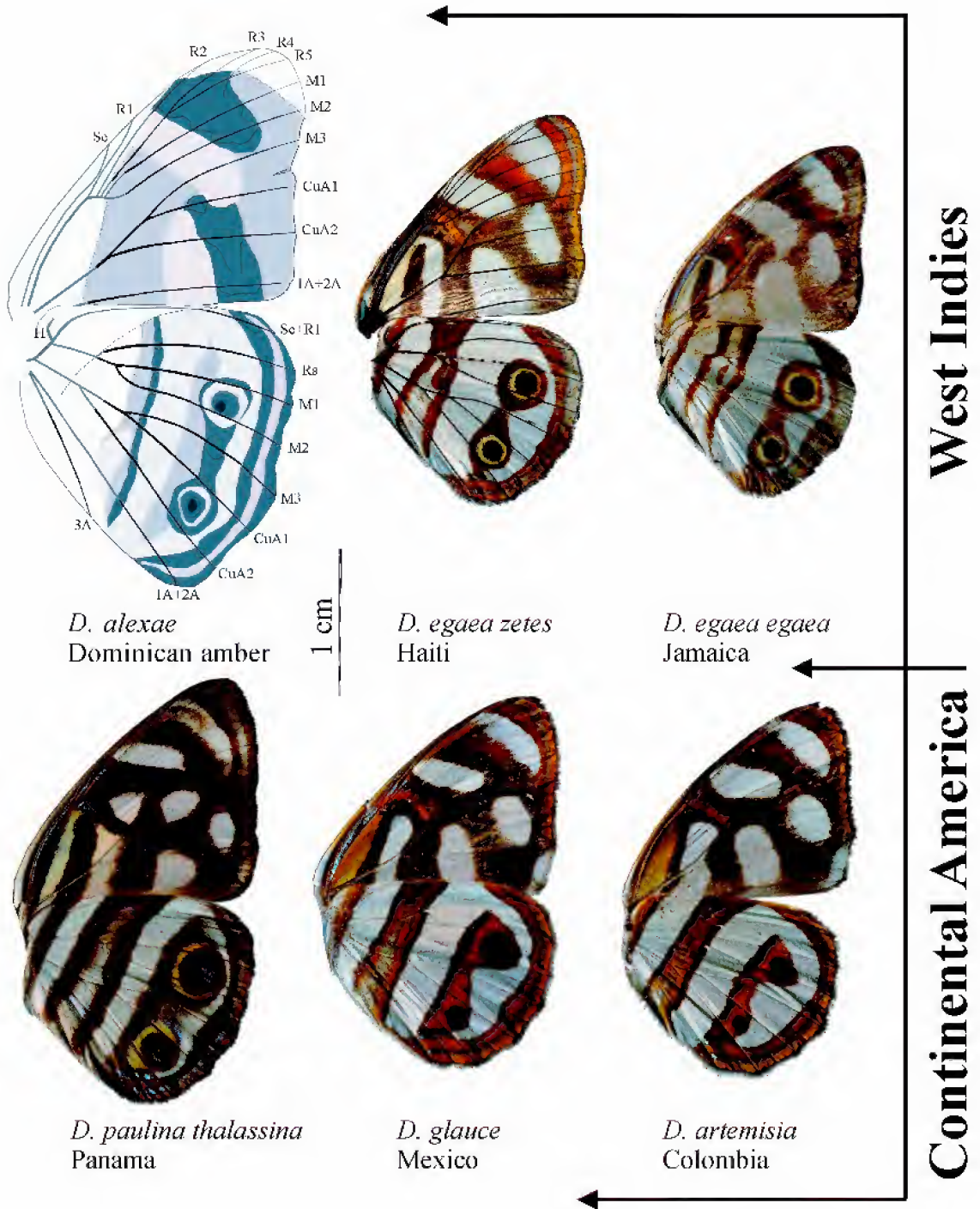


Fig. 4. Fossil and Recent wing venations and underside color patterns in males of the genus *Dynamine*. The reconstruction of the underside color pattern of *Dynamine alexae* n.sp. is adapted from several Recent species of *Dynamine* (fig. 3 shows the partly preserved color pattern), and the reconstruction of the wing venation (depicted as gray lines) is adapted from the venation of *D. egaea zetes* from Hispaniola. All specimens are from the AMNH collection. All to same scale.

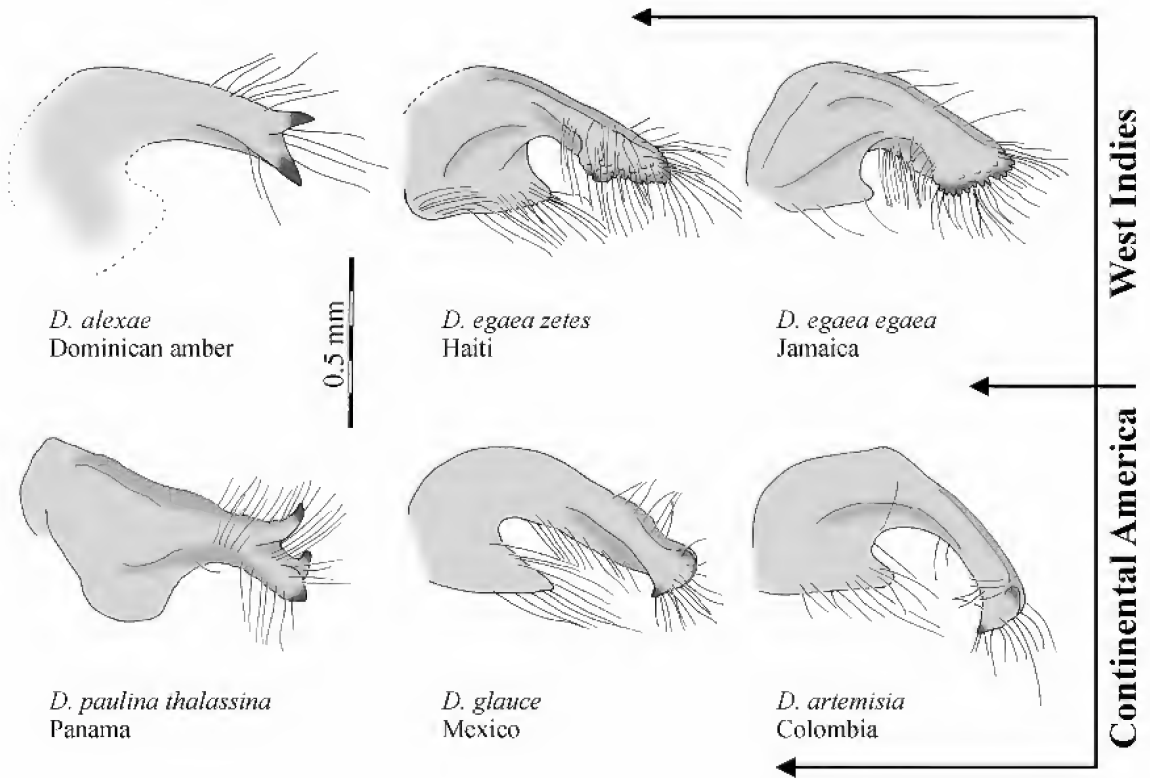


Fig. 5. Male genitalic valves of fossil and Recent species of *Dynamine*. All specimens are from the AMNH collection. All to same scale.

fossil record (e.g., Lewis and Grimaldi, 1997), and many specimens are unique, like the nymphalid described here. Normally, the inclusions are small, and on occasion there are preserved large insects like butterflies (Grimaldi, 1996; Grimaldi and Engel, 2005), but most butterflies and moths in amber are small, rarely larger than one centimeter (Weitschat and Wichard, 2002). Small vertebrates, including the remains of mammals, amphibians, and reptiles, have been also found (e.g., Rieppel, 1980; Poinar and Cannatella, 1987; Grimaldi, 1996; MacPhee and Grimaldi, 1996). This indicates voluminous production and exudation of resin by extinct species of *Hymenaea* during the Miocene, just as occurs with living species of the genus when wounded by storms or boring insects (Langenheim, 2003). There is also evidence that the Tertiary resin was very fluid. The wing surfaces of butterflies easily repel most fluids and are very resistant to wetting,

due to the vestiture of imbricate scales. Thus, only a very fluid resin could penetrate such surfaces completely and permit thorough fossilization. The nymphalid specimen has numerous gas bubbles trapped on the wing surfaces, due to the apparently original resistance against the fluids, but the rionidid specimen has no bubbles. Possibly, the scarce record of butterflies in Tertiary ambers is a consequence of a bias against the preservation of large insects, a hypothesis that agrees with the more abundant Tertiary amber record of moths. Moths and butterflies are rarely fossilized in lacustrine deposits perhaps because their broad, scaly wings resist wetting (Martínez-Delclòs et al., 2004).

Wing color patterns are commonly fossilized in both main types of Konservat-Lagerstätten in the insect fossil record, including laminated carbonates and amber. These color patterns have a chemical (pigments) or a physical (e.g., diffractive) origin.

Chemical color pattern is preserved in laminated rocks due to anoxic conditions in the bottom of some aquatic environments (Martínez-Delclòs et al., 2004). Fidelity in amber also includes chemical color patterns, surely due also to the anoxic conditions inside resin, but also to the complex mixture of terpenes and other hydrocarbons.

The genus *Dynamine* is generally recognized by their metallic markings, either on the hind-wing underside or on the upper side of both wings (DeVries, 1987), but these markings are preserved in amber as brown spots, not the original metallic optical effect. Some scales in the *Dynamine* specimen preserve the original color; for example, on the ventral part of both the abdomen and tibiae are scales that are preserved with their original white color. These white scales are not a taphonomic alteration since such scales are present precisely on the white abdominal and leg parts of extant *Dynamine*.

Hall et al. (2004) indicated that the five known adults of *Voltinia dramba* are females, and that caterpillars of Recent species of the subtribe Napaëina feed exclusively on the leaves of epiphytic plants (DeVries, 1997), and thus presumably near resin production in *Hymenaea* trees where the females oviposited. Subsequently, Vane-Wright (2004) agreed that this record of five females is not a random phenomenon. The new female specimen in the AMNH collection supports this hypothesis of taphonomic bias in the preservation of females. Members of the genus *Dynamine* are essentially forest butterflies and the extant subspecies *D. egaea zetes* in Hispaniola has the habit of congregating around trees of different species (Schwartz, 1989). This habit presumably facilitated the entrapment of *Dynamine alexae* in resin.

PALEOECOLOGY

Hall et al. (2004) indicated that caterpillars of *V. dramba* possibly fed on the leaves of epiphytic Bromeliaceae and Orchidaceae, because this species belongs to a group of genera whose larvae feed on these plants (DeVries et al., 1994). There are other groups of insects found in Dominican amber that today are associated with Bromeliaceae and Orchidaceae,

such as stalk-winged damselflies and orchid bees (Engel, 1999), and, in addition, some plant remains found in this amber could belong to orchids and indeterminate epiphytes (Poinar and Poinar, 1999). Minute bromeliads do occur in Dominican amber (AMNH collection).

The caterpillars of extant *Dynamine* are specialist feeders on flowers or bracts and developing leaves of the genera *Tragia* and *Dalechampia* in Euphorbiaceae (Brown and Heineman, 1972; DeVries, 1987). Schwartz (1989) observed *D. egaea zetes* adults in Hispaniola feeding on the flowers *Daucus* sp. (Apiaceae) and on *Lantana ovatifolia* (Verbenaceae), and Alayo and Hernández (1987) cited that caterpillars of *D.e.calais* can feed on *Tragia urens* (Euphorbiaceae). Indeed, the adults of *Dynamine* are generally uncommon except around *Dalechampia*. In several sites in Ecuador where two or three species of *Dynamine* are encountered (typically along streams and rivers), nine species were attracted to spots where potted *Dalechampia* plants were placed in forest gaps (P. J. DeVries, personal commun. 2005). Dominican amber contains abundant plant remains (including myriad flowers), but the plants are very poorly studied, so it is not surprising that *Dalechampia* is as yet unrecorded from this amber. Poinar and Poinar (1999) cited the families Euphorbiaceae and Urticaceae in this amber, and there is a euphorb flower in the AMNH collection. According to a paleobiogeographic scenario proposed for *Dalechampia* (Ambruster, 1994), it is probable that this important host plant genus for *Dynamine* lived during the Miocene in Hispaniola. Extant *Dalechampia* need resin-collecting bees for its pollination, and such bees (Meliponini: Proplebeia) are common in Dominican amber (Camargo et al., 2000). Lastly, the extant caterpillars of *Theope*, the other butterfly genus present in Dominican amber, feed on a wide group of plant families, which are: Sterculiaceae, Fabaceae, Bombacaceae, Cecropiaceae, Lecythidaceae, Euphorbiaceae, Convolvulaceae, and Cochlospermaceae (DeVries, 1997).

PALEOBIOGEOGRAPHY

The fossil butterflies in Dominican amber indicate there was significant extinction in the

Antillean fauna, to which we can add another example, *Dynamine*.

The family Riodinidae is poorly represented in the Antilles, as there is presently only one Recent riodinid species, of the genus *Dianesia* (Cuba and the Bahamas). Thus the genera *Voltinia* and *Theope*, both with fossil specimens in Dominican amber, have no species in the Greater Antilles today. *Voltinia* has nine living species on the Neotropical mainland; *Theope* is widely distributed in the Neotropics from Mexico, through Central America to northwestern Peru, throughout the Guianas to southeastern Brazil and Paraguay, and along the eastern slope of the Andes as far south as northern Argentina (Hall, 1999), including some islands. More than half of all named species of *Theope* are thought to occur only in the Amazon Basin (DeVries, 1997).

Many of the 70 species of nymphalids in the West Indies are endemic, sometimes to a single island; biogeographically there are species with Neotropical and Nearctic affinities and others with relatives on the African continent (Smith et al., 1994). There are about 30 species of *Dynamine* from the southern United States throughout Central and South America, and the greatest species diversity is in the Amazon Basin; some species are extremely restricted (DeVries, 1987). Central America contains 14 species and there are two species in the Antilles (*D. egaea* and *D. mylitta*), both of which are also well represented on the continent (each from Mexico to Paraguay-Argentina). According to Miller and Miller (1989) the *Dynamine* species in the West Indies are most closely related to those of Mexico and Central America, like most of the butterflies of the Greater Antilles. These authors further consider *Dynamine* to be good dispersers. Of the 36 species of nymphalids on Hispaniola, only one of them is in the genus *Dynamine*, specifically *D. egaea* (subspecies *D. e. zetes*), which is very similar to the Cuban subspecies *D. e. calais*. The subspecies *D. egaea dyonis*, occurring in Central America, more closely resembles the Jamaican subspecies *D. e. egaea* than the other two Antillean forms, and this has been attributed to the more recent separation of Jamaica from the Yucatán than for the other islands where this species occurs (Smith et al., 1994). We consider a vicariant

model for the Jamaican subspecies implausible, given such subtle differences between it and the mainland populations, and the millions of years of geological separation of these landmasses. *Dynamine mylitta* from Cuba and from the continent are identical, suggesting that they reached the island by dispersal, in contrast to the proposed vicariant distribution and subsequent divergence of island populations of *D. egaea*.

Miller and Miller (1989) reviewed theories and models for the biogeography of West Indian butterflies, indicating that historically these were dispersalist models. In contrast, Miller and Miller (op. cit.) proposed a combination vicariance/dispersal model, with emphasis on vicariance based on new geological evidence. These authors indicated that it is necessary to analyze the fossil record in order to determine the ages of butterflies, but only a few fossils were available. After study of the riodinid fossils, Hall et al. (2004) proposed that the rarity of Riodinidae in the Antilles today can be attributed to two primary factors; these butterflies are: 1) poorly dispersed over water, and 2) "disproportionately subject to Tertiary extinctions." Exactly what the "Tertiary extinctions" are is unclear, but presumably includes extinctions due to the insularization of Antillean land masses (there is, actually, one more possibility: that riodinids disperse well but do not colonize well). The finding by Hall et al. (2004) that *Voltinia dramba* is closely related to *V. danforthi* from northwestern Mexico actually contradicts the suggestion that a "probable cause" for the genus becoming extinct in the Antilles is xerophytization from Plio-Pleistocene cooling. *Voltinia danforthi* occurs in the xerophytic states of Sinaloa and Sonora.

We find it most likely that *Voltinia's* distribution in nuclear America included the Greater Antilles when these islands were closer to or actually fused with the mainland, perhaps in the Early Miocene or Late Oligocene. As the islands became more isolated through drift and/or rising sea levels, *Voltinia* and scores of other arthropod groups became extinct on the Antilles. Perhaps the best reflection of this is seen in the meliponine bees (Apidae: Meliponini). With the exception of a species living in Cuba that might have

been introduced, no meliponines occur in the Antilles, even on the large islands of Trinidad and Tobago close to Venezuela. Meliponines are notoriously poor dispersers, particularly over water, and opposite sides of the Amazon River are known to harbor different meliponine faunas (C.D. Michener to D.G. personal commun.). Yet meliponines were in the Antilles. There are three known species of the extinct genus of stingless bees *Proplebeia* in Dominican amber (Camargo et al., 2000), whose presence probably reflects a time when Hispaniola was close to the Central American mainland or after they had recently separated. If Hispaniola was directly connected to Central America when Dominican amber was being formed, we suspect the fossil meliponine fauna would be more reflective of continental diversity. We agree with Hall et al. (2004) that the poor dispersal ability (and possibly a poor colonization ability) keeps riordinids virtually nonexistent in the Antilles today, but their extinction from that region was probably due to the same reason why island faunas are generally depauperate.

COMMENTS ON THE AGE OF BUTTERFLIES

The age of butterflies is becoming a contentious issue. Some entomologists maintain that butterflies evolved in the Cretaceous (e.g., Miller, 1987; Miller and Miller, 1997; Vilorio, 1998; Hall et al., 2004; Braby et al., 2005 [see also the citations given therein]). Others maintain that butterflies evolved largely or wholly in the Tertiary (Shapiro, 1994; De Jong, 2003; Vane-Wright, 2004; Grimaldi and Engel, 2005), in approximately half the time of the other estimates.

Hall et al. (2004) supported a Cretaceous origin and divergence for butterflies on the basis of their study of the *Voltinia* fossil in Dominican amber. Assuming that the extinct *Voltinia dramba* and living *V. danforthi* diverged as a result of Caribbean separation from the Central American mainland, they estimated a divergence date of 40–50 million years. First, it is not at all apparent that this divergence coincided with island-mainland drift, even if a geological divergence took place 40–50 mya. It is possible that *V. dramba*

colonized Hispaniola just prior to the time in the Miocene when the amber was formed, either through long-range dispersal or across narrow water gaps during periods of low sea level. Even more obvious, though, is that an Eocene divergence date for these two species is implausibly old. Insects preserved in Eocene Baltic amber, for example, are generally very primitive compared to living genera (Weitschat and Wichard, 2002; Grimaldi and Engel, 2005). Using the 40–50 myo divergence date, Hall et al. (2004) concluded that this provided “additional support for a Gondwanan origin of many butterfly tribes and subfamilies,” citing Miller and Miller (1997) and Vilorio (1998), but to which they could apparently now add Braby et al. (2005). All of these authors contend that butterflies evolved as residents of wandering Gondwanan continents, and since Gondwana separated in the Cretaceous, butterflies are at least this old.

The study by Braby et al. (2005) was based on a comprehensive phylogenetic analysis of three genes and the genera of troidine swallowtails (family Papilionidae), which includes the famous bird wing swallowtails. The distribution pattern of troidines in their study appears to be compelling evidence for a Gondwanan distribution. The classic Gondwanan distribution comprises the southernmost, cool temperate forests of Africa, Chile, southeast Australia (including Tasmania), and New Zealand (reviewed in Grimaldi and Engel, 2005). However, no troidines occur in the temperate Austral region. In fact, the areas of endemism defined for each troidine genus by Braby et al. (2005) are unusually widespread, some of which are not even Gondwanan. The lineage that includes *Troides* and *Ornithoptera*, for example, extends from southeast Asia to the Solomon islands, New Guinea, and northern Australia, but which they referred to as “Australia”. Likewise, *Parides*, which is widespread throughout Central and South America, is referred to as “South America”. Another difficulty with the Braby et al. (2005) study is that they used the known ages of landmass separation to calibrate their estimates of taxon divergence, which is circular reasoning if one is testing whether taxa are Cretaceous in age. A third difficulty is that

molecular estimates of divergence dates are usually considerably older than evidence based on the phylogenetic study of fossils (Rodríguez-Trelles et al., 2002), but they can also give an illusion of precision (Graur and Martin, 2004). Also, there are Recent insect taxa that show classic austral disjunction, like certain chironomid midges, scolybythid and megalyrid wasps, primitive cyclorrhaphan flies, and others, but for which fossils of many occur in the Northern Hemisphere (Grimaldi and Engel, 2005), indicating formerly widespread distributions. Even if the biogeographic pattern of troidines was compellingly Gondwanan, which we maintain it is not, fossils in general remind us to be cautious about interpreting historical distributions entirely on the basis of the Recent fauna.

Lastly, Braby et al. (2005) make the typical appeal of incompleteness of the fossil record to support their hypothesis of Cretaceous butterflies, namely that Cretaceous butterflies have not been discovered given their rarity.

The fossil record of Papilionoidea, in fact, is quite good among macrolepidopterans. There are approximately 33 named fossil butterflies—more than any other group of macrolepidopterans—and all of them are Tertiary (reviewed in Grimaldi and Engel, 2005). This fact, plus the relatively derived phylogenetic position of butterflies among Ditrysia, makes it unlikely that they are much older than latest Cretaceous. If, according to Braby et al. (2005), troidine swallowtails existed by 90 mya, then the Papilionidae would need to have existed earlier than this, say 100 mya. In this scenario, Rhopalocera (including skippers and Hedyliidae) would need to be older still (say 120–130 myo), and Macrolepidoptera and Ditrysia origins would need to have originated in the Jurassic. This scenario defies all fossil evidence. Only small, primitive lepidopterans are known from the Late Jurassic and Early Cretaceous, and only one possible ditrysid (a leaf mine of an apparent gracilliaroid) is known from the Cretaceous (reviewed in Grimaldi and Engel, 2005). It is highly implausible that 80 million years of macrolepidopterans have simply escaped notice.

Tertiary evolution of the butterflies could easily be falsified by the discovery of

a Cretaceous specimen, but for the time being we contend that Vane-Wright (2004: 408) was entirely right in saying there is “no existing evidence to suggest that butterflies are older than about 70 million years.”

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