

Extinction and biogeography in the Caribbean: new evidence from a fossil rioidinid butterfly in Dominican amber

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We describe a new species of extinct rioidinid butterfly, *Voltinia dramba*, from Oligo-Miocene Dominican amber (15–25 Myr ago). This appears to be the first butterfly to be taxonomically described from amber, and the first adult rioidinid fossil. The series of five specimens represents probably the best-preserved fossil record for any lepidopteran. The phenomenon of extant *Voltinia* females ovipositing on arboreal epiphytes probably explains the discovery of multiple female *V. dramba* specimens in amber. *Voltinia dramba* appears to be one of many extinct butterfly species on Hispaniola. The northwestern Mexican distribution of the explicitly hypothesized sister species, the extant *V. danforthi*, supports the hypothesis that *V. dramba* reached Hispaniola by the ‘proto-Greater Antillean arc’, dating the divergence of *V. dramba* and *V. danforthi* to 40–50 Myr ago. This date is contemporaneous with the oldest known butterfly fossils, and implies a more ancient date of origin for many of the higher-level butterfly taxa than is often conceded.

Keywords: amber fossils; biogeography; Dominican Republic; extinction; Rioidinidae; *Voltinia*

1. INTRODUCTION

Amber from the Dominican Republic, which is derived from resin of the extinct leguminous tree *Hymenaea protera* (Poinar 1991), and that from Chiapas, Mexico, is unique among ambers of the world for its clarity (Grimaldi 1996), and is renowned for its systematically wide array of fossil inclusions (Poinar 1992). For example, mined Dominican amber pieces are known to contain at least 24 orders (Lewis & Grimaldi 1997) and 235 families (Poinar 1992) of insects alone. Lepidoptera inclusions are rare, and those of butterflies rarer still. Only three butterfly species have been reported from Dominican amber, two from single caterpillars (Nymphalidae and Rioidinidae; DeVries & Poinar 1997; Hammond & Poinar 1998) and one from several adults (Rioidinidae; Poinar 1992). All of these specimens came from mines in the northern part of the Cordillera Septentrional. Based on recent biostratigraphic and palaeostratigraphic data, amber material from this region is now estimated to be of an Upper Oligocene to Lower Miocene age, or 15–25 Myr ago (Grimaldi 1995; Iturralde-Vinent & MacPhee 1996). The butterflies have a known geological history beginning in Early Eocene rocks (Rasnitsyn & Quicke 2002).

The exquisite preservation of the wings, head and legs of the adult rioidinid fossils, upon which individual scales and sensilla can clearly be seen, allows us to determine with confidence that they represent a new species of the extant genus *Voltinia* (Rioidininae: Mesosemiini: Napaeina). This genus contains another nine externally heterogeneous species, most of which were previously placed in *Napaea*, which range from northern Mexico to southeastern Brazil (Hall 2003; Hall & Harvey 2004). Herein we first describe and name this adult rioidinid

butterfly, from five females in five pieces of amber that collectively represent probably the best-preserved fossil record for any lepidopteran. This appears to be the first butterfly described taxonomically from amber, and it is the first true fossil of an adult rioidinid. Two adult rock-compression fossils currently attributed to the Rioidinidae (Durden & Rose 1978; Jarzembowski 1980) are shown here not to belong to that family. We then discuss the butterfly palaeofauna of Hispaniola, and the implications of the *Voltinia* fossils and their phylogenetic position within the genus for the biogeography of the Caribbean region and the historical date of origin for *Voltinia* and thus, by extrapolation, the butterflies as a whole.

2. SYSTEMATICS

Voltinia dramba Hall, Robbins & Harvey, **new species**.

(a) Description

Female: Forewing (FW) length 20 mm. Wing shape: FW triangular, five FW radial veins; hindwing (HW) angular and pointed at vein M_3 . Dorsal surface: ground colour of both wings brown; three narrow white bars in discal cell of both wings, one immediately distally, and three at base of cell Cu_2 , darker brown between these markings, an extra faint spot at base of cell Cu_1 on HW; FW postdiscal band 4 elongate white spots in a straight, outwardly diagonal line in cells R_2 to M_2 , and three smaller, proximally displaced, white spots in cells M_3 to Cu_2 , HW postdiscal band five narrow white spots in cells M_1 to Cu_2 in a V-shaped pattern, darker brown scaling proximal to postdiscal band on both wings; roundly elongate FW submarginal spots in cells R_3 and R_{4+5} to Cu_2 pale (colour scheme in figure 1*i* a reconstruction adapted from sister species *V. danforthi*), large oval to semicircular HW submarginal spots largely black with a narrow pale border (depicted as yellow in figure 1*i* based on colour of

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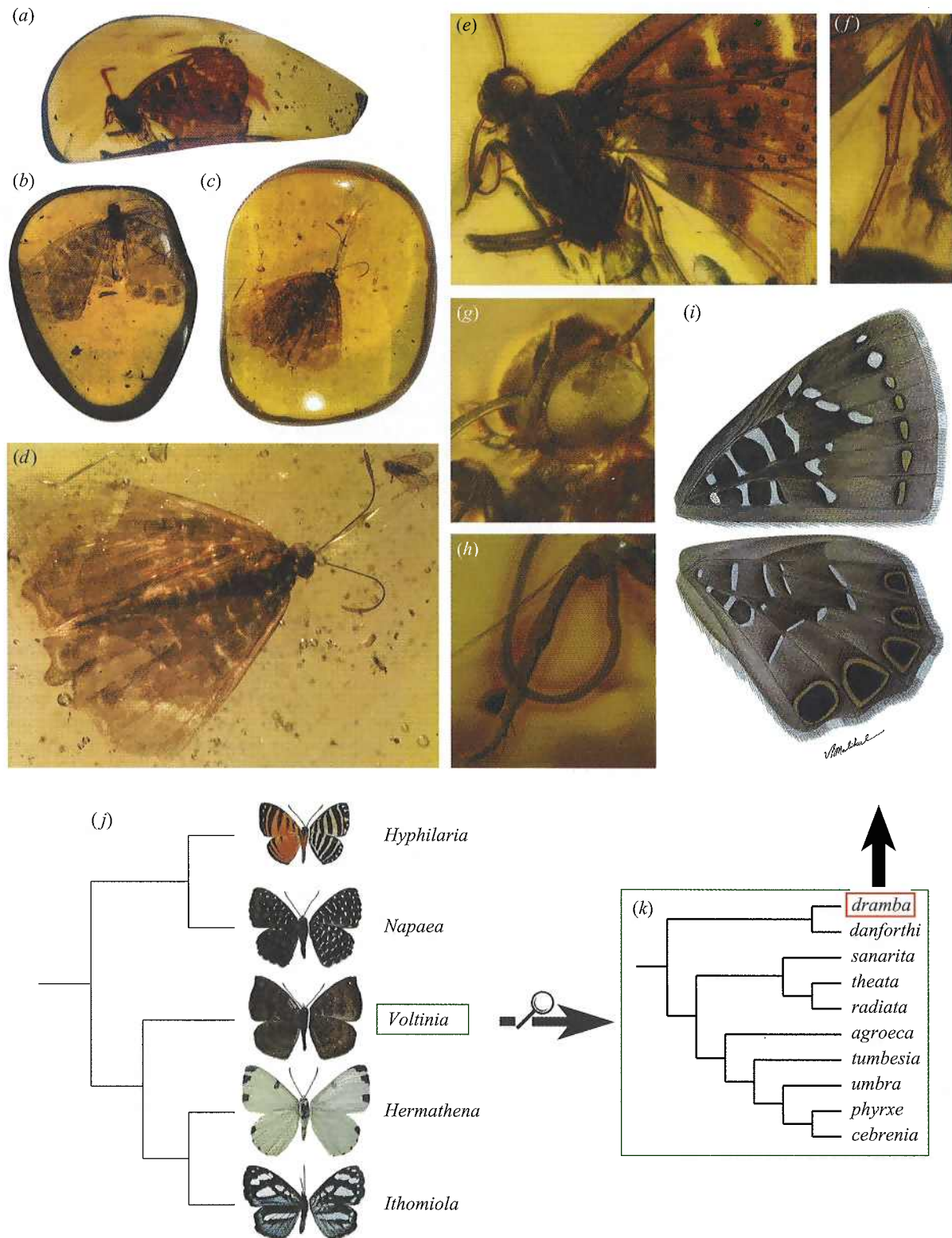


Figure 1. Amber specimens, wing reconstruction and systematic placement of the fossil riodinid butterfly *Voltinia dramba*. (a–c) Three Dominican amber pieces containing females of *V. dramba*—ca. 3.5–5.5 cm in length; (d) enlargement of fossil in (c); (e) head, thorax and wing base, (f) hindleg, (g) enlargement of head, and (h) foreleg of fossil in (a); (i) wing reconstruction of female *V. dramba* based on fossils in (a–c); (j) generic-level phylogeny for the riodinid subtribe Napaeina (Mesosemiini), indicating systematic placement of *Voltinia* (Hall 2003; Hall & Harvey 2004)—exemplar species for each genus are shown on the right; (k) species-level phylogeny for *Voltinia*, indicating systematic placement of *dramba* (Hall & Harvey 2004).

submarginal spots in close relatives), submarginal spots on both wings surrounded by darker brown; fringe colour on both wings indiscernible (pattern depicted in figure 1i

based on *V. danforthi*). Ventral surface: essentially same as dorsal surface. Head: eyes brown and bare, frons brown, palpi pale brown ventrally and dark brown dorsally

