THE ROYAL
SOCIETY

Received 30 October 2003
Accepted 14 January 2004

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

Jason P. W. Hall*, **Robert K. Robbins** and **Donald J. Harvey**

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0127, USA

We describe a new species of extinct riodinid 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 riodinid 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; Riodinidae; *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 Riodinidae; DeVries & Poinar 1997; Hammond & Poinar 1998) and one from several adults (Riodinidae; 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 riodinid 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* (Riodininae: 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 riodinid 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 riodinid. Two adult rock-compression fossils currently attributed to the Riodinidae (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

---

*Author for correspondence (hall.jason@nmnh.si.edu).

DOI 10.1098/rspb.2004.2691

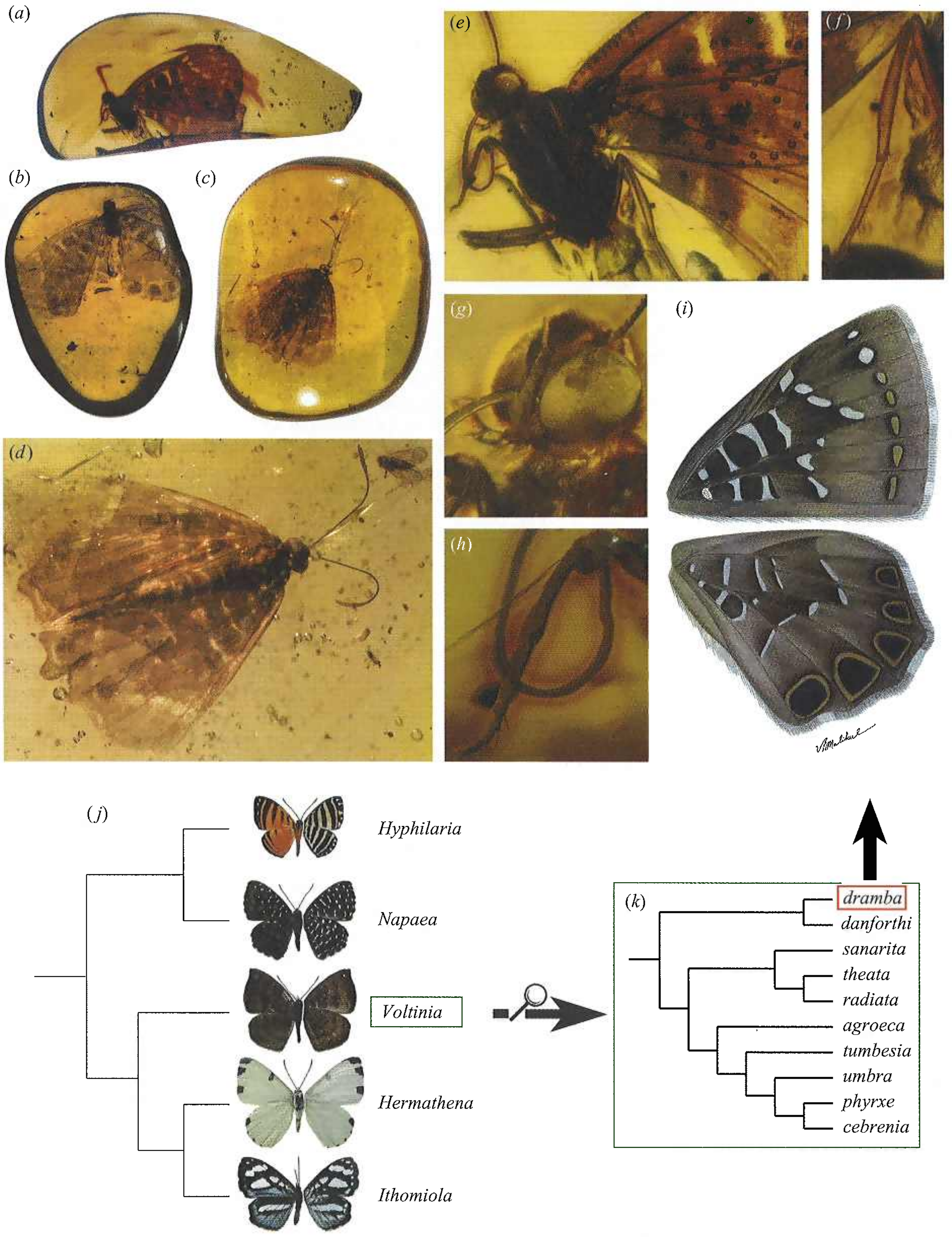

Figure 1. Amber specimens, wing reconstruction and systematic placement of the fossil riodinid butterfly *Voltinia dramba*. (*a–c*) Three Dominican amber pieces containing females of *V. dramba*—*ca*. 3.5–5.5 cm in length; (*d*) enlargement of fossil in (*c*); (*e*) head, thorax and wing base, (*f*) 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 1*i* 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 with elongate second and third segments, antennal segments brown with white scaling at base, antennal clubs brown. Body: both surfaces of thorax and abdomen brown, all legs brown, mid and hindlegs without a tibial spur (hindleg in figure 1*f* appears to have a tibial spur, but this seems to be an artefact of two overlapping spines; tibial spurs in *Voltinia* are confined to the species *V. radiata* and *V. theata*). Male: unknown.

(b) *Types*

Holotype female: Dominican Republic, Cordillera Septentrional; in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) (see figure 1*a*). Although the exact mine of origin is unknown, infrared spectroscopy indicates that the holotype fossil is embedded in highly polymerized, true Dominican amber.

(i) *Paratypes*

Same locality data, one female (figured in Murata 1998) in coll. M. Murata, Kyoto, Japan; two females (figure 1*b*,*c*) in coll. E. Morone, Torino, Italy. The fifth specimen is not designated as a paratype because we do not know its current deposition.

(c) *Etymology*

The species name is derived from the initials of its country of origin (i.e. Dominican Republic) and a phonetic feminine spelling of the word amber.

(d) *Systematic placement and diagnosis*

By having a central undivided patch of trichoid sensilla on the female foretarsus, the amber adult butterfly fossils can be placed in the Riodinidae (Harvey 1987). Although the presence of a costal vein on the HW, which defines the Riodininae (Harvey 1987), cannot be determined with certainty in the material examined, the wing venation of the fossils is otherwise consistent only with the Riodininae. By having five FW radial veins, and lacking a hindleg tibial spur and bristle-like scales on the palpi, the fossils can be placed in the tribe Mesosemiini (Hall 2003). Although none of the adult synapomorphies for the subtribe Napaeina is an external one that could be determined in the fossils, one such synapomorphy for the Mesosemiina, the only other subtribe in the Mesosemiini, is the presence of setose eyes (Hall 2003). As the fossils have naked eyes, we can place them in the Napaeina.

Phylogenetic and revisionary studies on the Napaeina suggest that the seven genera in current usage should be condensed to five, with *Cremna* a synonym of *Napaea*, and *Eucorna* a synonym of *Voltinia* (Hall 2003; Hall & Harvey 2004). A phylogenetic hypothesis for these five genera, *Hyphilaria*, *Napaea*, *Voltinia*, *Hermathena* and *Ithomiola*, is given in figure 1*j* (Hall 2003; Hall & Harvey 2004). Previously in the literature, the amber fossils have been referred to simply as a riodinid species or near *Napaea* (Poinar 1992, 1993; Grimaldi 1996; DeVries 1997; Murata 1998; Poinar & Poinar 1999; Poinar 2000; Vane-Wright 2003). However, *Napaea* as previously treated was polyphyletic, and the proper generic placement for these fossils has only now become possible (Hall 2003; Hall & Harvey 2004).

The colour pattern of the eye margins divides the Napaeina into three clades (Hall 2003; Hall & Harvey 2004). This scaling is yellow or white and medially divided by brown in *Hyphilaria* + *Napaea*, entirely brown in *Voltinia*, and entirely white in *Hermathena* + *Ithomiola*. The fossils have entirely brown eye margins. Additional characters excluding the fossils from the most similar genus, *Napaea*, include the lack of an isolated spot at the base of FW cell R_1 and individual pale spots at the costa of the dorsal HW. Another character excluding them from *Hermathena* + *Ithomiola* is the absence of a hindleg tibial spur (Hall 2003; Hall & Harvey 2004). Further evidence supporting placement of the amber fossils in *Voltinia* includes their entirely brown palpi and dark ocelli at the wing bases (Hall & Harvey 2004).

Phylogenetic revision of the Napaeina (Hall 2003; Hall & Harvey 2004) indicates that *V. dramba* is the sister species to the recently described *V. danforthi* (Warren & Opler 1999), which is endemic to the northwestern Mexican states of Sonora and Sinaloa (Warren & Opler 1999; Hall & Harvey 2004). The two species are similar, and alone in *Voltinia* in sharing the absence of a spot at the base of FW cell Cu_1 and prominent yellow to red submarginal markings on both wings, but *V. dramba* differs primarily by having a more proximally displaced anal section of the FW postdiscal band, and five large black submarginal HW spots that are surrounded by a narrow area of pale, probably yellow coloration. The HW submarginal spots in *V. danforthi* are small, narrowly elongate and entirely pale red, without any black pupils.

(e) *Other putative riodinid fossils*

Two adult rock-compression fossils currently attributed to the Riodinidae do not belong to that family. *Riodinella nympha* was described from the Early Eocene bed of the Green River Formation, Colorado, in the tribe Riodinini, subfamily Riodininae (Durden & Rose 1978). However, the fossil possesses five FW radial veins, a condition found within the Riodinidae only in the subfamilies Nemeobiinae and Euselasiinae, and the two most basal tribes of the Riodininae (Mesosemiini and Eurybiini; Harvey 1987; Hall 2003). In addition, the fossil has FW vein R_2 extending to the apex and vein R_3 ending at the distal margin, conditions found in no extant riodinid genus, but in some Papilionidae and Nymphalidae. Also, the fossil has FW vein R_2 originating distal to the discal cell end and FW radial veins two to five stalked. These character states are confined within the Riodinidae to a single species, *Styx infernalis* (Euselasiinae: Corrachiini), which has otherwise very different venation, but are present in some Pieridae and Nymphalidae. *Riodinella nympha* is not a riodinid, and it should be treated as an unplaced butterfly.

Lithopsyche antiqua was described as a geometrid moth (Butler 1889), but nearly 100 years later was transferred to the Riodininae (Jarzembowski 1980). Most of the FW costa in this fossil is missing and only parts of three radial veins can be seen. However, the central two-thirds of FW vein R_5 is unforked, a condition not found in any extant riodinid genus. The FW radial veins are unforked in certain Lycaenidae, but a HW humeral vein, which is present in the fossil, is very rare in that family. This fossil is too incomplete to confidently place it in any of the remaining butterfly families.

3. DISCUSSION

As well as producing invaluable systematic data on the age of appearance and evolution of organismal lineages and particular character traits, amber fossils can provide a wealth of insights into animal behaviour, the palaeoenvironment, biogeography, and the shifting patterns of taxon diversity and distribution through time. The riodinid butterfly fossils are no exception.

Individuals found in amber generally belong to those taxa that are most likely to be trapped in tree resin. It is not surprising that all five adult riodinid amber fossils found thus far are females belonging to the subtribe Napaeina, because this is the only clade of riodinids whose larvae feed exclusively on the leaves of epiphytic Bromeliaceae and Orchidaceae (Harvey 1987; Hall 2003; Hall & Harvey 2004). It seems likely that the *V. dramba* females became entangled in resin flows while ovipositing and resting on small epiphytes growing on the branches or trunk of *Hymenaea* trees.

The discovery of the *V. dramba* fossils provides a particularly clear-cut case of extinction for Hispaniola and the Antilles, because their butterfly faunas are well documented (Schwartz 1989; Smith *et al.* 1994) and only a single Antillean riodinid species exists today, namely *Dianesia carteri* (Riodininae: *incertae sedis*) from Cuba and the Bahamas. The Riodinidae are the most under-represented family of butterflies in the Antilles, where they constitute less than 1% of the total extant butterfly fauna (Smith *et al.* 1994) instead of the 15–20% typical of the Central and South American lowland mainland faunas (Robbins *et al.* 1996; Brown & Freitas 1999). This fact suggests that the family has been a particularly poor disperser over water and/or been disproportionately subject to Tertiary extinctions. As most riodinids are confined to intact wet forest habitats (DeVries 1997), Plio-Pleistocene cooling and subsequent habitat disturbance and xerophytization (Richards 1999) would have been one probable cause of Antillean riodinid extinctions. The *Theope* caterpillar (Riodininae: Nymphidiini) recently reported in Dominican amber (DeVries & Poinar 1997) represents a second tribal-level riodinid lineage now extinct in the Caribbean. Extinction in the Antilles of the *Dolichoderus* and *Azteca* ants (Wilson 1985) with which *Theope* caterpillars form obligate symbioses (DeVries 1997; Hall 1999) would additionally have doomed the survival of *Theope* in the region. The report of a nymphalid caterpillar similar to *Smyrna* in Dominican amber (Hammond & Poinar 1998) appears to represent a third example of a butterfly genus now extinct in the Antilles.

As a result of their highly preserved state, Dominican amber fossils can provide essential information for reconstructing the biogeographical history of the clades to which they belong and of the Caribbean region as a whole. Three main mechanisms have been proposed to explain the origins of the Antillean fauna:

(i) dispersal over water barriers during much of the Tertiary (Hedges *et al.* 1992; Hedges 1996);

(ii) continent–island vicariance, with a more-or-less continuous landmass between North and South America, the 'proto-Greater Antilles', beginning to move east into the Caribbean in the Middle Eocene (Rosen 1975, 1985); and

(iii) dispersal along a more-or-less continuous, short-lived, Oligocene landspan (the Aves ridge) stretching from northern Venezuela to the Greater Antilles (Iturralde-Vinent & MacPhee 1999).

Each of these mechanisms appears to have been responsible for shaping parts of today's Antillean butterfly fauna, which largely has affinities with South America, and particularly Central America (Miller & Miller 1989).

That the Antilles have not been substantially recolonized by riodinids since the hypothesized Pleistocene–Holocene extinctions shows that these comparatively sedentary butterflies, which tend to have smaller than average ranges for the Papilionoidea (Hall & Harvey 2002, 2004), are not good over-water dispersers (mechanism (i)). The sister-group relationship between the fossil *V. dramba* and the extant northwestern Mexican *V. danforthi* supports mechanism (ii) for the Antillean origin of *V. dramba*, and is inconsistent with mechanism (iii). If hypothesis (ii) is correct, then *V. dramba* and *V. danforthi* diverged *ca.* 40–50 Myr ago. This ancient hypothesized date of origin for *V. danforthi*, contemporaneous with the oldest known butterfly fossils (Rasnitsyn & Quicke 2002), is consistent with its basal position in the Mesosemiini, and thus the Riodininae (Hall 2003; Hall & Harvey 2004), and provides additional support for a Gondwanan origin for many of the butterfly tribes and subfamilies (Miller & Miller 1997; Viloria 1998). Heretofore, very few attempts have been made to ascertain the divergence dates of closely related, extant butterfly taxa. However, recent studies using molecular clock techniques have estimated that species-level taxa in the *Heliconius erato* group (New World Nymphalidae) diverged *ca.* 2–4 Myr ago (Brower 1994), the putative sister genera *Troides* and *Ornithoptera* (Old World Papilionidae) *ca.* 32–40 Myr ago (Morinaka *et al.* 1999), and the putative sister genera *Euryades* and *Cressida* (New and Old World Papilionidae, respectively) not more than 31 Myr ago (de Jong 2003). These data suggest that *V. danforthi*, like the papilionid *Baronia brevicornis*, which is similarly endemic to a small dry region of Mexico (Tyler *et al.* 1994), can be regarded as a 'living fossil'.

The authors thank S. Hendrickson, E. Morone and Y. Murata for arranging the loan of amber specimens; the Women's Committee of the Smithsonian Institution for the funds to purchase the holotype of *V. dramba*; F. Heuber, J. Langenheim and V. Comer for providing expertise on testing the authenticity of the fossils; C. Clark for taking the original photographs that appear as (*a*) and (*d*–*h*) in figure 1; V. Malikul for producing figure 1(*i*) from line drawings by the first author; and J. Burns, D. Grimaldi, C. Labandeira, A. Solis, K. Willmott and two anonymous reviewers for commenting on drafts of the manuscript.

REFERENCES

Brower, A. V. Z. 1994 Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proc. Natl Acad. Sci. USA* **91**, 6491–6495.

Brown, K. S. & Freitas, A. V. L. 1999 Lepidoptera. In *Biodiversidade do Estado de São Paulo, Brasil: Síntese do Conhecimento ao Final do Século XX*, vol. 5, *Invertebrados terrestres* (ed. C. A. Joly & C. E. M. Bicudo), pp. 225–243. São Paulo, Brazil: FAPESP.

Butler, A. G. 1889 Description of a new genus of fossil moths belonging to the geometrid family Euschemidae. *Proc. Zool. Soc. Lond.* **59**, 292–297.

de Jong, R. 2003 Are there butterflies with Gondwanan ancestry in the Australian region? *Invert. Syst.* **17**, 143–156.

DeVries, P. J. 1997 *The butterflies of Costa Rica and their natural history*, vol. II, *Riodinidae*. Princeton University Press.

DeVries, P. J. & Poinar, G. O. 1997 Ancient butterfly–ant symbiosis: direct evidence from Dominican amber. *Proc. R. Soc. Lond.* B **264**, 1137–1140. (DOI 10.1098/rspb.1997.0157.)

Durden, C. J. & Rose, H. 1978 Butterflies from the middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). *Pearce-Sellards Series: Tex. Mem. Mus.* **29**, 1–25.

Grimaldi, D. A. 1995 The age of Dominican amber. In *Amber, resinite and fossil resins* (ed. K. B. Anderson & J. C. Crelling), pp. 203–217. American Chemical Society Symposium 617. Washington, DC: American Chemical Society.

Grimaldi, D. A. 1996 *Amber: window to the past.* New York: H. Abrams & American Museum of Natural History.

Hall, J. P. W. 1999 *A revision of the genus Theope: its systematics and biology (Lepidoptera: Riodinidae: Nymphidiini)*. Gainesville, FL: Scientific Publishers.

Hall, J. P. W. 2003 Phylogenetic reassessment of the five forewing radial-veined tribes of the *Riodininae* (Lepidoptera: Riodinidae). *Syst. Entomol.* **28**, 23–37.

Hall, J. P. W. & Harvey, D. J. 2002 The phylogeography of Amazonia revisited: new evidence from riodinid butterflies. *Evolution* **56**, 1489–1497.

Hall, J. P. W. & Harvey, D. J. 2004 A phylogenetic revision of the Napaeina (Lepidoptera: Riodinidae: Mesosemiini). *Mem. Entomol. Soc. Wash.* (In the press.)

Hammond, P. C. & Poinar, G. O. 1998 A larval brush-footed butterfly (Lepidoptera: Nymphalidae) in Dominican amber, with a summary of fossil Nymphalidae. *Entomol. Scand.* **29**, 275–279.

Harvey, D. J. 1987 The higher classification of the Riodinidae (Lepidoptera). PhD dissertation, University of Texas, USA.

Hedges, S. B. 1996 Historical biogeography of West Indian vertebrates. *A. Rev. Ecol. Syst.* **27**, 163–196.

Hedges, S. B., Haas, C. & Maxson, L. 1992 Caribbean biogeography: molecular evidence for dispersal in West Indian terrestrial vertebrates. *Proc. Natl Acad. Sci. USA* **89**, 1909–1913.

Iturralde-Vinent, M. A. & MacPhee, R. D. E. 1996 Age and paleogeographic origin of Dominican amber. *Science* **273**, 1850–1852.

Iturralde-Vinent, M. A. & MacPhee, R. D. E. 1999 Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull. Am. Mus. Nat. Hist.* **238**, 1–95.

Jarzembowski, E. A. 1980 Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bull. Br. Mus. Nat. Hist.* (*Geol.*) **33**, 237–293.

Lewis, R. E. & Grimaldi, D. A. 1997 A pulicid flea in Miocene amber from the Dominican Republic (Insecta: Siphonaptera: Pulicidae). *Am. Mus. Nov.* **3205**, 1–9.

Miller, J. Y. & Miller, L. D. 1989 The biogeography of West Indian butterflies (Lepidoptera: Papilionoidea, Hesperioidea): a vicariance model. In *Biogeography of the West Indies* (ed. C. A. Woods), pp. 229–262. Gainesville, FL: Sandhill Crane Press.

Miller, L. D. & Miller, J. Y. 1997 Gondwanan butterflies: the Africa–South America connection. *Metamorphosis* **3**(Suppl.), 42–51.

Morinaka, S., Maeyama, T., Maekawa, K., Erniwati, D., Prijono, S. N., Ginarsa, I. K., Miyata, T. & Hidata, T. 1999 Molecular phylogeny of birdwing butterflies based on the representatives in most genera of the tribe Troidini (Lepidoptera: Papilionidae). *Entomol. Sci.* **2**, 347–358.

Murata, Y. 1998 Notes on the evolutionary process of butterflies and butterfly fossils (part I). *Butterflies* **20**, 4–17.

Poinar, G. O. 1991 *Hymenaea protera* sp. n. (Leguminosae, Caesalpinioideae) from Dominican amber has African affinities. *Experientia* **47**, 1075–1082.

Poinar, G. O. 1992 *Life in amber.* Stanford University Press.

Poinar, G. O. 1993 Insects in amber. *A. Rev. Entomol.* **46**, 145–159.

Poinar, G. O. 2000 Butterflies in amber. *Am. Butterflies* **8**, 22–27.

Poinar, G. O. & Poinar, R. 1999 *The amber forest: a reconstruction of a vanished world.* Princeton University Press.

Rasnitsyn, A. P. & Quicke, D. L. J. (eds) 2002 *History of insects*. Dordrecht, The Netherlands: Kluwer.

Richards, P. W. 1999 *The tropical rain forest.* Cambridge University Press.

Robbins, R. K., Lamas, G., Mielke, O. H. H., Harvey, D. J. & Casagrande, M. M. 1996 Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional del Manu, Perú. In *Manu: the biodiversity of southeastern Peru* (ed. D. E. Wilson & A. Sandoval), pp. 217–252. Washington, DC: Smithsonian Institution Press.

Rosen, D. E. A. 1975 A vicariance model of Caribbean biogeography. *Syst. Zool.* **24**, 431–464.

Rosen, D. E. A. 1985 Geological hierarchies and biogeographical congruence in the Caribbean. *A. Miss. Bot. Gard.* **72**, 636–659.

Schwartz, A. 1989 *The butterflies of Hispaniola.* Gainesville, FL: University of Florida Press.

Smith, D. S., Miller, L. D. & Miller, J. Y. 1994 *The butterflies of the West Indies and South Florida.* Oxford University Press.

Tyler, H. A., Brown Jr, K. S. & Wilson, K. H. 1994 *Swallowtail butterflies of the Americas. A study in biological dynamics, ecological diversity, biosystematics, and conservation.* Gainesville, FL: Scientific Publishers.

Vane-Wright, R. I. 2003 *Butterflies.* London: The Natural History Museum.

Viloria, A. L. 1998 Studies on the systematics and biogeography of some montane satyrid butterflies (Lepidoptera). PhD dissertation, King's College, London, UK.

Warren, A. D. & Opler, P. A. 1999 An unusual new *Napaea* metalmark from Sonora, Mexico (Lepidoptera: Riodinidae). *Hol. Lepid.* **6**, 25–29.

Wilson, E. O. 1985 Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science* **229**, 265–267.