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HYPOTHESES FOR THE RECENT HISPANIOLAN SPIDER FAUNA BASED ON THE DOMINICAN REPUBLIC AMBER SPIDER FAUNA

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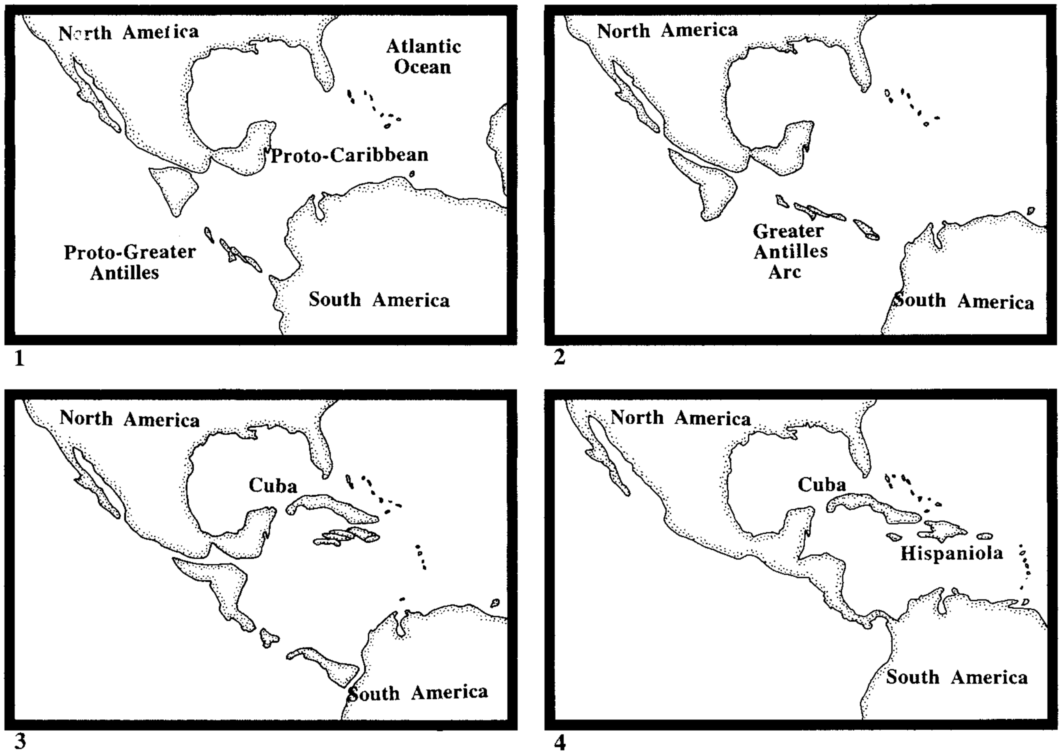
ABSTRACT. The Dominican Republic amber fossil spider record is examined and hypotheses generated concerning the Recent Hispaniolan spider fauna which is, at present, poorly known. The families Cyrtaucheniidae, Microstigmatidae, Nemesiidae, Ochyroceratidae, Tetrablemmidae, Palpimanidae, Hersiliidae, Symphytognathidae *s.l.*, Anapidae, Mysmenidae, and Hahniidae, known from the fossil, but not Recent, fauna are predicted to be components of the Recent fauna of Hispaniola. Based on a terrestrial invertebrate species longevity of less than ten million years, the presence of endemic and non-endemic species, and the assumption that Hispaniola has suffered no major ecological disruption that would cause the amber lineages to become extinct, the following hypotheses are made: Filistatidae and Desidae colonized Hispaniola after the Miocene amber formation; Drymusidae, Amaurobiidae, and Deinopidae were present on Hispaniola during the Tertiary, but avoided capture, or have yet to be found in the amber; and Scytodidae, Oecobiidae, Uloboridae, Dictynidae and Clubionidae have colonized Hispaniola since the Miocene amber formation but these families, which were present on Hispaniola during the period of amber formation, contain undiscovered endemic species.

Hispaniola is unique, in terms of its known spider fauna, in that more families are recorded from fossil species in Miocene Dominican Republic amber than are recorded from extant species (Wunderlich 1988; Penney 1999). Petrunkevitch (1928) considered the Greater Antillean spider fauna to represent an eastern outgrowth of the Central American fauna by way of a presumed earlier land connection and subsequent continent–island vicariance. However, a land connection appears not to have existed (Ross & Scotese 1988). Based on a quantitative computer model of platetectonics, these authors proposed that the Proto-Greater Antillean (Fig. 1) and subsequently the Greater Antillean landmass formed on the west of the Proto-Caribbean region during the late Lower Cretaceous. This landmass moved north-eastwards remaining close to the Yucatan Peninsula until the Eocene (Figs. 2, 3). During the Late Eocene–Oligocene this landmass was contiguous with Cuba and Puerto Rico before undergoing island–island vicariance (MacPhee & Iturralde-Vinent 1995). There is no evidence of island size change subsequent to this vicariance. During the mid-Tertiary the North and South American landmasses moved westwards relative to the Caribbean. During the period of amber-forming resin secretion (15–20 million years ago; Iturralde-Vinent & MacPhee 1996) the Haitian part of Hispaniola lay directly south of and close to the south-eastern part of Cuba. Since then, the separation of the islands has continued until the far-western tip of Hispaniola was clear of the south-easternmost tip of Cuba (Fig. 4) (e.g., Ross & Scotese 1988). Spiders, in general, are renowned for their good dispersal capabilities and presumably did not require a land bridge in order to colonize Hispaniola. There are 291 Recent species in 155 genera and 40 families recorded from Hispaniola (Penney 1999), but this fauna has not been intensively investigated using a variety of collecting techniques (e.g., Banks 1903; Bryant 1943, 1945, 1948). The fossil fauna consists of approximately 200 species in 46 extant families (Penney 1999). Eleven of the families are recorded only from the fossil fauna and five are recorded only from the Recent fauna which is an overlap of approximately 70%. Coddington et al. (1991) suggested that one hectare of typical neotropical forest probably supported 300–800 different spider species, supporting the idea that the Recent Hispaniolan spider fauna is poorly known.

Species longevity.—Based on observations from the fossil record and/or Lyellian per-



Figures 1–4.—Palaeogeography of Central America and the Caribbean (after Ross & Scotese (1988)). 1, Early Aptian (118.7 Ma); 2, Middle Campanian (84.0 Ma); 3, Late Eocene (44.1 Ma); 4, Recent (0.0 Ma).

centages (the percentage of species in the fossil record that exist today), Stanley (1985) suggested a few million years for a number of groups of terrestrial animals, whereas plants and some marine animals were found to have longer species durations. Prószyński (1986), in a footnote, requested information regarding species longevity, and suggested that a salticid species may survive a few million years. Prószyński's estimate was speculative and based on the disjunct distributions of Recent species which were assumed to have been caused by the Pleistocene glacial and interglacial periods. He has no additional data that would more accurately estimate the species longevity for this family (J. Prószyński pers. comm. 1998). Decae (1986), however, suggested that two species of *Cyrtocarenum* Ausserer 1871 (Ctenizidae) may both have a minimum age of 23 million years. Decae (1986) only mentioned that 23 million years was the minimum age of the species in the abstract of his publication. Evidence was given for a possible speciation event 23 million years ago resulting from vicariance (the separation of the Greek mainland into western and eastern parts divided by an oceanic trough).

Testing paleobiogeographic hypotheses.—With spiders, the analysis of Recent biogeographic patterns without evidence from the fossil record can be considered speculative at best. This is demonstrable by the numerous disjunct distributions between Recent spider families and genera and those preserved in the fossil record. Wunderlich (1994) discussed the biogeographic relationships of the extant and fossil central European spiders to the tropical and subtropical faunas. The families Archaeidae C.L. Koch & Berendt 1854, Deinopidae C.L. Koch 1851 and Cyatholipidae Simon 1894 (the fossils attributed to this family may be incorrectly placed; C. Griswold pers. comm.) were discussed with respect to their fossil (central Europe) and Recent (tropics and southern hemisphere) distributions. The presence of families and genera found in the fossil record in central Europe, which today are only found in southern Europe, or are rare in central Europe, for example, Ctenizidae Thorell 1887, Dipluridae Simon 1889, Leptonetidae Simon 1890, Hersiliidae Thorell 1870, Oecobiidae Blackwall 1862 and *Orchestina* Simon 1882 (Oonopidae Templeton 1835) was reported by Wunderlich (1994).

Decae's (1986) logic does not consider the ancestral area(s) of the taxa or their ancestor(s). Three hypotheses for the Recent distributions of the Afrotropical genera of the family Archaeidae may be generated. Vicariance resulted from Madagascar separating from the African mainland. The following evolutionary events may have occurred: 1) the Madagascan genus *Archaea* C.L. Koch & Berendt 1854 may have evolved from a population of the south African (e.g., Dippenaar-Schoeman & Jocqué 1997) genus *Afrarchaea* Forster & Platnick 1984 (one species *A. godfreyi* (Hewitt 1919) is found in Madagascar (Lotz 1996), is not endemic, and has probably been introduced from South Africa); or 2) vice versa; or 3) both genera evolved from a common ancestor.

Madagascar separated from northern Gondwanaland and moved southwards to its present position over approximately 150 million years beginning prior to the Middle Jurassic initiation of sea-floor spreading in the Western Somali Basin (Coffin & Rabinowitz 1987). The presence of fossil evidence, i.e., the genus *Archaea* in Baltic amber (e.g., Eskov 1992) rejects two of these hypotheses as follows. Madagascar is renowned for its unique fauna and flora; it is unlikely that *Archaea* would colonize the Baltic region so far north without also crossing the relatively narrow Mozambique Channel to colonize the African mainland. The fossil evidence and Recent distribution suggests a much wider distribution of this genus in the past (e.g., Eskov & Golovatch 1986) probably prior to the separation of Madagascar from the mainland (the family is also recorded from the Jurassic of Kazakhstan (Eskov 1987)). Thus two of the above hypotheses (1 and 3) are rejected because both genera may have evolved from a common ancestor, but prior to the vicariance event in question. There is no evidence to support the remaining hypothesis that *Afrarchaea* evolved from *Archaea*; however, this hypothesis is subject to falsification through the fossil record in the same manner as hypothesis 1.

Because fossils of Recent terrestrial animal species have not been found in rocks more than ten million years old, Eldredge (1985) proposed that all species alive more than about ten million years ago are extinct. All species described from Dominican Republic amber are extinct (with possibly a few exceptions, which warrant re-examination; e.g., Poinar 1992). Therefore a terrestrial invertebrate species longevity of less than 10 million years is a reasonable expectation. The obvious contraindication to this assumption are those Recent species considered to be 'living fossils', but these belong to extant clades known in the fossil record to show long and narrow clade shapes, i.e., occupying a long range of geological time and with few branches (Stanley 1985).

Hypotheses for the Hispaniolan spider fauna.—On the basis of the presence and absence data of spider families in the Dominican Republic amber, the Recent Hispaniolan spider fauna, and the Recent Neotropical spider fauna (Table 1–families known from all faunas and with both endemic and non-endemic Recent species not included) it is reasonable to expect that the families Cyrtaucheniidae Pocock 1903, Microstigmatidae Roewer 1942, Nemesiidae Simon 1892, Ochyroceratidae Fage 1912, Tetrablemmidae O.P.-Cambridge 1873, Palpimanidae Thorell 1870, Hersiliidae, Symphytognathidae *s.l.* Hickman 1931, Anapidae Simon 1895, Mysmenidae Simon 1922 and Hahniidae Bertkau 1878, have Recent representatives on Hispaniola which have yet to be discovered. These families are known from the Dominican Republic amber but not from the Recent Hispaniolan fauna, and are components of the Recent Neotropical fauna. Many of the smaller species (e.g., Ochyroceratidae, Tetrablemmidae, Symphytognathidae, Anapidae, Mysmenidae, Hahniidae), cryptic species (e.g., Cyrtaucheniidae, Microstigmatidae, Nemesiidae, Hersiliidae) or less common species (e.g., Palpimanidae) may have been overlooked in the early stages of a species inventory of Hispaniola, in favor of the larger and more common species. In the inventories listed by Bryant (1948) for Cuba, Puerto Rico, St. Vincent and the Virgin Islands the above families were represented only by the Hersiliidae recorded from Cuba,

Table 1.—Dominican Republic amber, Hispaniolan and Neotropical spider families considered in this paper, and the presence of Recent non-endemic and Recent endemic Hispaniolan species in those families.

Family	Dominican Republic (amber)	Recent Hispaniola (endemic)	Recent Hispaniola (non-endemic)	Recent Neo-tropical	Reference
Cyrtaucheniidae	+	−	−	+	Wunderlich (1988)
Microstigmatidae	+	−	−	+	Wunderlich (1988)
Nemesiidae	+	−	−	+	Schawaller (1981)
Ochyroceratidae	+	−	−	+	Wunderlich (1988)
Tetrablemmidae	+	−	−	+	Wunderlich (1988)
Palpimanidae	+	−	−	+	Wunderlich (1988)
Hersiliidae	+	−	−	+	Wunderlich (1988)
Symphytognathidae *s.l.*	+	−	−	+	Schawaller (1981)
Anapidae	+	−	−	+	Wunderlich (1988)
Mysmenidae	+	−	−	+	Wunderlich (1998)
Hahniidae	+	−	−	+	New amber record
Filistatidae	−	−	+	+	Platnick (1993)
Desidae	−	−	+	+	Platnick (1993)
Deinopidae	−	−	+	+	Bryant (1948)
Drymusidae	−	+	−	+	Bryant (1948)
Amaurobiidae	−	+	+	+	Platnick (1997)
Scytodidae	+	−	+	+	Wunderlich (1988)
Oecobiidae	+	−	+	+	Wunderlich (1988)
Uloboridae	+	−	+	+	Wunderlich (1988)
Dictynidae	+	−	+	+	Wunderlich (1988)
Clubionidae	+	−	+	+	Wunderlich (1988)

and the Palpimanidae recorded from all but the Virgin Islands. Subsequently, Tetrablemmidae was recorded from Cuba and the Virgin Islands and Anapidae from St. Vincent (Platnick 1989); Palpimanidae from the Virgin Islands (Platnick 1993); Ochyroceratidae and Mysmenidae from Cuba and St. Vincent (Platnick 1997).

Endemic *vs.* non-endemic species.—Some, if not all, of the families known from the Recent, but not amber, Hispaniolan spider fauna (Table 1) may have colonized Hispaniola since the period of amber-forming resin production in the Tertiary. The only known Hispaniolan filistatid, *Kukulcania hibernalis* (Hentz 1842), is widespread on the American mainland and the only known desid on Hispaniola, *Paratheuma insulana* (Banks 1902), is found in America and the West Indies (Platnick 1993). The only Hispaniolan deinopid, *Deinopis lamia* MacLeay 1839, is distributed throughout the Antilles; the only Hispaniolan drymusid, *Drymusa simoni* Bryant 1948, and two amaurobiids: *Tugana crassa* (Bryant 1948) and *Retiro gratus* (Bryant 1948) are endemic to Hispaniola. *Tugana cavatica* (Bryant 1940) is found on Cuba and Hispaniola (Alayón-Garcia 1992).

It is possible that those families containing species endemic to Hispaniola (Drymusidae Simon 1893 and Amaurobiidae Thorell 1870) were present on Hispaniola at the time of the Dominican Republic amber formation although this cannot be established unequivocally unless they are found in the amber or other fossils from the region.

Assuming a species longevity of less than 10 million years, families with only non-endemic species on Hispaniola (discovered and undiscovered) must have colonized Hispaniola since the Tertiary amber-forming period or have colonized other regions from Hispaniola since the Tertiary. It is more likely that most of the families known from only non-endemic species also have undiscovered endemic species present, particularly those families present in Dominican Republic amber, as detailed below. The families Scytodidae Blackwall 1864, Oecobiidae, Uloboridae Thorell 1869, Dictynidae O.P.-Cambridge 1871, and Clubionidae Wagner 1887, are recorded in Dominican Republic amber; Filistatidae

Ausserer 1867, Deinopidae, and Desidae Pocock 1895, are not. Many Recent genera of Desidae live in the intertidal zones of rocky coasts and may have been present on Hispaniola during the Miocene but avoided capture in resin because of their habitat.

Eskov (1990) reported Filistatidae from the Upper Jurassic of Kazakhstan (but this material has yet to be published), before the formation of the Proto-Greater Antillean land mass. It is probable, then, that Filistatidae colonized Hispaniola from the American continent, possibly via Cuba. The same may be true for the Desidae, but the Recent distribution of the deinopid species (Greater Antilles) suggests a colonization event originating from within the Greater Antilles, possibly Hispaniola.

Families that have colonized Hispaniola, but which lack endemic species, have probably not been on Hispaniola long enough to speciate; these families must have colonized the island since the amber formation and within the last ten million years. Families represented in the Dominican Republic amber and known from the Recent fauna of Hispaniola from only non-endemic species (Table 1) may either have colonized other regions from Hispaniola, or have colonized Hispaniola from other regions.

Uloboridae and Dictynidae include species with distributions restricted to the Greater Antilles and these families may have colonized other regions from Hispaniola; the clubionid *Elaver exceptus* (L. Koch 1866) (possibly present on Hispaniola) is distributed from Canada, through the USA to the West Indies (Platnick 1993). On Hispaniola, Scytodidae is known only from pantropical species and, despite the lack of evidence, the probability of Hispaniola being scytodid ancestral area is unlikely due to the relatively young age and isolated nature of the island, and the cosmopolitan distribution of Scytodidae. On Hispaniola, Oecobiidae is known from one species *Oecobius concinnus* Simon 1892, collected from Port-au-Prince, Haiti; elsewhere in the region it has a distribution throughout the Caribbean islands, Peninsula Florida, coastal Mexico, Central America, Venezuela and Columbia (Shear 1970). Many oecobiids are synanthropic, small, often overlooked, and are frequently inadvertently transported by man. All of the records of this species given by Shear (1970) are from coastal localities, so this was probably the means of dispersal for this species. Only 11 specimens are recorded from Hispaniola (Bryant 1948), compared with the hundreds of specimens collected from other regions, so this is probably an introduced species.

Families known from the Dominican Republic amber and recorded from the Recent Hispaniolan fauna from only non-endemic, presumably introduced species, unless their amber species lineages have become extinct since the Tertiary, might be expected to contain species endemic to Hispaniola that await discovery and description. The only known possible cause of major extinctions on Hispaniola since the amber formation might be the Pleistocene glaciations. Hispaniola lay in a tropical-subtropical zone with an arid glacial climate (in part, more arid than at present), and there is good evidence of a cooler Pleistocene climate from sedimentary and geomorphic data and alluvial terraces. However, extreme aridity and glaciation have not been documented for the Dominican Republic during the Pleistocene (Schubert 1988). Whilst the surrounding sea temperature dropped by approximately 2–3 °C during the glacial maxima (Prell et al. 1976), the albedo of Hispaniola was the same as it is at present (15–19%). The albedo increased during the last glacial maximum due to the expansion of savannah at the expense of tropical forest; e.g., Panama had a reflectivity of 15–19 percent during the last glacial maximum and at present has a reflectivity of 10–14% (Schubert 1988). Grimaldi (1996) presented a reconstruction of the Tertiary Dominican Republic amber-producing forest, based on fossil evidence, which differed little from a Recent Neotropical rainforest. It can be concluded that the Dominican Republic rainforest has suffered no drastic changes since the Tertiary that would cause the spider lineages present in the amber to become extinct.

Wunderlich (1988) recognized 25 Hispaniolan spider genera recorded only from fossil species. These genera may or may not be extinct. Considering the poorly known nature of the Recent Hispaniolan spider fauna, the lack of these genera in the Recent fauna cannot be construed as evidence for considering these genera extinct; they may contain extant species which have yet to be discovered.

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