

# Palaeoecological perspectives in Dominican amber

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**Abstract.** Palaeoecological and palaeobiogeographical aspects of Dominican amber are discussed based on the known insect fauna. Topics covered are examples of speciation, extinctions, longevity as well as associations between insects and plants, insects and vertebrates and various arthropod groups. Examples of camouflage, oviposition and predator-prey associations are presented. Ecological and medical implications from recently discovered vector-parasite associations (malaria, trypanosomiasis and leishmaniasis) are discussed. Paleosymbiotic associations, with examples of phoresis, mutualism, parasitism and pathogens, are examined. Insects in Dominican amber, together with their cohabitants, can assist in determining specific habitats and reconstructing ancient landscapes.

**Résumé. Perspectives paléocéologiques de l'ambre de la Dominique.** Les considérations paléocéologiques et biogéographiques de l'ambre de la Dominique sont discutées sur la base de la faune entomologique connue. Les sujets couverts concernent des exemples de spéciation, d'extinction, de longévité ainsi que des associations entre insectes et plantes, insectes et vertébrés et d'autres groupes d'arthropodes. Des exemples de camouflage, d'oviposition et de couples proies-prédateurs sont présentés. Les implications écologiques et médicales sont discutées à propos d'associations vecteurs-parasites récemment découvertes (malaria, trypanosomiase, leishmaniose). Des associations paléosymbiotiques sont discutées, avec des exemples de phorèse, de mutualisme, de parasitisme et de pathogénèse. Les insectes de l'ambre de la Dominique et leurs cohabitants, peuvent aider pour l'identification des habitats spécifiques et la reconstruction des paysages anciens.

**Keywords:** Dominican amber, paleosymbiosis, biogeography, speciation, extinctions.

## Introduction

Fossils in amber provide a unique opportunity to study not only the origin and evolution, but also the past distribution, ecology and associates of arthropod lineages. Dominican amber, which has provided a wealth of information about past tropical life, contains the largest number of insect fossils from one area in the Americas. The insect fauna in Dominican amber has been carefully tabulated (Arillo & Ortuño 2005; Pérez-Gelabert 1999) and examples of fossil behavior (paleoethology) in amber have been reviewed by Arillo (2007). A recent list of the known extant and extinct arthropod fauna of Hispaniola provides a basis for comparing lineages in Dominican amber with those found currently (Perez-Gelabert 2008). The present paper emphasizes various aspects of the micro- and macro- habitats and behaviour of Dominican amber biota and characterizes even further the ecology of the Tertiary amber forest in Hispaniola.

## Age and source of amber

The first dating of Dominican amber was based on foraminifera recovered from the Palo Alto mine, which provided a date of 23–20 million years (Baroni-Urbani & Saunders 1980). A range of ages for Dominican amber was later demonstrated by nuclear magnetic resonance spectroscopy (NMR) analyses (Lambert *et al.* 1985). In this study, exo-methylene carbons were used to obtain relative ages of amber from various mines, including the Palo Alto mine. The estimated actual ages were then calibrated from Baroni-Urbani and Saunderson's reported age of 23–20 million years for the Palo Alto mine. This provided a range of ages for Dominican amber with that from La Toca mine estimated to be between 30 and 40 mya (Lambert *et al.* 1985). By 1996, there were three additional age estimates of Dominican amber, one by Grimaldi (1996), who presented a range of 23 to 30 million years for amber from the “northern mountains”, another by Iturralde & MacPhee (1996), who estimated the age of the La Toca and Palo Alto mines at 15–20 mya based on foraminifera as well as previously known biostratigraphic and paleogeographic studies and

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a third by Cepek, who had obtained samples from the same mines and obtained a set of ages based on coccolith fossils. His results were published by Schlee (1990) and the estimated ages were 30–45 mya for the La Toca mine and 25–30 mya for the Palo Alto mine. There is clearly a discrepancy between the ages reported by the above authors. In addition, the 15–20 mya age could be low if the amber had been secondarily re-deposited for a significant amount of time and this would make a definite age determination based on stratigraphy difficult to almost impossible (Poinar & Mastalerz 2000).

Amber and copal deposits are spread throughout the Dominican Republic. In the West, most of the amber is derived from mines in the Cordillera Septentrional between the cities of Santiago and Puerto Plata and occurs in sandstone and limestone deposits associated with the El Mamey Group (Upper Eocene to Lower Miocene) (Draper *et al.* 1994). The most prolific mines there are La Toca, Palo Alto, Las Cacaos and La Cumbre which contain hard, clear, yellow to red amber. Amber in the eastern portion of the country near the city of Bayaguana mostly is derived from the Sierra de Agua and Comatillo mines, which contain hard, rather brittle, pale yellow to red and softer, yellow-grayish amber, respectively. Further north in the El Valle area are La Medita and Ya Nigua mines, which contain mostly hard, brittle, yellow to red amber, but also some light blue amber (Poinar 1992).

Based on floral and vegetative remains in amber collected from La Toca, as well as DNA studies (H. Poinar *et al.* 1993), Dominican amber was determined to be formed from resin produced by an extinct, leguminous tree, described as *Hymenaea protera* Poinar (1991). This species belongs to the primitive *Tachylobium* section of the genus and although most extant *Hymenaea* spp. occur in South America, the closest extant relative of *H. verrucosa* occurs in East Africa and adjacent islands. Both *H. protera* and *H. verrucosa* are characterized by the presence of two reduced scale-like petals, a character not found in any extant New World *Hymenaea* species. Both oceanic dispersal and vicariance events have been hypothesized as explaining this ampho-Atlantic distribution pattern of *Hymenaea protera* and its closest living relative, *Hymenaea verrucosa*. This aspect will be addressed more fully in the following section.

### **Biogeography, speciation and extinctions**

Because of the complexity and multiple opinions on the formation of Proto-Greater Antilles and its movement east on the Caribbean plate, tracing the past history of life on Hispaniola is difficult. There is a

general consensus that Hispaniola, as well as the other islands that make up the Greater Antilles, originated far in the past (some 100 mya) as result of a volcanic eruption in the Pacific ocean to the west of the present Central American isthmus.

This volcanic landmass, called the Proto-Greater Antilles, is thought to have first emerged above the sea some 65 million years ago (Ross & Scotese 1988), roughly the same time the famous meteor smashed into the earth and formed the Chicxulub Crater. Whether the collision was connected with the emergence of the Proto-Greater Antilles is unknown.

The Proto-Greater Antilles land mass began moving east on the Caribbean plate and for a period of time, formed a bridge between North and South America, roughly where Central America is located today. During this period, fauna and flora from North and South America colonized the young terrain. Eventually, around 60 mya, the Proto-Greater Antilles broke away from both continents and continued moving eastward, slowly breaking up into the various islands that form the Greater Antilles today (Cuba, Hispaniola, Puerto Rico, Jamaica). As it moved into the Caribbean, other life forms entered the landmass by air and water dispersal as well as over land bridges and island hopping during periods of low sea level. Thus the Dominican amber biota, as well as much of the present fauna and flora, represents both vicariance and dispersal events.

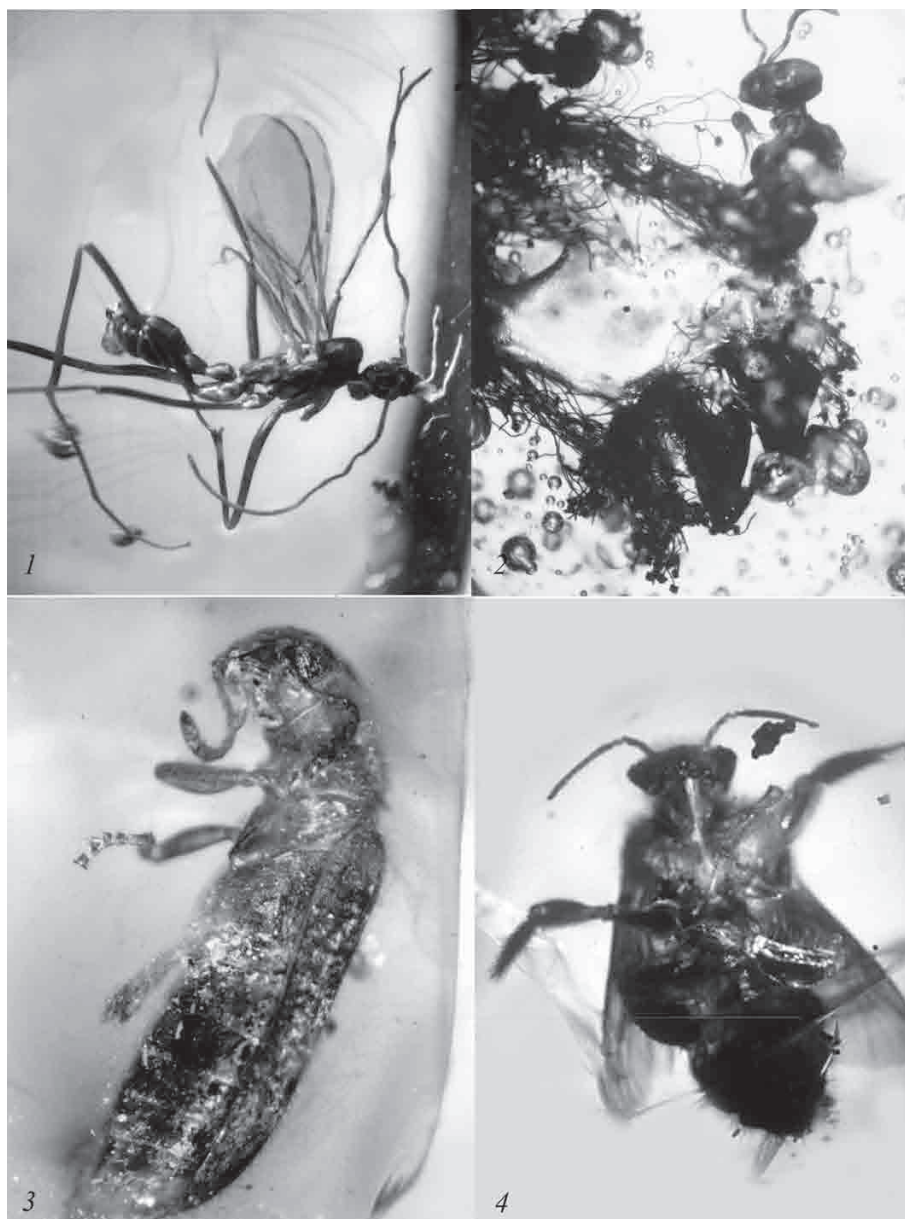
Hispaniola is thought to have reached its present location about 25 mya and ever since its emergence; it was never completely submerged (Lewis *et al.* 1990). The amber beds in Hispaniola were uplifted fairly recently, geologically speaking, only about 10,000–25,000 ybp (Ross & Scotese 1988).

The general pattern of speciation and extinction in Hispaniola as provided by amber fossils shows that a significant number of lineages entered the island mass, most probably when it was still connected to North and South America. As the area broke up into the various island groups, speciation of those lineages occurred and the forms preserved in Dominican amber represent a particular stage in this evolutionary event. Many of these lineages were extirpated from Hispaniola, from the entire Greater Antilles, from the Americas and many from the world (extinct genera, tribe and subfamily). The causes of these extinctions are complex, but climate change (drop in temperature and moisture levels) probably played an important role. Just removing some of the keystone species would have resulted in many subsequent extinctions. These extirpations of Dominican amber biota show a wide range of disjunct distributions between the amber biota and their nearest related lineages.

In some amber lineages both continuous and disjunct distributions occur. An example concerns the caddis fly genus *Antillopsyche* Banks. The species *A. oliveri* Wichard, one of the most common caddis flies encountered in Dominican amber, is amazingly still represented in the Antilles while all other species occur in the Ethiopian and Oriental Regions. Wichard (1987) felt that the generic lineage extended back to the

Mesozoic, at least to the mid-Cretaceous, when there was still a connection between the South American and African continents. This probably could be considered an example of phyletic speciation since both the amber and extant species in Hispaniola are closely related.

Another example of pseudoextinction in Dominican amber occurs in the *micrommatum* clade of the genus *Proceratium*, a genus that originated in the Afro-



**Figures 1–4**

**1**, a male *Leptomymex neotropicus*. Note the absence of a radial cell in the fore wing, which separates the Dominican amber species from its congeners in Australasia; **2**, a worker of *Proplebeia dominicana* associated with acacia flowers shows evidence of pollination behavior and flower selection; **3**, this checkered beetle, *Arawakis poinari* (Coleoptera: Cleridae), has its nearest extant relatives in South America and Africa; **4**, this orchid bee *Paleoeglossa* (Euglossinae: Apidae) indicates the presence of orchids in the amber forest (location of specimen unknown).

tropical Region (Baroni Urbani & de Andrade 2003). The two Dominican amber species in this clade (*P. dominicanum* de Andrade and *P. poinari* Baroni Urbani & de Andrade) apparently evolved into two extant species of the same clade (*P. taino* de Andrade and *P. longiscapus* de Andrade) now residing in Hispaniola. Further evidence of the endemism of these 2 extant forms is their absence outside of the Greater Antilles.

A second example was demonstrated with ants of the Neotropical genus *Cephalotes*, a genus characterized by a high level of polyandry, unlimited selection of food items, a high degree of morphological modifications related to passive defense and a high rate of spontaneous mutation (de Andrade & Baroni Urbani 1999). De Andrade & Baroni Urbani (1999) described two extinct species (*C. taino* de Andrade and *C. resiniae* de Andrade) in the *hamulus* clade in Dominican copal. Both are closely related to two members of the *hamulus* clade residing today in Hispaniola. This is especially interesting since radiocarbon dating of copal samples from Cotui revealed ages between 200 and 300 years. Was a few hundred years does long enough for phyletic extinction and speciation to occur as a result of the high rate of spontaneous mutation? The *Cephalotes* species in copal may still exist on Hispaniola but since *Cephalotes* ants are large and diurnal, it is strange they have not been discovered. Perhaps the “copal” containing the ants is really a light form of amber from one of the Eastern mines (e.g. Bayaguana). Or perhaps some of the Cotui copal may be much older than suspected. It is interesting that of the 12 extinct species of *Cephalotes* in Dominican amber, none of them are closely related to the 9 extant species that still inhabit Hispaniola, but belong to lineages now surviving in Central and South America.

There are many cases of extinct insect genera in Dominican amber that have closely related lineages in Central and South America today. Some examples are: the stingless bee *Proplebeia dominicana* (Wille & Chandler) (Michener 1982) (Hymenoptera: Apidae) (Fig. 1), the checkered beetle *Arawakis* (Coleoptera: Cleridae) (Opitz 2007) (Fig. 2), the orchid bee, *Paleoeglossa* (Hymenoptera: Apidae), still undescribed orchid bees (Fig. 3), the emesine bug, *Paleoploiarilo* Capriles, Santiago-Blay & Poinar (1993a) (Hemiptera: Reduviidae), a gnat bug, *Paralienates* Capriles, Santiago-Blay & Poinar (1996) (Hemiptera: Enicocephalidae), a resin bug, *Apicrenus* (Hemiptera: Reduviidae) (Capriles, Santiago-Blay & Poinar (1993b), a plant bug, *Stomatomiris* Capriles & Poinar (1995) (Hemiptera: Miridae), a sap beetle, *Palaeometopia* Kirejtschuk (Kirejtschuk & Poinar 2007) (Coleoptera: Nitidulidae) and a wasp, *Pterosclerogibba* Olmi (2003–2004) (Hymenoptera: Sclerogibbidae).

Disjunct species distributions between Dominican amber taxa and extant clades outside the Americas are shown in the study of *Proceratum* (Baroni Urbani & de Andrade 2003). Of the 12 species in the *stictum* clade, two Dominican amber fossils (*P. denticulatum* Lattke and *P. gibberum* de Andrade) show closest relationships to extant species (*P. cavinodus* de Andrade and *P. boltoni* Leston) in Australia and Africa, respectively.

Two additional classic examples of disjunct distributions involving clades outside the Americas are *Mastotermes* termites (Isoptera: Mastotermitidae) and *Leptomyrmex* ants (Hymenoptera: Formicidae), both of which represented an important part of the ecology of the Tertiary Dominican amber forest, but are complete gone from the Americas today (Poinar & Poinar 1999).

It is difficult to understand why the range of *Mastotermes* has contracted so drastically since the Tertiary because the single remaining Australian species, *Mastotermes darwiniensis*, has so many survival tactics. It can form colonies in a variety of substrates, the queens are long living (up to 17 years) with colony numbers reaching a million individuals and its diet includes not only logs and structural timbers, but also living trees, crops and even some synthetic materials. The range of *Mastotermes* in the Tertiary was apparently cosmopolitan, with fossils in Mexican amber as well as in European Miocene and Eocene deposits. Perhaps their large size was detrimental (alates reach up to 30 mm in length) or they succumbed to predators and/or diseases.

The second classic example of a disjunct distribution outside the Americas concerns the ant *Leptomyrmex neotropicus* Baroni Urbani in Dominican amber. This is one of the largest ants found in any amber deposit. European fossils show that these ants were widely distributed during the Tertiary, but today populations are reduced to just a dozen or so species confined to the Australasian region (Baroni Urbani & Wilson 1987). Possibly their large size is to blame or the wingless condition of the queens. The fact that the colonies were exposed on the forest floor could have made them susceptible to some external biotic or abiotic event.

The Dominican amber *Leptomyrmex* appears to be most similar to the extant *L. fragilis* living in New Guinea, Ceram, and Aru. However, a significant difference between the two is the wing venation. While all extant species have a well-developed radial cell, the alates of *L. neotropicus* lack this character completely (Fig. 4).

There are other groups in Dominican amber that show close affinities to Australasian taxa. Two species of *Pheidole* in Dominican amber (*P. primigenia* Baroni Urbani and *P. tethepa* Wilson) were more closely



related to extant species from the Malaysian and Australasian Regions, than to existing Neotropical lineages (Baroni Urbani 1995). This same pattern also was noted for Dominican amber ant species of *Anochetus* and *Aphaenogaster* (de Andrade 1994, 1995). The silverfish, *Hemirrinemura extincta* Mendes & Poinar (2004), belonged to a genus with three extant species restricted to Papua New Guinea, Melanesia and Polynesia. The Dominican amber marine water strider, *Halovelgia electrodominica* Andersen & Poinar (1998) has extant members of the genus occurring in the Indo-West Pacific Region. These extended disjunctions are difficult to explain, especially when the organisms occur on oceanic islands. Some of the larger islands like Madagascar and Australia were part of Gondwanaland and the lineages could have spread throughout that landmass when it was one giant continent. On the other hand, oceanic and aerial dispersion cannot be ruled out.

Some genera in Dominican amber appear to be completely unrelated to existing lineages. An example is the mantidfly, *Feroseta priscus* (Poinar 2006). This specimen lacks a pterostigma, which is one of the characteristic features of the family Mantispididae. Also, the flagellomeres are not pubescent and closely appressed to one another as in most mantispids, but are sparsely hirsute and separated as a result of an extended pedicel at the base of each flagellomere. In addition, the wing venation is highly variable and the tip of one forewing vein is represented by a row of macrotrichia. With these characters it is impossible to align the fossil to any extant lineage.

Fossil bees in Dominican amber also are excellent for extinction studies since some fossil genera, such as the stingless bee, *Proplebeia* (Apidae) and the orchid bee, *Paleo Euglossa* (Apidae) have disappeared over the past 20–30 mya, while other amber generic lineages, although absent today from the Greater Antilles, are represented in Central and South America. These include members of the solitary bee genera *Chilicola* (Colletidae), *Heterosaurus* (Andrenidae), *Oligochlora* (Halictidae), *Neocorynura* (Halictidae) as well as an orchid bee, *Euglossa* (Apidae).

Were these bees eradicated from the Greater Antilles at a recent date due to competition with imported honeybees (*Apis mellifera*)? Native bees were reported to be absent when Europeans introduced honeybees into the West Indies around 1656 (Purchas 1657) and no bees have been reported from the Cotui copal deposits that date between 200 and 300 years (Poinar 1999). It is hard to imagine that the Casimirod and Taino cultures, which extend back some 4000 B.C., had agricultural practices that would have been unfavorable to the native bees. The recent “colony

collapse” disorder of honeybees in various parts of the world has focused attention on disease as an agent of bee declines. Disease is definitely a possibility. Abiotic factors that would have affected all forms were cooling and drying events. Over the past 4 million years, the closing of the Central American Isthmus and glacial activity were two events that caused climatic changes resulting in a 5–6 °C temperature drop in Panama and the Amazon basin (Colinvaux 1996). This event and an accompanying dry period would have affected all life forms in the Greater Antilles, especially bees and their preferred food plants (Poinar & Poinar 1999, Poinar 1999).

Climatic change would have affected other arthropod populations. Being more generalist predators, spiders might not have fared so badly, however Wunderlich (2003) concluded that of the 82 genera of spiders in Dominican amber, 33% are extinct and about 30% are congeneric with extant taxa. No data is given for the other 34%.

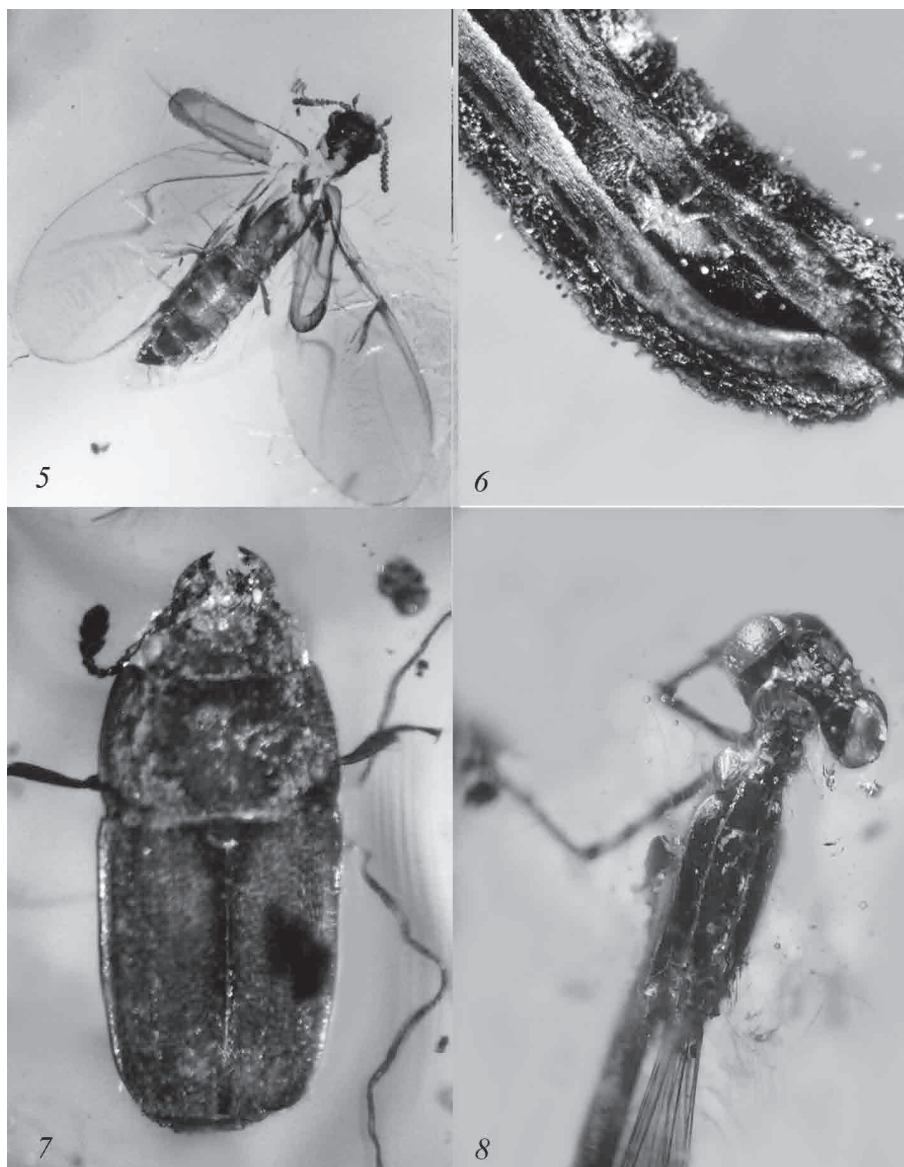
Biogeographical distributions and extinction events of plant genera in Dominican amber parallel those of the arthropods. Certainly the resin producing tree, *Hymenaea protera*, was a keystone species in the amber forest and its extinction was followed by others that depended on it. Thus the study of plant genera in Dominican amber is an important aspect for reconstructing the ecology of the Dominican amber forest. While *Hymenaea courbaril* is the only species of the genus in Hispaniola today, it is not closely related to the Dominican amber tree (*H. protera*). The nearest relative is *H. verrucosa*, which occurs today in East Africa. How can this amphiatlantic distribution pattern of *H. protera* and *H. verrucosa* be explained? One theory is that the progenitor of *H. protera* colonized West as well as East Africa during Tertiary times and the highly resistant fruits (pods) were washed into streams and carried to the ocean where they were picked up by the south equatorial current and dispersed to the Antilles and the eastern shores of South America (Hueber & Langenheim 1986). Another explanation involves a vicariance event where the progenitor of both species spread across the South American and African landmasses in the mid Cretaceous when the continents were still part of Gondwanaland. The retreat of *Hymenaea* populations in Africa since the Tertiary left a single living relict (*H. verrucosa*) in east Africa, while evidence of this lineage in the New World is limited to *H. protera* in Dominican amber (Poinar 1991).

Regional and global extinctions of plant genera in Dominican amber have also occurred. The Dominican amber *Trithrinax dominicana* has its nearest congeners in South America (Poinar 2002). However, two Dominican amber plant genera are extinct globally

today. One is the unique legume, *Lasiambix dominicensis* Poinar, Chambers & Brown (2008a) (Fabaceae) and the other an apparent parasitic plant, *Trochanthera lepidota* Poinar, Chambers & Brown (2008b).

The general pattern of speciation, survival and extinction for much of the biota in Dominican amber appears to follow the pattern explained above for the bees. Climatic changes during the Pliocene-Pleistocene greatly affected the stenotopic tropical lineages that

were unable to survive extended periods of cooling. There were few protected habitats available and little opportunity to migrate to warmer areas. When tropical conditions returned, the fauna and flora was depauperate. There was little chance for the re-invasion of related lineages from Central and South America since the ocean acted as a barrier and the prevailing winds in the Caribbean are from the northeast (Poinar 1999).



**Figures 5–8**

5, dominican amber fossils of primitive, yet highly specialized *Micromalthus* beetles (Coleoptera: Micromalthidae) are considered co-specific with the extant *Micromalthus debilis*; 6, This thrips (Thysanoptera) was probably feeding on pollen when the stamen was preserved; 7, This sap beetle, *Palaeometopia dominicana* (Coleoptera: Nitidulidae) is indirect evidence of a feeding association (on tree exudate) with the resin-bearing tree; 8, Based on extant species of the genus, this stalk-winged damselfly, *Diceratobasis worki* (Zygoptera: Coenagrionidae) probably bred in tank bromeliads.

Dominican amber can be used to study species longevity. While insect species in general survive at least for 2–3 million years (the late Frank Carpenter, personal communication), Dominican amber micromalthid beetles so closely resemble the only known extant species, *Micromalthus debilis*, that they are considered conspecific (Fig. 5) (Hoernschemeyer *et al.* “*in lit*”). This lineage may have remained stable because of its generalist habits of feeding on dead and decaying wood. Another apparently unchanged Dominican amber lineage with similar habits is the tenebrionid beetle, *Lorelus wolcottii* Doyen & Poinar (1994). The few minor differences between extant specimens and those in the amber could be attributed to intraspecific variability. Once a successful pattern of survival between a species and its surroundings is established, evolutionary stasis may persist for long periods, until upset by other biotic and abiotic factors.

### Associations between arthropods and plants

Insects utilize plants for food and shelter. Determining host plants for various insects in amber can be difficult since while there are many examples of leaf, flower and bud damage in Dominican amber, it is usually impossible to determine what organisms were responsible since many invertebrates aside from insects (gastropods, diplopods, etc.) are also phytophagous. One way to determine the likely existence of specific plants in the ancient forest is to determine the host plants of closely related descendants of Dominican amber insects. For example, since fig wasps are highly adapted to pollinate fig flowers, these plants were certainly present in the original habitat. The same reasoning can be applied to palm bugs and palm beetles as showing evidence of palms and this has been substantiated by the discovery of palm flowers in Dominican amber (Poinar 2002). Butterfly caterpillars of the genus *Vanessa* suggest the presence of the nettle genus *Urtica* (Urticaceae). Metalmark butterflies of the genus *Napaea* reveal orchids and bromeliads and orchid bees also confirm the presence of orchids. These findings were further substantiated by an orchid seed in Dominican amber (Poinar & Poinar 1999). Since today, flower thrips are well known for feeding on pollen, a member of this group in a legume anther in Dominican amber was probably showing a similar behavior (Fig. 6). Resin can serve a number of purposes. For *Hymenaea* trees, it could be a repellent against leaf feeding insects and certain fungi (Stubblebine & Langenheim 1977; Arrhenius *et al.* 1983). However some insects have found important uses for this exudate. Resin is collected by stingless bees today for nest construction and *Proplebeia* bees in Dominican

amber with resin balls attached to their hind basitarsi show an early date for this behavior. It is likely that the great majority of stingless bees captured in Dominican amber were in the resin-collecting period of their life since very few carry any significant amount of pollen grains. And apparently most of these became entombed before they began collecting the material since their legs lack any trace of resin.

Another group of insects that utilized resin in Dominican amber were the resin bugs (Hemiptera: Reduviidae: Apiomerinae). These bugs coat the long, silky setae on their fore tibiae with globs of resin in order to facilitate prey capture, which includes stingless bees. Present day representatives do not limit their prey to bees but also use this method to capture grasshoppers, flies and beetles (Poinar 1992b). Studies on extant South American resin bugs showed that some may actually obtain sugars and other substances from the resin, as well as using it for catching prey (Bérenger & Pluot-Sigwalt 1997).

Indirect evidence of other associations between plants and insects in Dominican amber are bark, platypodid, cerambycid and sap beetles. Members of the former three groups could be carrying symbiotic fungi that grow on the host plant and provide nourishment for their developing larvae. Regarding the latter group, two species of sap beetles in the extinct genus *Palaeometopia* Kirejtschuk in Dominican amber (Fig. 7) probably fed on sap from the Dominican amber tree, which is a typical food item for their closest relatives in the tribe Nitidulini (Kirejtschuk & Poinar 2007).

A completely separate category is the association between arthropods and plants with phytotelmata. The evidence for tank bromeliads is indirect and based on either the presence of insects that feed on these plants today, such as the caterpillars of *Napaea* butterflies, or those extant groups that live in the water collected in the leaf bases. One of the latter is the stalk-winged damselfly, *Diceratobasis worki* (Poinar 1996) (Fig. 8), whose present day representatives deposit eggs in tank bromeliads. Diving and marsh beetles, as well as tadpoles also show evidence of phytotelmata. White worms of the family Enchytraeidae (Annelida) today occur in epiphytic bromeliads and that could have been the natural habitat of *Palaeoenchytraeus dominicanus* Poinar (2007) in Dominican amber.

### Associations between arthropods (non-vectors) and vertebrates

Vertebrates are rare in amber, however there are a number of invertebrates, especially bloodsuckers that indirectly demonstrate the presence of various

vertebrate groups. This applies to the male of the soft tick, *Ornithodoros antiquus* Poinar (1995) (Fig. 9) in Dominican amber. Normally it would have been difficult to assign a vertebrate host to this extinct species since members of the genus *Ornithodoros* feed on mammals, birds and reptiles today. However, adjacent to the tick was a mammal scat and hair, both of which had rodent characteristics. With these two clues, we can safely assume that *O. antiquus* fed on rodents.

Hard ticks belonging to the genus *Amblyomma* also occur in Dominican amber but since species of the genus feed on a wide range of vertebrates today, it is generally impossible to identify the host. However in one case where three *Amblyomma* larvae were associated with a lizard skull in Dominican amber, we can presume that these species fed on reptiles, at least in the larval stage (Fig. 10).



**Figures 9–12**

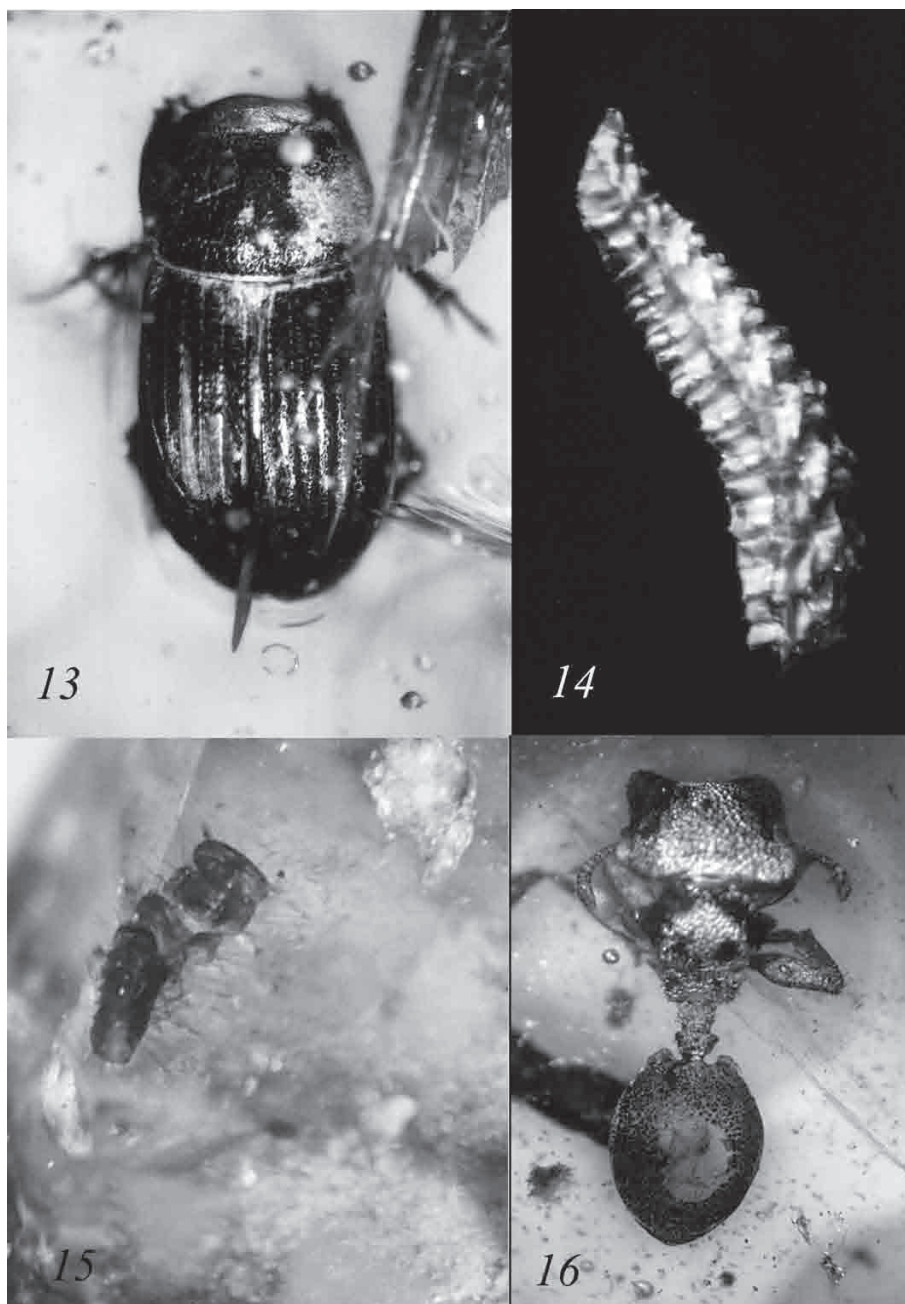
**9**, *Ornithodoros antiquus* (Acari: Argasidae) adjacent to a fecal pellet resembling that of a rodent. Rodent hair adjacent to the scat supports this conclusion; **10**, One of three ixodid tick larvae (Acari: Ixodidae) in a piece of amber containing a decomposed lizard head; **11**, A parasitic mite attached to a lizard torso shows a rare case of vertebrate parasitism; **12**, Based on studies of recent species, this fur beetle larva (Coleoptera: Staphylinidae: Amblyopinae) could have had a mutualistic association with rodents in the Tertiary.



Another piece of Dominican amber contained the torso portion of a lizard, together with three large mites. One of the mites had its mouthparts inserted between the scales of the lizard (Fig.11), while the other two mites were free in the adjacent amber. The

mites resemble members of the family Smariididae, however if that is the case, this would represent a new type of behavior since members of this family today are only known as predators and not parasites.

An interesting group of staphylinid beetles are



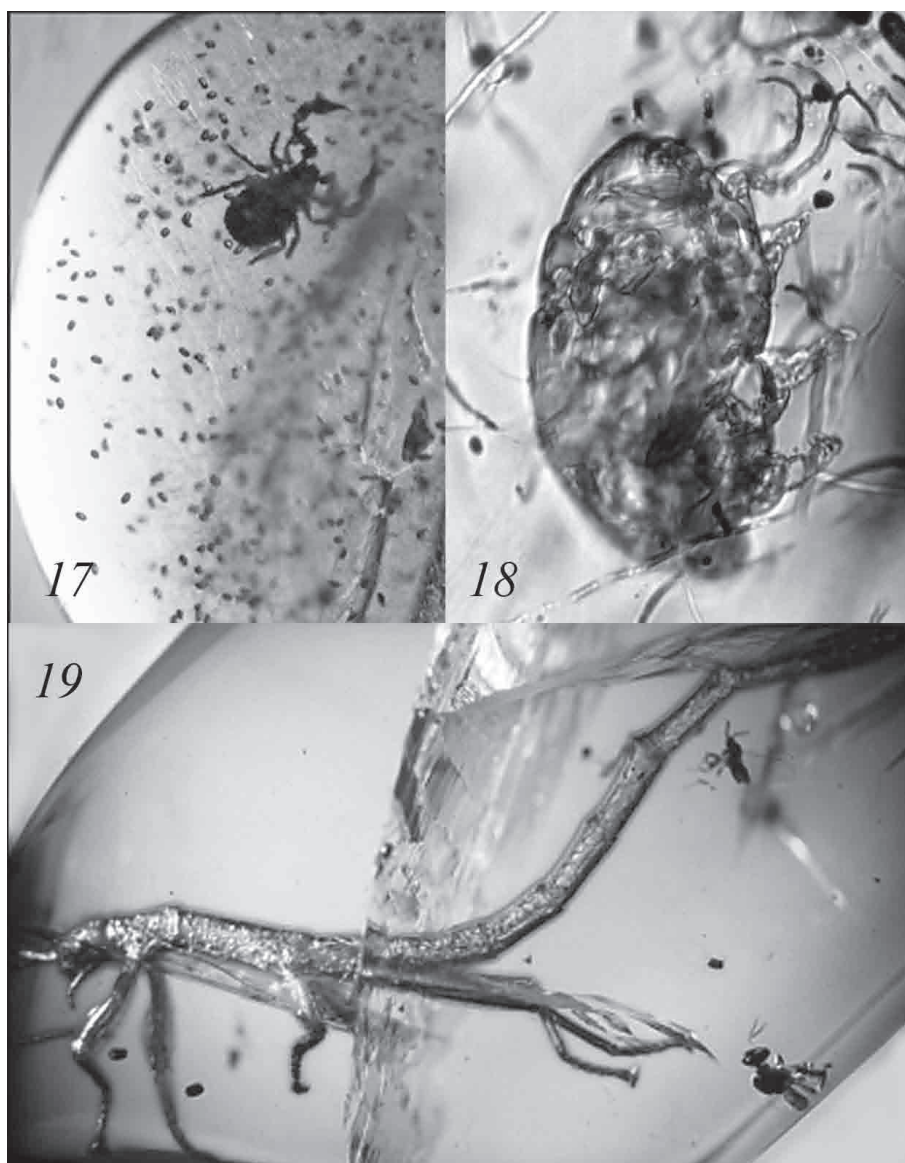
**Figures 13–16**

**13**, Dung beetles provide indirect evidence of the presence of various types of vertebrates; **14**, Calliphorid larva (Diptera: Calliphoridae) similar to the one figured here have been recovered from amber containing decomposing frog and bird remains; **15**, A dermestid larva that was feeding on the remains of a nestling bird (location of specimen unknown); **16**, A worker *Cephalotes* ant with a damaged abdomen is surrounded by hundreds of nematode eggs similar to those of the extant *Myrmeconema* that parasitizes *Cephalotes* ants today.

the amblyopinines that occur in the pelt of small mammals, especially rodents and marsupials in the Neotropics and Australia. Two individuals of this group were discovered amidst a large tuft of rodent hair in Dominican amber (Poinar 1988). Extant members of this group gather clumps of hair with their mandibles, but are not parasitic as originally thought. They do not feed on blood, epidermal cells or host secretions, but are predatory on ectoparasites in the nests of their vertebrate hosts. Since their natural hosts tolerate the beetles, it was concluded that this association is a case of

mutualism (Ashe & Timm 1987; Timm & Ashe 1989). It is possible that the specimen shown here (Fig. 12) preyed on listrophorid mites that were also associated with the rodent hair in Dominican amber and that the beetle may have had a mutualistic relationship with its rodent host.

The presence of horseflies (*Stenotabanus*), mosquitoes (*Culex*, *Anopheles*), biting midges (*Culicoides*), sand flies (*Lutzomyia*) and fleas in Dominican amber also indicate the presence of various vertebrates in the Tertiary forest.



**Figures 17–19**

17, Some pieces of amber contain syn-inclusions that represent a microcosm in themselves. This pseudoscorpion is surrounded by a large population of tardigrade-like invertebrates. Mites, nematodes, protozoa and fungi were also present. 18, one of the enigmatic tardigrade-like invertebrates shown in Fig. 17; 19, A walking stick (Phasmida) represents a case of morphological camouflage (location of specimen unknown).

Coprophagous and necrophagous insects suggest the presence of vertebrates.

Various dung beetles (Fig. 13) in Dominican amber depended on living vertebrates while calliphorid (Fig. 14) and dermestid larvae fed on cadavers. A dermestid larva (Fig. 15) in a piece of amber containing bones, feathers and feet of a nestling bird illustrates a typical habitat for this group.

Birds were certainly an important component of the original forest, however their remains are rare in Dominican amber and only two groups have been identified, a woodpecker was determined from a feather and a hummingbird from an eggshell (Poinar *et al.* 2007). They would have fed on insects, dispersed fruits and carried ectoparasites and endoparasites.

Based on recent findings and the presence of a nematode-parasitized *Cephalotes* ant in Dominican amber, we can surmise that canopy birds not only fed on these ants, but also were important in transmitting the parasite. The extant nematode parasite of ants, *Myrmeconema neotropicum* Poinar & Yanoviak, occurs in Central and South America and parasitizes the canopy ant, *Cephalotes atratus*. Studies on the life history of this parasite indicated that birds played an important role in its transmission from one ant generation to the next (Yanoviak *et al.* 2008). Internal infections are initiated in the larval stage of the ants and the parasites are carried through the pupae and into the adult ants. The gasters of parasitized adult ants turns from black to red and the petiole becomes weakened. The diseased individuals expose themselves on branches and continuously wave their red gasters. Frugivorous and omnivorous birds mistake the red gasters for fruit and the nematode eggs are passed through the bird's alimentary tract and deposited in their feces in the canopy. Continuation of the parasite's life cycle is facilitated when the worker ants gather bird feces to feed to the developing brood. Spherical to slightly oval and smooth, nematode eggs 36 (30–56)  $\mu\text{m}$  in diameter (Fig. 16) adjacent to a Dominican amber *Cephalotes* sp. with a damaged gaster are similar in size and shape to the eggs of *Myrmeconema* and show that this complex life cycle involving ants and birds was present in the mid-tertiary.

In some small pieces of amber are microcosms rarely preserved by other types of fossilization. One such piece of Dominican amber contained a multitude of minute life forms (Fig. 17). A pseudoscorpion represented the top predator and probably preyed on all the other invertebrates in the system, which included nematodes, mites and numerous tardigrade-like forms (Fig. 18). There were also protozoa as well as filaments and spores of algae and fungi. The nematodes, which

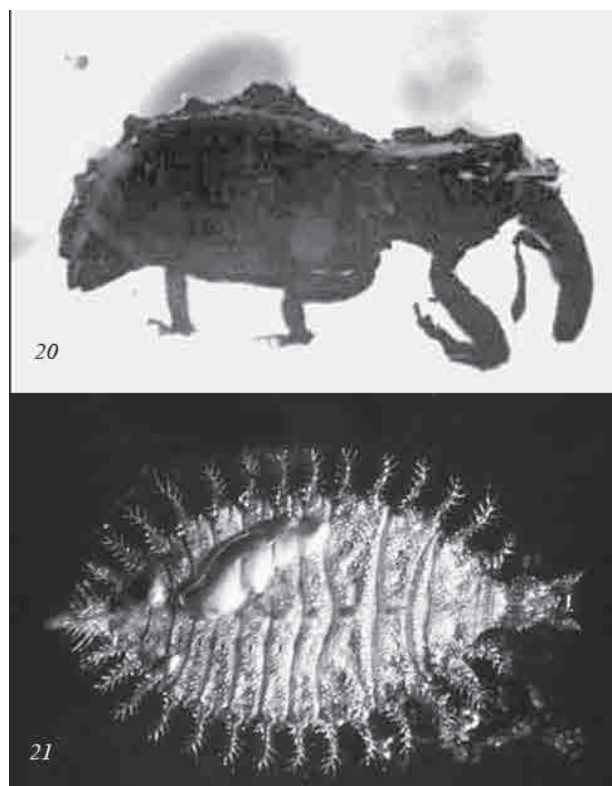
probably fed on bacteria and fungi, would have served as food for the mites and tardigrades as well.

The Dominican amber onychophoran, *Tertiapatus dominicanus* Poinar (2000), was preserved in the act of emitting deposits of slime from its oral papillae. Whether that was a response to falling in the amber or was directed at a mycetophilid fly entombed in the same piece of amber is unknown. However, onychophorans efficiently catch insect prey by entangling them with ejected slime deposits.

### Camouflage in Dominican amber

Camouflage is any morphological or behavioral condition that makes it difficult to detect an organism against its background, thus protecting it from predators or parasites or allowing it to be undetected by potential prey. Fossil evidence of camouflage is rare because in most cases color patterns fade over time but some examples occur in Dominican amber.

Camouflage can be accomplished by bearing structures that resemble shapes of other natural objects in the environment, as shown by walking sticks



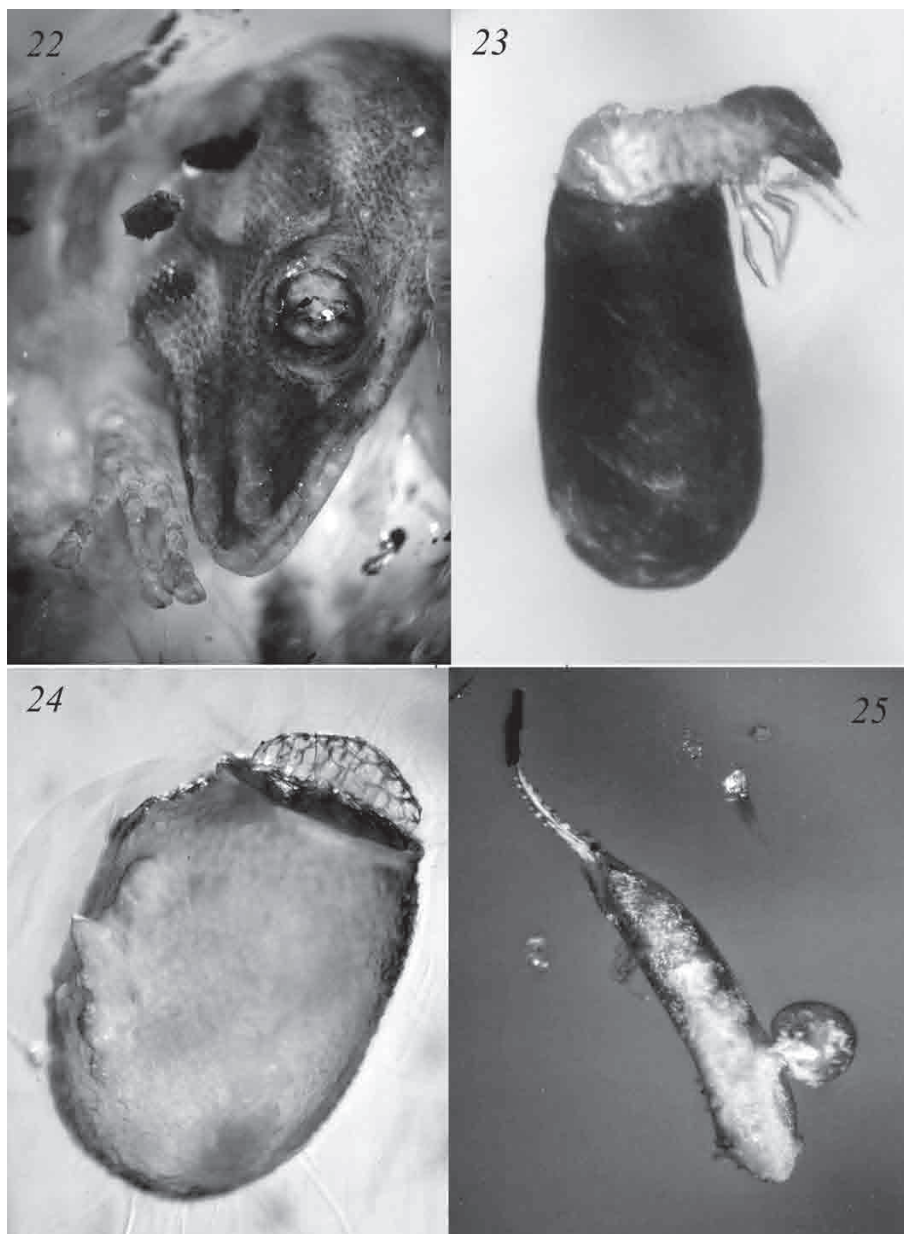
**Figures 20–21**  
**20**, The weevil, *Velatis dominicana*, is camouflaged with its cuticular protuberances; **21**, abdominal protuberances on this brachypsectrid beetle larva are another type of structural camouflage (Cardoen collection).



that appear as twigs (Fig. 19) or with insects that support various types of protuberances. Tree hoppers (Hemiptera: Membracidae) are classic examples of the latter and many support morphological modifications such as various thorn or spine-like projections on their thorax that resemble the spines or other features of their plant host. The Dominican amber weevil, *Velatis*

*dominicana* Poinar & Voisin (2003) (Fig. 20), has large protuberances on its body causing it blend into the background. Some beetle larvae bear abdominal protuberances to escape detection (Fig. 21) while others (Fig. 15) use long dorsal hairs for the same purpose.

Camouflage can be achieved by adapting a color pattern matching the background, as occurs on the



**Figures 22–25**

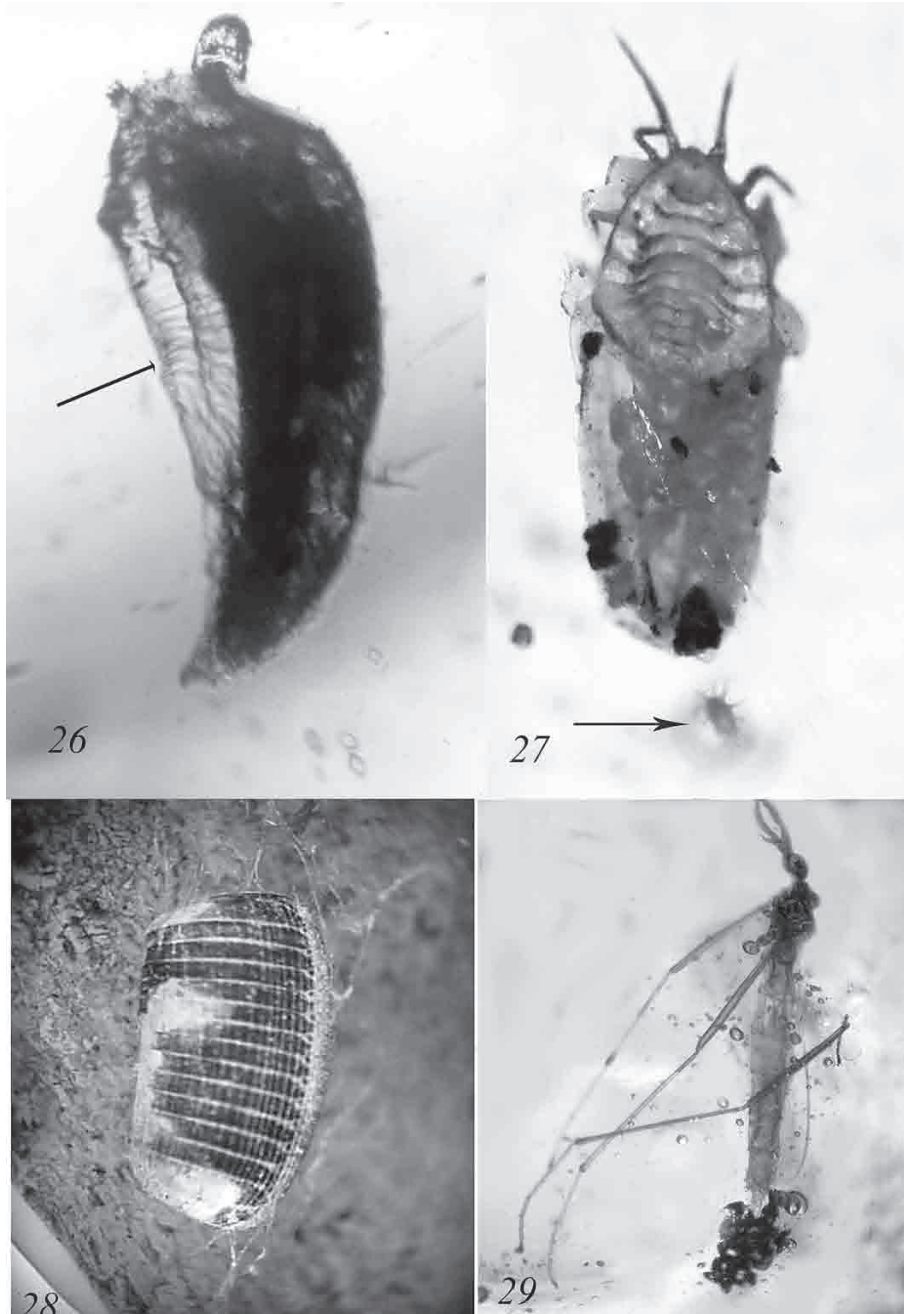
**22**, Color patterns on this Gecko's head are another type of camouflage to avoid detection. Lizards and birds would have been significant vertebrate predators of insects in the amber forest (location of specimen unknown). **23**, some leaf beetle larvae (Coleoptera: Chrysomelidae: Cryptocephalinae) construct solid, protective cases from fecal material and plant debris as a means of camouflage; **24**, Some insect eggs, like this walking stick egg, are strongly constructed for survival on the forest floor. Hatching may not occur for weeks. **25**, an adaptation of this muscoid egg for insertion in moist habitats is a respiratory horn for air intake.



back of some flat bugs (Aradidae: Hemiptera) that rest on tree bark or on the wings of emesine bugs that stealthily creep up on their victims. Such patterns also commonly occur on lower vertebrates such as frogs

and geckos (Fig. 22).

Some insects hide under a pile of debris for protection or construct a case out of detritus that surrounds their entire body. However this type of debris case of-



**Figures 26–29**

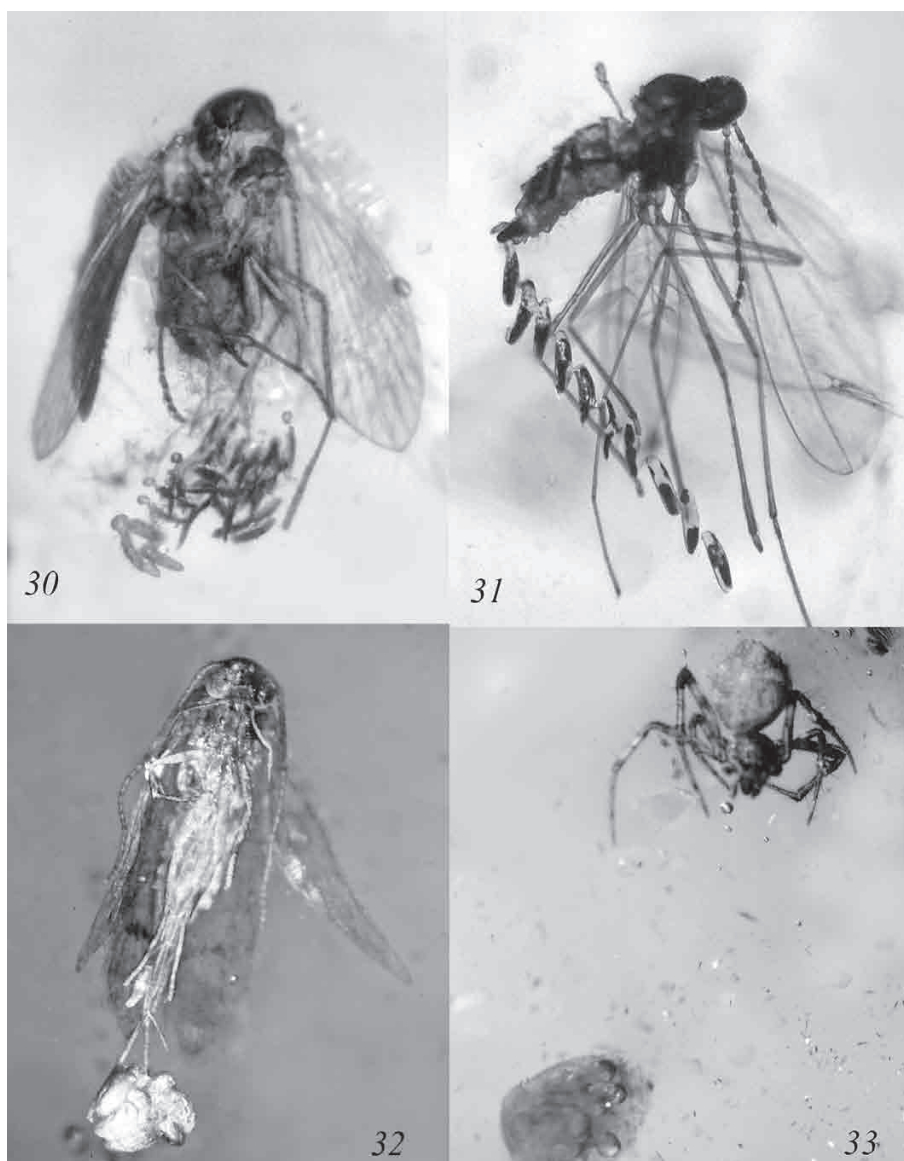
**26**, a special adaptation on this egg of *Anopheles dominicana* was a float (arrow) to keep it on the water surface; **27**, some insects, like this scale insect (Hemiptera: Ortheziidae), carry their egg sacs throughout the hatching process. One hatchling (arrow) is located in the amber behind the egg sac. **28**, eggs of cockroaches often occur in strongly chitinized ootheca, which protect the embryos until hatching; **29**, Evidence of oviposition by a crane fly (Diptera: Limoniidae) in Dominican amber.

fers little protection once the occupant is detected. A more secure form of protective camouflage is the construction of hardened cases that can accommodate the entire organism. These cases are strong, portable and can be quickly entered. The entrance is then usually blocked from predators and parasites by the thick, sclerotized head capsule of the occupant. Leaf beetle larvae cement together fecal matter into a thick-walled portable case with saliva (Fig. 23). One organism mimicking another (Batesian mimicry) is an additional way insects can escape from predators. Examples in

Dominican amber include cerambycid and staphylinid beetles mimicking ants.

### Eggs, oviposition and maternal care

Fossil evidence of eggs, oviposition and maternal care are rare but some cases occur in Dominican amber. Insect eggs may have specific adaptations related to the environment. Walking sticks eggs are very durable and their sturdy construction protects them as they drop to the forest floor (Fig. 24). They can survive exposed to potential predators and pathogens for up to several



**Figures 30–33**

**30**, oviposition by a moth fly (Diptera: Psychodidae); **31**, a series of eggs laid by a gall midge (Diptera: Cecidomyiidae) in Dominican amber; **32**, a moth (Lepidoptera) depositing eggs; **33**, a spider that was guarding her adjacent egg sac.

months before hatching. Some of the advanced flies have eggs with respiratory horns (Fig. 25) that provide an unobstructed flow of air after they are deposited in rotting vegetation, mature fruit or animal dung. Eggs of *Anopheles* mosquitoes deposited on water surfaces are often equipped with floats that keep them from sinking (Fig. 26). Some eggs of scale insects are borne in sacs attached to the body of the female. Hatching

many occur sporadically with the young larvae leaving over a period of time (Fig. 27).

Another way to protect eggs is to incorporate them into hard, chitinized egg cases, such as the oothecae of cockroaches. Oothecae are formed by oviduct cell secretions that glue together groups of eggs that are protected by the hardened capsule wall. These are often just deposited in the environment and the newborn



**Figures 34–37**

**34**, *Triatoma dominicana* (Hemiptera: Reduviidae) was a vector of the bat pathogen, *Trypanosoma antiquus*, in the Dominican amber forest; **35**, The discovery of *Anopheles dominicana* (Diptera: Culicidae) could explain how some types of malaria were transmitted in the Americas during the Tertiary. Arrow indicates the position of the egg shown in Fig. 26. **36**, the Dominican amber *Lutzomyia adiketis* vectored the leishmanial parasite, *Paleoleishmania neotropicus*; **37**, a pedunculated oocyst of *Plasmodium dominicana* in the mosquito, *Culex malariager* provides evidence that malaria existed in the Americas in the Tertiary.

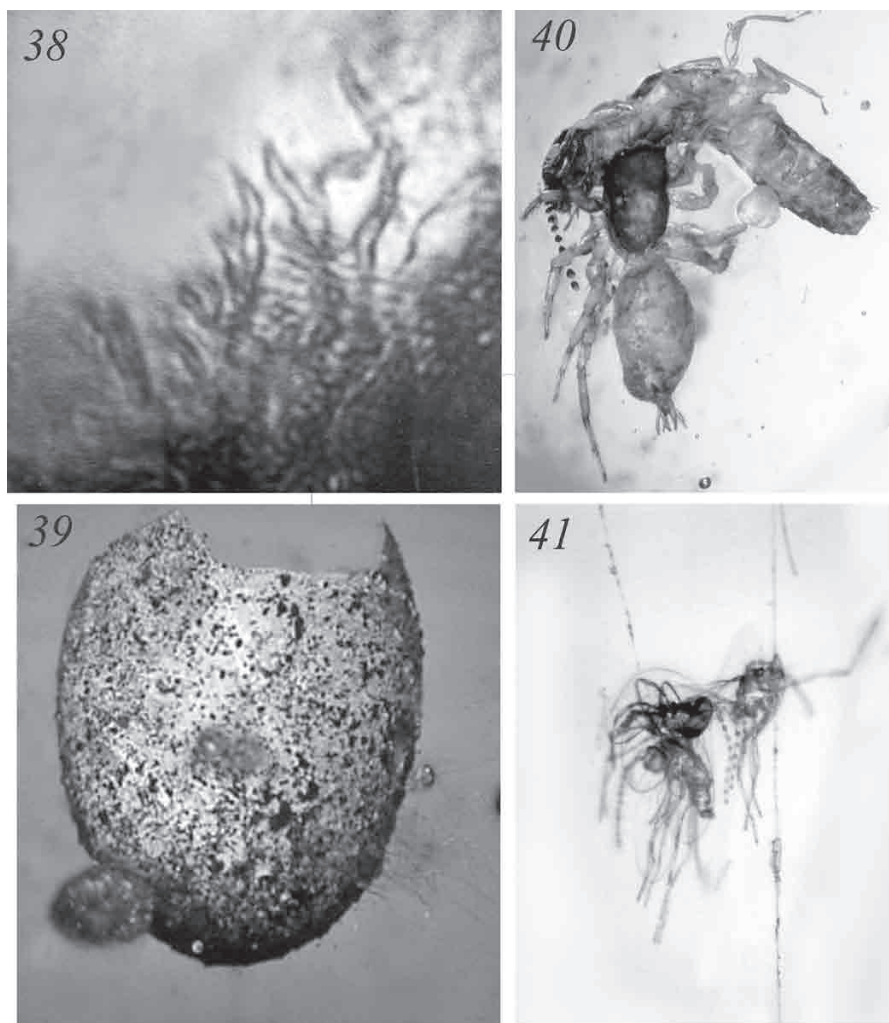
escape when the two halves of the ootheca partially separate (Fig. 28).

There are many cases of ovipositional behavior in amber, but the cause is still a mystery. Is it because the desire to reproduce is so strong that dying females release their eggs in a final attempt to continue the lineage or does the trauma of falling into the resin cause an involuntary relaxation of the sphincter muscles or the ovipositor? Perhaps the pressure from the resin alone physically forces out any eggs residing in the oviduct.

Some flies in Dominican amber deposited a series or cluster of eggs at once, like the crane fly in Fig. 29 (Diptera: Limoniidae), the psychodid (Diptera: Psychodidae) in Fig. 30 and the gall midge (Diptera: Ce-

cidomyiidae) in Fig. 31. These eggs were unprotected and would have perished shortly after deposition unless they had been placed in a moist environment. One of the eggs of the gall midge was in the process of being deposited. It was compressed to enable it to squeeze through the narrow lumen of the ovipositor but would have resumed its original shape after deposition (Fig. 31, arrow). Lepidopteran eggs can be extruded singly or in groups, as seen in this cluster in Dominican amber (Fig. 32).

Maternal care in amber is rare. Examples of females that carry their egg sacs such as some cockroaches, the scale insect mentioned above and some spiders (Fig. 33) could be regarded as fossil evidence of maternal care.



**Figures 38–41**

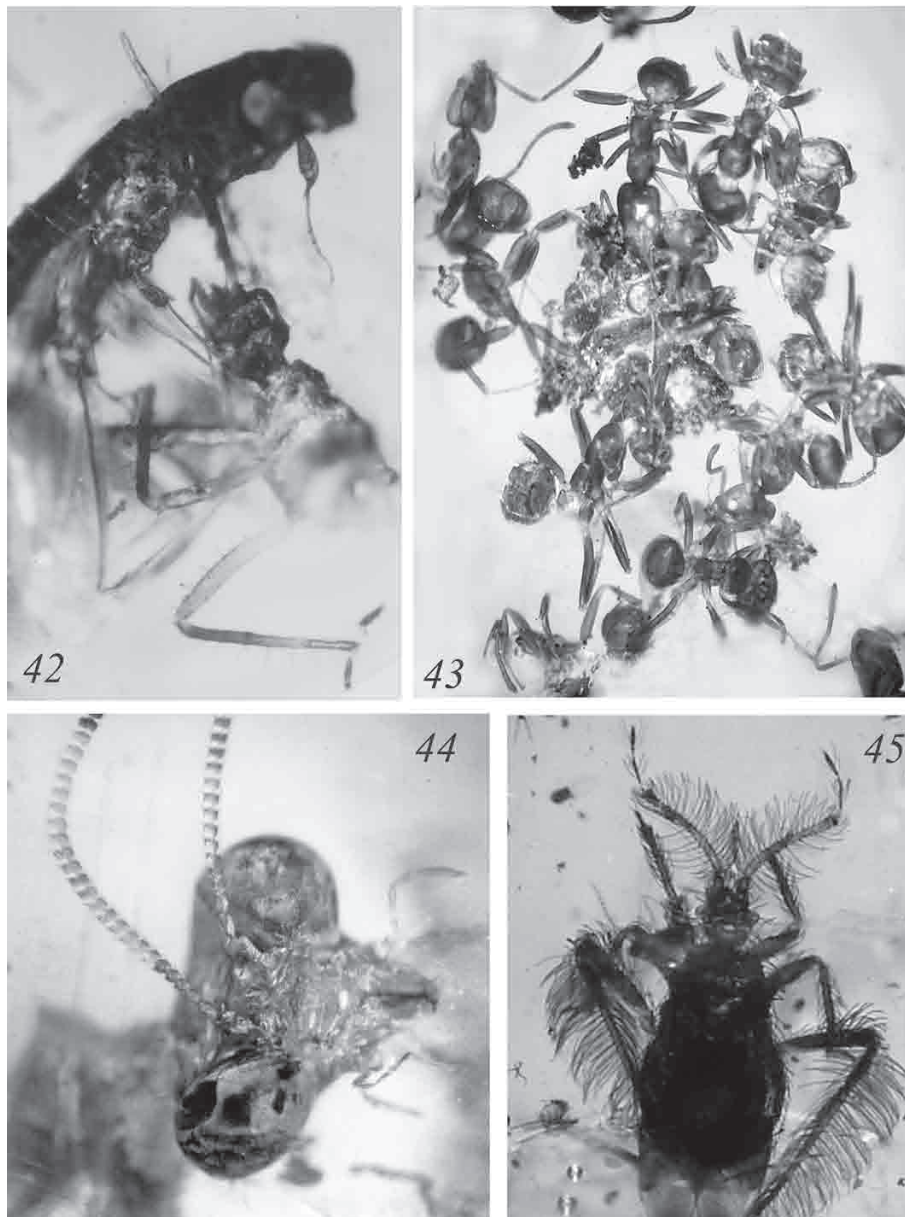
**38**, Sporozoites of *Plasmodium dominicana* being released from an oocyst in the mosquito, *Culex malariager*. Sporozoites were also in the salivary glands of the mosquito, thus indicating a parasite-vector association. **39**, this hummingbird egg shell is indirect evidence of insect predation by birds as well as a pollination agent (location of specimen unknown); **40**, a spider attacking a termite illustrates a predator-prey association; **41**, three gall gnats (Diptera: Cecidomyiidae) in a spider web show evidence of spider predation.



### Arthropod vector-pathogen associations

All amber deposits, including the Dominican, contain biting arthropods that could have served as vectors of vertebrate diseases. One of the exciting discoveries in Dominican amber was the first fossil record of a hematophagous hemipteran, *Triatoma dominicana* (Poinar 2005c) (Fig. 34). Because of their habits of feeding on

the faces of sleeping human victims, these bugs are often called “kissing bugs”. The fossil was represented by a fifth instar nymph exuvia with well-developed meso and metanotal wing lobes and was almost 20 mm in length. As one of the most speciose and wide-ranging genera in the tribe Triatomini, *Triatoma* spp. mostly feed on birds or mammals. Several bat hairs adjacent to the fossil triatomine indicated that the vertebrate host



**Figures 42–45**

42, A predatory gnat bug (Hemiptera: Reduviidae: Emesinae) attacking a platypodid beetle; 43, a group of *Azteca alpha* ants (Hymenoptera: Formicidae) carrying a portion of an insect's abdomen back to their nest; 44, the mantisfly, *Feroseta priscus* (Neuroptera: Mantispidae), represents an extinct generic lineage in Dominican amber; 45, Specific predator–prey associations are indicated by the presence of insects such as this ant bug, *Praecoris dominicana* (Hemiptera: Reduviidae). This is a specialist predator of ants and its long hairs protect it from the bites of its ant victims.

of *T. dominicana* was a bat. Since there are no endemic triatomines in Hispaniola today, this is yet another example of the extinction of a generic lineage from Hispaniola since the mid-Tertiary.

Species of *Culex*, the most common genus of mosquitoes in Dominican amber, transmit a wide range of vertebrate pathogens today. One Dominican amber mosquito, described as *Culex malariager* Poinar (2005a), contained the sexual stages of a *Plasmodium* malaria. Further discussion of this first record of a fossil mosquito vectoring a vertebrate pathogen will be covered below. Also of special interest in vector associations was the discovery of *Anopheles dominicanus* Zavortink & Poinar (2000) in Dominican amber (Fig. 35). The fossil was placed in the subgenus *Nyssorhynchus*, which today exists in southern North America, Central America, South America and the Greater Antilles. Larvae of members of the subgenus have been recovered from a wide range of habitats, ranging from tree holes to ponds and stream margins.

A number of phlebotomine flies have been described from Dominican amber, most of which have been assigned to the genus *Pintomyia* Costa Lima. Since diagnostic characters for species are based in large part on male genitalia, most of the descriptions are based on males. However, because the females are bloodsuckers and thus transmit pathogens, to parasitologists, they demand more attention than males. A female sand fly, described as *Lutzomyia adiketis* Poinar (2008) (Fig. 36), was discovered vectoring a leishmanial pathogen in Dominican amber. *L. adiketis* differs from all previously described Dominican amber sand flies by its forked Sc vein. Extant species of *Lutzomyia* are restricted to the New World and their host range is quite extensive, including over 30 families of mammals, birds, reptiles and amphibians. Several extant members of the subgenus *Lutzomyia* feed on humans and are proven vectors of *Leishmania chagasi*, the causal agent of American visceral leishmaniasis. The specific vertebrate host of *L. adiketis* is undetermined. These three vectors were all carrying pathogens and provide a unique view of vertebrate diseases in the Dominican amber forest.

Species of *Triatoma* are well known for vectoring protozoan trypanosomes of man and animals. Extant members of these large bugs hide in the thatched roofs of villages in South America during the day and come out at night to feed on the sleeping occupants. The trypanosomes are not directly transmitted by the bite of the insect. The type of transmission is called "posterior station" and involves the insect voiding its gut contents just after feeding, usually on or adjacent to the feeding wound. Irritation from the saliva introduced during

feeding causes the victim to scratch the area and the trypanosomes in the fecal deposit are smeared over and enter through the feeding wound of the victim. Two fecal droplets in the amber adjacent to *T. dominicana* contained the infective stages of a trypanosome. The flagellates had been naturally fixed from chemicals in the resin and could be easily seen. This parasite, described as *Trypanosoma antiquus* Poinar (2005c), was considered to be closely related to *Trypanosoma cruzi*, the notorious human parasite.

Because bat hairs were adjacent to the bug, it was likely that it had been feeding on a bat infected with *Trypanosoma antiquus*. Trypanosomes have been reported from many extant genera of bats and triatomine bugs and are the suspected vectors of all Neotropical bat trypanosomes. The Dominican amber *Triatoma* most probably had habits similar to the extant Jamaican *Triatoma obscura* (Maldonado & Farr) that resides in hollow tropical hardwood trees and is thought to feed on bats. South American triatomine bugs living in hollow trees also have been noted to feed on bats under natural conditions. Since bat trypanosomes are morphologically indistinguishable from the human pathogen, *Trypanosoma cruzi*, it is possible that *T. antiquus* was a bat parasite and the progenitor of strains that became infective to other mammals, perhaps eventually, even humans. Bats could have carried the infection between mainland Central and South America and Hispaniola in the Tertiary.

The first fossil evidence of a malaria-mosquito association was found in Dominican amber (Poinar 2005b). In the anterior portion of the body cavity of the vector, *Culex malariger*, were four pedunculated oval oocysts, two of which were mature and entire (Fig. 37) and two that had just burst and released large numbers of sporozoites into the resin (Fig. 38). The released sporozoites ranged from 10 to 14  $\mu\text{m}$  in length and 1 to 3  $\mu\text{m}$  in width, which is similar to the size of sporozoites of extant species of *Plasmodium*. Sporozoites were also in the tubules of the salivary glands and there was even an ookinete and a microgametocyte with emerging microgametes in the mosquito's gut lumen. The presence of these stages indicated that a true vector relationship had been established between the mosquito and malarial parasite.

The mosquito phase of malarial organisms is the sexual part of the cycle beginning with male and female gametocytes acquired while feeding on an infected vertebrate. The male microgametocyte produces slender microgametes (sperm) that fertilize the female macrogametocyte (egg). After fertilization, the zygote becomes a sausage-shaped active stage (ookinete) that penetrates into the mosquito's gut and forms an

oocyst on the body cavity side of the gut epithelium. Sporogony within the developing oocyst eventually produces numerous sporozoites which when mature, break out of the oocyst, enter the hemocoel and migrate to the salivary glands. Most of the above developmental stages were present in *Culex malariager*.

Based on the size and shape of the oocysts and sporozoites and the culicine vector, the fossil malarial organism, described as *Plasmodium dominicana* Poinar (2005b), showed most similarities with the extant avian pathogen, *Plasmodium juxtannucleare*. There are many species of *Plasmodium* in birds, and some have a fairly wide host range although the known hosts of *Plasmodium juxtannucleare*, which is widely distributed in Central and South America, are members of the order Galliformes.

If the host range of *P. dominicana* was similar to that of *P. juxtannucleare*, it would provide indirect evidence of galliform birds in the amber forest in Hispaniola. While there are no records of extinct or extant native galliforms from the entire West Indies, some could have inhabited Hispaniola in the Tertiary. A likely candidate would have been a chachalaca (*Ortalis* sp.) of the family Cracidae. One species (*O. ruficauda*) of this predominately Central-South American group occurs today in the Lesser Antilles (Grenadines) and could represent the remains of a population that extended throughout the Greater Antilles in the mid-Tertiary. Fossils of chachalacas occur in North American Eocene through Pliocene deposits. Perhaps *P. dominicana* caused their extinction, since *P. juxtannucleare* infects 7 species in 3 families of Galliformes and can be quite lethal, especially for chickens.

The presence of a *P. juxtannucleare* clade in Hispaniola in the mid-Tertiary could be explained in two ways. If this clade is endemic to the Americas, as it would appear to be, infected birds could have entered the Proto-Greater Antillean archipelago from North or South America when it formed a bridge between the two continents in the early Tertiary. This scenario would apply to galliforms, since they are essentially non-migratory today. However, it is likely that *P. dominicana* had a fairly wide range of bird hosts, so the possibility of dispersal over water is also possible. That is how *P. dominicana* could have been widely distributed in Central and South America.

The presence of a Tertiary species of *Plasmodium* in Hispaniola addresses the controversial question of whether some species of human malaria originated in the Americas, rather than being imported by soldiers and slaves from Europe and Africa, respectively. Some studies indicate that the human malarial pathogen, *Plasmodium falciparum*, may have been established

as a result of a lateral transfer from birds (mosquitoes acquiring the infection from birds and passing it on to mammals). In fact, the lateral transfer of malaria from birds to mammals by culicine mosquitoes was demonstrated experimentally. It is then possible that *Culex malariager* or other species of *Culex* that were infected with *Plasmodium dominicana*, transferred the infection to mammals, especially monkeys, in the late Tertiary. This scenario is supported by reports of *Culex* transmitting human and simian malaria. There were certainly simians in South and Central America at that time and also evidence they some inhabited Hispaniola then (Poinar & Poinar 1999).

Another possible scenario for the transfer of *P. dominicana* to mammals is that *Anopheles dominicanus* could have picked up the infection from diseased birds and passed it on to other vertebrates. Once established in a simian host, *Anopheles dominicanus* could have transmitted the pathogens to humans when they arrived on the scene. The South American simian malarial parasite, *Plasmodium brasileanum*, is capable of infecting humans and the exoerythrocyte stages of *P. brasileanum* are quite similar to those of the cosmopolitan human malarial parasite, *P. malariae*. Lateral transfers could have shifted *Plasmodium dominicana* from birds to mammals, including simians and then to humans. When Europeans first arrived in South America, Amerindians were well aware of the value of cinchona bark for curing “fevers” caused by malaria, which is indirect evidence that they had experienced human malaria, probably *P. malariae*, for some time (Poinar 2005b).

The origin of vertebrate parasitic flagellates and their acquisition by sand flies is a controversial topic. The oldest fossil record of a sand fly- *Leishmania* vector association is in Early Cretaceous Burmese amber, suggesting a Palaeartic origin of *Leishmania*.

The discovery of a leishmanial parasite, described as *Paleoleishmania neotropicus* Poinar (2008), in a sand fly in Dominican amber shows that vector associations had been established by the mid Tertiary in the Neotropics. The single, anteriorly directed flagella, compact kinetoplast and nucleus places *P. neotropicum* in the family Trypanosomatidae and the presence of amastigotes and paramastigotes in the proboscis of *Lutzomyia adiketis* is evidence that *L. neotropicum* was digenetic, since amastigotes and metacyclic stages are only formed in the vertebrate host and extant sand flies are not known to be infected with monogenetic flagellates.

The presence of amastigotes (the stages produced in vertebrates) indicates that the vector had taken a blood meal quite recently; while the paramastigotes



(the stages produced in the sand fly that are infective to the vertebrate), show that an earlier blood meal had been taken. Female sand flies normally engorge blood at least twice during their lifetime, with a batch of eggs laid after each blood meal. The round amastigotes of *Paleoleishmania neotropicum* are similar in size (4–7 µm) and morphology to those of extant species of *Leishmania* and the promastigotes are similar in size (6–10 µm) to those of extant *Leishmania* spp. It is not possible to determine if *P. neotropicum* was a progenitor of the extant *Leishmania* clade, but it could be, since the only digenetic trypanosomatids that have sand fly vectors today belong to the genus *Leishmania*.

Vector-borne diseases are quite ancient with some types of malaria and at least two types of trypanosomatids (*Leishmania* and *Trypanosoma*) extending back to the mid-Cretaceous as revealed in vectors entombed in Burmese amber. It is quite possible that *Plasmodium* also has that long a heritage. With such ancient origins, these pathogens had ample time to disperse globally either through infected hosts or vectors and evolve means of avoiding the host's defenses.

### Predator-prey associations

Dominican amber has the remains of a number of vertebrates that would have fed on insects. These include complete or partial specimens of frogs, lizards, snake (partial cast skin), rodents (hair and a scat), bats (hair), insectivores (bones), birds (feathers, decaying remains and an egg shell) and carnivores (hair). The only known egg shell (Fig. 39) was identified as belonging to a hummingbird and although nectar is the main source of nourishment for these small creatures, spiders and minute insects supply protein for the developing young. While there are small and large portions of feathers in amber, only one has been identified as a woodpecker of the family Picidae (Laybourne *et al.* 1994).

Bat hair has been recovered twice in Dominican amber, once adjacent to a nymphalid caterpillar, indicating an attempted predatory association with the caterpillar targeted as prey and again adjacent to *Triatoma dominicana*, indicating a vector-parasite association between the bug and the mammal. Insectivore bones found in Dominican amber were thought to belong to the extinct *Nesophontes*, which was eradicated fairly recently from the Dominican Republic as a result of human occupancy (MacPhee & Grimaldi 1996). These shrew-sized creatures would have selected a wide range of insects as food items.

There are numerous groups of predatory insects and arachnids in Dominican amber and all of them would have dined on insects. Spiders were certainly

important generalist predators of insects. Some 152 species of spiders have been described from Dominican amber and Wunderlich (2004) illustrated examples of spider predation on a wide range of arthropods, including beetles, bark lice, ants, planthoppers, termites (Fig. 40), caddis flies, flies (Fig. 41), parasitic wasps, scale insects, springtails, roaches, aphids, a web spinner, weevils, bristle tails, insect larvae, myriapods, other spiders, mites, and pseudoscorpions. Other arachnid generalist predators in Dominican amber are scorpions, pseudoscorpions, predatory mites, harvestmen, wind scorpions, schizomids and tailless whip scorpions.

Additional generalist predators in Dominican amber would have been centipedes (Chilopoda), velvet worms (Onychophora), damselflies (Odonata: Coenagrionidae) (Fig. 8), gerrid water striders (Hemiptera: Gerridae), nabid bugs (Hemiptera: Nabidae), *Halovelia* water bugs (Hemiptera: Gerridae), assassin bugs (Hemiptera: Reduviidae), gnat bugs (Hemiptera: Enicocephalidae) (Fig. 42), preying mantids (Mantidodea: Mantidae), ground beetles (Coleoptera: Carabidae), lady bird beetles (Coleoptera: Coccinellidae), antlike stone beetles (Coleoptera: Scydmaenidae), rove beetles (Coleoptera: Staphylinidae), robber flies (Diptera: Asilidae), biting midges (Diptera: Ceratopogonidae), dance flies (Diptera: Empididae), soldier flies (Diptera: Stratiomyidae), tabanid fly larvae (Diptera: Tabanidae), ants (Hymenoptera: Formicidae) (Fig. 43), sphecid wasps (Hymenoptera: Sphecidae), mantisflies (Neuroptera: Mantispidae) (Fig. 44), ant lions (Neuroptera: Myrmeleonidae), owl flies (Neuroptera: Ascalaphidae), dusty wings (Neuroptera: Coniopterygidae), brown lacewings (Neuroptera: Hemerobiidae), green lacewings (Neuroptera: Chrysopidae) and dobson flies (Megaloptera: Sialidae) (Poinar & Poinar 1999). A record of a group of *Azteca alpha* ants carrying a portion of their prey back to the nest (Fig. 43) is an example of frozen behavior that only could have been documented in amber.

There are also a few specific predators in Dominican amber (Poinar & Poinar 1999). One of these is the ant bug, *Praecoris dominicana* (Fig. 45). These bugs are noted for the long, thick hairs covering most of their body and a pair of secretory glands located on the ventral surface. They station themselves near a column of ants, raise their body to expose the gland openings and wait. Eventually, an ant will be attracted to the glandular secretions and began to imbibe the excretory product, which apparently also has a narcotic effect. After the ant becomes disorientated, the bug inserts its beak into the victim. There are also specific predators among the ants. One of these in Dominican amber

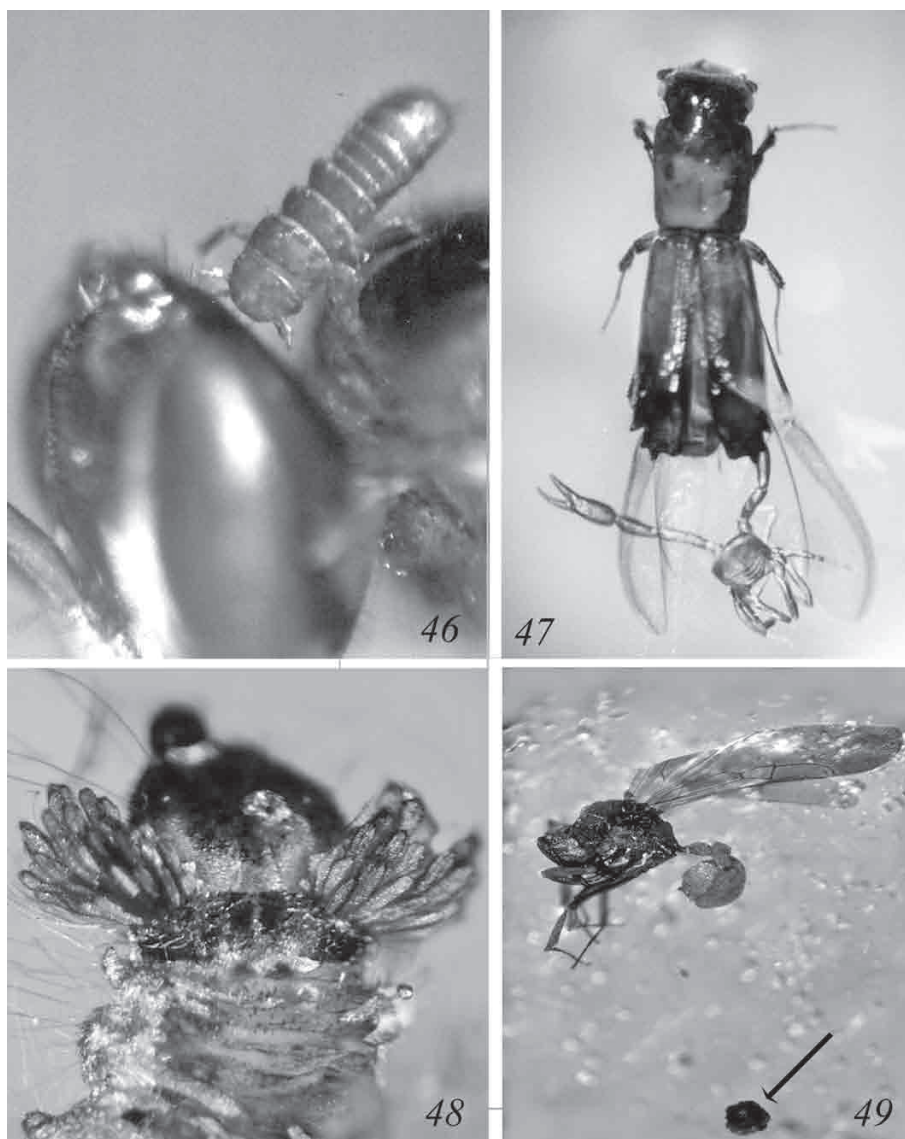


is a dacetine ant of the genus *Acanthognathus*. These ants have elongate mandibles that employ a snap-trap method of catching prey and specialize on springtails (Collembola) (Poinar & Poinar 1999).

### Paleosymbiosis

Because the death of insects encountering resin is usually rapid, symbiotic associations unlikely to occur with other types of fossilization are often preserved as

they were in life. The main types of paleosymbiosis (involving two individuals belonging to separate species) encountered in amber are commensalism, mutualism and parasitism. Commensalism implies a benefit to one member without harm or benefit to the other. Mutualism is when both members benefit and neither is harmed, and parasitism is when one organism takes nourishment from the other, and in so doing, harms the other (host) at some level.



**Figures 46–49**

**46**, a triungulin of a blister beetle (Coleoptera: Meloidae) phoretic on the bee, *Proplebia dominicana* (Hymenoptera: Apidae). The triungulin is holding to a single hair in its mandibles; **47**, pseudoscorpions today and in the past attached themselves to platypodid beetles in phoretic associations with one chela grasping the posterior edge of the beetle's elytron. This position does not restrict the beetle's flight abilities; **48**, balloon setae protruding behind the head capsule on this metalmark butterfly larva (Lepidoptera: Riodinidae: *Theope*) produce compounds that summon attending ants for protection; **49**, A *Cyphomyrmex* fungus gardening queen ant on her way to establish a new colony was bringing a ball of fungal inoculum (bromatia) (arrow), which was released when she fly into the resin.

Phoresis, in which one organism is transported on the body of another organism, is probably the most typical type of commensalism found in amber. There are many examples of mites and pseudoscorpions transported by insects in Dominican amber. These associations are defined as commensalism because the arachnids benefit by being conveyed to an environment with a new food supply. The carrier only serves as a transporting agent, does not receive any benefit from the association and is generally not harmed, although its brood may be destroyed in part. Future studies may show, however, that in some cases, both carrier and rider benefit.

A classic example of phoresy in Dominican amber is pseudoscorpions that are carried by platypodid beetles (Fig. 46). This is a successful dispersal mechanism that is continuing today and a vital one for the pseudoscorpion, who lives in a transitory habitat on the bark of a tree. Thus it is not surprising that adaptations for the detection of carriers, attachment and release have occurred over the eons. The most important adaptation is the way in which the pseudoscorpion grasps the beetle so that it does not interfere with flight. The favored position is the posterior portion of the beetle's elytron and this area is clasped by the pseudoscorpion with one chela. Although not proven, this association may be more than just a phoretic one, especially if the beetle benefits from the feeding habits of the pseudoscorpion. One example would be if the pseudoscorpion feeds on potential egg or larval predators of the beetle. (Poinar *et al.* 1998).

Blister beetles (Coleoptera: Meloidae) have an interesting biology. The adults are generalist herbivores but the larvae develop at the expense of insects, especially bees. Blister beetles possess a type of development called hypermetamorphosis, where the first stage insect larva is free-living and is modified for mobility and the detection of potential hosts. The succeeding stages however are only slightly mobile and often grub like. These first stage mobile larvae are often referred to as triungulins, a term also used for hypermetamorphic larvae of Strepsiptera, Mantispidae and Ripiphoridae. Triungulins possess legs and are very active and those species parasitic on bees climb up plants and collect around the flowers. The triungulins attach themselves to passing bees by grasping a single hair in their tightly clenched mandibles. They are carried back to the host's nest and after releasing their hold, attack the host's egg and proceed to feed on the stored pollen reserves. Since the morphology of the triungulins has played a dominant role in the systematics of the Meloidae, it was possible to describe a triungulin in the genus *Meloe* that was grasping a hair on the occiput of a stingless

bee in Dominican amber (Poinar 2009) (Fig. 47).

While all members of the genus *Meloe* parasitize bees, there are no records of extant meloids parasitizing social stingless bees. However several species of *Meloe* have been reported developing on eggs, larvae and/or provisions of the honeybee (*Apis mellifera* L.) and a member of the meloidid genus *Nemognatha* is known to attack both honeybees and bumblebees.

The oldest example of fossil mutualism is represented by Paleozoic lichens, which is an association between an alga and a fungus. A number of mutualistic associations, aside from a fossil lichen, occur in Dominican amber. One striking example is a stingless bee (*Proplebeia dominicana*) that had an orchid pollinarium (described as *Meliorchis caribea*) attached to its thorax (Ramirez *et al.* 2007). This not only demonstrated unknown aspects of this bee's behavior but also showed the existence of a particular orchid lineage (subtribe Goodyerinae) that existed in Hispaniola in the mid-Tertiary. The authors noted that the normal position of pollinaria of that orchid group is usually on the mouthparts of bees and not on the thorax. However, since no other *Proplebeia* specimens in Dominican amber have been reported with this type of pollinarium, this case could be a chance encounter.

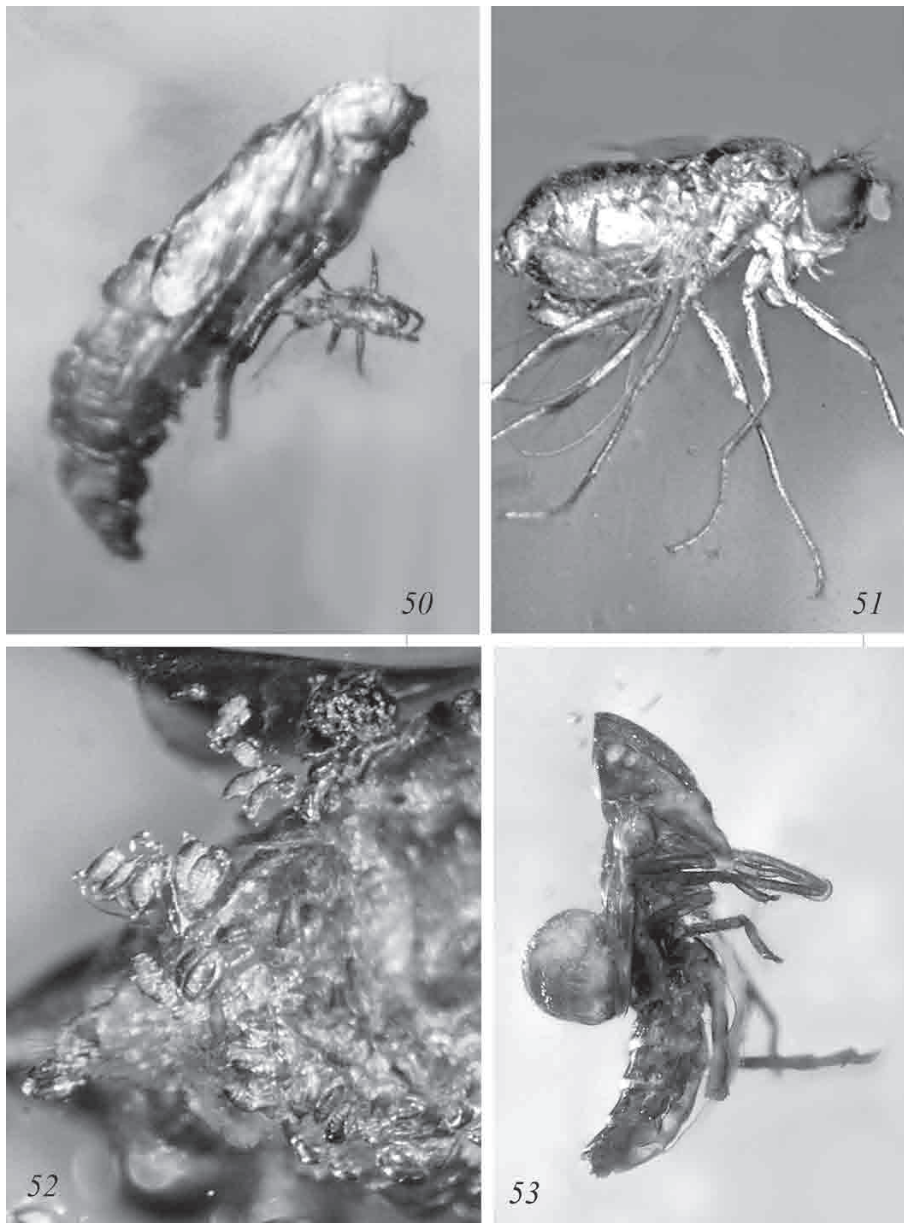
An example of insect-insect mutualism is demonstrated by a rare fossil riodinid butterfly larva in Dominican amber. Specialized morphological features of this *Theope* caterpillar indicating a symbiotic association were balloon setae (Fig. 48) and vibratory papillae in the neck area, and tentacle nectary organ openings on the eighth abdominal tergite. Extant *Theope* caterpillars associated with ants have similar features. The tentacle nectary organs provide a treat for the ants, which guard it. When an enemy threatens the caterpillar, the vibratory papillae beat against the head capsule and make a sound audible to ants and the balloon setae emit a chemical signal picked up by nearby ants. The ants then defend the caterpillar against predators to protect their source of nectar (de Vries & Poinar 1997).

Representatives of at least 3 genera of fungus gardening ants, which includes the famous leaf-cutting ants, occur in Dominican amber. All of them provide evidence of paleomutualism between ants and fungi. Members of the leaf-cutting genus *Atta* search the surroundings for suitable plants to cut up and carry back to the nests for their fungal gardens (Wheeler 1973). Species of *Atta* are well known for their devastation to cultivated crops in Central and South America. Based on a Dominican amber species of *Apterostigma* with an adjacent leaf fragment, these ants also used leaves for their fungal gardens in the Tertiary.

Most species in the other seven extant genera of these American ants are little noticed. Representatives of the attine genus *Cyphomyrmex* are inconspicuous and extant species build nests in the ground under logs or stones. They cultivate their fungus on caterpillar feces and plant debris and the mycelium of the nourishing fungus forms bodies called bromatia. These bromatia

are eaten by the brood and workers and when a queen is ready to leave the colony and establish a new one, she will transport at least one bromatia in her mandibles. In the queen *Cyphomyrmex* preserved in Dominican amber, the bromatia is dislodged but still clearly visible in the amber beneath her (Fig. 49).

Other direct and indirect evidence of mutualistic



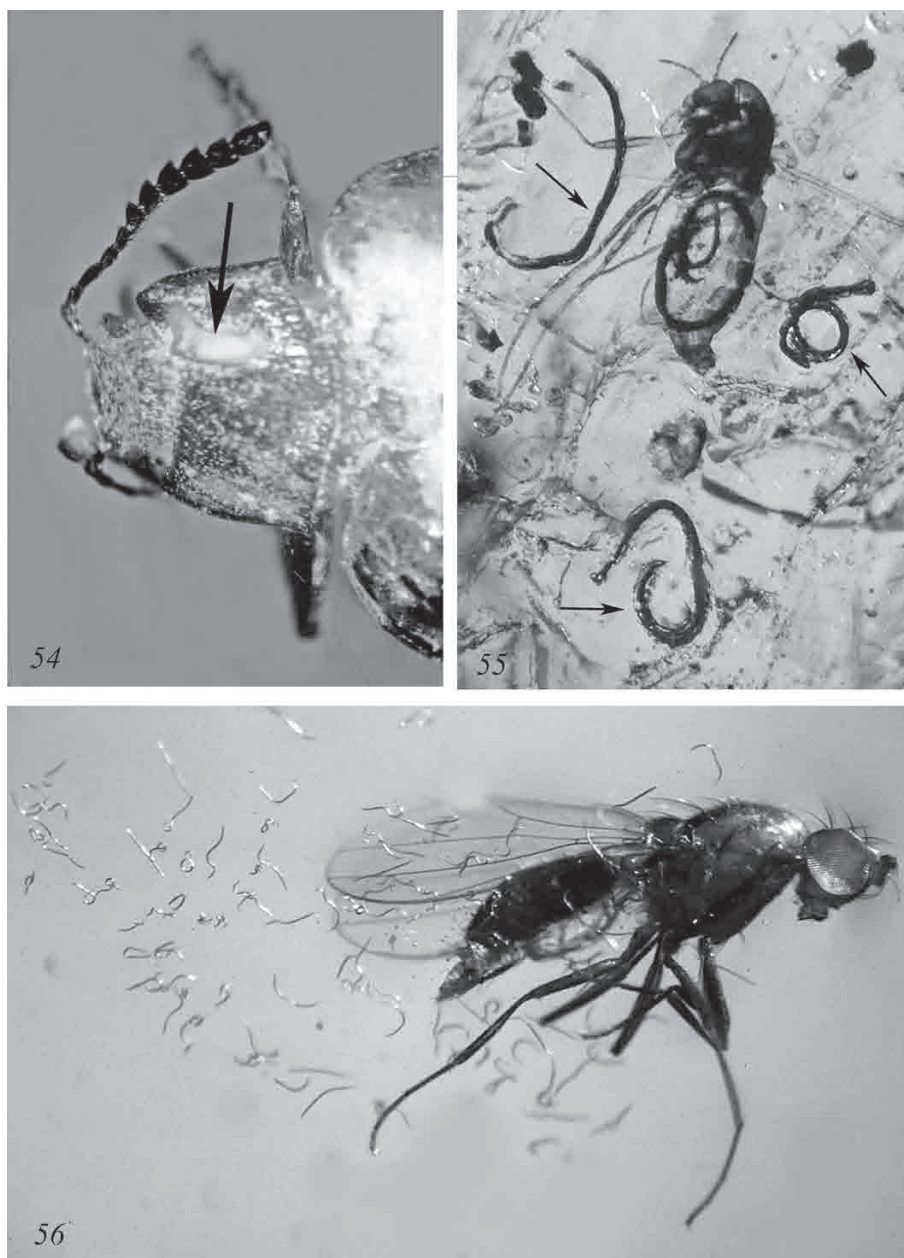
**Figures 50–53**

**50**, a rare example of a parasitic mite feeding on a moth pupa; **51**, three macrochelid mites are attached to the abdomen of this drosophilid fly in a phoretic association. Only two of them can be seen in the photo. **52**, Strepsiptera triungulins cover the abdomen of their planthopper host. They recently left their mother's brood pouch and were ready to begin the short free-living stage of their life cycle. **53**, the larvae of sac wasps (Hymenoptera: Dryinidae) develop in a pouch outside the host's body, which makes these examples of endoparasitism easy to detect.

associations in Dominican amber are termites containing certain types of protists and bacteria (Weir *et al.* 2002), bark beetles indicating the presence of blue-stain fungi and braconid and ichneumonid wasps indicating the presence of polydnaviruses.

Parasitism by insects is difficult to verify in the fossil record. There are many records of amber insects

(especially wasps and flies) whose descendants today are parasitic on a wide range of organisms, but to discover an actual host–parasitic association is rare. This topic can be divided into paleoectoparasitism, with the parasites clearly visible and attached to the exoskeleton of the host and paleoendoparasitism, where the parasite develops in the body cavity of the host.



**Figures 54–56**

54, fly egg (arrow) deposited on the pronotum of a leaf beetle (Coleoptera: Chrysomelidae); 55, a midge (Diptera: Chironomidae) heavily parasitized by nematodes (Nematoda: Mermithidae). Three of the parasites (arrows) left the host, while a fourth still resides in the midge. Insects are usually killed by mermithid nematodes. 56, juvenile nematodes (Nematoda: Allantonematidae) leaving their drosophilid host. This group of nematodes usually sterilizes, but does not kill the host.



In Dominican amber, most ectoparasites are larvae of parasitic mites belonging to the families Trombidiidae or Erythraeidae. The mites feed on the host's hemolymph by inserting their mouthparts through the cuticle (Fig. 50), and when satiated, leave the insect and molt to the nymphal and adult stages, which normally are free-living predators. Such parasitic mites are not to be confused with phoretic ones, which are only transported by and obtain no nourishment from the carrier (Fig. 51).

Cases of paleoendoparasitism are usually discovered when the parasite attempts to leave its host after it became entombed. This behavior has revealed cases of parasitism by insects and various types of worms. Actual evidence of insect parasitism is provided by epipyropids (Lepidoptera: Epipyropidae), sac wasps (Hymenoptera: Dryinidae) and twisted winged insects (Strepsiptera).

Strepsipterans have a fascinating biology. Both sexes develop as parasites in the body cavity of insects, however the females normally remain in the host with their head and thorax exposed, while the adult males are winged and search for females. After mating, which occurs on the host containing the wingless females, first instar triungulin larvae eventually appear in the female's brood pouch. A parasitized planthopper (Hemiptera: Delphacidae) in Dominican amber was entombed when the triungulin larvae were exiting from the female's brood chamber and 25 of them were still adjacent or in contact with the host's abdomen (Fig. 52). Under normal circumstances, these larvae would start searching for another host, which they would enter by direct penetration.

Epipyropids are one of the few members of the Lepidoptera that have adapted a parasitic way of life. The larvae, which are highly modified and appear as spheres with legs, parasitize hemipterans. One representative in Dominican amber is the only fossil member of this family.

Sac wasps are so named because the larvae develop in pouches formed by the stretched body membranes of their hosts. The sacs make them very conspicuous and easy to detect in amber (Fig. 53).

Evidence of fly parasitism of leaf beetles (Coleoptera: Chrysomelidae) in Dominican amber is shown with an adult beetle in the subfamily Aulascoscelinae with a fly egg attached to its prothorax (Fig. 54). The fly egg (probably a tachinid) is open and flattened on one side, suggesting that the fly larva had already hatched and entered the body cavity of the beetle.

Worm parasites are detected when they attempt to exit from their hosts. In a piece of Dominican amber containing a parasitized adult chironomid, three

mermithid nematodes (Nematoda: Mermithidae) had already exited the host after it had entered the resin, while one remained in the body cavity (Fig. 55). Under normal conditions, the exit would have occurred over water and the nematodes would have entered debris on the bottom of the water source where their potential host larvae would be developing. Here the nematodes would have mated and oviposited. The juveniles leaving the eggs would penetrate directly through the host's cuticle and initiate development in the body cavity.

In the case of the allantonematids (Nematoda: Allantonematidae) parasitizing a fruit fly in Dominican amber, the released juveniles seen in Fig. 56 would normally have developed to the adult stages in the host's environment, then mated. The fertilized infective stage females would penetrate into fly larva and commence their development, eventually depositing numerous eggs that would hatch in the body cavity of the fly. The young would develop up until the third stage juvenile, then leave the host.

Another type of worm parasite is the hairworm (Nematomorpha: Gordaceae). Hairworms normally occur in the body cavity of larger insects, especially orthopteroids, and are rarely fossilized. However two hairworms were discovered in the process of leaving the body of their cockroach host in Dominican amber. The life cycle of hairworms is complex since they utilize a paratenic (transport) host to reach their developmental host. The paratenic host is usually an aquatic insect that scavenges the hairworm eggs from the debris at the bottom of a pond or other water source. After being ingested by the aquatic paratenic host, the hairworm eggs hatch and the microscopic larvae burrow through the gut wall and enter the insect's hemocoel. A host encapsulation reaction surrounds and encysts the larvae and they remain "trapped" inside their cysts until the paratenic host is eaten by a host in which the hairworms can complete their development. In the case of the amber fossils, the developmental host was a cockroach.

All of the above fossil worms still parasitize the same types of hosts today and with the exception of the allantonematid, fossil remains of the other two groups (mermithids and hairworms) have been found in Early Cretaceous amber, thus showing the antiquity of these host-parasite associations.

### **Insect pathogens**

Insect pathogens include representatives of viruses, bacteria, protozoa, fungi and certain types of nematodes. Records of fossil insect pathogens are almost non-existent however the following fungal pathogens have been reported from Dominican

amber: an *Entomophthora* from a termite, a species of *Beauveria* on an ant, an unidentified fungus on a bark louse (Psocoptera) and an ectoparasitic fungus on an adult mosquito (Poinar & Poinar 1999, 2005).

The mosquito parasite had some features of members of the Trichomycetes, a group of cosmopolitan, microscopic fungi that usually occur inside the alimentary tract of insects and other arthropods. Three types of fungal bodies were found protruding from the intersegmental abdominal segments of the fossil mosquito (Fig. 57). One type was pointed and unbranched, another type was straight to slightly curved with the tips rounded to pointed and the third

type consisted of spherical-shaped thalli containing oval spores. Since no extant members of the Trichomycetes are known to occur on the external surface of adult insects, the actual identity of these bodies remains unknown.

One of the difficulties in looking for fossil parasitic fungi (or insect parasitic fungi in general) is how to eliminate various saprophytic types that colonize dead insects or in the case of the fossils, those not yet completely covered by the resin. Saprophytic fungi were ruled out in this case because the mosquito was complete and preserved in a life-like poise with all of its appendages attached and showed no sign of decay. There was no mycelium present and the thalli occurred at specific locations, not over large areas of the body as occurs with most saprophytic forms.

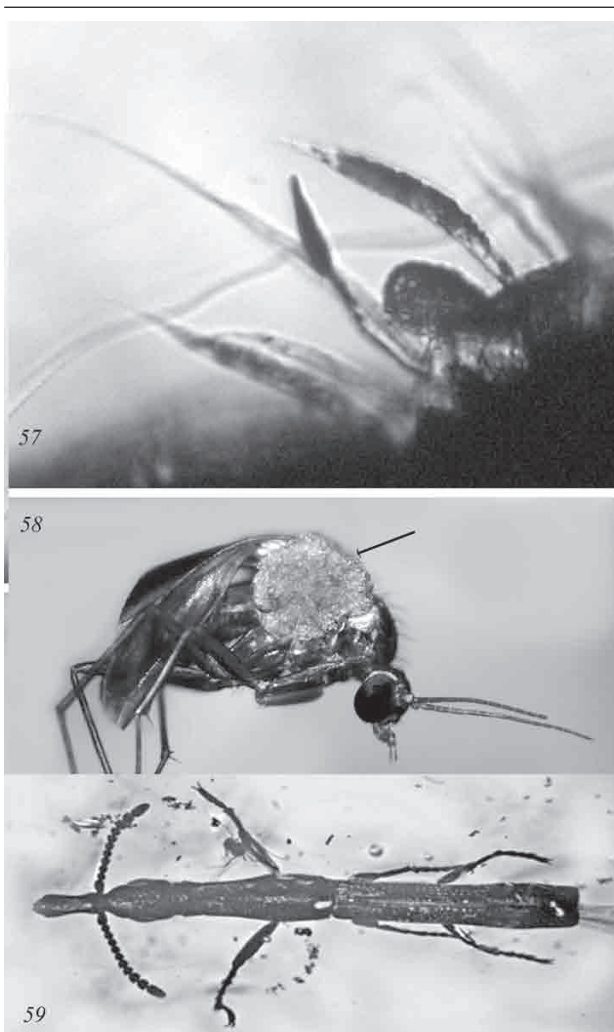
Another case of fungal parasitism in Dominican amber involved a mat-like growth on portions of the abdomen and thorax of a fungus gnat (Diptera: Mycetophilidae) (Fig. 58).

The fungal patch was orange to brownish-orange in color with an irregular surface covered with cracks and ridges. Large thick-walled cells bordering the growth could have been cystidia, which indicates an Entomophthoraceae infection similar to those reported on extant fungus gnats. *Entomophthora* produces a felt-like hymenium over the surface of recent fungus gnats and the infection is often limited to the dorsal and lateral regions of the insect, which is similar to the condition observed on the fossil mycetophilid.

#### Arthropods providing evidence of specific habitats and organisms

Dominican amber arthropods can provide evidence of specific habitats. Diving beetles (Coleoptera: Dytiscidae), caddisflies (Trichoptera), and damselflies (Odonata) all provide evidence of aquatic habitats. Aquatic conditions can occur in a variety of micro and macrohabitats in a tropical forest. Aside from streams, ponds and lakes, a large aquatic fauna is known to develop in phytotelmata, or water collected in portions of epiphytic plants. The damselfly (Fig. 8) in Dominican amber belonged to a genus whose modern representatives deposit eggs in tank bromeliads. Diving and marsh beetles as well as many midges and mosquitoes are associated with tank bromeliads and that is where many of those in Dominican amber probably developed (Poinar & Poinar 1999).

Evidence of ground pools in the Dominican amber forest comes from the discovery of *Anopheles dominicanus*, the first fossil anopheline mosquito from the New World. This mosquito belongs to a group that normally breeds in ground water. On the other hand,



Figures 57–59

57, thalli of an ectoparasitic fungus emerging from the cuticle of a mosquito; 58, fungal mat (arrow) of an Entomophthoraceae growing on the integument of a fungus gnat (Diptera: Mycetophilidae); 59, dorsal view of the brentid weevil, *Dominibrentis leptus* Poinar. This species long, narrow body would allow it to enter the galleries of bark beetles for oviposition and possible predation.

a pigmy mole cricket (Orthoptera: Tridactylidae) in Dominican amber indicates the presence of an aquatic habitat with sandy shores as found along the banks of a stream or lake.

The discovery of a marine insect, *Halovelvia electrodominica*, presents a puzzle regarding its occurrence in Dominican amber. Its congeners occur throughout the Indo-West Pacific region, from the Red Sea and the east coast of Africa to the Pacific Islands. If the fossil had the same habits as present day members of the genus, it would have lived in mangrove swamps or in the intertidal zone. During high tides, it would have retreated to cavities in corals, surrounding itself with an air bubble during periods of submergence (Andersen & Poinar 1998). How then did it end up entombed in amber?

While arthropods can provide evidence of specific habitats, can their absence provide evidence of an absence of specific habitats? The case of the absence of blackflies (Diptera: Simuliidae) in Dominican amber is an example. Earlier mentions of the family Simuliidae in lists of Dominican amber insects were actually members of the family Scatopsidae (Poinar 1992; Poinar & Poinar 1999). A number of blackflies are endemic to Central and South America, so why haven't any been found in Dominican amber? Two species have been reported in Hispaniola today (Pérez-Gelabert 2008) but both of them (*Simulium ochraceum* Walker and *Simulium bipunctatum* Malloch) appear to be recent introductions. Since blackfly larvae are modified to catch food from fast flowing water, does that mean there were no rushing streams or rivers close to the Dominican amber forest or was there another reason? The presence of black flies in Baltic amber shows that they do get captured in resin so they do rest on trees.

The brentids or straight snouted weevils (Brentidae: Cyphogoginae) are very rare as fossils and the long, slender adult of *Dominibrentis leptus* Poinar in Dominican amber shows a fine example of functional morphology (Fig. 59). Its presence is evidence of other boring insects (Scolytidae and Platypodidae) in the Dominican amber forest. This species slender form would allow it to enter scolytid and platypodid galleries for oviposition and possible predation of the previous occupants, which are the habits of their extant descendants (Poinar 2009).

A dipterous group whose larvae are dependent on fast flowing streams is the net-winged midges or Blephariceridae. There are no fossils recorded from Dominican amber nor are there any extant species in the Greater Antilles. Some groups of stoneflies (Plecoptera) prefer fast flowing streams, however the

single specimen in Dominican amber, *Dominiperla antiqua* Stark & Lentz (1992), belongs to the family Perlidae, most of whose extant representatives develop in sluggish, turbid rivers. There are no extant members of stoneflies in the Greater Antilles today (Pérez-Gelabert 2008). So were there ever endemic blackfly or net-winged midge lineages on Hispaniola and was the absence of fast-flowing streams, at least in the vicinity of the amber forest, the reason? Future discoveries may change this scenario since fossils only tell us what lineages were present at a certain time and place and not which were absent.

### Reconstructing Ancient Landscapes

Placing together all of the jigsaw pieces of faunal and floral evidence in Dominican amber will continue far in the future as more and more fossils are discovered and described. They all are important in reconstructing the natural environment at the time Dominican amber was formed. The behavior of the fossil organisms can in large part be surmised from the biology of their descendants today, at least at the species and genus level (Boucot 1990). Gaps in the puzzle will always occur since amber is a selective trap and is biased towards capturing fauna associated with forested habitats containing the resin-forming trees. While amber does contain insects from adjoining ecological zones, those living in aquatic habitats and grasslands will always be under represented because they were too distant from the trees, too large to be held in resin or their behavior did not bring them into contact with the resin-forming trees.

### Future studies

Dominican amber contains a wealth of information available for a range of studies in speciation, extinction, biogeography, ecology and biodiversity. An increasing interest for collecting and describing fauna and flora in Dominican amber has occurred in the last decade and this will certainly continue in the coming years. As more data is accumulated, these deposits can be better compared to fossils from other formations around the world. Of special interest are the Mexican Chiapas amber deposits, which are relatively the same age, occur in the same general region (Mesoamerica) as the Dominican ones and were produced by trees of the same genus (*Hymenaea mexicana* Poinar & Brown 2002). With these similarities, comparative studies of the fauna and flora in these separate deposits should not only help us to understand the origin, extinction and biography of select lineages. Comparing changes over time in two different systems, one on an island and the



other continental should lead to insights into island biogeography and extinctions. One of the difficulties in all of these studies is the problem of homoplasy. Structural resemblances due to convergent evolution rather than common ancestry are widespread in various groups and careful evaluation of several characters in amber fossils may be required to differentiate between this condition and phyletic evolution.

Other future studies on biota in Dominican amber could include descriptions of microhabitats based on syninclusions in individual pieces of amber. An example presented here was the small piece with a wealth of micro-invertebrates and microscopic life (Fig.17). With the development of new techniques, such as propagation phase contrast synchrotron X-ray imaging, that obtains an image of life forms that would otherwise be masked by the opacity of the amber, our knowledge of past biodiversity and ecological associations will increase.

Perhaps some day, it will be possible to perfect the application of x-ray tomography to decipher the structure of internal organs, the gut contents and the hemocoel to analyze diets and parasites of insects and other invertebrates in amber. And with the advent of new molecular techniques for the recovery and repair of small amounts of DNA, studies on extracting DNA from amber flora and fauna can be resumed.

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