

CHRYSOMELIDAE IN FOSSILIZED RESIN: BEHAVIOURAL INFERENCES

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Abstract

A listing of the chrysomelid beetles known from amber deposits is presented, along with the first report of a Mesozoic sagine chrysomelid from Canadian Cretaceous amber. A discussion of the possible plant hosts of this Cretaceous fossil is presented in light of fossil cycads from that period and location and a possible sedge (Cyperaceae) seed found in the same amber deposits. New findings of chrysomelids in fossilized resin (amber and copal) are presented, along with indications of past behavioural patterns and associations including evidence of predation, gregariousness, feeding behaviour, host plant selection, parasitism, defence mechanisms, mimicry and symbiotic associations.

Introduction

Previous reports of fossil Chrysomelidae have been summarized by Santiago-Blay (1994). All of the Mesozoic and many of the Tertiary fossils are represented by compression fossils in rock layers which are incomplete specimens. Criticisms that most of these are poorly described, rarely show morphological features that provide synapomorphies in cladistic analyses and are debatable as belonging to the Chrysomelidae, are valid. However, identifiable fossils such as those that occur in amber can provide important phylogenetic and biographical information (Reid, 1995).

Chrysomelid fossils occur in a range of amber and copal deposits around the world (Table 1). Copal is defined as immature amber. When resin is no longer pliable by hand, it falls into the category of copal (Poinar, 1992). Over time and through the processes of oxidation and polymerization, semi-fossilized copal acquires the physical characteristics of amber. This is thought to occur within 2-4 million years. But copal can be as young as 50 years and as old as 50,000 years. Some early reports of insects in amber were actually specimens in copal, especially material from Africa. This is why it is important to verify all early reports of amber fossils and most of the specimens described in the 19th Century need to be restudied. A list of the reported genera and species of Chrysomelidae in amber appears in Table 2. No chrysomelids from copal deposits have yet been officially described.

Specimens in fossilized resin have the advantage of being preserved in their entirety, usually without noticeable distortion. Obstructing material can often be polished away, allowing the entire specimen to be viewed from several sides. Unfortunately, characters associated with the reproductive system and around the mouth are usually concealed from view, so only certain external characters can be used for identification purposes.

Table 1. Deposits of amber and copal containing Chrysomelidae

Deposit	Location	Estimated age	References
Canadian	Alberta, Canada	79 mya	present work
Baltic	Northern Europe	40 mya	Bachofen-Echt, 1949 Spahr, 1981 Keilbach, 1982 Poinar, 1992
Dominican	Dominican Republic	15-45 mya	present work Poinar, 1992 Santiago-Blay et al., 1996
Mexican	Chiapas, Mexico	22-26 mya	present work Gressitt, 1963, 1971 Poinar, 1992 Santiago-Blay et al, 1996
Colombian	Colombia, S.A.	less than 1000 yrs	present work; Poinar, 1996
Madagascar	Madagascar, Af	less than 1000 yrs	present work
Zanzibar	Zanzibar, Af	untested but probably less than 1000 yrs	Hope, 1836

Table 2. Identified genera and species of Chrysomelidae from amber deposits

Deposit	Taxon	Reference/ author
Baltic	<i>Altica</i> Geoffroy 1862	Spahr, 1981
	<i>Anisodera</i>	"
	<i>Cassida</i> L. 1858	"
	<i>Chalepus</i> Thunberg 1805	"
	<i>Chrysomela minutissima</i>	Schaufuss 1891
	<i>C. succini</i>	Giebel 1856
	<i>Colasposoma</i>	Spahr, 1981
	<i>Crioceris</i> (<i>Criocerina</i>) <i>pristina</i>	Germar, 1813
	<i>Cryptocephalus sericeus</i>	Helm 1886
	<i>Donacia</i> Fab. 1875	Spahr, 1981
	<i>Electrolema baltica</i>	Schaufuss, 1891
	<i>Eumolpus</i> Weber 1901	Spahr, 1981
	<i>Galerucella</i> Crotch 1973	"
	<i>Hadrosceles</i>	"
	<i>Haemonia</i>	"
	<i>Hispa</i>	"
	<i>Inclusus</i>	Spahr, 1981
	<i>Lema</i> Fab. 1898	"
	<i>Luperus</i> Geoffroy 1862	"
	<i>Monolepta</i> Erickson 1843	"
	<i>Nodonota</i> Lefevre 1885	"
	<i>Ochrosis</i>	"
	<i>Oposispa scheelei</i>	Uhmann, 1939
	<i>Pachnephorus</i>	Spahr, 1981
	<i>Protanisodera glaesi</i>	Quiel 1910
	<i>Pseudocolaspis</i>	Spahr, 1981
<i>Sucinagonia javetana</i>	Uhmann, 1939	
Mexican	<i>Profidia nitida</i>	Gressitt, 1963 Santiago-Blay et al., 1996
	<i>Asiorestia</i> (<i>Crepidodera</i>) <i>antiqua</i>	Gressitt, 1971 Santiago-Blay et al., 1996

Table 2. Cont.

Deposit	Taxon	Reference/ author
Dominican	<i>Alethaxius</i> Lefevre 1885	Santiago-Blay et al., 1996
	<i>Chalcosicya</i> Blake 1830	"
	<i>Colaspoides</i> Laporte 1833	"
	<i>Cryptocephalus</i> Geoffroy 1862	"
	<i>Diachus</i> LeConte 1880	"
	<i>Glyptoscelis</i> LeConte 1833	"
	<i>Leptonesiotes virkkii</i>	"
	<i>Metachroma</i> LeConte 1858	"
	<i>Sceloenopla ambarensis</i>	"
	<i>Walterianella</i> Bechyne	"
	Cassidinae	present work

First amber fossil of a Mesozoic Chrysomelidae

From the Canadian Cretaceous deposits of Alberta, the first Mesozoic amber chrysomelid has been recovered (Fig. 1). This specimen has been identified as a member of the Sagrinae. Although part of the body is obscured by fungal growth, the enlarged hind femora bearing rows of teeth are clearly visible, a feature characteristic of this subfamily of chrysomelids (Lawrence & Britton, 1991). Fossil sagrines are quite rare and have come from only two sites. *Mesosagrines multipunctatatus* Martynov 1935 was described from a single damaged elytron from the Late Jurassic Kara Tau deposits and its placement remains doubtful



Fig. 1. Sagrine chrysomelid in Canadian Cretaceous amber (79 mya). Note thickened and toothed hind femora.

(Santiago-Blay, 1994). More convincing are the specimens of *Eosagra obliquata* Haupt 1950 and *E. subparallela* Haup 1950 from the Eocene "brown coal" deposits near Geiseltal, Germany, which establishes this group in the Palaearctic in the early Tertiary.

The present find places the sagrines in the Nearctic during the Late Cretaceous and shows that the New World distribution of this group has been reduced during the past 79 million years to two relictual populations in South America. Such disjunct distributions of past and present populations of insect taxa are not unknown. Recently a genus of marine water striders was recovered in Dominican amber with the nearest species in the Indo-West Pacific (Andersen & Poinar, 1998). An interesting fossil amber beetle in the family Armatopodidae also demonstrates this point. Some twenty years after Crowson (1973) described the "extinct" genus *Electribius* from Baltic amber, stating that it was most closely related to modern representatives from Central America, two species in the same genus were described from Mexico and El Salvador, respectively (Lawrence, 1995). In all of these cases, the disjunct distribution probably was a result of population reduction caused by extinction events.

It is possible to speculate on the probable host plant of the Canadian fossil sagrine. There are several hypotheses as to the early food plants of sagrines and of chrysomelids in general. One suggests that the early Sagrinae lived on Cycadaceae (Schmitt, 1988) and the extant Australian *Carpophagus banksiae* has been noted visiting *Macrozamia* (Jolivet, 1988), (Table 4). The fossil sagrine could have fed on cycads since fossil evidence has shown that the climate was warm-temperate to subtropical and the cycad, *Nilssonia* has been reported from the Edmonton flora of the Upper Cretaceous of Alberta while *Pseudoctenis* and *Pseudocycas* have been found in the Upper Cretaceous Dunvegan flora of Alberta and British Columbia. Both sites date roughly the same as the amber location (Tidwell, 1998). Thus there is evidence that, as suggested by Jolivet (1988), cycads might have been the ancient hosts for this "stemgroup" of all Chrysomelidae.

Another theory is that the original plant hosts of the sagrines were Angiosperms (Tables 3 & 4) and feeding on monocots is a synapomorphy for all of the known subfamilies, as proposed by Reid (1995). Thus the host plant of the Canadian fossil sagrine could have been some type of reed or rush. By chance, a seed was found in a piece of amber from the same Alberta deposit where the sagrine originated (Fig.2). Botanists have been unable to match this seed with any known plant genus or family, but the morphology closely resembles extant genera of the sedge family (Cyperaceae). This would also agree with the current information known about the depositional site which indicates that the amber was formed in, or adjacent to a fresh-water marsh (Pike, 1995). One might speculate that the spines on the hind femur of the sagrines evolved as a means of grasping stems when feeding or ovipositing on semi-aquatic plants, since falling into water could result in drowning or predation by aquatic organisms.

Chemical analysis of the amber indicated that it was produced by trees of the genus *Agathis* (Araucariaceae) (Lambert *et al.*, 1996). This genus of trees is now restricted to the southern hemisphere where they have a Gondwanian distribution (New Zealand, Australasia and New Caledonia) similar to the Sagrinae which also have presently a nearly Gondwanian distribution with representatives in Australia, India, Africa, South America and southern Asia. These beetles are basically a warm-climate group, most being confined to the tropics or subtropics (Crowson, 1981). The Eocene "brown coal" fossils in Germany and the present find establishes this group in the Northern hemisphere and confirms a past Laurasian dis-



Fig. 2. Seed of a tentative sedge (Cyperaceae) in Canadian Cretaceous amber (79mya) from the same deposit as the sagrine shown in Fig. 1. Length of seed = 3 mm, greatest width = 0.5mm, bristles from the base range from 2.5 – 3.0 mm in length. The basal 40% of the bristles are dark while the upper 60% are hyaline and barely show in the photo.

Table 3. Host plants of larval Sagrinae

Genus	Locality	Plant host	Reference
<i>Atalasis</i>	Neotropical	<i>Sphaeralcea</i> , <i>Malvastrum</i> , <i>Sida</i> , <i>Gossypium</i> (Malvaceae)	Jolivet, 1988
<i>Mecynodera</i>	Australia	<i>Lomandra</i> (Xanthorrholaceae)	Lawrence & Britton, 1991
<i>Sagra</i>	Pantropical	Leguminosae, Rutaceae Euphorbiaceae, Rhizophoraceae Convolvulaceae, Verbenaceae Rubiaceae, Dioscoreaceae Acanthaceae, Meliaceae	Jolivet, 1988; Reid, 1995

tribution of the Sagrinae. It also provides evidence that the subfamily extended back to the time of Pangaea, having radiated over most of the warm areas of the land masses. It appears that past climatic conditions in the Northern hemisphere have been harsher than those in the Southern, explaining why so many more relict species of plants and animals occur in the southern hemisphere today.

Table 4. Plants associated with adult Segrinae

Taxon	Plant	Association	Reference
<i>Carpophagus banksiae</i>	<i>Macrozamia</i> (Cycad)	sitting on leaves	Jolivet, 1988 Reid, 1995
<i>Diaphanops</i> sp.	<i>Melaleuca</i> (Myrtaceae)	feeding on pollen	Reid, 1995
<i>Mecynodera</i> sp.	<i>Acacia</i> (Mimosaceae)	feeding on pollen	Reid, 1995

Evidence of behaviour in amber fossil Chrysomelidae

Aside from demonstrating the presence of a particular taxon at a specific period in the earth's history, the excellent preservation of specimens in fossilized resin can also indicate something about the behaviour of extinct organisms.

Evidence of predation

There is a curious type of predation that sometimes occurs on insects trapped in fossilized resin (Poinar, 1998). This type of predation has been also detected on chrysomelids in Madagascar copal (Fig. 3). It is presumed that the predation occurs after the beetle has



Fig. 3. A chrysomelid in Madagascar copal, with its elytra and internal tissues removed by a predator.

become stuck to the surface of a resin deposit. The predator or predators, which remain unknown at this time, surgically and carefully cut away the cuticle of the prey, which in this case meant removing the elytra of the entrapped leaf beetle. The predator may ingest the elytra or simply cut it away to expose the soft underparts, which are then completely removed with fine precision. Thus the body cavity of the entrapped adult is completely consumed and an air bubble remained in its place when a subsequent resin flow finally completely entombed the specimen. Although the identity of this particular predator remains unknown, it may have left some clues as to its presence since a cluster of elongate scales overlay the air bubble that now fills the empty body cavity of the victimized beetle.

Evidence of gregariousness

Evidence of gregariousness in a population of flea beetles (Alticinae) from the Greater Antilles can be obtained from a single piece of Dominican amber containing eleven adult beetles (Fig.4). The beetles must have been feeding on a leaf that was close to the resin deposit on the Dominican amber tree (*Hymenaea protera*: Poinar, 1991) when they were disturbed. Quite possibly a predator arrived which caused the beetles to jump or fall off the leaf (thanatosis?) into the resin or something might have brushed the leaf into the resin flow.



Fig. 4. Eleven adult flea beetles in a piece of Dominican amber provides evidence of gregarious behaviour some 20-40 million years ago.

Evidence of feeding behaviour

Although pieces of fossilized resin containing plant damage along with leaf beetles have not been reported, some leaves in Dominican amber demonstrate feeding damage which is characteristic of that caused by leaf beetles (Fig. 5).

Evidence of host plant selection

Again, unless a recognizable plant part with insect damage is found together with larval or adult chrysomelids, it is impossible to correlate a particular insect with a specific plant to establish host-plant associations. However, many tropical families of plants have characteristic plant hairs and sometimes insects in fossilized resin are associated with them. An example is presented here where a chrysomelid larva (probably a Galerucinae) in Colombian copal has a simple trichome attached to the ventral surface of its body (Figs. 6,7). This type of trichome is characteristic of several plant families, including members of the Combretaceae and Acanthaceae (Gentry, 1993). It would be difficult to specify exactly the plant host without further knowledge of the trichome structure of plants growing in Colombian forests. However, amber insects have been discovered with more characteristic trichomes, like T-shaped hairs characteristic of members of the family Malpighiaceae (Poinar & Poinar, 1999).

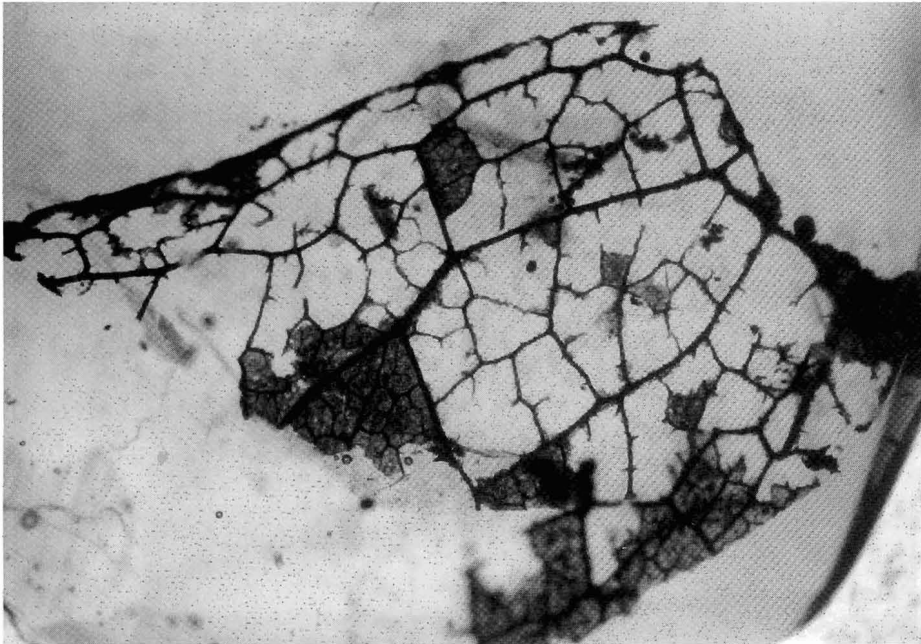


Fig. 5. Feeding damage to a leaf in Dominican amber is characteristic of leaf beetle activity.



Fig. 6. A larval chrysomelid (probably a Galerucinae) in Colombian copal.

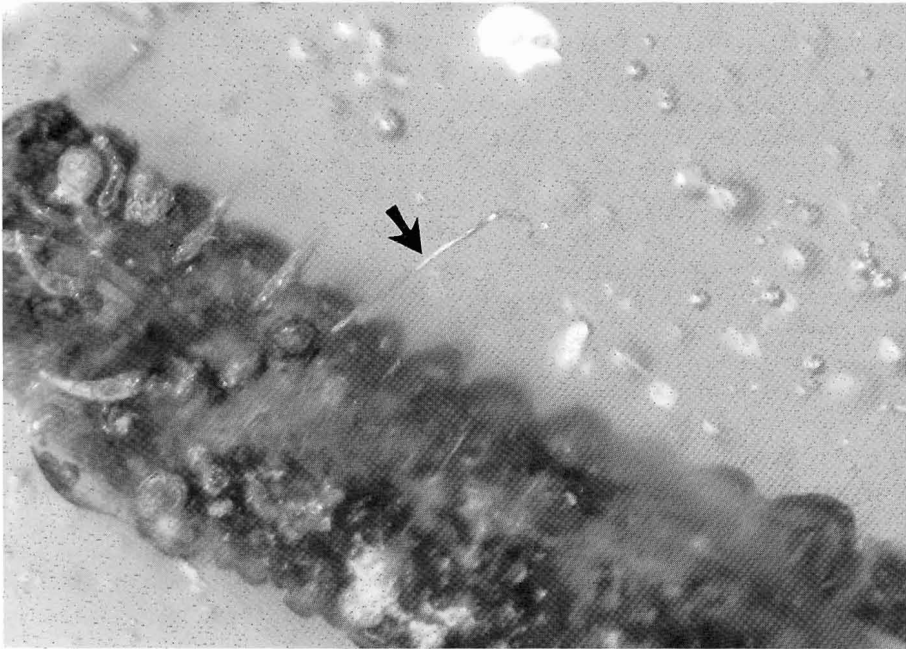


Fig. 7. Detail of galerucine larva in Fig 6 showing plant trichome (arrow) attached to underside of body.

Evidence of parasitism

While leaf beetles with emerging parasites have not been reported in fossilized resin, genera of parasitic wasps with representatives known to parasitize extant chrysomelids have been recovered from amber deposits containing leaf beetles. For instance the oil palm leaf-mining hispid, *Hispolepsis subfasciata* Pic which occurs in South America is parasitized by species of Eulophidae, Encyrtidae, and Braconidae (Mariau, 1988), all of which groups are represented in Dominican amber with the fossil hispine, *Sceloenopla ambarensis* Santiago-Blay, Poinar & Craig (1996). More specifically, the prepupa of *H. subfasciata* is parasitized by a species of *Brachymeria*, a genus which occurs in Dominican amber (Fig. 8). This genus of Chalcididae also parasitizes larvae and pupae of tortoise beetles (Buzzi, 1988) which are represented in Dominican amber. Although it is impossible to say that the *Brachymeria* depicted in Fig.8 parasitizes leaf beetles, there is a good possibility that some of the amber ones did.

Defense mechanisms and mimicry

Several Eumolpines in Dominican amber are quite rounded, smooth and shiny. This is especially true with some members of the genus *Metachroma* whose bodies can be characterized as smooth metallic (Fig.9). These modifications are often used by leaf beetles as a protective measure against ants, that find it difficult to grasp the beetle's bodies (Selman, 1988).

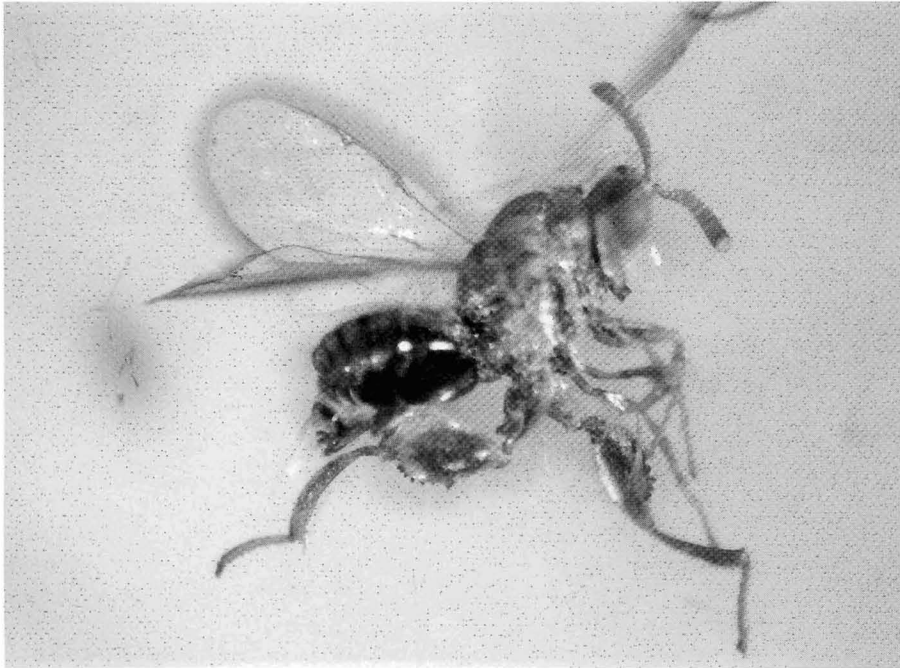


Fig. 8. An adult *Brachymeria* (Chalcididae: Hymenoptera) in Dominican amber that could have parasitized leaf beetles.



Fig. 9. The smooth, rounded body of this *Metachroma* sp. in Dominican amber may have served as a defence against ants.

Regarding protective coloring or mimicry, eye spots on insects in general are thought to frighten predators by representing the eyes of general, unidentifiable species, although the interpretation of small eye spots is still open to discussion (Balsbaugh, 1988).

The dark spots on the anterior and posterior portions of each elytron on *Leptonesiotes virkkii* Santiago-Blay *et al.*, 1996 in Dominican amber merge into two eyespots when the wings are closed (Fig. 10). These spots could serve as a defense against some types of predators.

Perhaps the clearest evidence of defensive behaviour of chrysomelids in amber is the presence of case-bearing Camptosomata in Dominican amber. A mantle covering the eggs of this group is periodically enlarged upon with faecal material from the growing larvae, forming a protective case which is carried around by the insect. This group abounds in the Neotropics so it is not unexpected that their cases would appear in tropical amber. All of the cases reported to date appear to belong to the Cryptocephalinae (Santiago-Blay *et al.*, 1996) and a recently discovered one in Dominican amber belongs in that same group (Fig.11). This latter case closely resembles extant cases made by members of the genus *Cryptocephalus* (Erber, 1988). It is not clear whether the feeding habits of *Cryptocephalus* larvae include decaying plant material on the forest floor or living leaves on trees and shrubs. The presence of these case-bearing larvae in amber suggests that they did at least crawl on the bark of trees.

Larvae of the Cassidinae do not make cases, but possess caudal and lateral outgrowths which retain excrement, exuviae and debris to conceal themselves (Buzzi, 1988). Two early larval representatives of this group have been found in Dominican (Fig. 12) and



Fig. 10. When the elytra of *Leptonesiotes virkkii* are folded at rest, the color patterns merge to make a pair of eyespots.



Fig. 11. A larval cryptocephaline (probably *Cryptocephalus* sp.) partially protruding from its protective case.

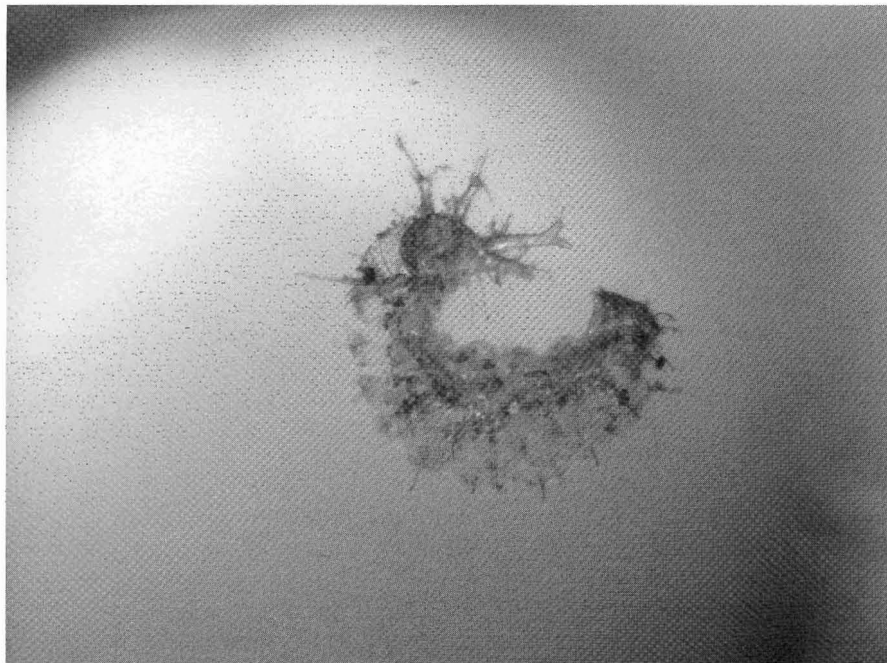


Fig. 12. A larval Cassidinae in Dominican amber.

Baltic amber (Fig. 13). Although debris is absent in these forms (possibly because it came off in the resin), the caudal spines that serve to hold the material are evident.

Symbiotic associations

Aside from evidence of parasitism by nematodes, fungi, protozoa and viruses, symbiotic associations involving mutualism have rarely been reported involving Chrysomelidae. However the pronotum of *L. virkkii* in Dominican amber (Santiago-Blay *et al.*, 1996) contains a large central cavity (Fig. 14), which is probably not an artifact since the remainder of the body shows no sign of distortion. This cavity is lined with a whitish powdery material which may represent some type of microorganism or the product of an organism that has a parasitic or mutualistic association with the adult beetle.

Preservation of internal tissue in amber Chrysomelidae

A study that examined Dominican amber eumolpines with pyrolysis-gas chromatography/mass spectrometry showed that the volatile components in the resin penetrated both the cuticle and internal tissues of the adult beetles (Stankiewicz *et al.*, 1998). Straight chain hydrocarbons and bicyclic resin products from the fossil tissue were abundant, even in tissues not directly in contact with the amber. It was presumed that resin molecules formed chemical cross links which explained the detailed preservation of the internal tissue, even

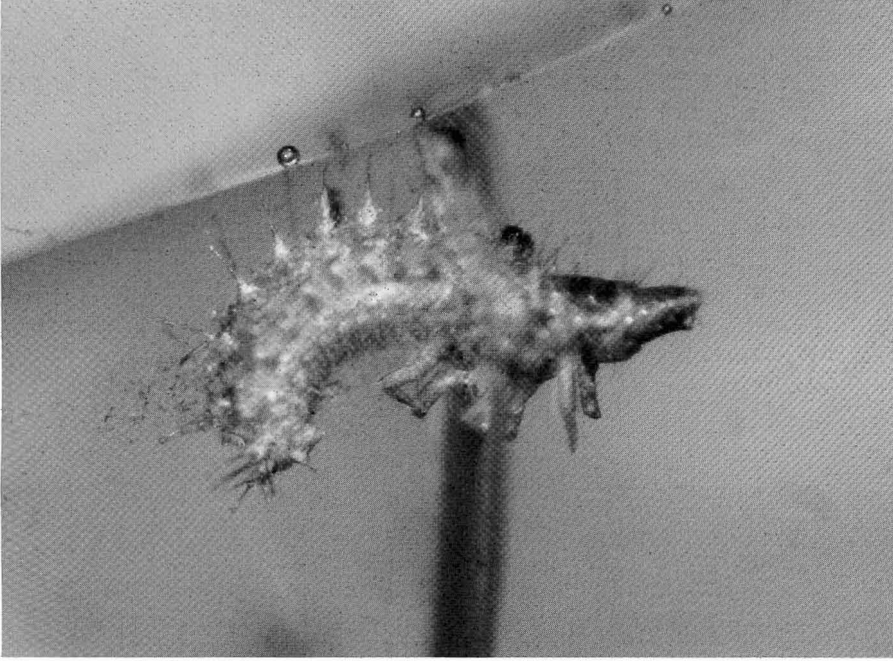


Fig. 13. A larval Cassidinae in Baltic amber.

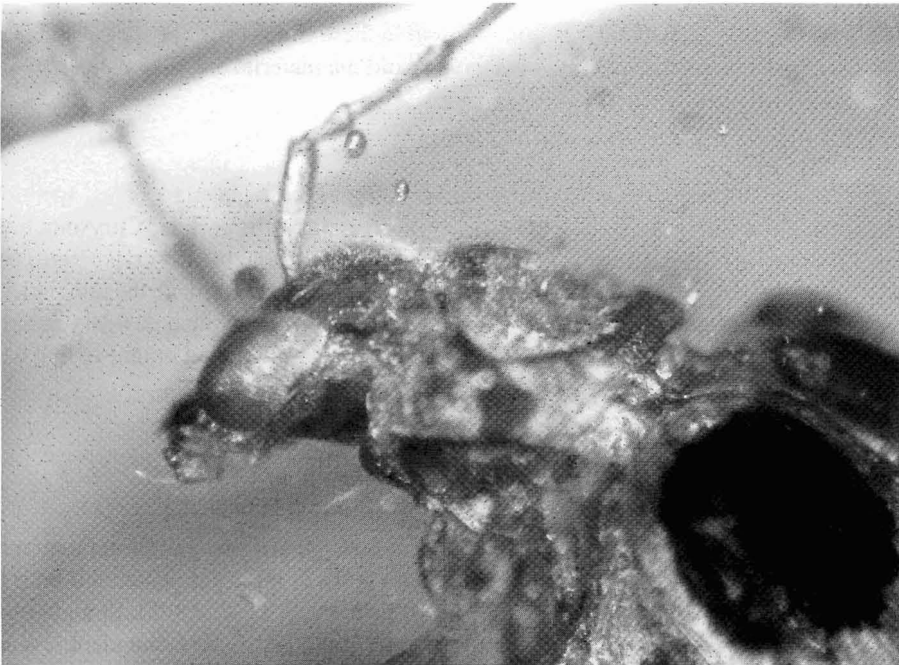


Fig. 14. The pronotum of *L. virkkii* in Dominican amber contains a cavity filled with a powdery substance which could indicate some type of symbiotic or parasitic association.

though the cuticle was degraded. Unfortunately, the study failed to explain how DNA is preserved in amber specimens, although insect DNA sequences, still awaiting analysis, were obtained from a *Metachroma* sp. in Dominican amber (Hendrik Poinar, personal communication).

Conclusions

Aside from establishing the presence of leaf beetles at a particular time and location in the past, amber fossils can also be used to interpret aspects of a wide range of behaviour and interactions that occurred in fossil taxa. Interpretation is dependent in a large part on the habits of extant chrysomelids, since as has been adequately demonstrated by Boucot (1990), the habits of organisms tends to remain steady over time, following the principle of behavioural constancy.

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