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Paleoethology: fossilized behaviours in amber

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ABSTRACT

When organisms became trapped in sticky resin they usually expired so quickly that they could fossilize in almost lifelike circumstances. Based on frequent description in literature of many examples we propose in this paper a classification of these paleobehaviours.

KEYWORDS | Amber. Paleoentomology. Amber fossils. Paleoethology. Paleobehaviour.

INTRODUCTION

Amber is fossilized resin secreted by a wide range of plant families. It occurs in several deposits throughout the world. Fossiliferous ambers have a range of ages from Lower Cretaceous to subrecent hardened resins called copal. When the resin is still fresh and sticky many sorts of organisms (mainly short sized) can eventually be trapped and become fossilized when the resin hardens. The results are fossil preserved in exquisite three dimensional details even with ultrastructural cellular details. A huge number of fossil species preserved as amber fossils have been described mainly from Cenozoic Baltic, Dominican and Mexican ambers, but in recent years fossil faunas from other ambers are also being studied, including Mesozoic ambers.

When organisms become trapped in sticky resin they usually die so quickly that they could fossilize in almost lifelike circumstances. Many examples of this kind of "frozen" behaviours have been described in literature. So we can study, not only the fossil species that lived in the amber producing forest, but we could eventually study the behaviour of fossil species and even fossil associations between species.

When two organisms are preserved in the same piece of amber we call it a syninclusion (term proposed by Koteja, 1986): two organisms embedded in the same resin flow probably lived and died in the same day and thus we can be sure that they lived in the same habitat and were parts of the same paleoecosystem. However, if two organisms are preserved in the same resin flow, it only means that they were contemporaneous as they may have ended up together by accident and an association between both species is not real.

Interaction between trapped organisms and the fresh resin is also very important. Usually trapped animals struggle to escape and their movements could "fossilize" changing the resin flows. Sometimes this struggle could be erroneously interpreted as the normal behaviour of the animal; for example when an animal bites another trying to escape it could be interpreted as a predation association.

In this paper I try to classify paleobehaviors preserved in amber in three sections: 1) Intraspecific relations, 2)

Interspecific relations, and 3) Interactions with fresh resin.

1) Intraespecific relations are subdivided into: a) reproductive behaviour that includes mating (Figs. 1A and 1B), mate guarding, egg lying and progeny care, and b) social /gregarious behaviour that include swarms (Figs. 1C-1D), and food carriage.

2) Interspecific relations (symbiosis *sensu lato*) are subdivided into: a) predation, b) parasitism (Figs. 1E-1F), c) mutualism (symbiosis *sensu stricto*), d) phoresy, and e) defence behaviour.

3) Interactions with the fresh resin include: a) stress behaviour, such as egg laying (Fig. 1G), defecation, ejaculation, etc., b) movements into the fresh resin, c) lost of pieces, and d) secretion of repugnatory glands

Acronyms and age of ambers used in the text: (LA) Lebanese amber (Lower Cretaceous), (SA) Spanish amber (Lower Cretaceous), (MA) Myanmar amber (Upper Cretaceous), (NJA) New Jersey amber (Upper Cretaceous), (TA) Taymyr Siberian amber (Upper Cretaceous), (CA) Canadian amber (Upper Cretaceous), (BA) Baltic amber (Eocene), (BitA) Bitterfeld amber (Eocene) and (DA) Dominican amber (Miocene).

INTRAESPECIFIC RELATIONS

Reproductive behaviour

Mating

Mating behavior is widely reported from different ambers. Examples among Coleoptera include fireflies (Lampyridae) in DA (Poinar and Poinar, 1999, fig.135; Grimaldi and Engel, 2005, fig. 10.46); Byturidae in BA (http://www.brost.se); Cantharidae in BA (Wichard and Weitschat, 2004, p. 79). A very interesting example of mating is a piece of DA containing a mating couple of *Halovelia electrodominicana* (Velidae: Hemiptera) (Andersen and Poinar, 1998). Leafhoppers (Cicadellidae: Homoptera) are known mating in DA (Grimaldi and Engel, 2005, fig. 2.27). Mating behaviour examples are common among different Diptera families as *Trichoneura vulgaris* LOEW, 1850 (Limoniidae) in BA (Kosmowska-Ceranowicz, 2001, fig. 85) Limoniidae in BA (Janzen, 2002, fig. 346); Limoniidae in DA (Grimaldi, 1996, p. 86); Ceratopogonidae in BA (Ross, 1998, fig. 92; Wichard and Weitschat, 2004, p. 24); Chironomidae in BA (Ross, 1998, fig. 138; Kobbert, 2005, p. 142; Wichard and Weitschat, 2004, p. 142); Scatopsidae in DA (Ross, 1998, fig. 63; Wu, 1997, fig. 493; Grimaldi and Engel, 2005, fig. 12.32); Mycetophilidae in BA (Fig. 1A, Collection of the Museo de Ciencias Naturales de Álava, MCNA-11.115; Janzen, 2002, fig. 349; Wichard and Weitschat, 2004, p. 24); Cecidomyiidae in DA (Poinar, 1993); Dolichopodidae in BA (Weitschat and Wichard, 1998, fig. 86e; Wichard and Weitschat, 2004, p. 24; Kobbert, 2005, p. 149; Fig 1B, Collection of the University of Barcelona, Spain); Phoridae in BA (Weitschat and Wichard, 1998, fig. 87g). Examples among Hymenoptera include Bethylidae in DA (http://www.ambericawest.com). Apart from insects, "mating" spiders have also been recorded in BA (http://www.brost.se).

Mate guarding

An example of mate guarding is know in DA; the male remains close to the female after the copula warding off all others. The example is a couple of water striders, *Electrobates spinipes* (Gerridae: Hemiptera; Andersen and Poinar, 1992)

Egg lying

Females egg-lying are known preserved in amber but this is a kind of not natural behaviour as it is caused by the stress of struggling against the sticky resin and, in some cases, it could be even a *post-mortem* process. This behaviour is known among Diptera. Grimaldi (1996, p. 86) reports a Nematocera in DA, Grimaldi and Engel (2005, fig. 2.28) reported one cecidomyiid in DA, Wu (1997, figs. 498-499) reported two female Ceratopogonids ovopositing in DA and Martínez-Delclós et al. (2004, fig. 2G) reported one Keroplatidae in DA; one Sciaridae (http://www.brost.se) and one Mycetophilidae (Kobbert, 2005, p. 141) are known in BA; a Drosophilidae is known in DA (Wu, 1997, fig. 508) and an undetermined Brachycera is known in DA (Poinar and Poinar, 1994).

Progeny care

Progeny care behaviour is not commonly fossilized in amber except among social insects (mainly ants). Poinar and Poinar (1999, fig. 72) recorded a Pholcidae spider in DA carrying her silk case with eggs. A female millipede (Diplopoda) in DA with her young has also been recorded (Poinar and Poinar, 1999, fig. 89). In ants there are several examples of progeny care. A well known example is the piece called "Jorge Caridad"; it is a piece of DA where a colony of ants (*Technomyrmex caritatis*) is carrying eggs and pupae (Brandao et al., 1999). Another Formicidae in DA carrying a pupa is recorded in Grimaldi (1996, p. 90). In BA ants carrying a larva are also known (Weitschat and Wichard, 1998, fig. 71e; Kobbert, 2005, p. 122). Sometimes an adult just emerging from its pupal

case could be trapped in fresh resin and it could erroneously be interpreted as an association between an adult with a juvenile stage. For example Anisopodidae (Diptera) in BA (Weitschat and Wichard, 1998, fig. 82d) or in DA (Grimaldi, 1991).

Social/ gregarious behaviour

Swarms

Swarms are common in amber. Mating swarms are common among winged insects. Some species have winged adults just for mating swarms as termites: good examples are recorded in DA (Grimaldi, 1996, p. 85; Wu, 1997, fig. 269) and in BA (Wichard and Weitschat, 2004, p. 107), but it is also common in Colombian copal (Martínez-Delclòs et al. 2004, fig. 3D). Diptera are also known swarming in amber pieces as Dolichopodidae in DA (Grimaldi, 1996, p. 84) or Mycetophilidae in BA (Ross, 1998, fig. 1). Mesozoic Diptera swarms are also known: a swarm of *Prioriphora intermedia* (Phoridae) is known in CA (Brown and Pike, 1990) and a swarm of Microphoridae is recorded in SA. Platypodidae beetles are known swarming in a piece of DA (Martínez-Delclòs et al. 2004, fig. 3E). Swarming winged ants (Formicidae) are sometimes reported in DA (Martínez-Delclòs et al. 2004, fig. 3C; Fig. 1C, Collection of the University of Barcelona, Spain).

Some pieces of amber could preserve groups of organisms of the same species due to different types of gregarious behaviour: most evident of them are ants, for example a piece of DA containing part of a colony of *Azteca* sp. (Grimaldi, 1996, p. 92). Some juvenile spiders could also show a gregarious behavior as in a piece of DA (Poinar and Poinar, 1999, fig. 73) or in BA (Weitschat and Wichard, 1998, fig. 20h). Another example is a group of Alticinae chrysomelids (Coleoptera) in DA gregariously feeding on a leaf (Poinar, 1999a).

Food carriage

Food carriage is known fossilized in amber among social species. Best example is *Proplebeia dominicana* (Apidae: Hymenoptera) in DA carrying pollen (or resin to construct their nests) on their hind legs (Poinar, 1992 fig. 111). Other examples are: a *Neivamyrmex* sp. ant in DA carrying a wasp pupa (Poinar and Poinar, 1999, fig. 104); several ants in DA carrying a Diplopoda (http://www.brost.se); a gardening ant (*Apterostigma* sp.) in DA carrying a chewed-off leaf (Poinar and Poinar, 1999, fig. 109). A special intraspecific feeding relation among social insects is trophalaxy (when one individual is feed by another) as in a piece of DA where one *Nasutitermes* sp. termite is feeding one chemical squirting soldier (whose heads are cone shaped for chemical defence, lacking mandibles) (http://www.brost.se).

INTERSPECIFIC RELATIONS (SYMBIOSIS *SENSU LATO*)

Predation

Predation behaviour is sometimes recorded in amber. Empididae (Diptera) in BA are known attacking ants (http://www.brost.se) and Chironomidae (Janzen, 2002, fig. 385); Spiders are known predating on termites and ants (Poinar and Poinar, 1994; Poinar, 1995). Spiders constructing their silk web are also known in BA (Weitschat and Wichard, 1998, fig. 20b) and preys trapped in silk web are known in DA, as one Psychodid (Diptera) or an ant (Poinar and Poinar, 1999, figs 70-71) and in BA where one scale-insect, one ant and one Auchenorrhyncha trapped in silk are known (Kobbert, 2005, pp. 84, 167, and 169). Oldest spider-web is known from LA (Zschokke, 2003).

Poinar (2001a) reported a piece in DA where an ant (*Azteca alpha*) is clutching a pseudoscorpion. It could represent a predation behavior but probably it is related with a case of phoresy and probably also with a stress behaviour (see 3.1).

Parasitism

Endoparasitism

Endoparasitic behaviour could be recorded in amber when parasite emerges from the host when it dies in the fresh resin or when the parasitic female is putting her eggs into the host.

Parasitic Nematodes emerging from their hosts are widely recorded in amber. Poinar et al., 1994a recorded one Mermithidae (*Cretacimermis libani*) emerging from a Chironomidae in LA (Azar pers. comm). Grimaldi et al. (2002) and Grimaldi and Engel (2005, fig. 2.29) reported also two Mermithidae emerging from one Chironomidae in MA. Mermithids are also known associated with insects in BA: Schlee and Glöckner (1978), Poinar (1984a, 2003) and Eichmann (2002) reported them emerging from Chironomids; Weitschat and Wichard (1998) reported also Nematodes emerging from Limoniidae (Diptera) (figs. 7a-7b), Chironomidae (fig. 7e), and Nematocera (fig. 7c). One Nematode emerging from one Nematocera in BA is also known in the Collection of the Museo de Ciencias Naturales de Álava (Fig. 1E, MCNA-11.088) Other Nematode emerging from a Chironomidae are shown in Janzen (2002, fig. 364) and Kobbert (2005,

p. 183. Poinar (2001b) recorded a Mermithid (*Heydenius brownii*) in BA parasite of an Achilidae (Homoptera), another, *Heydenius araneus*, in BA parasite of a Thomisidae spider (Poinar, 2000) and Poinar (2002) recorded another in BA, *Heydenius formicinus* parasite of an ant (*Prenolepis henschei* MAYR). Mermithids are also known in DA, Poinar (1992, fig. 138, 1998a) reported them emerging from Chironomidae. Another Mermithidae (*Heydenius dominicus*) was found in DA emerging from a Culicidae (Poinar, 1984b). A third Mermithidae (*Heydenius mirmecophila*) was described emerging from an ant (*Linepithema* sp.) in DA, (Poinar et al., 2006). Allantonematidae (Nematoda) are known in DA emerging from *Chymomyza primaeva* (Drosophilidae: Diptera; Poinar, 1984c). Another example is 44 juvenile Allantonematidae in DA surrounding a Staphylinidae (Coleoptera) (Poinar and Brodzinsky, 1985). Poinar (1999b) reported two hairworms, *Paleochordodes protus* (Nematomorpha) in DA emerging from their cockroach host.

Not only Nematodes are known as endoparasites in amber: Poinar and Miller (2002) described a parasitoid wasp larva (Braconidae) in BA emerging from a *Lasius* ant. Alonso et al. (2000, fig. 12-1) reported a Stigmaphronidae (Hymenoptera) ovopositing into a Sciaroidea (Diptera) in Mesozoic SA. Wunderlich (1986) reported an Ichneumonidae (Hymenoptera) ovopositing into a caterpillar in BA.

Strepsiptera are also known parasiting their hosts in amber; Eichmann (2002) reported a Strepsitera parasiting an ant in BA and Poinar (2004a) reported a Strepsiptera parasiting an *Augochloropis* sp. (Halictidae) in DA.

Ectoparasitism

Ectoparasitism is widely reported in the amber record. Mites are the most usual ectoparasits. *Leptus* sp. mites (Erythraeidae) and other parasitic mites are known in BA parasiting Mycetophilidae (Weitschat and Wichard, 1998, fig. 14c), Limoniidae (Weitschat and Wichard, 1998, fig. 14d), Anisopodidae (Kobbert, 2005, p. 181), Empididae (Kobbert, 2005, p. 180), Dolichopodidae (Weitschat and Wichard, 1998, fig. 14e; Kobbert, 2005, pp. 178-179), or even a Dolichopodidae with two mites attached (Fig. 1F, collection of Leif Brost, Swedish Amber Museum). Water mites (Hydracharina) are known in BA parasiting Chironomidae (Schlee and Glökner, 1978); Bachofen-Echt (1949) recorded also a water mite attached to a Trichoptera. Mites are also recorded in DA parasiting a Drosophilidae (Diptera) (Ross, 1998, fig. 74); four Hydracharina in DA are known attached to the abdomen of a Chironomid (Poinar, 1985) and one Trombidid is known attached to a Sciaridae (Diptera) (Poinar and Poinar, 1999, fig. 154). Erythaeidae are also known in DA as parasites of moths (Gracillariidae and Tineidae) (Poinar et al., 1991). Parasitic mites attached to their hosts are also known in Mesozoic ambers: in CA Poinar et al. (1993) reported a Microthrombidiidae (Acari) attached to a Ceratopogonidae and Poinar et al. (1997) recorded an Erythraeidae (Acari) attached to a *Metriocnemus* female (Diptera: Chironomidae). In LA two pieces of amber with *Leptus* (Erythreaidae) parasiting Ceratopogonids are known (Poinar and Milki, 2001, pl. 17; Poinar et al., 1994b). *Leptus* are also known in SA parasiting a Chironomid (Alonso et al., 2000, fig. 9-4) and a Microphoridae. A possibly Erythraeidae mite is known attached to a Cecidomyiid (Diptera) in Cretaceous NJA (Grimaldi et al., 2000, fig. 42h).

Mites attached to scale insects (Coccinea) have been recently summarized by Koteja and Poinar (2005). They report 1) an Inkaidae (*Inka minuta*) parasited by a Heterostigmata mite (*Protophenax kotejai*) in TA; 2) several Pitycoccidae parasited by undetermined mites in BA and BitA; 3) an Electrococcidae (*Turonicoccus beardsleyi*) parasited by an undetermined mite in NJA; 4) a Kuwaniidae parasited by an undetermined mite in BA; 5) a Steingeliidae parasited by an undetermined mite in LA, and 6) an Ortheziidae parasited by an undetermined mite in BA.

One *Leptus* sp. parasiting one Epipsocidae (Psocoptera) is known in BA (Wichard and Weitschat, 2004, p. 70).

Eichmann (2002) has recently recorded several mite-Diptera parasitics associations in BA including Cecidomyiidae, Chironomidae, Sciaridae, Ceratopogonidae and Dolichopodidae.

Dryinidae (Hymenoptera) are one of the ectoparasitic insect group best recorded in amber. Their presence is known due to the sac-like structures (containing a larva) protruding from the body of the host; they are known in DA parasiting Fulgoroidea (Homoptera; Poinar, 1992, fig. 140; Poinar, 2001a; Poinar and Poinar, 1999, fig. 140; Ross, 1998, fig. 73; Grimaldi and Engel, 2005, fig. 11.37). Other parasitic Hymenoptera are recorded attached to their hosts: Poinar (1992, fig. 141) reported a Polysphinctini Ichneumonid in DA attached to a Clubionidae spider.

A parasitic moth larva (Epipyropidae) is known in DA attached to a Cicadellidae (Homoptera; Poinar and Poinar, 1999, fig. 151).

Poinar (2004b) reported an Ichneumonidae larva (Hymenoptera) making its coccon over the eggs of a Clubionidae spider in BA.

Finally, lice (Phthiraptera) are known attached to mammal hairs in BA (Weitschat and Wichard, 1998, fig. 92a - 92b).

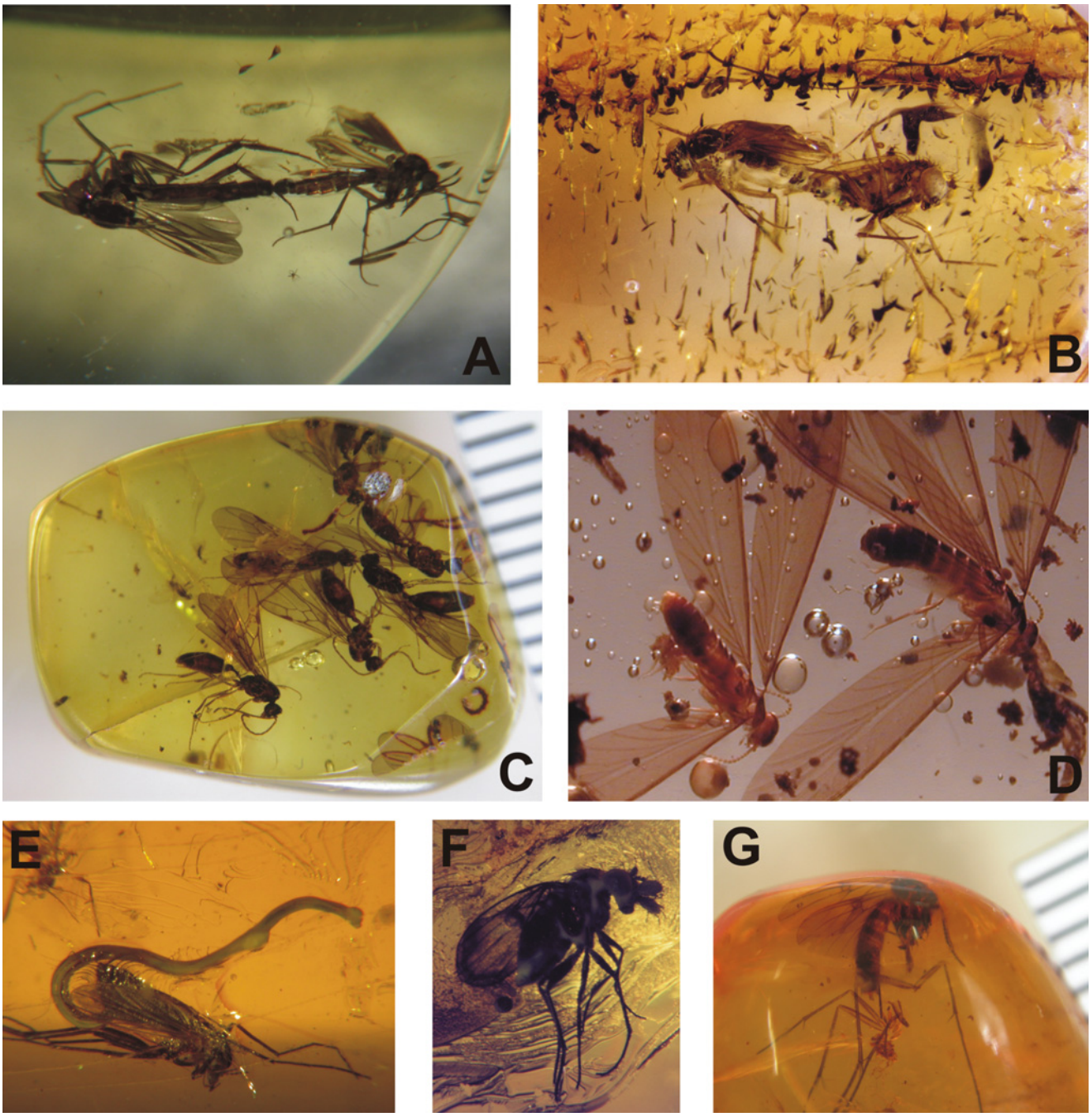

FIGURE 1 | **Different paleobehaviors preserved in amber. MCNA: Museo Ciencias Naturales de Álava; EPGM: Collection of the Dept. Estratigrafia, Paleontologia i Geociències Marines, University of Barcelona. A) Intraspecific relations (reproductive behaviour): Mycetophilids (Diptera Mycetophylidae) in copula in Baltic amber (MCNA-11.115). B) Dolichopodids (Diptera Dolichopodidae) in copula from the Baltic amber (EPGM-RD-BA-0059). C) Intraspecific relations (social /gregarious behavior): Swarm of winged ants (Formicidae) in Dominican amber (EPGM-RD-060). D) Swarm of termite imagoes in Colombian copal (EPGM-RD-0061). E) Interspecific relations (parasitism): Nematode emerging from a Nematoceran Diptera in Baltic amber (MCNA-11.088). F) Diptera Dolichopodidae with two parasitic mites in Baltic amber (Collection Leif Brost). G) Interactions with the fresh resin (stress behaviour): Keroplatidae from the Dominican amber laying eggs (EPGM-RD-0048).**

Mutualism (Symbiosis *sensu stricto*)

Mutualism is known between ants and Homoptera. In several pieces of DA winged ant queens belonging to genera *Azteca* and *Acropyga* have been recorded carrying Coccoidea (Homoptera; Poinar and Poinar, 1999, fig. 108; Johnson et al., 2001; Grimaldi and Engel, 2005, fig. 8.35). Also one ant carrying one Aphidoidea is known in BA (Wichard and Weitschat, 2004, p. 87).

Phoresy

Some pseudoscorpions use different insects as a way of transport. A Platypodidae beetle (*Mitosoma rhinoceroide*) is recorded in DA transporting a pseudoscorpion (Schawaller, 1981) and a *Proplebeia dominicana* (Apidae) is known transporting a pseudoscorpion in DA also (Wu, 1997). Other phoretic pseudoscorpions are known in BA: attached to a Braconidae (Hymenoptera; Bachofen-Echt, 1949, fig. 56; Weistchat and Wichard, 1998, fig. 11a), to a harvestman (Opiliones; Weitschat and Wichard, 1998, figs 11b-11c), to a Mycetophilidae (Kosmowska-Ceranowicz, 2001, fig. 2), to Rhagionidae (Ross, 1998, fig. 75; Wichard and Weitschat, 2004, p. 71) and to a moth (Lepidoptera; Poinar et al., 1998).

Phoretic behavior is widely known among mites. Uropodids (Mesostigmata: Acari) are recorded in BA being transported by a Cleridae (Coleoptera; Weitschat and Wichard, 1998, figs. 14a-14b). Hypopus phase of Astigmata (Acari) are also known in DA being transported by a Platypodid (Coleoptera; Poinar and Poinar, 1999, fig. 59) and by a *Proplebeia dominicana* bee (Apidae; Poinar, 1992, fig. 135). Macrochelid mites are also known in DA phoretic on Drosphilidae (Poinar and Grimaldi, 1990). Undetermined mites are known in DA being transported by one Scolytidae and one Colydiidae (Coleoptera; Wu, 1997, figs. 121 and 140). Eichmann (2002) reported several examples of phoretic mites in BA on Dolichopodidae, Chironomidae and Sciaridae among Diptera and on Cupedidae and Mordellidae among Coleoptera.

Meloidae (Coleoptera) first larva instars, called triungulins, are known in DA being transported by a *Proplebeia dominicana* bee (Apidae; Poinar and Poinar, 1999, fig. 153) and in BA being transported by a Protolithurgus ditomeus bee (Megachilidae) (Engel, 2005). While triungulins are phoretic, rest of larval instars, once in the host's nest, are predator on pollen provisions and on immature bees.

Poinar (2004c) reported a phoretic scale insect (Hemiptera: Coccinea) on a Salticidae spider in BA.

Some *Parasitodiplogaster* (Nematoda) use fig wasps (Agaonidae, Hymenoptera) as a way of being transported to a fig plant when is being pollinated by the wasp. An example of this phoretic behavior is known in DA (Poinar and Poinar, 1999, fig. 23).

Defense behaviour

Defense behaviour is sometimes recorded in amber: Grimaldi (1996, p. 93) reported a praying mantis attacked by ants in DA. *Nasutitermes* cone shaped soldiers are frequent in DA although never found in defensive action (Poinar and Poinar, 1999, fig. 117). Sometimes stress behaviour could be erroneously interpreted as defense behaviour; this is probably the case of a *Nasutitermes* soldier producing a defense secretion (Poinar, 1998b)

INTERACTIONS WITH THE FRESH RESIN

Stress behaviour: egg laying, defecation, bitting, ejaculation…

Virtually all examples of animal behaviour "frozen" in amber are distorted due to the interaction of the organism struggling against the sticky resin. This is the case of female's ovopositing in resin (see "Egg lying" above). But also defecation is reported as a stressed behaviour in resin: Geirnaert (2002, fig. 160) reported a Coleoptera from amber without locality (probably BA) and Poinar (1998b) reported a termite in DA. A frequent stress behaviour in amber is bitting, one ant, struggling with the resin bites another trapped ant trying to pull itself free of the resin; some examples are known in BA (http://www.brost.se) (Kobbert, 2005, pp. 123-126) and in DA (Ross, 1998, fig. 76; Wu, 1997, fig. 604). Finally an ejaculation as stressed behaviour in a Mymarommatidae (Hymenoptera) is known in SA (Martínez-Delclòs et al., 2004).

Movements into the fresh resin

It is very frequent that struggle of trapped animals in fresh resin produce distortion in the resin flows (Martínez-Delclòs et al., 2004, fig. 2C).

Lost of pieces

Sometimes trapped organism in sticky resin brake off some of their pieces (mainly legs) in their effort to escape for example Ross (1998, fig. 62) reported a Limoniidae in BA and Krzemisnka and Krzeminski (1992, fig. 142) a harvestman (Opiliones) in BA with broken legs.

Secretion of glands

Some organism could make secretions of their glands when they become trapped in amber. These secretions could react with the resin and produce a halo around the animal, for example a Staphylinidae in BA (Krzeminska and Krzeminski, 1992, fig. 102). Scretions could also produce bubbles in the fresh resin, for example a Throscidae in DA (Grimaldi and Engel, 2005, fig. 10.41).

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