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Taphonomy of insects in carbonates and amber

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Abstract

The major taphonomic processes that control insect preservation in carbonate rocks (limestones, travertines and nodules) are biological: insect size and wingspan, degree of decomposition, presence of microbial mats, predation and scavenging; environmental: water surface tension, water temperature, density and salinity, current activity; and diagenetic: authigenic mineralisation, flattening, deformation, carbonisation. The major taphonomic processes that control the preservation of insects in fossil resins (amber and copal) are different, but can be considered under the same headings – biological: presence of resin producers, size and behaviour of insects; environmental: latitude, climate, seasonality, resin viscosity, effects of storms and fires, soil composition; and diagenetic: resin composition, insect dehydration, pressure, carbonisation, thermal maturation, reworking, oxidation. These taphonomic processes are geographically and temporally restricted, and generate biases in the fossil record. Nevertheless, where insects occur they may be abundant and very diverse. Taphonomic processes may impact on phylogenetic and palaeobiogeographic studies, in determining the timing of the origin and extinction of insect groups, and in identifying radiations and major extinctions. Taphonomic studies are an essential prerequisite to the reconstruction of fossil insect assemblages, to interpreting the sedimentary and environmental conditions where insects lived and died, and to the investigation of interactions between insects and other organisms.

Keywords: fossil insects; preservation; limestone; resin

1. Introduction

Insects are by far the most diverse and successful group of macroscopic organisms and they play an important role in all the terrestrial ecosystems that they inhabit. The fossil record of insects and their diversity through time have been reviewed (Carpenter, 1992; Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996; Ross et al., 2000; Jarzembowski, 2001b) as well as the palaeobiology of insect feeding (Labandeira et al., 1994; Labandeira, 1997). The earliest record of the Insecta is from the Lower Devonian of Gaspé (Québec) (Labandeira et al., 1988), but the group is not evident in the fossil record in significant numbers until the Upper Carboniferous (Brauckmann et al., 1995). The number of

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insect orders present in the Permian was similar to that of now; the record of families identifies major periods of origination in the Permo–Carboniferous, Early Jurassic, Early Cretaceous and Palaeocene (Jarzembowski and Ross, 1996). The degree to which the recorded diversity of insects is a reflection of taphonomic processes is very difficult to determine. A knowledge of the conditions that led to the preservation of insect biotas, and of the biases introduced by taphonomic processes, is also essential for interpreting the role of insects in terrestrial ecosystems, such as organic matter recycling and the pollination and distribution of plant taxa. Here we review the major taphonomic processes that affect insects.

Insects lack biomineralised tissues and are usually considered by palaeontologists as soft-bodied organisms. Exceptional conditions are normally required to ensure their preservation, but where taphonomic processes are favourable, insects may be extremely abundant. However, there is clearly a significant range in susceptibility to decay, for example between flies and beetles, reflecting contrasts in the degree of sclerotisation of the cuticle. Nonetheless, laboratory experiments have shown that even fly carcasses may survive in quiet sedimentary settings for more than a year without disarticulating (Martínez-Delclòs and Martinell, 1993).

The most exceptionally preserved insects in sedimentary rocks occur in fine-grained laminated carbonates in lacustrine and shallow marine settings, where conditions may be suitable for the preservation of truly labile soft-tissues (e.g. Solnhofen, Germany: Frickhinger, 1994). They provide a basis for contrasting preservation with that in amber. The different taphonomic processes that control the preservation of insects in carbonate rocks and in amber result in samples of different insect communities. Amber normally preserves insects regardless of their susceptibility to decay, but selective preservation is often a feature of insect assemblages in carbonates. The occurrence of insects is normally considered to identify a fossil deposit as a Konservat-Lagerstätte or conservation deposit (sensu Seilacher, 1970) where the emphasis is on the quality of preservation rather than the abundance of fossils. Konservat-Lagerstätten which preserve non-biomineralised tissues are a critical source of palaeobiological data that are not available from the ‘shelly’ fossil record (Briggs, 1995a). The preservation of delicate structures allows for more detailed comparison with recent organisms. The controls on the preservation of non-biomineralised tissues, so-called soft-bodied fossils, are more complex than those on shelly taxa, which are dominantly sedimentological (Kidwell, 1991) – they include organic matter input, microbial activity, and environmental geochemistry (Allison and Briggs, 1991a,b; Briggs, 2003a).

Insect body fossils occur in a variety of environmental settings including peat deposits (Kenward, 1976; Hayashi, 1994; Lavoie et al., 1997), deserts (e.g. Chihuahuan Desert, USA, Quaternary: Elias, 1990; desert sands Mauritania, Quaternary, Azar pers. commun.), lakes and rivers (e.g. Montsec and Las Hoyas, Spain, Lower Cretaceous: Martínez-Delclòs, 1995; Meléndez, 1995; Sézanne and Auriol travertines, France, Eocene: Nel and Blot, 1990; Papazian and Nel, 1989), deltas (e.g. Vosges, France, Middle Triassic: Gall, 1996; Marchal-Papier, 1998), lagoons (e.g. Solnhofen, Germany, Upper Jurassic: Malz, 1976; Frickhinger, 1994), open marine environments (e.g. northern Switzerland, Lower Jurassic: Etter and Kuhn, 2000), and deeper marine turbidites (e.g. Borredà, Spain, Eocene: Gaudant and Busquets, 1996). The spatiotemporal distribution of these palaeoenvironments was a major control on the insect fossil record.

Where insects are preserved in calcium carbonate, precipitation may occur as calcite mud (e.g. Green River, USA, Eocene: Ferber and Wells, 1995), aragonite mud (e.g. Rubielos de Mora, Spain, Miocene: Peñalver, 1998), and dolomite mud (e.g. Karatau, Kazakhstan, Upper Jurassic: Seilacher et al., 1985). Fossil insects also are preserved in a variety of other sedimentary contexts: clays and marls (Nel, 1986), siltstones (Martínez-Delclòs and Nel, 1991), sandstones (Nel et al., 1993), lacustrine diatomites (Hong, 1985; Riou, 1995), cherts (Whalley and Jarzembowski, 1981), evaporites (Priesner and Quievreux, 1935; Schlüter and Kohring, 2001), phosphates (Handschin, 1944), coal measures (Bartram et al., 1987; Shear and Kukalová-Peck, 1990; Jarzembowski, 2001a), and asphalt (Miller, 1983, 1997; Iturralde-Vinent et al., 2000). Here we focus on the two most important sources of fossil insects, carbonates and amber.

Repositories are abbreviated as follows: MNHN, Muséum National d'Histoire Naturelle, Paris, France; PIN, Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia; MCAM, Museu de la Ciència, Fundació 'La Caixa', Barcelona, Spain; EPGM, Dept. Estratigrafia, Paleontologia i Geociències Marines, Univ. Barcelona, Barcelona, Spain; MCNA, Museo Ciencias Naturales de Álava, Vitoria–Gasteiz, Spain; MCCM, Museo de Ciencias de Castilla–La Mancha, Cuenca, Spain; MPV, Museu Paleontològic de València, València, Spain; JME, Jura-Museum, Eichstätt Germany; QM, Queensland Museum, Brisbane, Australia; IEI, Institut d'Estudis Ilerdencs, Lleida, Spain.

2. The importance of insect Konservat-Lagerstätten

Konservat-Lagerstätten reveal the diversity of insects in the past. Different taphonomic processes bias the preservation of insects in carbonates and amber in different ways. A more diverse range of taxa and sizes is preserved in carbonates whereas amber is usually dominated by particular taxonomic groups and size categories (Zherikhin et al., 1999). In the Lower Cretaceous of Spain, for example, only a few families of insects occur in both the Montsec limestones (Peñalver et al., 1999) and Álava amber (Martínez-Delclòs et al., 1999; Alonso et al., 2000). The occurrence of insect compression fossils in sediment that also yields insect-bearing resin is extremely rare. Notably, a well preserved cockroach wing was found associated with amber from the Palaeocene Due Formation at Urtuy, on the Naiba River of Sakhalin Island, Russia (Zherikhin, pers. commun., 2001). Fossil insects also have been found in both limestone and amber from the same exposure. Such amber localities include the Lower Cretaceous of Lebanon (Azar, 2000) and the Upper Cretaceous of New Jersey (Grimaldi et al., 2000).

Evidence of ecologic relationships between insects and other animals is sometimes preserved in limestones, where it is usually confined to plant–insect interactions (Labandeira, 1998; Waggoner, 1999). Such behaviour is inferred on the basis of functional morphology, or gut contents (Schaal and Ziegler, 1992; Krassilov et al., 1997) or more commonly coprolites (Rothwell and Scott, 1988), or an array of primary evidence for insect feeding (Rößler, 2000; Labandeira and Phillips, 2002). Amber, on the other hand, commonly reveals interactions, such as reproduction (mating, egg laying), commensalism and parasitism between different insects, and between insects and other organisms such as nematodes, spiders, pseudoscorpions, mites and ticks, and vertebrates (Poinar, 1984; Poinar et al., 1994; Grimaldi, 1996; Weitschat and Wichard, 1998). Plant damage is very rarely recorded in amber (e.g. Poinar and Brown, 2002).

Konservat-Lagerstätten reveal other features of an ecosystem. The presence of certain taxa, such as termites (Nel and Paicheler, 1993), or assemblages of insects, may indicate particular climatic conditions (McCobb et al., 1998; Poinar et al., 1999; Duringer et al., 2000; Miller and Elias, 2000). Adult and worker termites have been found in the Lower Cretaceous of Spain and Siberia indicating that social behaviour had evolved in this group by this time, earlier than it did in ants or bees (Martínez-Delclòs and Martinell, 1995). Some taxa imply the presence of others. Rasnitsyn (1968) described the oldest cephid sawflies (Hymenoptera, Cephidae) from the Lower Cretaceous of Baissa in Transbaikalia. Cephid sawflies are associated exclusively with angiosperms and, as predicted, angiosperm leaves and seeds subsequently were found at the locality (Rasnitsyn, pers. commun.). The occurrence in the Lower Cretaceous ambers of Spain of wasps (Evaniidae), for example, which are parasitic on the eggs of cockroaches, suggests that cockroaches were present even though they have not been recorded.

Konservat-Lagerstätten provide evidence of factors controlling the growth of authigenic minerals in sediments and amber. In carbonate rocks fossil insects are usually preserved as organic remains of the cuticle, or as a mould where the cuticle has been lost during diagenesis or weathering (Martínez-Delclòs et al., 1995). Early mineralisation may replicate insect morphology in calcite (McCobb et al., 1998; X.M.-D., pers. observation in Las Hoyas), pyrite transformed to goethite (Grimaldi and Maisey, 1990), or in calcium phosphate (Duncan et al., 1998). 3-D preservation may occur in calcium sulphate, such as gypsum from the Miocene of Alba, Italy (Chiambretti and Damarco, 1993; Schlüter and Kohring, 2001). Authigenic minerals rarely form in resin. Pyrite may penetrate amber along fracture planes (Karwowski and Matuszewska, 1999), coating the insect inclusion (Schlüter and Stürmer, 1982; Krzeminska et al., 1992; Grimaldi et al., 2000).

Exceptionally preserved deposits may yield ancient biomolecules. DNA has been reported from insects in amber (Desalle et al., 1992; Cano et al., 1992, 1993) but its preservation is controversial due to its susceptibility to both hydrolytic and oxidative damage (Lindahl, 1993; Smith and Austin, 1997; Austin et al., 1997), and to the difficulty of eliminating contamination by recent DNA. Decay-resistant tissues, such as the cuticles of some insects, have a higher preservation potential that is controlled by three major factors (Briggs, 1999): (1) the nature and composition of the cuticle, exemplified by its better preservation in the thick sclerotised elytra of beetles than in other insects; (2) the depositional environment, such as resin vs. sediment, which influences decay rate; and (3) diagenetic history, including polymerisation, which is controlled by thermal effects and reaction time. The chitin and protein in insect cuticle have only been reported from later Cenozoic deposits (Miller et al., 1993; Stankiewicz et al., 1998a; Flannery et al., 2001); weevil cuticle in the Oligocene lacustrine shales of Enspel, Germany, preserves the oldest traces (Stankiewicz et al., 1997b). In older examples the original biomolecules are altered to kerogen (Briggs and Eglinton, 1994; Stankiewicz et al., 1997a, b; Briggs, 1999). Stankiewicz et al. (1998b) demonstrated that chitin is not preserved in Dominican amber, confirming that the preservation of DNA is highly improbable (Austin et al., 1997).

3. The role of microbial mats in insect preservation

Microbial mats may facilitate the preservation of insects in a number of ways (Briggs, 2003b). Mats are complex communities of photosynthetic prokaryotes (cyanobacteria), diverse unicellular algae, and chemautotrophic micro-organisms (Gall, 1990). Anaerobic and aerobic species coexist. Cyanobacteria may be spherical or filament-like and they form a mat by secreting mucilage. Details of fossilised microbial mats may be revealed by scanning electron microscopy (Gall et al., 1985).

Where microbial mats form on the surface of standing bodies of water, they may trap insect carcasses and transport them to the sediment–water interface when the mat sinks (Gall, 1995; Harding and Chant, 2000). Where a carcass is overgrown by a mat, it is protected from erosion and from scavengers and burrowing animals (Gall, 1990, 1995) and is prevented from floating. Microbial mats may reduce decay by acting as a barrier and promoting conditions unfavourable to certain bacteria (Gall, 1990, 2001). Microbial mats may also prevent the transfer of ions, leading to concentrations within the carcass sufficient to promote mineralisation of soft-tissues or of the mat itself (Briggs and Kear, 1993; Gall et al., 1994; Sagemann et al., 1999). Where the mat becomes mineralised, as in fossils from the Messel Shale and from Enspel (Wuttke, 1983; Toporski et al., 2002), it may form a pseudomorph of the carcass, preserving the gross morphology of the soft-tissues.

Microbial mats develop today in extreme environments, such as sabkhas, intertidal flats, and anoxic marine bottom water, conditions that are hostile to most organisms. Marine microbial mats have been reported in the Upper Jurassic Solnhofen Limestone, Germany, which yields a significant assemblage of insects (Keupp, 1977; Frickhinger, 1994). Most of these insects are preserved as moulds or by precipitation of calcite or pyrolusite; phosphate mineralisation is rare, amounting to $<8\%$ of individuals (Wilby et al., 1995). Lacustrine microbial mats have been reported in the Miocene basins of Rubielos de Mora and Bicorp, Spain, which yield important assemblages of insects (Peñalver et al., 2002a). 3-D caddisfly pupae are preserved in Miocene freshwater limestones in Saint-Gérard-le-Puy, France, associated with possible mats (Hugueney et al., 1990). However, more decay prone soft-tissues may not be mineralised even where microbial mats occur, as in the Middle Triassic Grès à Voltzia, Vosges, France, which yields a diversity of insects (Gall, 1990; Marchal-Papier, 1998). Additionally, insects have not been reported from the Upper Jurassic of Cerin, France, which preserves phosphatised soft-tissues in association with microbial mats (Gall et al., 1985; Wilby et al., 1996).

4. Resin as a preservational medium

Resins are produced by specialised tree cells and exuded through fissures. Amber is a fossilised natural resin with properties similar to amorphous polymeric glass (Poinar, 1992). Resins are a complex mixture of terpenoid and/or phenolic compounds (Anderson and Crelling, 1995). Their chemical composition is diverse but they are soluble in alcohol and insoluble in water. Terpenoids may be volatile, where mono- and sesquiterpenes provide fluidity and act as plasticisers, or they may be non-volatile, as in the case of diterpenoids or sometimes triterpenoids (Langenheim, 1995). Among terpenoids, the most common are oxygenated terpenes: acids, alcohols and esters secreted from plant parenchyma cells. The polymerisation of non-volatile terpenoids promotes copal and amber formation, as volatile terpenoids escape to the atmosphere. The chemical composition of amber is only partially known, due to its insolubility. Notably, Lebanese amber has been dissolved with chloroforms, but the chemical composition has not been published (Azar, 1997). Infrared Spectrometry (IRS) has been employed in comparative studies of fossil and modern resins, allowing the tree producers to be identified (Beck, 1999; Kosmowska-Ceranowicz, 1999), and the categorisation of amber into different types. A classification of fossil resins was proposed by Anderson and Crelling (1995).

Oils, oleo-resins and resins are produced by both gymnosperms and angiosperms for defence against herbivores and pathogens such as insects and fungi. They are common and diverse in recent tropical ecosystems (Farrell et al., 1991). Neither oils nor oleo-resins are known to be a source of amber (Langenheim, 1995). Copals are resins with a low oil content, mainly from the araucariacean *Agathis* (Philippines, New Zealand) and the leguminoseans *Hymenaea* and *Copaifera* (Africa, Caribbean and South America), used to make hard and elastic varnishes. Some dipterocarpaceans from Southeast Asia produce dammar resins. Fossil copal of both araucariacean and leguminosean origin with insect inclusions is known from several localities in the Southern Hemisphere (Poinar, 1991a; Schlüter, 1993). Araucariacean copal occurs in northern New Zealand and Victoria, Australia, where it is known as kauri, and in the South Pacific region, Indonesia and the Philippines, where it is known as Manila copal. Leguminosean copal occurs mainly in Africa, in the Caribbean and South America. Copal from *Hymenaea* spp. is known from northwestern Madagascar, in the eastern parts of Kenya and Tanzania, the Santander region in Colombia, Minas Gerais in Brazil, and the eastern part of the Dominican Republic. Copals produced by *Copaifera* are known from West Africa, and that produced by dipterocarpaceans from Malaysia and Sumatra, where it is known as dammar. Insects and other arthropods are abundant in copals, particularly in kauris from New Zealand and copals from Madagascar, Kenya, Tanzania and Colombia. Due to the young age of these resins, which range up to a thousand years old, the entombed insect associations are similar to those of today (Schlüter, 1993).

Resin is produced by at least three families of conifers and twelve of angiosperms, but only some of these generate amber in the fossil record. The conifers are Pinaceae, Araucariaceae and Taxodiaceae (Taxodiaceae is now included within Cupressaceae: Stefanovic et al., 1998); the angiosperms are Leguminosae, Burseraceae, Dipterocarpaceae, Hamamelidaceae (Langenheim, 1995), and Combretaceae (Nel et al., in press). The Leguminoseae include the Southern Hemisphere *Hymenaea* which yields copious quantities of resin (Langenheim, 1995). Dominican and Mexican ambers were produced by an extinct relative of the West Indian locust (*H. protera*) (Poinar, 1991b). Most Mesozoic ambers and Eocene Baltic amber are considered to be a product of araucariacean conifers as shown by their similarity to the resin of Recent *Agathis* (Langenheim, 1995; Beck, 1999). Anderson and LePage (1995) suggested, however, that Baltic amber originates from a pinaceous conifer similar to *Pseudolarix*.

5. Distribution of amber through time

It is difficult to produce a comprehensive list of insect occurrences in carbonates due to the enormous number of localities involved and the range in quality of preservation and assemblage diversity (Allison and Briggs, 1991b). Amber deposits, on the other hand, are geographically and temporally restricted (Poinar, 1992; Grimaldi, 1996). The earliest known fossilised resins are from Upper Carboniferous pteridosperms of England (van Bergen et al., 1995), but amber did not become abundant until the Early Cretaceous with the rise of the coniferous Araucariaceae, particularly in tropical and subtropical forests. The earliest ambers with inclusions are from Jezzine and Hammana, in the Lower Cretaceous of Lebanon. More than 60% of the insects in amber from Hammana are flies, including taxa that indicate

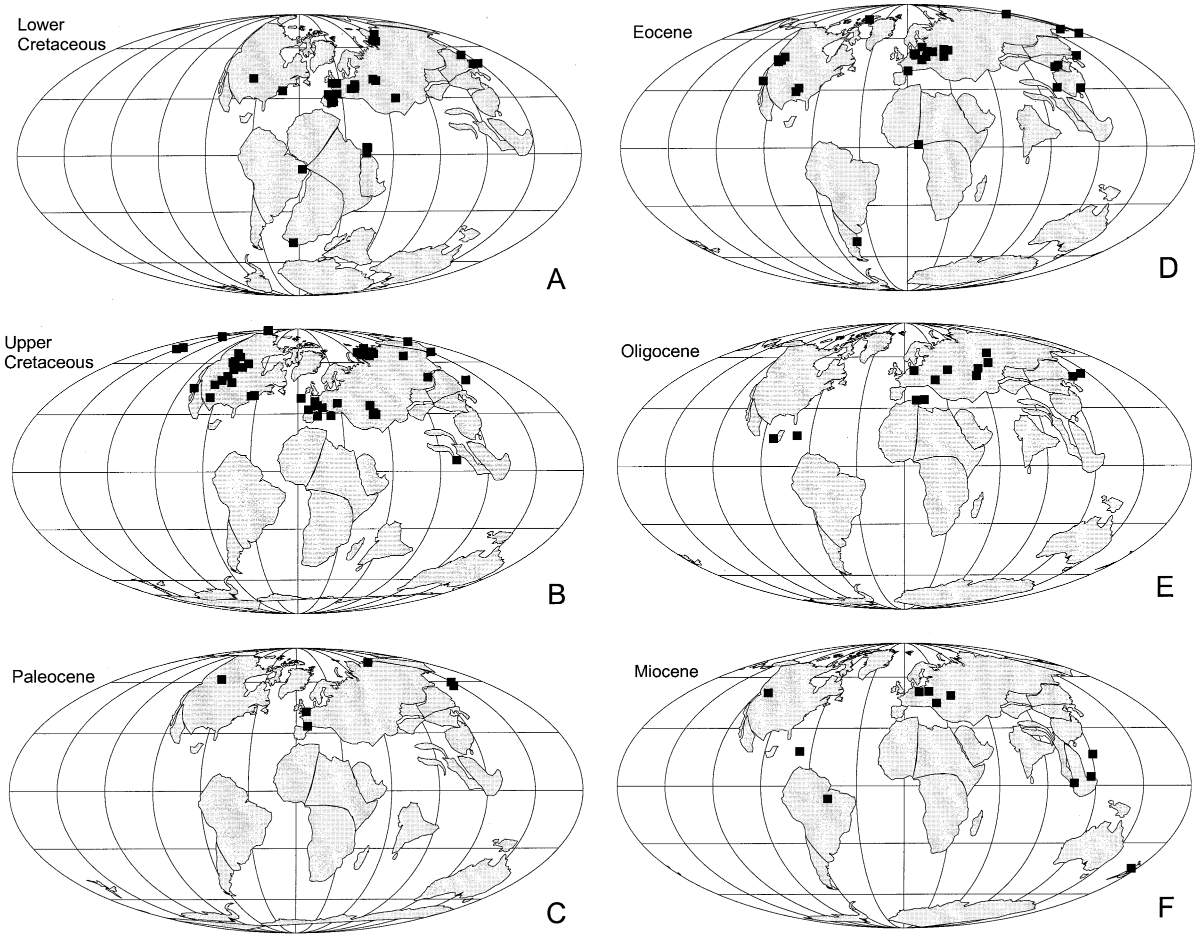


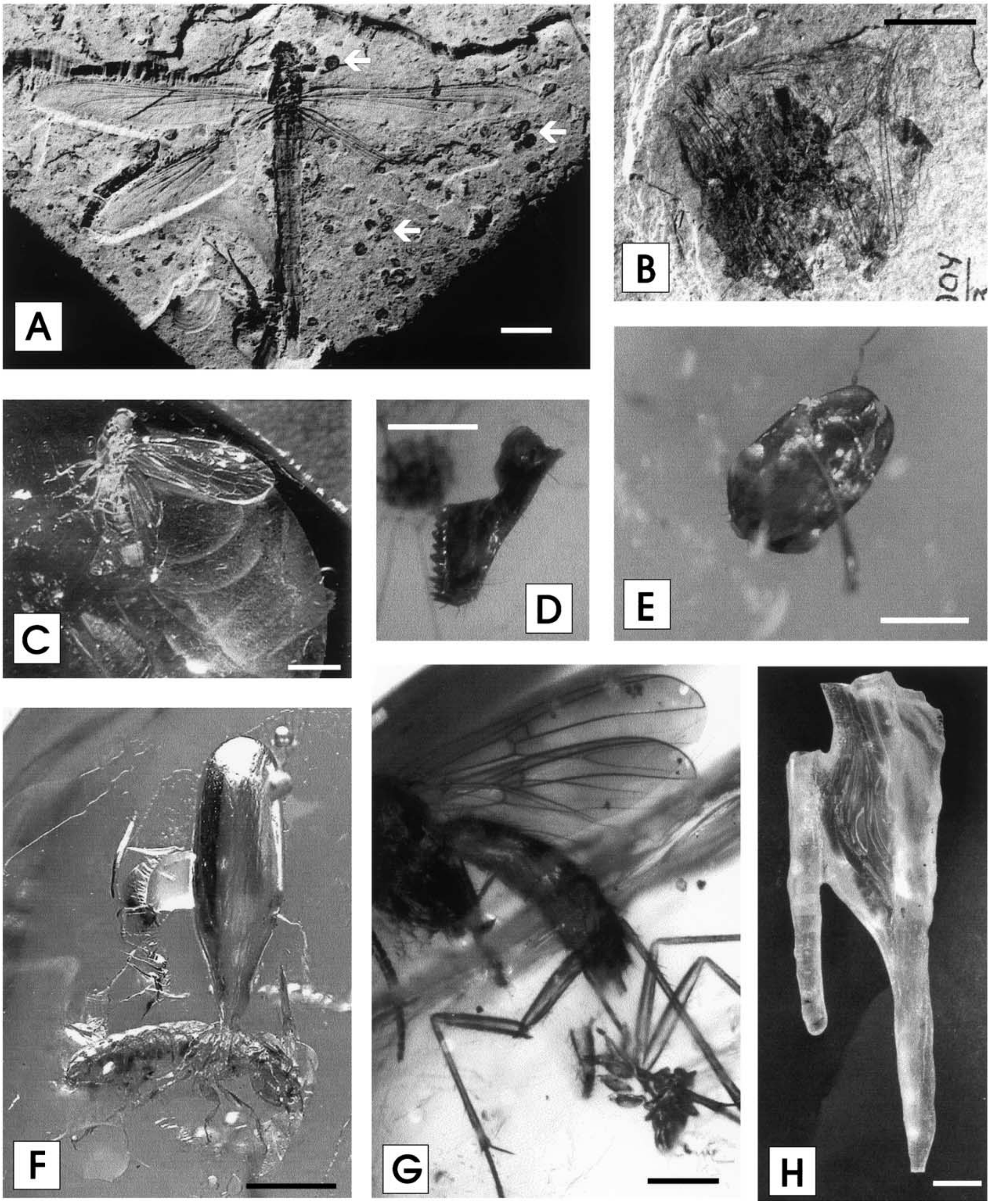
Fig. 1. Palaeogeographic maps showing the principal localities (see Appendix 1) that yield amber. (A) Lower Cretaceous. (B) Upper Cretaceous. (C) Palaeocene. (D) Eocene. (E) Oligocene. (F) Miocene.

that the resin formed in a warm climate within a wet leafy forest (Azar, 2000). While some of the earliest Cretaceous amber-bearing deposits (Fig. 1A) formed between the equator and 4°N (Israel and Lebanon), they are concentrated in northern mid-latitudes, between 29°N (Azerbaijan) and 50°N (Japan), the moist megathermal zone based on vegetation distributions of Morley (2000). By the end of the Early Cretaceous, while occupying a similar equatorial range, amber extended north from 27°N (Spain) to near 70°N (Khatanga, Russia), coinciding with the moist megathermal zone of the Northern Hemisphere. Galle (2000) regarded the climate of the Tethys Region, where a large number of amber-bearing localities are to be found, as generally humid during the Lower Cretaceous and becoming more arid in the Upper Cretaceous. The presence of amber in extensive lower-latitude coals in the Lower Cretaceous of Lebanon and Spain is consistent with very humid conditions (Barrón et al., 2001). A small number of localities, such as those in northern Siberia, represent cool temperate conditions. Equatorial occurrences, corresponding to hot, relatively dry conditions, occur in Brazil and the Middle East. Only one amber locality is known in the Southern Hemisphere, in South Africa (Gomez et al., 2002).

No Upper Cretaceous amber is known from the Southern Hemisphere (Fig. 1B). The only equatorial occurrence is from the earliest Upper Cretaceous of Burma, which predates the widespread development of megathermal angiosperm-rich forests in equatorial latitudes towards the end of the Cretaceous (Morley, 2000). Localities are mainly in the northern, moist, megathermal zone along the northern margin of the Tethys Ocean and in North America. Barron and Peterson (1990) considered that the Tethys Ocean would have been dominated by two clockwise gyres of ocean surface currents during the Cretaceous, with a dominantly easterly flow along its the northern side. Climate modelling (Barron et al., 1989) predicted a strongly developed monsoon in the Tethys area during the Cretaceous. Elevated temperatures resulted in high rates of evaporation and precipitation, which produced very high seasonal rainfall on the northern and southern borders of the Tethys Ocean (Barron et al., 1989), allowing the formation of coals (Parrish et al., 1982). In North America amber localities border the epicontinental seaway flanked by warm temperate wet vegetation (biome 5 of Horrell, 1991), which includes Cupressaceae. The insect amber assemblage from the Upper Cretaceous Raritan Formation of New Jersey (Grimaldi et al., 2000) suggests a warm temperate or subtropical climate, similar to that of Siberian and Canadian Upper Cretaceous amber forests. Grimaldi et al. (2000) estimated a palaeolatitude of 32°N for this amber, but palaeogeographic considerations place it at 40°N. Greenhouse conditions, with particularly high temperatures during the Middle Cretaceous (Huber et al., 2002) are evidenced by the nature of the terrestrial vegetation which indicates a cool temperate regime even at high latitudes. In this context, ambers are found at $>80°$N in Alaska. Berner (1990) considered that levels of atmospheric CO_2 were eight to ten times those of the present day, reaching a maximum at the beginning of the Late Cretaceous.

The climatic history of the Cenozoic can be divided into two episodes (Pickering, 2000): the Palaeocene to Eocene interval was characterised by a continuation of the greenhouse conditions of the Upper Cretaceous whereas cooling occurred during the Oligocene to Recent period with occasional short and warmer episodes. There is a paucity of Palaeocene amber (Fig. 1C): only 0.5 major occurrences per million years, compared to 1.65 in the Upper Cretaceous and nearly 2 in the Eocene. There also are no Palaeocene occurrences in the Southern Hemisphere nor in the tropical rain forests of the equatorial Palmae Province. The few amber occurrences are in the northern rain forests of the Boreotropical Province, or in temperate latitudes further to the north.

The number and geographical spread of amber localities is much more extensive during the Eocene (Fig. 1D). Amber is represented in the tropical rain forests of the Southern Megathermal Province (Argentina) and the African Province (Nigeria) but the majority of localities (including Baltic amber) occur in the Boreotropical Province. Amber is present in the dry subtropics of China and the Kamchatka Peninsula to the south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of the Boreotropical Province and in more temperate latitudes to the north.

Following the terminal Eocene cooling event the global extent of rain forests was substantially reduced. Tropical rain forest remained in the Caribbean region, as evidenced by Dominican Republic and Mexican amber derived from *Hymenaea*, and apart from localities in Tunisia and Sicily where the climate was presumably dry, most Oligocene amber is found in a mid-latitude belt across Eurasia (Fig. 1E). Oligocene amber is unknown from the Southern Hemisphere, but the mid-latitude belts and tropical rain forests have yielded amber during the Miocene in both the Northern and Southern Hemispheres (Fig. 1F). Most Mesozoic ambers and Eocene Baltic amber are a product of araucariacean conifers (but see Anderson and LePage, 1995). As the climatic constraints on the distribution of these taxa are poorly known, they cannot be used directly to infer the climatic controls on amber.

6. Insect taphonomy

Taphonomy deals with the incorporation of organic remains into sediments or other contexts, such as resin, and the fate of these materials after burial. It is normally divided into: necrolysis, referring to death and its causes; biostratinomy, involving the sedimentary history of the remains prior to burial; and diagenesis, comprising physical and chemical modifications within the sediment or resin.

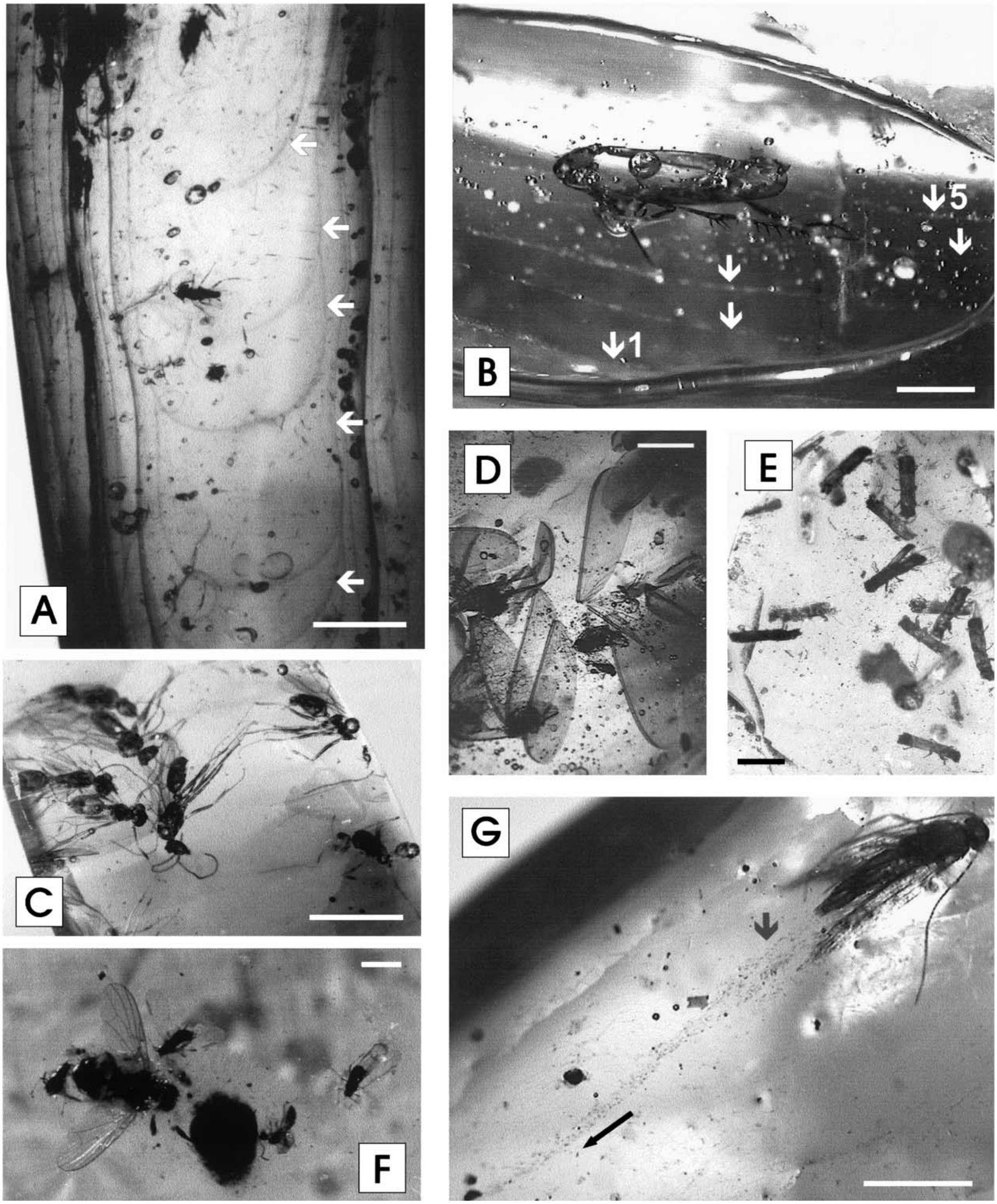
6.1. Necrolysis

6.1.1. Necrolysis in aquatic settings

Where fossil insects occur in carbonates, biomineralised and non-biomineralised remains of other organisms are found in association, and often soft-tissues or delicate structures are preserved, as in the Lower Cretaceous of Liaoning, China (Fig. 2A). Insect assemblages preserved in carbonate are often dominated by species that rely on water for ecological reasons such as habitat, for hunting, or for laying eggs. Assemblages of mayflies, termites, and flying ants, for example, may be the result of a mass mortality, and/or show a bias toward a particular size range. Smith (2000), for example, demonstrated that the insect assemblage that accumulated around a recent ephemeral lake in Arizona is biased towards smaller robust species, and also to ground-dwelling forms. She compared the diversity of living insects, mainly beetles, that occur in different environments around the lake with the assemblage preserved in the shallow, subsurface sediments along the lakeshore. 65% of living beetle families and 28% of living beetle genera were represented in the sediments; 100% of the families and 91% of the genera found dead were present in the live fauna. The relative abundance of beetle families in the living assemblage is significantly different from their relative abundance in the sediments, from which the best represented groups are the families of hymenopterans (62%) and coleopterans (30%).

Soft-tissues of all organisms are quickly degraded by bacteria and fungi, which may completely destroy a carcass in a few days, depending on its size, the water temperature and other ambient factors. Martínez-Delclòs and Martinell (1993) studied the death of insects in aquatic environments to determine the taphonomic processes that influence insect fossilisation. Observations were made on cockroaches, crickets, earwigs, ter-

Fig. 2. (A) *Bellabrunetia catherinae*, terrestrial dragonfly with aquatic conchostracans (white arrows). MNHN-LP-R 55232a, Upper Jurassic/Lower Cretaceous, Liaoning (China); photo by A. Nel; scale bar = 10 mm. (B) Coprolite or regurgitate with dragonfly wings. PIN 2904/3; Upper Jurassic, Karatau (Kazakhstan); scale bar = 10 mm. (C) Homopteran showing wings and body movements. MCAM0043; Miocene amber from Hispaniola (Dominican Republic); scale bar = 5 mm. (D) Isolated insect mandible. MCAM0005; Miocene amber, Hispaniola; scale bar = 0.5 mm. (E) Isolated ant head. MCAM0095; Miocene amber, Hispaniola; scale bar = 1 mm. (F) Worker termite with an air bubble extending from its body due to the activity of gut microbes. MCAM0508; Miocene amber, Hispaniola; scale bar = 2 mm. (G) Female of Diptera, Keroplatidae laying eggs during entrapment, EPGM-RD-0048; Miocene amber, Hispaniola; scale bar = 1 mm. (H) Copal stalactites, Martín-Closas collection, EPGM; Holocene, Madagascar; scale bar = 10 mm.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restrial bugs, mayflies, true flies, wasps, ants, beetles, snakeflies, lacewings, and butterflies. Three different stages were considered: (a) on the water surface, during death and while the body was floating, (b) during sinking, while the insect was alive or immediately following death, and (c) on the bottom at the substrate–water interface. They compared their experimental results with fossil insects preserved in lithographic limestones.

The results of this study indicated that different types of insects behave in varied ways when they enter water. There are two patterns.

(1) *Non-winged insects* show two types of behaviour when they fall into water. Those with a density less than water, such as worker ants, walk easily on the surface allowing them to escape. They raise the abdomen with rhythmical movements presumably allowing them to breathe. Larger wingless forms, such as earwigs, penetrate the surface tension because of their violent movements and sink rapidly, dying by asphyxia on the bottom.

(2) *Winged insects* also show two types of behaviour. Those with some capacity to escape, especially hymenopterans such as winged ants and wasps; dipterans such as house flies and horse flies; snakeflies and lacewings; beetles such as weevils, ladybirds and carabids; and true bugs such as acantosomatids, pentatomids, pirrocorids and reduviids fold the wings and raise them above the water while trying to take off. If the insect fails to fly or escape to the edge it dies exhausted with the wings extended. Wasps flex the abdomen anteriorly when they die. The death throes do not exceed 2 h. Cockroaches are unusually resilient; they can move rapidly and survive on the surface of the water for up to 36 h. If the cockroach is removed from the water during this time, it will remain still for some minutes before flying and walking normally. Nevertheless, cockroaches are common in carbonates from the Late Carboniferous to the Cretaceous. Their reduced abundance thereafter is unlikely to be a reflection of preservation potential; the tegmina of blattoids have been sclerotised since the Carboniferous. They are rare in Tertiary limestones, although an exception is their elevated representation in the Palaeocene of Menat, France (Nel, pers. commun.). Cockroaches are more common in Tertiary than in Cretaceous amber, where they are rare, except for Lebanese amber (Azar, pers. commun.).

Winged insects that are unable to escape include small-bodied taxa with a wing span less than 5 mm, such as planthoppers, aphids, flies and wasps and those taxa with a large wingspan like butterflies and grasshoppers. These taxa lack sufficient strength to escape the water surface. They become exhausted after a few minutes and die by asphyxia within an hour. Winged grasshoppers remain lying on their side with the wings folded dorsally. They can move on the water surface but may die in this position. Laterally flattened crickets are very common in limestones (Martínez-Delclòs and Martinell, 1993; Peñalver, 1998). The death throes of insects produce surface ripples that attract predators, including other insects, fish, birds and pterosaurs. Fish and crocodiles usually eat the whole insect but wings and highly sclerotised parts may be regurgitated intact or defecated (Fig. 2B).

When aquatic insects die from environmental agents or predation, the carcass does not have to penetrate the surface tension to sink to the bottom. For example, cases of caddisfly larvae are abandoned as the insect emerges and may be buried in the sediment, forming, for example, *In-*

Fig. 3. (A) Successive flows (white arrows) that include several insects. EPGM-RD-0049; Lower Miocene, Hispaniola; scale bar = 2 mm. (B) Homoptera, Cicadellidae, covered by five successive flows of resin. Insect was trapped in flow 1 and finally covered by flow 5 (white arrows). EPGM-RD-0050; Miocene amber; Hispaniola, scale bar = 1 mm. (C) Swarm of ant imagoes. MCAM0409; Miocene amber; Hispaniola, scale bar = 10 mm. (D) Isolated termite wings that separated along the humeral suture after nuptial flight. EPGM-CC-0051; Pleistocene–Holocene, Santander (Colombia); scale bar = 2 mm. (E) Platypodid borer beetle swarm. MCAM0034; Miocene amber, Hispaniola; scale bar = 2 mm. (F) Small living insects trapped by surface tension and decomposed before sinking, scale bar = 2 mm. (G) Butterfly wing scales (grey arrow) displaced from the body by successive flows, after partial decomposition; black arrow shows the flow direction; copal stalactite, Martín-Closas collection, EPGM; Holocene, Madagascar; scale bar = 2 mm.

dusia cypridis from the Late Eocene of Florissant, Colorado, a case constructed of the shells of the ostracod *Cypris florissantensis* (Meyer, 2003). Sukatsheva (1982) even proposed a Mesozoic and Tertiary continental biostratigraphy based on caddisfly cases.

Insects may also be introduced into aquatic settings following forest fires. Grimaldi et al. (2000) found a large diversity of fusanised insect remains in Upper Cretaceous clays from New Jersey that also yielded fossiliferous amber. These fusanised insects represent a fossil scrub community prone to wildfire. Jarzembowski (2001a) reported beetle remains preserved as fusain from the Lower Cretaceous of the Weald, southern England, showing ultrastructural details.

6.1.2. Necrolysis in resins

Amber, in contrast to sedimentary rock, may retain evidence of the death throes of the insects fossilised within it. For example, wing movement (Fig. 2C), disarticulation of body parts (Fig. 1D–E), escape of decay gases, typically as a stream of bubbles (Fig. 2F), and egg laying (Fig. 2G), are commonly preserved. Poinar (2000) reported the preservation of spermatophores with sperm in a springtail in Baltic amber. Shedding of spermatophores commonly occurs during decay of Recent insects, but is rarely observed in the fossil record. The oldest known example is from a tiny wasp from the Lower Cretaceous Álava amber of Spain (Fig. 8C).

Resin may form in plant parenchyma cells and accumulate in internal channels and cracks within the wood and under and within the bark as well as on the surface of the tree (Fig. 2H). Sometimes trunks may even burst due to resin pressure. When resin escapes it may form stalactites, drops and flows (Weitschat and Wichard, 1998). The position of these structures affects their exposure to polymerising agents. Free radicals, which are induced by solar radiation and exposure to air, contribute to the polymerisation of *Hymenaea* resin (Cunningham et al., 1977). Polymerisation of *Agathis* resin is also thought to be dependent on exposure to both air and light (Whitmore, 1977). Alternating flow and drying of resin results in the differentiation between darker and lighter layers (Fig. 3A). Resins are produced not only by bark and wood but also by roots and leaves. Neither variation in the position and type of resin, nor its impact on insect inclusions, have yet been studied in the amber record.

Trees may produce several different kinds of resins with different functions. The antimicrobial, antifungal resin of the kaurí tree *Agathis australis*, for example, produces five types, depending on whether it is exuded by leaves, trunk, branches or roots (Henwood, 1992a; Langenheim, 1995). The amount of secretion is controlled by the viscosity of resin, which is determined by both environmental temperature and the internal pressure of the sap. Both temperature and pressure are higher during spring and summer, with the result that resins are exuded more frequently. Drops and flows form on the bark, usually daily, stalactites on bark and branches, usually yearly. During higher daily temperatures, resin is fluidised and exuded by the tree, while during the night, the temperature decreases, causing an increase in viscosity and slowing down of exudation. Resin production also is known to fluctuate seasonally. This has been confirmed in Baltic amber based on the presence of the stellate hairs of oak tree flowers which appear predominantly during spring and early summer (Weitschat and Wichard, 1998). Richardson et al. (1989) recorded that up to 60% of the Baltic amber contains these hairs, and was therefore produced at the same time as the major seasonal abundance of insects. Sontag (2001) surveyed 3875 pieces of amber (42.6 kg), a random sample from unselected Baltic material, and found that only 28% contained these plant remains. Similar stellate hairs occur in Lebanese amber, and may be a product of other plants (Azar, pers. commun.). In any event, seasonal changes in resin production influence the fossil assemblage preserved in copal and amber.

A number of explanations have been offered for resin production: (1) as a defense mechanism against fungal infestation or insect attack (True and Snow, 1949; Janzen, 1975; Farrell et al., 1991); (2) as a reaction to physical damage (Meyer and Leney, 1968; Henwood, 1992a); (3) as storage of unwanted products of cellular metabolism or growth (Henwood, 1993); (4) as a protective barrier to reduce temperature and water loss (Dell and McComb, 1978; Langenheim, 1995); and (5) to attract insect pollinators (Langenheim, 1994; Gonçalves-Alvim, 2001). The first two of these functions are thought to be the most important. It is well documented that some resin components act as herbivore deterrents (although they may also act as attractants; see Labandeira et al., 2001) and have fungicidal properties (Messer, 1985; Richardson et al., 1989). Some chemical compounds (such as alkanes and monoterpenes) in conifer resins are toxic to fungi transmitted by boring beetles (Cobb et al., 1968). Some resins have insecticidal properties, e.g. resin from *Dipterocarpus kerrii* kills workers of the termite *Zootermopsis angusticollis* (Richardson et al., 1989). However, copious production of resin could also be a reaction to damage. The effects of hurricanes may extend for hundreds of square kilometres (Vandermeer et al., 2000), and living *Hymenaea courbaril* is prone to hurricane damage (Wadsworth and Englerth, 1959). It is likely that the Caribbean was subject to tropical storms in the Tertiary, just as it is today. However, observations on *Hymenaea courbaril* in Panama showed that the controls on copious exudation are complex, and physical damage was not the only cause (Henwood, 1992a, 1993).

Saproxilic beetles depend on the availability of damaged wood. When the woody structure of a tree is damaged, it normally creates a chemical or physical barrier with phytolexins to prevent invasion by insects (Lehong and Laks, 1994). Oleoresins and other resins provide such a barrier and usually trap saproxilic organisms. Interaction between the tree and beetles takes place during the earliest stages following damage (Mamaev, 1961). For example, the Buprestidae, a family of beetles whose larvae often rely exclusively on wood, bore large tunnels that also permit other organisms to invade the wood. Similar wood-boring beetles are first recorded in the Triassic, and other xylophagous families such as Cerambycidae and saproxilic ones such as Elateridae and Eucinetidae appear during the Jurassic (see Ross and Jarzembowski, 1993; Labandeira, 1994). Nevertheless, the first record of substantial amber production and of insect inclusions in amber is Early Cretaceous. Molino-Olmedo (1999) showed that 78% of beetles embedded in amber are associated with a saproxilic habitat, while 64% of saproxilic families of beetles are first recorded in the Cretaceous. During the Early Cretaceous 32% of the total number of saproxilic families of beetles appear. The first record of the beetle family Scolytidae is also Lower Cretaceous; this family includes important borers in the Oligo–Miocene *Hymenaea* forests that produced Dominican and Mexican ambers and also in cool-temperate swamp forests near the North Pole that contained resin-producing conifers (Labandeira et al., 2001). 26.6% of all families of beetles appear in the Lower Cretaceous, and 73.7% of these are related to saproxilic habitats; all constituent species found in amber belong to these saproxilic families (Molino-Olmedo, 1999). Bored wood from amber-bearing lithologies from the Lower Cretaceous of Archingeay, France, may have been invaded by xylophagous beetles such as Cerambycidae, Buprestidae and Scolytidae, and termites (Néraudeau et al., 2002). The first records of termite sociality are also from Lower Cretaceous amber, namely a few specimens from Jezzine and Hammana, Lebanon (Azar, 2000), and many from Montsec, Spain (Martínez-Delclòs and Martinell, 1995). In the Lebanese amber a few adults of dry wood termites (Kalotermitidae), which live in ill-defined galleries inside the wood on which they feed, have been found. In Spain many specimens of adults and workers of damp-wood termites (Hodotermitidae), have been found; they also feed on dead wood and may live in underground colonies, although they may invade the tree directly without ground contact.

The evolution of herbivorous insects can be compared with the phylogeny of resin producers among angiosperms and gymnosperms (Dussourd and Eisner, 1987). The fossil record of amber shows that resin production became widespread during the Early Cretaceous, coincident with the expansion of some groups of boring insects (Chaloner et al., 1991). It has been suggested (Molino-Olmedo, 1999) that this expansion of araucariaceans and other resin-producing conifers coincides with the first occurrence of some groups of xylophagous insects, principally beetles and termites. Although there may be a link between the Early Cretaceous radiation of araucariaceans and the appearance of new groups of xylophagous insects, this remains to be documented (but see Sequeira and Farrell, 2001); the xylophagous insect record extends back to the Triassic (Labandeira, 1994).

Palaeogeography determines not only the distribution of the resin producers, but also what insects are available for trapping. Henwood (1993) argued that periods of extensive production do not reflect pathological conditions; the quantity of resin produced by healthy modern trees is sufficient to explain the amount of amber in the fossil record. Alternative explanations, not all of which are amenable to testing with fossil deposits, include: (1) prolonged and regular storm damage due to palaeoenvironmental changes; (2) abundance of mature trees, as resin production is low in immature trees (Henwood, 1992a); or (3) high prevalence of forest fires that lead to bark splitting.

An important question is why so much amber does not include fossil insects. Only five of 65 Lower Cretaceous amber localities in Lebanon yielded fossil insects (Azar, 2000). Similarly, of more than 45 Lower Cretaceous amber localities in Spain, only five yielded organism inclusions, and in only one, Álava amber of Peñacerrada, is the number of individuals abundant (> 4000 specimens). It is unlikely that resins that do not contain insects formed within the bark of trees, because amber formed in such situations should display a platy or lenticular morphology. Some amber without insect inclusions may have accumulated in soil, but only occasional pieces contain a high quantity of organic matter or sediment, and the soil organisms that might be trapped are usually not present. However, many soil organisms are present, for example, in the Lower Cretaceous amber of Archingeay, France (Néraudeau et al., 2002). Another hypothesis is that the large quantity of resin without inclusions may have been exuded into water, perhaps in response to a flooding event. While this is unlikely to explain the volume of resin that lacks insects, it could be tested by observations of extant resin-producing trees. The concentration of amber inclusions in a relatively small number of pieces from a restricted number of outcrops remains to be explained.

Resin trapping may be biased toward certain organisms (Brues, 1933; Poinar, 1992; Henwood, 1992a). A number of factors promote preservation of some groups of insects and not others:

(1) *Resin viscosity*. Resin viscosity, stickiness, and drying depend on its volatile content, which controls the effectiveness and longevity of the resin as a trap. These properties of the resin are influenced by its position on the tree. The more viscous the resin the higher the surface tension, and the less the likelihood that it will be penetrated by insects. Large insects can penetrate more easily than smaller ones, but they are also more likely to struggle free (Henwood, 1993); there are few records of large insects and small vertebrates in amber. Large insects may, however, adhere to the resin surface and be predated (Fig. 3B) before a new flow covers them completely, or they may leave appendages behind (Weitschat and Wichard, 1998). Amber inclusions tend to be dominated by small organisms. An investigation of insect size revealed a predominance of small to very small individuals of less than 5 mm long in Cretaceous ambers while Tertiary ambers include not only small insects but also middle to large sized ones of more than 5 mm long (Poinar, 1992). However, these differences may be the result of variation in the viscosity of the resin or durability of the amber. The intense polymerisation of Cretaceous ambers renders them extremely fragile and large insect specimens are rare (Azar, 2000; Grimaldi et al., 2000): less than 3% of more than 2500 insects prepared from the Álava Lower Cretaceous amber are more than 4 mm long (Martínez-Delclòs et al., 1999; Alonso et al., 2000).

(2) *Insect behaviour*. The behaviour of insects influences the likelihood of their entrapment in amber. Certain categories are more at risk than others: insects that live in bark or usually rest on it, xylophagous insects that bore into wood and bark or feed on leaves (Poinar and Poinar, 1999), and swarming insects including dipterans such as Chironomidae and Dolichopodidae and hymenopterans such as Formicidae (Fig. 3C). Swarm-

ing favours the inclusion of large numbers of individuals in amber (Koteja, 1996). Isolated wings of adult termites are preserved in Pleistocene–Holocene copal from Colombia (Fig. 3D); they shed their wings after nuptial flight by disassociation along the humeral suture. Gregariousness promotes the inclusion of large numbers of insects in resin when it penetrates colonies of ants, termites and beetles (Fig. 3E). Up to 40 aphid specimens are known from a single piece of Upper Cretaceous amber from Grassy Lake, in Alberta, Canada (Pike, 1993).

Some recent bees forage for resin (Henwood, 1992a; Gonçalves-Alvim, 2001). This behaviour increases the chance of becoming trapped and explains why *Proplebeia* is the most common bee found in Dominican amber. Several specimens of *Proplebeia dominicana*, with hind-leg baskets filled with pollen and resin, have been reported from Dominican amber (Roubik, 1989).

Some groups of parasitic and symbiotic insects are brought to the trees by other organisms, or carried by wind due to their small size. More than 90% of ∼400 hymenopterans in the Lower Cretaceous amber of Álava, Spain, are small wasps that parasitise other groups of insects (Martínez-Delclòs et al., 1999). Different larval stages of insects parasitic on mammals or birds, such as haematophagous adults, eggs or larvae, often make their first appearance in the fossil record in Eocene Baltic amber (Larsson, 1978; von Schlee, 1990). Phoretic arthropods, particularly mites, are usually entombed on the host insect (Larsson, 1978; Grimaldi, 1996; Poinar et al., 1998).

Even aquatic insects may be trapped in resin. Larvae of mayflies, caddisflies and stoneflies, pupae of some other groups of flies, and adult riparian and limnic beetles and bugs are represented in Tertiary ambers (Baltic: Weitschat and Wichard, 1998; Dominican: von Schlee, 1990; Poinar and Poinar, 1999). Wichard and Weitschat (2001) reported that at least 30% of Baltic amber inclusions are aquatic insects, but this figure includes pupae, larvae and adults, not all of which are aquatic. Aquatic insects represent 14% of all inclusions in the New Jersey Upper Cretaceous amber (Grimaldi et al., 2000). Weitschat (2001) reported the presence of adults of the ostracod *Cyclocypris* in Baltic amber. Thus in some cases there was presumably standing water near the amber trees (Poinar, 1992; Poinar and Poinar, 1999; Grimaldi et al., 2000).

Grimaldi (1996) recorded a crab from Miocene amber from Chiapas, Mexico, which occurs in lignites interbedded with marine sandstones and silts. Associated pollen indicates that the amber was deposited in a mangrove environment. Such crabs live today in forests close to the seashore in Costa Rica, in tunnels between the roots of *Hymenaea courbaril* (pers. observation). It is possible that resin could have been eroded from the soil to accumulate among the mangrove roots (Langenheim, 1995). Resins could also have accumulated in tunnels and trapped the crab. Nevertheless, the resin producer must have been rooted in water to account for trapping of the crab; transported resin cannot trap organisms.

(3) *Insect habitat*. Zherikhin and Sukatcheva (1990) documented insect assemblages in resins produced by living Eurasian temperate conifers and showed that they contain a large number of snakeflies, alderflies, earwigs, and stoneflies. The small number of fly species and the absence of mayflies and caddisflies emphasise that the composition of these assemblages is clearly distinct from those in any known amber. This difference is attributed to the formation of known fossil amber in tropical rainforests rather than temperate conifer stands.

The location of resin production affects the trapping of insects. Insects that live around resin-producing trees are most prone to entombment. Small insects from elsewhere may have been carried to the resin by wind, although this might be prevented in very dense forest. This hypothesis could be tested in New Zealand today in forests of the araucariacean *Agathis*. Insects from wet soil, bark, and leaf habitats are well represented in amber but those from habitats other than forest, for example prairie or dry environments, are rarely represented (Krzeminska et al., 1992; Poinar and Poinar, 1999). Accumulations of *Agathis* resin persist in surface layers of soil for thousands of years (Thomas, 1969). Resin concentrations also occur around *Hymenaea* individuals where they not only fall from the tree, but are produced by the roots (Langenheim, 1967). Henwood (1992a, 1993) suggested that extensive underground accumulations of resin occur principally around the root systems of large trees. Accumulations of resin are found buried around Recent *Agathis*, *Copaifera*, and *Hymenaea*, sometimes up to 1.8 m below ground (Howes, 1949; Whitmore, 1980; Langenheim, 1967). Some authors (Howes, 1949) discussed whether such resin and copal accumulations were produced totally by roots or are the result of both aerial and underground production. The presence of an underground soil fauna in the amber suggests that at least some of these resins were produced in situ by roots. Amber has only been found in association with a developed root system in the Lower Cretaceous of Jordan (Nissenbaum and Horowitz, 1992). Bandel et al. (1979) suggested that the resin was concentrated in 'parautochthonous' lignite beds; the resins and other tree remains that produced the lignite beds may have been trapped by mangrove roots, although such root systems are not characteristic of the resin producers.

(4) *Plant defence*. Volatile resin products may deter or attract groups of insects. Resins protect trees from insects, fungi and bacteria. Floral resins may attract pollinators to flowers (Armbruster, 1984). Some leaf-cutter ants are deterred by a terpenoid compound secreted by the leaves of *Hymenaea courbaril* (Ales et al., 1981). In Recent rainforests, diverse associations of resin-producing plants may enhance their defence against folivores and pathogens (Langenheim, 1995). Pollen of diverse resin producers, including araucariaceans, cupressaceans and cheirolepidaceans, occurs in the Lower Cretaceous amber of Spain (Barrón et al., 2001). The diversity of such associations is lower in more xeric environments.

(5) *Environmental factors that influence resin production*. Abiotic factors, such as light, temperature, moisture, and nutrients play an important role in controlling the nature and quantity of resins, and of insect inclusions (Langenheim, 1995). Elevated temperature promotes resin exudation: trees exude more resin during spring and summer than in autumn and winter. For this reason the majority of insects in Tertiary ambers are spring and summer taxa. The unusual occurrence of representatives of some living winter and crepuscular dipterans, such as Trichoceridae and Culicidae, respectively, in Baltic amber suggests that the resin-trapped insects lived proximal to the trees (Krzeminska et al., 1992). Resin that is produced underground is subjected to different and more constant temperature and humidity than that in the open air, and is protected from UV light, which promotes polymerisation.

Soil type and water availability also influence resin production. In the extant *Copaifera mitijuga* forests of Brazil, trees living in clayey soils produce more resin than those living in sandy soils (Alencar, 1982). Resin production is greater in *Hymenaea courbaril* trees of similar size with more available water (Langenheim, 1967). Solar radiation also increases resin production in *Hymenaea*, whereas darkness and soil nitrogen reduce it. Resin production may vary widely among individuals of the same species, even when they occupy similar habitats (Adams, 1977). Additionally, resin composition differs between geographically separate populations of *Hymenaea courbaril* (Langenheim, 1984).

Resin may be produced following splitting of bark as a result of fires (Hillis, 1987). Siegert et al. (2001) investigated exceptional fires in the dipterocarp-dominated rain forests of Borneo (Indonesia) resulting from droughts promoted by 'El Niño' between 1997 and 1998. Dipterocarps are angiosperms that are exploited to produce dammar resin (Heywood, 1998). 2.6 million hectares of rain forest were burned, resulting in damage varying from moderate (25–50% trees killed) to near total ($>80\%$ vegetation killed). The fire affected mainly lowland dipterocarps (40.5% of the total area of distribution burned), as well as secondary forest and peat swamp forests. The highland dipterocarps were only partially affected, by $<8.5\%$ of the total area of distribution burned. *Canarium strictum* (Burseraceae) is also burnt to induce the production of dammar resin, causing tree exudations for about ten years (Henwood, 1993). Fusanised flowers and insects, and fire-damaged amber, are found associated with cretaceous amber in New Jersey. These constituents suggest that resin production may have been induced by fires (Grimaldi et al., 2000). Levels of atmospheric oxygen during the Cretaceous were among the highest during the Phanerozoic, close to 30% compared to 20% today, leading to a much higher prevalence of fires (Robinson, 1989).

(6) *Other biological factors*. Small disarticulated fragments of insects and other arthropods are common in amber. Kutscher and Koteja (2000) offered three explanations for the origin of these inclusions. They are parts of exuviae, components of the faeces of a predator, or detritus produced by mites, microorganisms and/or physical factors. They concluded that the inclusions are most likely to be the remains of faeces. Insect faeces or frass also have been recorded in amber (Grimaldi et al., 2000; Néraudeau et al., 2002) as have prey carcass refuse heaps that have been attributed to spiders (Weitschat and Wichard, 1998).

6.2. Biostratinomy

The first studies on insect biostratinomy were published by Schäfer (1972) and Lutz (1984, 1990). Schäfer (1972) described the necrolysis and biostratinomy of Recent *Libellula quadrimaculata*, and other insect orders such as beetles, flies and wasps, from the North Sea. Lutz (1984) described the disarticulation of one element of cockroach elytra. In 1990 he discussed the different stages of insect preservation evident in the Messel oil-shale (Eocene, Germany), and documented and interpreted the first actualistic experiments on the biostratinomy of insect carcasses (Lutz, 1990). Wilson (1980, 1988) compared insect assemblages from nearshore and offshore settings in several Palaeogene lakes in North America, and concluded that insects are well represented in nearshore deposits, although they are more fragmented in offshore settings. Dipterans, hymenopterans and heteropterans are better represented than other groups in offshore zones, while trichopterans and coleopterans are more common in nearshore zones. Martínez-Delclòs and Martinell (1993), Lutz (1997), (Rust, 1998), Peñalver (2002) and Duncan et al. (2003) have contributed actualistic studies on insect biostratinomy.

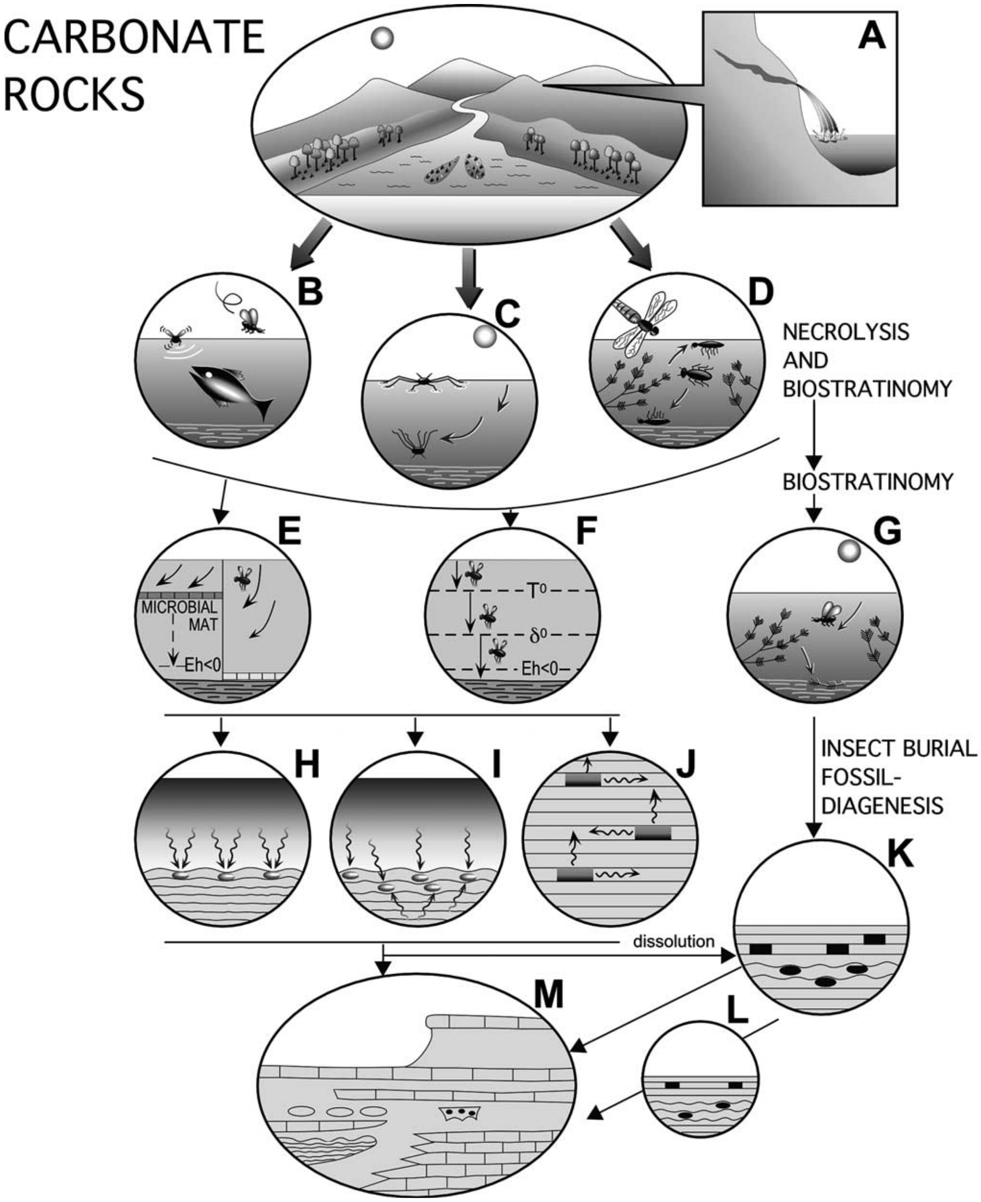
6.2.1. Biostratinomy in aquatic settings

Biostratinomic processes are a very important control on insect preservation in carbonates. Winged insects that fall into water are affected by diverse biostratinomic processes (Fig. 4). The time spent floating varies even within the same insect taxon (Martínez-Delclòs and Martinell, 1993). Insects that die in aerial or terrestrial conditions and are later introduced to water float for longer than insects that drown. Insects may float in the calm water of tanks for more than 6 months. Where fishes are present, they eat the majority of insects within a few hours and they are clearly an important taphonomic filter in lakes, rivers and lagoons.

Insects with a large wingspan, such as butterflies and dragonflies, and very small insects cannot penetrate surface tension and usually decompose, disarticulate and fragment on the water surface (Fig. 3F). Butterflies have scaly wings that soak easily, and when they fall onto water, they are trapped by the surface tension (Martínez-Delclòs and Martinell, 1993). Two days after death the body shows considerable decomposition, and any biological or physical disturbance promotes fragmentation and rapid decay. Many hundreds of individuals may be preserved in exceptional circumstances, as are lepidopterans in offshore marine diatomites in the Palaeocene of Denmark (Rust, 2000). Rust (1999) interpreted these lepidopteran accumulations as a result of rapid penetration of surface tension due to strong wind or rain. Where insects with a large wingspan and/or very small ones are well preserved elsewhere (Leestmans, 1983), this is often due to the development of cyanobacterial mats (Martínez-Delclòs and Martinell, 1993; Etter and Kuhn, 2000).

Observations on outdoor tanks in Barcelona during the spring, summer and autumn of 1990–1991 revealed a ratio of small to large (>5 mm) insects of more than 25:1 counted every two days for two weeks. This proportion is reduced considerably after a rainy or windy day, but fragments and disarticulated parts are present on the bottom. Large insects may remain on the water surface for 4–14 days (Martínez-Delclòs and Martinell, 1993). Water entering the tracheal system may increase the weight of the carcass sufficiently to allow it to sink. Wetting and sinking are hastened by decomposition. Sinking is also promoted by the growth of fungi or algae on the insect carcass (Martínez-Delclòs and Martinell, 1993), both of which usually begin on the articulations of the abdominal segments. However, fungi and algae may also hold the carcass together, inhibiting disarticulation. Fungi and algae are preserved through mineralisation in association with insects from the Tertiary of Riversleigh, Queensland (Duncan et al., 1998).

Experimental observations in tanks show that sinking of an insect carcass is usually slow and vertical. Orientation varies depending on the position in which the carcass is stable on the substrate. This is true even for insects enveloped by algae or fungi. Normally only insects trapped by cyanobacterial mats in the water column exhibit



varied positions. The presence of a thermocline, with or without a halocline, represents a density change that prevents sinking and promotes decomposition before carcasses are deposited on the bottom. Carcasses may remain articulated for almost one year on the bottom of tanks in undisturbed ambient conditions. Disarticulation and fragmentation are promoted by biological or physical agents (Tischlinger, 2001; Duncan et al., 2003).

Carbonate rocks which yield fossil insects often show evidence of anoxic conditions (Martill, 1993; Etter and Kuhn, 2000) and the insects may be relatively complete. Disarticulation and fragmentation presumably occurred during floating and sinking in the oxygenated zone above a thermocline or halocline, or as a result of displacement by decay gases. Chitinophagous bacteria that degrade cuticle live almost exclusively in oxygenated environments, although some are capable of anaerobic metabolism.

The disarticulated elements that commonly occur in carbonate rocks are: head and thorax, head with antenna, thorax with legs, thorax with wings, and thorax and abdomen. Other isolated structures, including palps, cerci and tarsi, are rare. Early disarticulation and disintegration may be the result of predation and scavenging by vertebrates and invertebrates at the air–water interface, sediment–water interface, and within the sediment. It may be difficult to distinguish fragments left by predators from those produced by physical agents. Predators and scavengers may control the composition of fossil arthropod assemblages (Plotnick, 1986, 1990). Their absence is critical for the preservation of insect carcasses (Duncan et al., 2003). Fragments of insects also occur as gut contents of amphibians (Peñalver, 2002), fishes (Richter and Baszio, 2001), some mammals, such as bats or anteaters (Schaal and Ziegler, 1992), and in coprolites (Ansorge, 1993) (Fig. 2B).

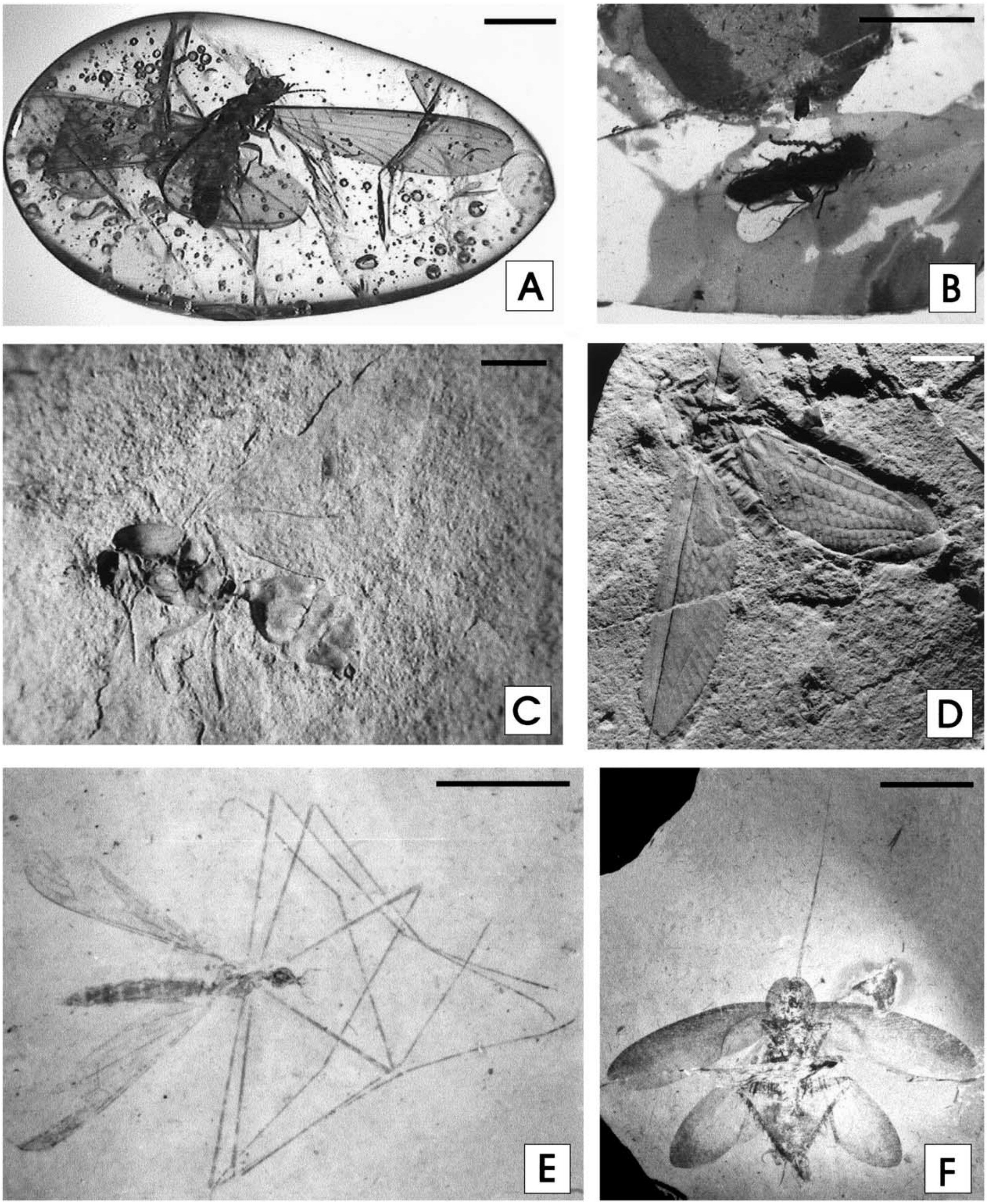
6.2.2. *Biostratinomy in resins*

The biostratinomy of insects entombed in resins can be regarded as commencing only when the resin is first transported. By this definition the entombment of the insect in the resin is not synonymous with burial of a carcass in sediment, but is a pre-burial process that generally takes a very short time, from seconds to a few days. However, it is not always possible to differentiate between factors affecting insect inclusions before and after resin burial, and therefore the process of entrapment is also considered here.

Insects usually die by asphyxia and only large insects, which require more than one resin flow to overwhelm them, perish as result of fatigue or predation. The time required for resin to overwhelm an insect depends on its viscosity, the frequency of flow, and how the resin is deposited: if resin falls as drops (Wagensberg et al., 1996), burial is rapid. When insects are trapped in resin by the legs or wings, another drop may disarticulate the carcass, particularly when it has dried (Fig. 3G). Twisted wings, abnormal positions, or assemblages displaying oriented body structures (legs, antennae, scales, etc.) usually reflect resin flow (Fig. 5A).

Occasionally amber preserves alternating clear and dark bands, representing successive flows

Fig. 4. Carbonate taphonomy. (A) Travertines form in fluvial settings or springs with high alkalinity, and preserve terrestrial and aquatic insects. (B)–(D) Carbonate rocks preserve terrestrial, semiaquatic and aquatic insects. Unlike aquatic insects, terrestrial and semiaquatic taxa need to penetrate the surface tension before sinking. (E) During sinking insects may be trapped by microbial mats that live in the water column, or they may be coated by algae or fungi that inhibit disarticulation. Microbial mats also grow at the sediment–water interface; where they also trap insect carcasses. (F) Sinking may be delayed by the thermocline or halocline; anoxic bottom conditions delay decomposition. (G) Travertines may be produced under water, but insects are rarely preserved; typically plant and algal remains are found. (H) Immediately after burial, insects may be mineralised by diagenetic minerals such as calcite or pyrite. (I) Insects may decay, or the early diagenetic minerals may dissolve to leave a cavity in which other minerals may precipitate, forming a cast. (J) When pressure and temperature affect fossil insects, the volatile components of organic structures may be lost and the original organic compounds diagenetically transformed. (K) In travertines organic matter is rarely preserved, and insects and plants are usually found as moulds. (L) The space left by degradation of the insect may or may not be infilled by a second generation of minerals. (M) Carbonate rocks that preserve fossil insects are usually those deposited in continental or shallow marine environments.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(Weitschat and Wichard, 1998). The darker layers, usually thinner than the clear ones, are the result of rapid drying by sunlight and wind. These dark layers may contain insects that were not completely encapsulated until the arrival of the next flow or drop of resin (Fig. 3B). Some examples show that insect structures, such as wings, can prevent rapid drying of the resin (Fig. 5B).

The majority of amber outcrops are allochthonous. Only in the Lower Cretaceous of Jordan is amber found in association with tree roots, possibly the producer plant (Nissenbaum and Horowitz, 1992). Amber may occur in association with coal seams, as in the Upper Cretaceous of Grassy Lake, Canada, or in the Lower Cretaceous of Wadi Zerka, north of Amman, Jordan (Poinar, 1992; Bandel et al., 1979). Some authors (Pike, 1993; Bandel et al., 1997) have interpreted such deposits as 'in situ', but they may represent transported accumulations. Where fragile structures such as stalactites or individual drops are preserved, it suggests that they have not been transported far, or that they have been carried by water without any contact with the bottom sediment. The presence of aquatic animals in amber indicates the proximity of water to the trees. Some species of *Hymenaea* in the Amazonian rainforest today may be periodically inundated (Langenheim, 1995), and likewise *Agathis australis* of New Zealand.

The transport and deposition of resins are poorly understood (Fig. 6). Amber is rarely found within fossil wood, suggesting that they are normally transported separately or that the amber is destroyed during diagenesis. Clastic sediments that yield amber are frequently rich in organic matter, but rarely in wood or bark fragments. Where amber is preserved in wood, this may provide important evidence of the source plant and the part of the tree from which the amber originated. Small pieces of amber occur in the wood of *Metasequoia glyptostroboides* from the Middle Eocene of Axel Heiberg Island, probably as a result of insect infestation (Labandeira, pers. commun.). Dejax in Azar (2000) suggested that Lebanese amber is produced by the cheirolepidacean *Protopodocarpoxylon* sp., congeneric with *P. subrochii*, from the Upper Jurassic of Morocco, and not by an araucariacean as previously thought. Ghiurca (1988) proposed a taxodiacean origin for Romanian Miocene amber. Knowlton (1896) proposed a cupressacean origin for some pieces of amber from the Upper Cretaceous of New Jersey, but Grimaldi et al. (2000) considered a pinacean or taxodiacean origin more likely based on chemical analysis of the amber.

Although resins are produced by plants that would be expected to accumulate in deltaic and lacustrine sediments, remains of resins are rarely reported in studies of plant taphonomy in these environments. Gastaldo et al. (1987) reported no resin in their taphonomic study of plant remains in the Holocene crevasse splay in the Mobile Delta of Alabama, USA, nor in the backswamps of a Holocene oxbow lake of the Alabama River, where an important swamp cypress (*Taxodium*) community lived (Gastaldo et al., 1989). When resins occur in association with other plant remains in some sedimentary environments, they tend to be preserved as rare fragments. Resins are found as palynodebris in most delta-plain subenvironments associated with parenchyma tissues and wood debris, and sometimes in distributary channels, such as the Middle Miocene of the Niger Delta amid an angiosperm dominated forest

Fig. 5. (A) Termite, Rhinotermitidae, with rolled wings. EPGM-RD-0052; Miocene amber, Hispaniola; scale bar = 2 mm. (B) Wasp, Scelionidae, showing that wings inhibit rapid drying and polymerisation of the resin (dark layer). MCNA-9244; Lower Cretaceous, Moraza (Spain); scale bar = 1 mm. (C) Ants preserved in large numbers due to precipitation of authigenic carbonate. TJ-0213-MCCM; Miocene, Tres Juncos (Spain); scale bar = 2 mm. (D) Neuroptera, Chrysopidae, showing elongation of left forewing due to tectonic deformation. ADR-0029-I/MCCM; Barremian, Las Hoyas (Spain); scale bar = 5 mm. (E) *Dicranomyia*, Diptera, Limoniidae, preserving delicate structures. MPV-69-RM; Lower Miocene, Rubielos de Mora (Spain); scale bar = 5 mm. (F) *Aktassoblatta fusca*, cockroach preserving organic rich cuticle. PIN 2239/347; Upper Jurassic, Karatau (Kazakhstan); scale bar = 5 mm.

(Oboh, 1992). Phytoclasts in the Recent Mahakan River Delta in Borneo (Gastaldo and Huc, 1992) include dipterocarpacean resins (dammar) as either duct infills or amorphous to cylindrical clasts associated with other plant debris. These structures occurred in high energy depositional environments. Resin clasts may be up to several centimetres long and over 1 cm in diameter, and usually are rounded. These resins account for up to 4.5% of plant parts recovered on the delta front and in tidally influenced interdistributary areas (Gastaldo, 1994). The Lower Cretaceous amber of Álava, Spain, occurs in sandy channels of the delta plain (Alonso et al., 2000).

6.3. *Diagenesis*

Insect carcasses that survive biostratinomic processes may be buried (Fig. 4). Subsequently they may be affected by a number of processes: (1) early mineralisation; (2) flattening; (3) deformation; (4) thermal maturation; and (5) reworking. Other factors, such as bioturbation, decomposition and weathering also may lead to biases in fossil insect assemblages.

(1) *Early mineralisation*. The preservational state of fossil insects depends on the degree of decomposition when an insect arrives at the burial environment. Decay-resistant tissues may survive to be preserved as organic material; diagenetic changes result in transformation to more stable molecules than those of the original (Briggs, 1999). Preservation of labile tissues requires replication by authigenic minerals before the loss of morphological detail. The type of mineral involved depends on the chemistry of the environment and the prevalent microbial processes (Efremov, 1950; Allison, 1988). Both types of preservation – of resistant and labile tissues – may occur at the same fossil locality and even within the same fossil (Peñalver et al., 1993).

(2) *Flattening*. Flattening includes collapse of the carcass due to decomposition, and compaction as a result of overburden pressure. The degree and nature of flattening is determined by the grain size and composition of the sediment, the morphology and composition of the carcass, its orientation to the bedding, the nature and timing of diagenesis, and processes involved in cavity infill. 3-D preservation of insects in limestone implies that mineralisation of the soft-tissues (Duncan and Briggs, 1996) and/or early cementation of the surrounding sediment (McCobb et al., 1998) was initiated prior to appreciable decay (Fig. 5C). The effects of compaction may be differentiated from tissue collapse through evidence of distortion of the mineral infill, replacement, or coating (Allison and Briggs, 1991a). 3-D preservation is normal in amber. Subsequent compaction of the host sediment may result in 'engraving' of the surface and flattening of a piece of amber (Alonso et al., 2000; Zherikhin and Ross, 2000) but rarely affects the inclusions.

(3) *Deformation*. Fossil insects are sometimes distorted tectonically and this may lead to taxonomic misidentification (Peñalver, 1996) (Fig. 5D). Limestone is more resistant to weathering and erosion than amber, which may be very fragile due to intense polymerisation.

(4) *Thermal maturation*. Maturation results in the transformation of the organic components of a fossil insect to a kerogen-like composition (Stankiewicz et al., 2000). It causes amber to become darker and more fragile by promoting the loss of volatile terpenes and increasing the rate of polymerisation. It may also increase amber plasticity.

(5) *Reworking*. Amber with insect inclusions is often reworked. Fossil insects in carbonates are only likely to be reworked if they are preserved in nodules.

6.3.1. *Diagenesis in carbonate rocks*

Rapid burial favours exceptional preservation (Seilacher et al., 1985) by eliminating scavengers and promoting anaerobic conditions that inhibit bioturbators. It results in the preservation of articulated carcasses (Fig. 5E). Low rates of decay are necessary to allow authigenic minerals to form quickly enough to preserve the most labile soft-tissues (Briggs, 1995b). If decay outpaces mineralisation, only the most decay-resistant tissues and structures will be preserved. Organic remains survive only where chemical (hydrolysis, oxidation) and biological (enzymatic and microbial activity) degradation is prevented (Briggs, 1999).

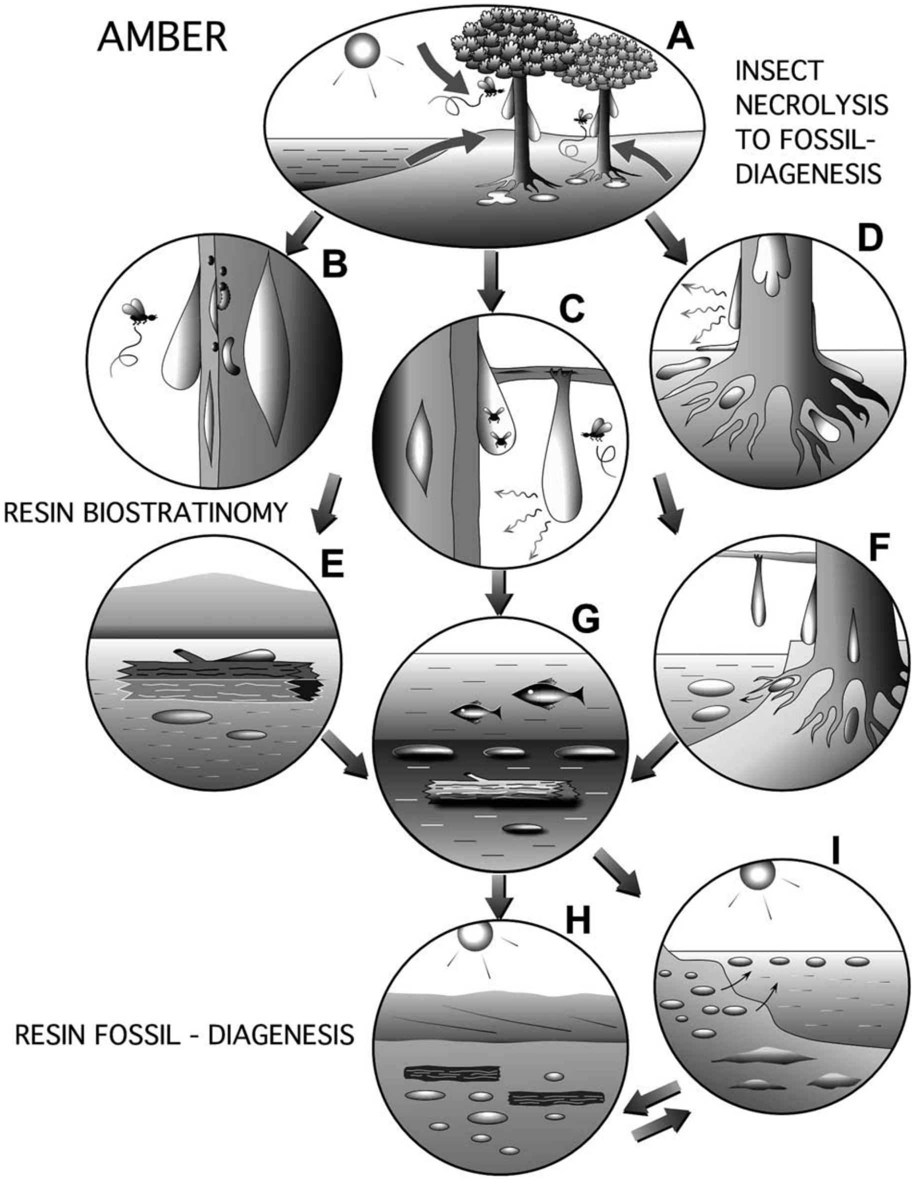
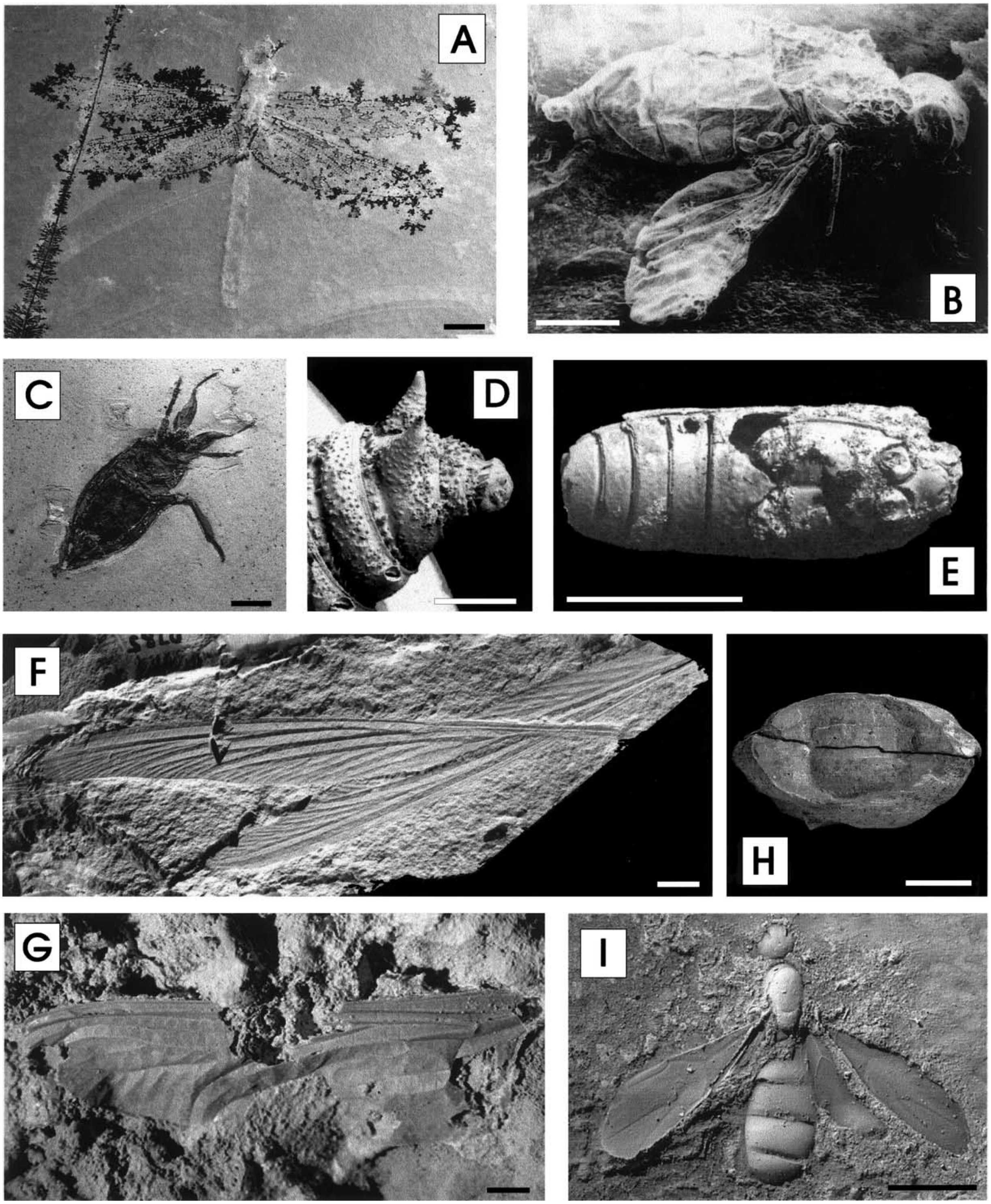


Fig. 6. Amber taphonomy. (A) Terrestrial, aquatic and underground insects are trapped by resin. (B) Resin may accumulate in the internal cracks and pockets within the wood, under and between the bark. (C) When resin is unconstrained it may form stalactites, drops and flows, and may trap insects and other organisms. Under subaerial conditions resins lose volatiles. (D) Subterranean deposits of resins also form, produced by roots and by the aerial parts of the tree, and accumulate as large masses around the tree base. (E) In the majority of cases it is not known whether resin is transported to the deposit in which it becomes fossilised with the tree or separately. (F) Resins are introduced into water directly from the tree or following erosion of the soil. (G) Initial deposition of the resin, usually associated with organic rich sediments. (H) Diagenesis of the resin begins with burial. Nevertheless, some prediagenetic processes that affect insects in resins are difficult to distinguish from the effects of diagenesis (see text). (I) Amber is usually reworked and deposits are time-averaged.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Insects are preserved in carbonate rocks in six major ways: (1) as cuticle remains, usually as a diagenetic product of the original organic composition; (2) by preservation in an authigenic mineral, often calcium carbonate, pyrite or calcium phosphate, or infilling of a decay void by minerals such as calcite, silica, or pyrolusite which may be recrystallised or altered during diagenesis; (3) as a mould of the exoskeleton, resulting from the loss of organic remains; (4) in travertine, usually as a mould or carbonate coat; (5) in a concretion, often as a moulds or through replication by authigenic minerals. More than one type of preservation may occur at the same locality and in the same specimen.

(1) *Cuticle remains*. Insects are usually preserved as cuticle remains (Fig. 5F). Loss of the organic remains may result in preservation as a mould. Both of these types of preservation commonly occur in the same sequence: in the laminated Lower Cretaceous limestones of Las Hoyas, Spain, for example, cuticle commonly survives in dark laminae, but has been lost in the lighter coloured laminae (Fregenal-Martínez et al., 1992). Cuticle may be preserved in three dimensions due to sclerotisation or early mineralisation of the enclosing lithology (McCobb et al., 1998). Aquatic Heteroptera are preserved in three dimensions at Las Hoyas where the content of organic matter in the sedimentary matrix is low. Where more organic matter is present, compaction results in 2-D preservation (Martínez-Delclòs et al., 1995).

The chemistry of the cuticle of fossil arthropods has been investigated using pyrolysis–gas chromatography/mass spectrometry which allows insoluble macromolecular material to be analysed in very small quantities (Stankiewicz et al., 1997a; Briggs et al., 1998; Briggs, 1999). Arthropod cuticles are composed of chitin and proteins, cross-linked via catecholamine and histidyl moieties (Stankiewicz et al., 1997b). Traces of cuticle chitin and protein may survive in Cenozoic strata: the oldest so far reported are in a curculionid beetle from Oligocene volcanoclastic lacustrine sediments at Enspel, Germany (Stankiewicz et al., 1997b). In Eocene and older deposits, the organic components of arthropod cuticle are altered to aliphatic compounds, as in the water boatman *Iberonepa romerali* from Las Hoyas in Spain (Stankiewicz et al., 1997a). Aliphatic pyrolysates are interpreted as a product of polymerisation of free or ester-bound aliphatic compounds and the simultaneous alteration of labile polymers such as proteins and chitin (Stankiewicz et al., 2000). Such a process may also lead to the formation of aromatic moieties (Harvey et al., 1983) in fossil crustaceans and other organisms (Stankiewicz et al., 1997a).

(2) *Mineralisation*. There are three main modes of mineralisation of insects: preservation of tissue morphology, pseudomorphing and infilling to form a cast. Labile soft-tissues may be replicated in apatite (Duncan et al., 1998), which preserves remarkable detail, or in pyrite/goethite. Decay-resistant cuticles may be fossilised by the precipitation of authigenic minerals such as apatite or pyrite in their structural spaces, as in the insects of the Crato Formation in Brazil (Grimaldi and Maisey, 1990). Labile soft-tissues are more commonly preserved in outline, by bacteria that colonise the carcass and become mineralised them-

Fig. 7. (A) *Cymatophlebia longialata*, dragonfly, with wing venation replaced by pyrolusite during diagenesis. 1959.73.Ka/J.M.E.; Upper Jurassic, Solnhofen (Germany); scale bar = 10 mm. (B) Fly preserved in silica in a nodule from the Barstow Formation; Middle Miocene, Southern California (USA), photo by L. Park; scale bar = 1 mm. (C) Aquatic Heteroptera preserved secondarily in goethite, originally in pyrite, EPGM-RD-0053; Lower Cretaceous, Crato Formation (Brazil); scale bar = 10 mm. (D) Abdominal apex of caddisfly larva preserved in authigenic calcium phosphate, QM F34594, Oligocene–Early Miocene of Riversleigh (Queensland), scale bar = 0.1 mm. (E) Beetle 3-D preserved in authigenic calcium phosphate, QM F34595; Oligocene–Early Miocene, Riversleigh (Queensland); scale bar = 0.5 mm. (F) *Reisia sodgianus*, isolated dragonfly wings preserved as moulds. PIN 2785/4; Upper Triassic, Dzhayloutcho (Kirghizistan); scale bar = 5 mm. (G) *Aeshna isosceles*, dragonfly hindwing preserved as a mould in 5000-year old travertine. IPM-R.08356; Holocene, Auriol (France), photo by A. Nel; scale bar = 5 mm. (H) Carbonate nodule from Lower Miocene, Izarra (Spain), IZA-001; scale bar = 10 mm. (I) Imago ant preserved as a mould in the Izarra nodule, JFP-001; scale bar = 5 mm.

selves. Such microbial films can be preserved in various minerals. This type of preservation has been recorded in animal tissues preserved in the deposits of Eocene Lake Messel (Wuttke, 1983), for example, but has not been reported in the insects from the same site, which are preserved as diagenetically altered organic material. Infilling occurs where the void left following decay is subsequently filled by a mineral, as in pyrite infilled beetles from the Eocene London Clay of southeastern England (Britton, 1960; Jarzembowski, 1992). The diagenetic minerals that most commonly form casts are calcium carbonate, pyrolusite and silica (Fig. 6A,B). In the Cretaceous of Las Hoyas and the Jurassic Solnhofen Limestone of Bavaria, calcite and pyrolusite precipitate in the spaces left following decay and form casts. Sometimes pyrolusite is confined to the wing veins. In contrast, calcite infills the void left when insects decay in the Eocene Bembridge Limestone and may replicate the soft-tissues (McCobb et al., 1998). Silica, celestine, apatite and gypsum form casts and replace the cuticle of the insects in carbonate nodules from the Miocene Barstow Formation, USA (Park and Downing, 2001).

A variety of authigenic minerals may replace soft-tissues (Allison, 1988). Labile tissues can only be replicated where mineralisation is rapid relative to decay. The principal authigenic minerals that replace insect soft-tissues in carbonate rocks are calcite/aragonite, apatite and pyrite (Fig. 7C). In most freshwater and marine environments, concentrations of the bicarbonate ion exceed those of the phosphate ion, and calcite/aragonite formation is favoured. The solubility product of calcium phosphate must be greater in order to precipitate apatite (Briggs and Wilby, 1996). Early diagenetic pyritisation requires rapid burial, low organic matter content, and the presence of sulphates, and it is favoured by high concentrations of reactive iron (Brett and Baird, 1986; Briggs et al., 1996).

Decay can be rapid under anaerobic conditions. Preservation of soft-tissues in such circumstances is due mainly to the link between decay and mineral formation, rather than to limited decomposition. Mineralisation is favoured by elevated microbial activity, which establishes the geochemical gradients required for precipitation. The locus of mineral precipitation is determined by geochemical gradients from the decaying organism into the surrounding sediment (Canfield and Raiswell, 1991).

Calcium carbonate and calcium phosphate (apatite) are the two major types of mineral that occur in limestones. The controls on the formation of these minerals are amenable to experimentation (Briggs and Kear, 1994; Sagemann et al., 1999). For example, shrimps decayed in marine media at 15°C under oxic conditions underwent limited weight loss when indigenous bacteria alone were present. This resulted in the formation of a variety of $CaCO_3$ crystal bundles, including discs, rods and dumbbells, but there was no soft-tissue preservation. In contrast, where decay rates were elevated by the addition of an inoculum of bacteria, anaerobic sulphate reduction was intense, causing more extensive weight loss, pH decreased, and some muscle tissue was replicated in apatite. Thus, while calcium carbonate is normally favoured due to the high concentrations of the bicarbonate ion, it may be inhibited due to reduced pH, allowing apatite to form. A limiting factor is that continental water bodies are characterised by low concentrations of phosphorus. Only highly alkaline waters, poor in Ca, retain much phosphate in solution. Consequently, calcium carbonate minerals are normally associated with fossil insects. Bacterially induced $CaCO_3$ precipitation results in single crystals or in crystal bundles in the form of rods, spheres, and brushes (Buczynski and Chafetz, 1991). In a liquid medium, circulation and ion diffusion rate are both high, precipitation is rapid, and aragonite forms. Where diffusion is lower, as within the gelatinous secretions of bacteria and/or algae, calcite is precipitated.

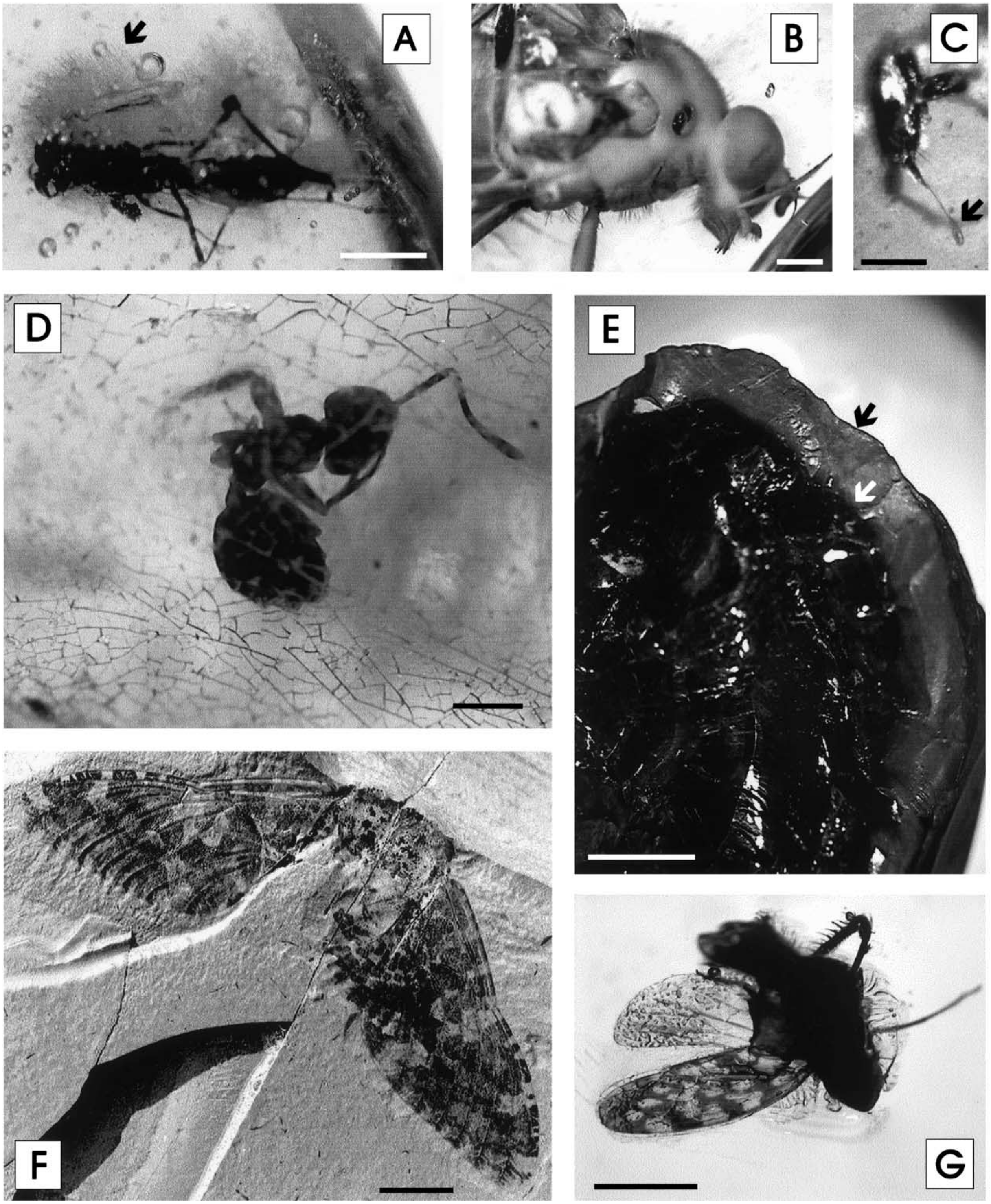
Calcium carbonate does not normally replicate the structure of soft-tissues (but see McCobb et al., 1998). Its importance in preserving insects is in infilling voids left following the decay of soft-tissues, but more importantly in promoting rapid lithification, particularly the formation of nodules. In the eutrophic conditions of some lakes and lagoons, high productivity of organic matter is associated with anaerobic bottom conditions. Bicarbonate ions released by decay react with calcium or iron to produce authigenic carbonates. Limestone precipitation is favoured by bicarbonate saturation that results from CO_2 production by bacteria, algae, and plankton. Fossils are characteristically flattened and preserved as impressions in the carbonate matrix or coated by other minerals.

Phosphatisation can result in the replication of soft-tissues over a period of weeks or months. Apatite forms more rapidly and yields higher fidelity of detail at the cellular level than any other mineral (Duncan and Briggs, 1996). Phosphatisation is more prevalent in organisms such as arthropods, fishes and cephalopods (Wilby and Briggs, 1997) that have a relatively high reserve of organically bound phosphate in the carcass (Fig. 6D,E). This process frequently occurs in marine environments, particularly in plattenkalks, as in the Upper Jurassic limestones of Solnhofen, Germany, and Cerin, France, the Upper Cretaceous Hakel and Hjoula limestones of Lebanon, and Eocene limestones of Monte Bolca, Italy (Wilby and Briggs, 1997). However, such deposits do not always yield insects, although the Solnhofen Limestone is an exception (Frickhinger, 1994; Viohl, 1998). In contrast, a number of important freshwater plattenkalks that do yield insects, including the Lower Cretaceous of Montsec and Las Hoyas, Spain, and the Eocene Green River Formation of the Western Interior of the USA, do not normally preserve phosphatised soft-tissues.

Phosphatisation of insect soft-tissues normally requires a build-up of phosphorus in the upper layers of the sediment in order to provide more than is available within the carcass itself. This may be accomplished by adsorption to clays and iron hydroxides (Wilby et al., 1995). Phosphorus may be derived from decay of organic matter, dissolution of biogenic apatite in skeletons, and from the water column (Wilby et al., 1996). In order to be available for incorporation into fossils phosphorus must be prevented from recycling back into the water column. Microbial mats may achieve this by controlling the redox boundary, often as a site of transitory fixation (Soudry, 1992; Reimers et al., 1988). Microbial mats prevent carcasses from floating and accordingly protect them from scavengers and currents (Gall et al., 1994). These mats also favour early mineralisation because they create low oxygen conditions and reduced pH around the carcass (Chafetz and Buczynski, 1992; Neumeier, 1999). Mineralisation of soft-tissues may take several weeks, or even months, if decay is inhibited (Briggs et al., 1993). Microbial mats are evident in association with fossil insects at several localities (see Section 4).

Pyrite is ubiquitous in organic-rich, fine-grained sediments. It forms in both marine and freshwater anoxic settings (Allison, 1988), but is usually sulphate-limited in the latter due to low sulphate concentration in freshwater. It is rare in continental limestones, where most fossil insects occur. Framboids and crystal aggregates are the most common textures observed in pyritised insects (Peñalver et al., 1993). Insects in the Lower Cretaceous Crato Formation of Brazil are preserved in two and three dimensions in goethite (iron oxide hydroxide; Fig. 7C) (Grimaldi and Maisey, 1990). The exceptional detail (Grimaldi and Maisey, 1990; Martill, 1993) reflects mineralisation prior to significant decay. These sediments were deposited in a lake that evolved under arid or semiarid tropical conditions, with a possible seasonal monsoon climatic regime that may have favoured permanent stratification of the water body. Rapid burial may have been due to major sediment input during particular events, or by high sedimentation rates of > 1 cm/yr associated with a delta (Lopes-Neumann, 1999). A low organic matter content, evidenced by a matrix that is 99% calcite (Lopes-Neumann, 1999), together with the presence of pore-water sulphates, favoured pyrite precipitation during insect decay and decomposition. Santana insects may have been mineralised initially in pyrite and then altered to goethite during diagenesis.

(3) *As a mould*. In preservation as moulds only an impression of the external characters of the insect remains (Fig. 7F). Where the tissues of the insect decay rapidly, mould formation requires early diagenetic cementation of the surrounding lithology. More decay resistant cuticles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may survive lithification of the sediment, only to be removed during diagenesis or weathering. The result may be an external mould. External moulds of insects commonly occur in limestones with a low organic matter content (Martínez-Delclòs et al., 1995), in travertines (Nel and Blot, 1990), and in carbonate nodules (Barrón et al., 2002).

(4) *In travertine*. Travertines are freshwater carbonates that form in fluvial settings or springs with a high alkalinity. The major sources of carbonate in such settings are inorganically precipitated carbonate, carbonate precipitated as a result of photosynthesis, biogenic debris from calcareous plants and animals, and allochthonous material from carbonate rocks in the drainage basin (Dean and Fouch, 1991). Precipitation of $CaCO_3$ on the surface of organic remains results in their preservation as moulds. While plants are often preserved in such settings, insects are rare, exceptions being a dragonfly wing from the Holocene of Auriol, France (Fig. 7G; Papazian and Nel, 1989), and insects in the Miocene of Böttingen, Germany (Zeuner, 1931). Traces of insect activity are even more rarely preserved in travertines, such as galls produced by the cecidomyid fly *Harmandiola* in leaves of *Populus*, from the Pleistocene of the Matarranya River in Teruel, Spain (Peñalver et al., 2002b), and the feeding in wood by a Quaternary beetle of the family Scolytidae, from Thüringens, Germany (Claus, 1958).

(5) *In nodules*. Insects are not often preserved in concretions. Examples include the famous Upper Carboniferous biotas of Mazon Creek, Illinois, USA, and Montceau-les-Mines, France, and the Middle Miocene biotas of the Barstow Formation of the Mojave Desert, California, USA, and of Izarra, Álava, Spain (Figs. 6I and 7H). The Barstow Formation insects and other arthropods are preserved in three dimensions and are typically replaced by minerals, such as quartz (Fig. 7B), apatite, celestine, gypsum and zeolites, but in some cases the structure of the soft-tissues of these organisms is preserved (Palmer, 1957; Park, 1995; Park and Downing, 2001). The insects of Montceau-les-Mines (France) and Izarra (Spain) are preserved as moulds (Caurel et al., 1994; Barrón et al., 2002). 3-D preservation indicates that nodules are formed by early diagenetic processes, prior to decay collapse. In these localities insects do not always occur in the centre of the nodules. Nodule formation begins with decay and release of CO_2 and NH_3. This promotes an increase in concentration of the bicarbonate ion (HCO_3^-) promoting $CaCO_3$ precipitation around the carcass (Berner, 1968; Raiswell, 1987; Raiswell and Fisher, 2000). Calcareous nodules from the Montceau-les-Mines basin are dominated by siderite and pyrite with traces of phosphate; they may be traversed by calcite veins. This suggests an anoxic setting rich in organic matter, with a pH of 7 or lower (Caurel et al., 1994). The Miocene Barstow Formation concretions, on the other hand, were formed under dysaerobic, low energy conditions in a distal saline–alkaline lake (Park, 1995). No geochemical studies have been carried out in Izarra.

Colour is rarely preserved in insect fossils because the majority of chemical compounds that cause it are lost rapidly after the death of the organism. The oldest preserved colour in insects is known from several Upper Carboniferous deposits associated with coals (Carpenter, 1992). Ex-

Fig. 8. (A) Hymenoptera with fungal covering. EPGM-RD-0055; Miocene amber, Hispaniola; scale bar = 1 mm. (B) Brachycerous Diptera showing a white aureole produced by decay and decomposition of labile tissues. This aureole is best developed on the side of the amber where the insect was trapped initially. EPGM-B-0056; Eocene, Baltic Sea (Lithuania); scale bar = 0.5 mm. (C) Spermatophore (black arrow) at the apex of the abdomen of a tiny wasp (Mymarommatidae, Hymenoptera). MCNA 9127; Lower Cretaceous amber, Moraza (Spain); scale bar = 0.05 mm. (D) Detail of copal stalactite showing cracking of the external surface that may affect insect preservation. EPGM-CM-0054; Holocene, Madagascar; scale bar = 0.5 mm. (E) Rugose and darker crust (black arrow) produced by weathering of amber; crystalline amber (white arrow), EPGM; Lower Cretaceous, Escucha (Spain); scale bar = 5 mm. (F) *Wonnacottella pulcherrima*, palaeontinid (Homoptera) showing colour pattern in wings preserved in carbonate. LP-0026-G/IEI; Barremian, El Montsec (Spain); scale bar = 10 mm. (G) *Xestocephalus*, leafhopper showing colour pattern. EPGM-RD-0057; Miocene amber, Hispaniola; scale bar = 10 mm.

amples of colour preserved on insects are known mainly from carbonate rocks (Fig. 8F) but also from amber (Fig. 8G). In some Mesozoic dragonflies from carbonate rocks the wing venation pattern is only preserved where the wings were coloured; wing zones that lacked colour are not preserved. This suggests that the properties of the coloured wings in dragonflies, perhaps the presence of melanin, may have promoted preservation. In other groups of insects that preserve colour, such as leafhoppers and scorpionflies, the venation is preserved throughout. The metallic colours which are preserved in some beetles from the Eocene of Messel, Germany, for example, are not chemical in origin, but a product of multilayer reflectors (Parker and McKenzie, 2003).

6.3.2. Diagenesis in resins

Processes such as dehydration and carbonisation begin as soon as the insect is trapped but before the resin is buried. It is not always clear which processes occur before and after burial of the resin so here we consider the diagenesis of insect inclusions to begin when they are first trapped, whereas diagenesis of the resin only begins when it is buried in a sedimentary deposit (Fig. 6). Resins have antiseptic and antibiotic properties that protect an insect carcass from decay, unlike those in limestones. The development of fungi around carcasses in amber where the hyphae clearly are not oriented by the flow of the resin indicates that the fungus grew after the insect was trapped; thus in some cases the resin does not have fungicidal proprieties and may not harden quickly (Fig. 8A). Resin-encapsulated insects provide an opportunity to investigate diagenetic changes in organic matter that has been protected from external agents.

Insect remains in copal and amber are usually restricted to the cuticle. After the insect is embedded in resin, anaerobic degradation occurs as a result of autolysis and the activity of endogenous bacteria (Allison and Briggs, 1991a,b). These processes may be inhibited by rapid dehydration, however, and labile tissues are sometimes preserved. Experiments have shown that early dehydration is critical to this process (Henwood, 1992a,b; Grimaldi et al., 1994). Henwood (1992b) argued that insects with well preserved internal organs represent individuals that dehydrated prior to complete entombment. Poinar and Hess (1982) suggested that such mummification might be the result of an extreme case of inert dehydration. They considered that organic compounds such as sugars and terpenes in the resin might combine with water in the tissues to aid in the dehydration process. Grimaldi et al. (1994) argued that the role of terpenes is probably more significant than that of monosaccharides and other compounds, because terpenes occur in higher concentrations and would perfuse tissues more rapidly. During early diagenesis, fluids produced by decay and decomposition of labile tissues may react with sugars and terpenes in the resin, resulting in a white aureole around the carcass (Fig. 8B) that has been interpreted as a foam of microscopic bubbles (Mierzejewski, 1978; Weitschat and Wichard, 1998). This frequently occurs in insect larvae with a high proportion of labile tissues, but also in adults, particularly in Baltic and Dominican amber. Where foam is present on only one side of a carcass the other probably was exposed to the atmosphere long enough to become dehydrated before it was covered by a subsequent flow. Grimaldi et al. (2000) reported New Jersey amber that is turbid due to foams. If soft part preservation is a function of dehydration, reduced evaporation underground might contribute to the lower preservation rate of subterranean organisms, but this is more likely a reflection of their low mobility compared to flying insects. Internal soft-tissues are preserved in both Dominican and Baltic amber (Grimaldi et al., 1994), but more commonly in the former, which sometimes yields cellular details, including mitochondria and nuclei (Poinar and Hess, 1982; Henwood, 1992a). Membranous structures, such as musculature, air sacs or tracheae, are generally better preserved than proteinaceous ones (Grimaldi et al., 1994). Internal soft-tissues also have been reported from Lebanese amber (Azar, pers. commun.). Gas exchange with the atmosphere may occur (Hopfenberg et al., 1988; Cerling, 1989), but this is unlikely to promote decay.

Some macromolecules are more decay-resistant than others. DNA is highly susceptible to both hydrolysis and oxidation (Lindahl, 1993) and is rare in fossils more than 100 000 years old. Reports of DNA from insects in amber (Desalle et al., 1992; Cano et al., 1993) probably reflect contamination (Austin et al., 1997; Walden and Robertson, 1997; Cooper and Poinar, 2000). Proteins are known to decay rapidly; some of them, such as albumin, have similar characteristics to DNA (Poinar et al., 1996), while others, such as collagen, osteocalcin or keratin, are more resistant (but see Bada et al., 1999). Cellulose and chitin are carbohydrates that are easily biodegraded unless they are part of structural tissues through cross-linking with other molecules. Recognisable traces of these biomolecules may last for millions of years (Briggs et al., 1998; Briggs, 1999).

Low molecular weight fractions such as mono- and sesqui-terpenes readily diffuse from the resin into carcasses. Insect preservation in Baltic (gymnospermous origin) and Dominican (angiospermous origin) ambers differs (Grimaldi et al., 1994). Dominican amber usually preserves membrane structures, musculature, and nerve tissue, whereas preservation of these features is less frequent in Baltic amber where inclusions tend to be surrounded by a milky coating due to microbial decomposition, autolysis or reaction between decay fluids and compounds in the resin. Baltic amber contains a high concentration of resin acids, mainly succinic and communic. Dominican and Mexican ambers are similar to Baltic amber and fossil kauri, but differ in the stereochemistry of the methyl group and its side-chain. Thus they are not derived from communic acid but from ozic acid and its hydroxy derivative zanzibaric acid (Beck, 1999). The preservation of amino acids in insect tissues from ambers of various ages is attributed to anhydrous conditions (Wang et al., 1995). Low temperatures are a more important factor in determining whether amino-acids might be preserved in amber than is the age of the deposit (Halpine, 1995; Wang et al., 1995). Traces of chitin and protein are present in bees from 2000-year old African copal, but bees and beetles from Dominican amber preserve neither. The cuticle of the Dominican taxa has been transformed into long, straight chain hydrocarbons (Stankiewicz et al., 1998b). Encapsulation of the insects in resin precludes an external source for the aliphatic polymer, which is interpreted as a diagenetic product of polymerisation of the insect cuticular waxes and body lipids (Stankiewicz et al., 2000).

Resin prevents carcasses from collapsing and allows them to retain their 3-D morphology. The preservation of decay-prone tissues is doubtless a product of reaction with constituents in the resin, although the details of this process remain to be elucidated. Henwood (1993) suggested that diterpene resin acids, such as copalic and enantiopinifolic acids, reacted with organic inclusions. Stankiewicz et al. (1998b) considered the preservation to be a result of cross-linkage with resin components connected via sulphur and/or other terminal olefinic groups of the diterpenoid units. The loss of volatiles during polymerisation of copal under atmospheric conditions promotes cracking of the surface (Fig. 8D).

Amber may be reworked. Amber deposits are known to have been eroded and redeposited in the Baltic Sea region during the Quaternary (Masicka, 1972; Weitschat and Wichard, 1998). Baltic amber even has been found in the UK (Jarzembowski, 1999). The ease with which resin pieces are transported varies with their density, which depends on the nature of the inclusions and degree of polymerisation, and with the salinity of the transporting medium. The density of resin is similar to that of water (copal: 1.03–1.08; amber: 1.04–1.10). Dominican amber shows little evidence of reworking or transport and its age can be used to calibrate rates of molecular evolution of the included taxa (Iturralde-Vinent and MacPhee, 1996).

Amber oxidises rapidly when exhumed, indicating, together with the results of studies of Recent kauri gum (Poinar, 1991a), that preservation is favoured by burial in anoxic sediment. The processes that affect amber-bearing rocks also affect their inclusions. Darkening of amber, usually from yellow to red, has been correlated with oxidation and weathering, as well as temperature increase: amber from both the Baltic (Eocene) and northern Spain (Middle Cretaceous) exhibits a darkening of the edges of abundant organic inclusions. A comparison of the maturity of amber with that of the enclosing rock matrix, as determined by the study of the vitrinite content, may reveal whether or not the amber has been reworked (Poinar and Mastalerz, 2000).

The major processes that affect amber-bearing deposits during diagenesis are overburden pressure and elevated temperature. Intensely polymerised amber is brittle, while less polymerised amber is more plastic and deformable and may become flattened or disc-shaped (Zherikhin and Eskov, 1999). Release of pressure may result in fracturing around the discontinuity formed by an insect inclusion. Fractures and haloes around carcasses are common, particularly in Baltic amber. Dark amber layers, which have been polymerised by sunlight and wind, are more prone to fracturing. Increased temperature may induce darkening. Moreover, amber may melt (melting point: 200–380°C) or fragment completely. Differences in degree of tectonic deformation are reflected in differences in the infrared spectra of amber from two localities in the Cordillera Septentrional of the Dominican Republic: La Toca and Palo Alto (Henwood, 1992a). The La Toca site has undergone tectonic deformation (Grimaldi, 1995).

Weathering destroys amber through oxidation, which results in the formation of a friable crust that increases in thickness and darkness with time (Fig. 8E). Diagenetic minerals, such as pyrite, occur in some ambers. Pyrite may penetrate amber to form dendrites along fissures, or precipitates as a coat at the boundary between the amber matrix and the insect carcass (Schlüter and Stürmer, 1982; Baroni-Urbani and Graeser, 1987). Pyrite most commonly occurs within amber in sulphur-rich coal-bearing sediments (Garty et al., 1982; Alonso et al., 2000). Few examples are known of completely pyritised insects: five specimens in Lebanese amber (Azar, pers. commun.), and two in New Jersey amber (Grimaldi et al., 2000). The mode of formation is unknown, but is likely to reflect microfractures that connect the insect to the surface of the amber piece. Schlüter (1989) found microscopic crystals of marcasite in the interior of some insects from Cenomanian amber of northwestern France.

Collecting methods may introduce biases into insect assemblages and distort palaeoecological conclusions. Pike (1993) compared the insects from five samples of amber that were prepared by picking with those from three samples that were prepared by sieving. Fewer insects per kg were found in the picked samples than in the sieved ones. Sieving evidently retrieved small pieces containing significant inclusions. Amber preserves many small insects such as thysanopterans and aphids, but this size range is very rare in limestones. This bias may be partly a result of collecting methods, as limestones are usually sampled in the field, whereas amber is sampled using a microscope in the laboratory.

7. Conclusions

Localities that yield fossil insects are uncommon compared, for example, to those preserving mollusc shells: insects are treated as an exotic group of fossil arthropods in the majority of palaeontology texts, and are sometimes not mentioned. In recent years, however, a large number of papers have been published on fossil insects: they are the fossil group to have received the most attention between the publication of *The Fossil Record* in 1967 (Crowson et al., 1967) and *The Fossil Record 2* in 1993 (Ross and Jarzembowski, 1993; Labandeira, 1994). Today more species of fossil insect are known than any other group of fossil arthropods, and there are more families of fossil insects than of combined fossil and recent vertebrates.

The fossil record of insects preserved in carbonate rocks is very different from that in amber. Evidence of the death of the insect is usually preserved in amber, but not in carbonate rocks. Biostratinomic processes are much more significant in sediments, although insects in amber may be transported together with the preservation medium. The diagenesis of insects entombed in resin is poorly understood, but dehydration, reactions with chemical components within the resin, and polymerisation are important. The diagenesis of insects found in carbonate rocks is more complex and diverse. Specimens may be preserved as organic remains, albeit altered to a more stable composition; by replication or replacement in an authigenic mineral, usually calcium carbonate, pyrite or calcium phosphate; as an external mould of the exoskeleton; or as a cast in calcite, silica, or pyrolusite. Insects are usually flattened in limestones, while they are preserved in three dimensions in amber.

Although fossil insect localities are rare and scattered in time and space, where these arthropods do occur, they tend to be abundant and diverse. Few insect localities are known from the Triassic, Upper Cretaceous and Palaeocene. Thus the insect fossil record fluctuates with global taphonomic conditions. Family level data across the Cretaceous–Tertiary (K–T) boundary reveal little impact of the extinction on insects (Whalley, 1987; Ross et al., 2000; but see Christianson and Pike, 2001), but no major occurrences of insects of Maastrichtian or Danian age are known (Labandeira et al., 2002). Evidence of plant–insect associations, however, suggests that there was a major extinction of insect herbivores at the K–T boundary, at least in North America (Labandeira et al., 2002). Fluctuations in the quality of the insect fossil record generate problems for the study of fossil insects: in analyzing phylogeny (some groups are less represented than others); in palaeobiogeography (e.g. the lack of insect records for most of Gondwanaland); in determining the true timing of the origin and extinction of some groups; and in identifying the history of diversity of the group as a whole and the timing of important radiations and extinctions, such as the impact of the Permo–Triassic and K–T boundary events.

This review of the major taphonomic processes that affect the preservation of insects in carbonates and amber will assist in the identification of the factors that promote biases in the insect fossil record. It also highlights questions that require further research. Why are biological inclusions absent at most amber localities and how was this barren amber produced? How is amber transported from the producing tree to the sediment in which it is preserved? What controls 3-D preservation and concretion formation in carbonates?

The study of taphonomic processes is important not only for the reconstruction of the fossil insect assemblage, but also for the interpretation of the sedimentary setting and palaeoenvironment where the insect lived (climate) and died (anoxia, presence of microbial mats), as well as the ecological importance of insects in Phanerozoic terrestrial ecosystems. Reworking of amber may result in time-averaging and mixing of insects from different ecosystems. An understanding of the taphonomy of insect assemblages is essential to determining the palaeoenvironment and interpreting possible relationships among insects, interactions between insects and other organisms, and their role in ancient ecosystems.

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Appendix

	Amber deposits	Age	Coordinates	Palaeolatitude	Palaeolongitude
1	Aukland Prov. (New Zealand)	Miocene–Pliocene	37S 175E	−44.31	175.411
2	Luzon Island (Phillipines)	Miocene–Pliocene	16N 121E	16	121
3	Romania	Upper Miocene	44N 26E	43.851	24.761
4	Yazov (Ukraine)	Upper Miocene	48N 39E	48.294	37.477
5	Okanagan Highlands (British Columbia)	Lower Miocene–Middle Miocene	50N 119W	50.106	−112.591
6	Bayaguana–El Valle (Dominican amber)	Lower Miocene	19N 69W	17.512	−67.53
7	Merit–Pila (Malaysia)	Lower Miocene	2N 113E	4.428	117.304
8	Burghammer (Lausitz, Germany)	Miocene	51N 14E	50.437	12.342
9	Central Sumatra	Miocene	0 102E	1.157	106.602
10	Machów (Poland)	Miocene	51N 22E	50.705	20.258
11	Pará (Brazil)	Miocene	5S 53W	−6.745	−48.228
12	Goitsche mine (Germany)	Upper Oligocene–Lower Miocene	52N 12E	51.193	7.935
13	Bitterfeld (Germany)	Upper Oligocene–Lower Miocene	52N 12E	51.193	7.935
14	Catania (Sicily)	Upper Oligocene	37N 15E	34.338	14.153
15	Santiago–P. Plata (Dominican amber)	Middle Oligocene–Miocene	19N 71W	15.54	−68.83
16	Mexican amber (Chiapas–Simojovel)	Middle Oligocene–Miocene	17N 93W	14.081	−83.643
17	Chilikty Fm. (Pavlodar, Kazakhstan)	Middle Oligocene	52N 77E	56.044	75.29
18	Chulym–Enisey basin (Siberia)	Middle Oligocene	58N 85E	62.376	83.34
19	Rechnoy Peninsula (Tavrichanka, Russia)	Oligocene	43N 132E	47.39	134.406
20	Uly–Zilansik River Basin (Kazakhstan)	Oligocene	49N 65E	52.385	62.729
21	Iwaidzumi–Iwate (Japan)	Oligocene	40N 142E	48.971	143.454
22	Korzhindy Fm. (Aral Sea, Kazakhstan)	Lower–Middle Oligocene	45N 60E	48.08	58.016
23	Kantemirovka (Veronezh, Russia)	Lower Oligocene	50N 40E	51.549	36.338
24	Colti (Buzau, Romania)	Early Oligocene	45N 27E	45.507	24.102
25	Ben Metir (Aïn Draham, Tunise)	Oligocene or earlier	37N 9E	34.227	8.356
26	Klesov (Ukraine)	Upper Eocene–Lower Oligocene	51N 27E	51.356	21.207
27	Uglovka Fm. (Primorye, Russia)	Eocene–Oligocene	55N 20E	54.267	12.89
28	Seattle (Washington, USA)	Eocene–Oligocene	48N 122W	45.767	−101.135
29	Avekova Fm. (Magadan, Russia)	Eocene–Oligocene	60N 151E	65.524	166.927
30	Königsaue (Aschersleben, Germany)	Upper Eocene	52N 11E	50.119	5.513
31	Palmnicken (Samland, Russia)	Upper Eocene	55N 20E	54.267	12.89
32	Zwenkau (Leipzig, Germany)	Upper Eocene	51N 12E	49.277	6.786
33	Dnepr River basin (Belorussia and Ukraine)	Upper Eocene	47N 34E	48.435	29.504
34	Kasyanovo (Veronezh, Russia)	Upper Eocene	50N 40E	52.205	34.602
35	Verkhne–Sinevidnoe (Ukraine)	Upper Eocene	49N 20E	48.422	15.069
36	Sambian Peninsula	Upper Eocene	55N 20E	54.267	12.89
37	Parczew (Poland)	Early Upper Eocene	52N 23E	51.768	16.942
38	Shansi Prov. (China)	Middle–Upper Eocene	35N 112E	43.043	114.627
39	Shensi Prov. (China)	Middle–Upper Eocene	34N 109E	42.17	111.203
40	Kwangtung (China)	Middle–Upper Eocene	23N 113E	30.459	118.924
41	Yungchang (Yunnan, China)	Middle–Upper Eocene	26N 100E	30.79	103.126
42	Tiger Mountain Fm. (Issaquah, Washington, USA)	Middle Eocene	48N 122W	45.767	−101.135

Appendix (*Continued*).

	Amber deposits	Age	Coordinates	Palaeolatitude	Palaeolongitude
43	Claiborne Fm. (Arkansas, USA)	Middle Eocene	36N 92W	31.062	−74.884
44	Napan Fm. (Kamchatka, Russian)	Middle Eocene	58N 159E	62.63	175.052
45	Visloe (Belgorod, Russia)	Middle Eocene	51N 37E	52.763	31.185
46	Helmstedt (Germany)	Middle Eocene	52N 11E	50.119	5.513
47	Leonhard (Geiseltal, Germany)	Middle Eocene	51N 12E	49.277	6.786
48	Baltic amber (Samland Peninsula)	Lower–Middle Eocene	55N 20E	54.267	12.89
49	Guchenzgi Fm. (Fushun, Liaoning, China)	Eocene	42N 124E	48.61	137.14
50	Malverne (Arkansas, USA)	Eocene	34N 93W	29.148	−76.044
51	Simi Valley (California, USA)	Eocene	34N 119W	35.089	−102.457
52	Tastakh Lake (Siberia)	Eocene	71N 144E	77.457	164.343
53	Patagonica Fm. (Puerto Madryn, Argentina)	Lower–Middle Eocene	43S 65W	−50.66	−41.917
54	Latdorf–Nienburg (Germany)	Eocene	52N 12E	50.254	6.451
55	Nietleben (Halle, Germany)	Eocene	51N 12E	49.277	6.786
56	Ameki Fm. (Umuahia–Bende, Nigeria)	Eocene	6N 7E	1.352	6.924
57	Eureka Sd Grp (Axel Heiberg+Ellesmere Island, Canada)	Eocene	80N 85W	73.568	−53.205
58	Gablitz (Wien, Austria)	Eocene	48N 16E	46.89	11.532
59	Douzens (Aude, France)	Lower Eocene	43N 3E	40.239	0.512
60	Quesnoy (Oise, France)	Lowermost Eocene	51N 3E	46.543	11.429
61	Hat Creek (British Columbia, Canada)	Early–Middle Eocene	51N 121W	48.62	−99.467
62	Nanaimo (Vancouver, Canada)	Early–Middle Eocene	49N 124W	46.969	−102.794
63	Princeton (British Columbia, Canada)	Early–Middle Eocene	49N 121W	46.647	−99.957
64	Bykovskaya Fm. (Lena Delta, Siberia)	Palaeocene	72N 127E	73.946	101.574
65	Naiba River (near Urtay Creek mouth, Russia)	Palaeocene	52N 143E	59.508	148.527
66	Sakhalin Island (Russian Far East)	Palaeocene	49N 143E	57.192	144.891
67	London Clay Fm. (UK)	Palaeocene	51N 1E	41.722	7.473
68	Wabamun Lake (Alberta, Canada)	Palaeocene	54N 114W	61.695	−74.752
69	Corbières (Pirenean, France)	Danian	43N 2E	33.705	8.015
70	Lance Fm. (Niobrara, Wyoming, USA)	Upper Maastrichtian	43N 104W	51.426	−59.433
71	Hell Creek Fm. (Glendive, Montana)	Upper Maastrichtian	47N 105W	55.375	−57.831
72	Laramie Fm. (Boulder, Colorado)	Upper Maastrichtian	40N 105W	48.921	−62.264
73	Timmerdyankh–Khaya Hill (Yakutia, Russia)	Maastrichtian–Danian	66N 174E	74.869	162.467
74	Edmonton (Alberta, Canada)	Maastrichtian	54N 113W	63.899	−60.676
75	Grande Prairie (Alberta, Canada)	Maastrichtian	55N 119W	66.419	−66.885
76	Vilada (Barcelona, Spain)	Maastrichtian	41N 2E	28.713	13.446
77	Terlingua Formation (Brewster County, Texas)	Late Campanian–Early Maastrichtian	30N 103W	38.951	−64.788
78	Fruitland Fm. (San Juan Basin, New Mexico)	Campanian	37N 107W	46.362	−66.119
79	Cedar Lake (Manitoba, Canada)	Campanian	53N 100W	59.264	−47.468
80	Foremost Fm. (Medicine Hat, Alberta, Canada)	Campanian	50N 111W	59.775	−62.183
81	Baja California (Mexico)	Campanian	∼29N 115W	44.442	−80.791
82	Dinosaur Prov. Park (Patricia, Alberta, Canada)	Campanian	51N 112W	60.952	−62.465
83	Taber (Alberta, Canada)	Campanian	50N 112W	60.05	−63.342

Appendix (*Continued*).

	Amber deposits	Age	Coordinates	Palaeolatitude	Palaeolongitude
84	Taneichi and Kunitan Fms. (Kuji, Japan)	Campanian	40N 142E	48.635	136.675
85	Wainright (Alaska)	Campanian	71N 161W	88.037	−168.067
86	Yantardakh (Khatanga, Russia)	Late Santonian	72N 103E	67.044	84.297
87	Maymecha River Siberia	Santonian	71N 100E	65.709	83.422
88	Merchantville Fm. (New Jersey)	Santonian–Campanian	40N 75W	40.112	−32.378
89	Baikura–Neru Bay (Taimyr, Russia)	Coniacian–Santonian	73N 82E	65.083	69.34
90	Kheta Fm. (Khatanga, Russia)	Coniacian–Santonian	72N 103E	67.044	84.297
91	Gorchuchaj river (Laèinskij, Azerbaijan)	Coniacian	40N 47E	29.391	53.467
92	Shawarshawan (Armenia)	Coniacian	45N 45E	34.241	51.22
93	Koti (Noemberyan, Armenia)	Coniacian	40N 45E	29.259	51.716
94	Mamalichay river basin (Azerbaijan)	Coniacian	40N 47E	29.391	53.467
95	Tamagawa Fm. (Okawame–Kuji, Japan)	Late Cretaceous	40N 142E	48.635	136.675
96	Arctic Coastal Plain and Foothills, Yukon Delta	Late Cretaceous	63N 164W	80.108	−147.563
97	Arctic Coastal Plain and Foothills, Umnak Islands	Late Cretaceous	53N 169W	69.791	−150.23
98	Arctic Coastal Plain and Foothills, Unalaska	Late Cretaceous	54N 167W	70.975	−147.231
99	Arctic Coastal Plain and Foothills, Killik Bend	Late Cretaceous	69N 154W	86.275	−111.297
100	Ajka (Hungary)	Upper Cretaceous	47N 18E	35.635	28.337
101	Magothy Fm. (Maryland, USA)	Turonian–Coniacian	39N 77W	39.786	−34.739
102	Bouches-du-Rhône (France)	Turonian	44N 5E	33.104	17.136
103	Ledyanaya Fm. (Khatanga, Russia)	Turonian	72N 103E	67.044	84.297
104	Raritan Fm. (New Jersey)	Turonian	40N 75W	40.112	−32.378
105	Kiya and Simonovo Fm. (Chylym–Enisey, Siberia)	Cenomanian–Turonian	73N 81E	64.967	68.704
106	Arkagala Fm. (Magadan, Russia)	Cenomanian–Turonian	60N 160E	66.974	150.995
107	Timmerdyakh Fm. (Siberia) Yakutia	Cenomanian–Turonian	66N 174E	74.869	162.467
108	Dolgan Fm. (Agapa, Russia)	Upper Cenomanian	71N 89E	64.133	75.839
109	Seward (Nebraska)	Upper Cretaceous	41N 97W	47.576	−53.226
110	Taimyrskoje lake (Taimyr, Russia)	Upper Cretaceous	75N 105E	69.884	81.242
111	Lena (Yakutia, Russia)	Upper Cretaceous	64N 126E	64.075	111.719
112	Arctic Institute Islands (Karsk Sea, Taimyr)	Upper Cretaceous	75N 82E	66.904	67.304
113	Baigul Fm. (Olov, Chita, Russia)	Upper Cretaceous	52N 114E	50.453	108.418
114	Grassy Lake (Alberta, Canada)	Upper Cretaceous	50N 101W	56.918	−51.199
115	Adzikend (Azerbaijan)	Cenomanian	41N 46E	30.32	52.492
116	Agapa river (Tajmyr)	Cenomanian	71N 89E	64.133	75.839
117	Angoulêmes (Aquitanian Basin, France)	Cenomanian	46N 10E	28.785	22.578
118	Anjou region (France)	Cenomanian	47N 1W	36.468	12.364
119	Bezonnais, *Durtal* and Fouras (France)	Cenomanian	48N 13W	38.492	2.397
120	Bezonnais, Durtal and *Fouras* (France)	Cenomanian	46N 1W	35.473	12.237
121	Salignac (Alpes, France)	Cenomanian	45N 1E	34.341	13.82
122	Hukawng Valley (Myitkyina, Myanmar)–Burmese	Cenomanian	26N 95E	5.518	100.275
123	La Monjoya Fm. (Asturias, Spain)	Lower–Middle Cenomanian	43N 6W	32.1	7.326
124	El Caleyu Fm. (Asturias, Spain)	Lower Cenomanian	43N 6W	32.1	7.326
125	Murovdag Range (Azerbaidzhan)	Lower Cenomanian	40N 47E	29.391	53.467

Appendix (*Continued*).

	Amber deposits	Age	Coordinates	Palaeolatitude	Palaeolongitude
126	Ullaga Fm. (Asturias, Spain)	Upper Albian	43N 6W	31.973	20.475
127	Begichev (Uts–Enisey, Russia)	Albian–Cenomanian	70N 84E	64.067	81.885
128	Charente (France)	Albian–Cenomanian	45N 0	32.144	26.674
129	Ellsworth County–Kanopolis Lake (Kansas)	Albian–Cenomanian	39N 98W	41.208	−34.699
130	Aabediyé (Central Lebanon)	Albian	34N 36E	3.442	43.801
131	Khetana river (Khabarovsk, Russia)	Albian	48N 135E	54.487	144.659
132	Wadi Zerka (Amman, Jordan)	Albian	52N 36E	40.404	55.56
133	Ensenada del Camello (Santander, Spain)	Albian	43N 4W	31.156	21.899
134	Escucha Fm. (Rubielos de Mora and others, Spain)	Lower–Middle Albian	40N 1W	27.418	22.207
135	Nograro Fm. (Peñacerrada, Spain)	Lower–Middle Albian	43N 3W	30.752	22.61
136	Crato Fm. (Araripe, Brazil)	Upper Aptian–Lower Albian	7S 40W	−7.563	2.1
137	Caza Aaley (Central Lebanon)	Upper Aptian	34N 36E	3.442	43.801
138	Hammana 3 (Central Lebanon)	Upper Aptian	34N 36E	3.442	43.801
139	Ogneva Fm. (Khatanga, Russia)	Aptian–Albian	72N 103E	69.191	91.91
140	Reocín (Cantabria, Spain)	Aptian–Albian	43N 4W	31.156	21.899
141	Yakovleva (Taimyr, Russia)	Aptian–Albian	71N 83E	64.762	80.049
142	Stary Oskol (Belgorod, Russia)	Aptian	51N 38E	39.6	57.361
143	Hadath El Joubbeh (Lebanon North)	Early Aptian	34N 36E	3.442	43.801
144	Hammana 3 (Central Lebanon)	Early Aptian	34N 36E	3.442	43.801
145	Jezzine 3 (South Lebanon)	Early Aptian	34N 35E	3.793	43.049
146	Morella (Castelló, Spain)	Early Aptian	41N 0W	27.867	23.531
147	Wessex Fm. (Isle of Wight, UK)	Early Barremian	51N 1W	38.163	26.102
148	Patuxent Fm. (Atlantic Coastal Plain)	Barremian	39N 73W	34.108	−11.841
149	Mont Liban localities (Central Lebanon)	Upper Neocomian (Hauterivian)	34N 36E	3.442	43.801
150	Kimigahama Fm. (Nagasaki–Chōshi, Japan)	Hauterivian	36N 141E	49.282	148.596
151	Bloudan (Syria)	Hauterivian	34N 36E	3.442	43.801
152	Viena and Salzburg (Austria)	Hauterivian	48N 16E	35.219	39.868
153	Kirkwood Fm. (Eastern Cape Prov. South Africa)	Middle–Upper Valanginian	33S 25E	−47.787	−4.802
154	Mont Hermon (Qiryat Chmouma, Israel)	Valanginian–Hauterivian	33N 36E	0.736	43.02
155	Amber in *Dorset*, Kent and Sussex (UK)	Valanginian	51N 3W	38.216	24.502
156	Amber in Dorset, *Kent* and Sussex (UK)	Valanginian	51N 1E	38.123	27.702
157	Amber in Dorset, Kent and *Sussex* (UK)	Valanginian	51N 0	38.141	26.902
158	Hammana 1 and 2 (Central Lebanon)	Middle Neocomian	34N 36E	3.442	43.801
159	Jezzine 1 and 2 (South Lebanon)	Middle Neocomian	34N 35E	3.793	43.049
160	Mont Liban localities (Central Lebanon)	Middle Neocomian	34N 36E	3.442	43.801
161	Quanat and Bcharre (North Lebanon)	Middle Neocomian	34N 36E	3.442	43.801
162	Mont Liban localities (Central Lebanon)	Lower Neocomian	34N 36E	3.442	43.801
163	Moravske Trebove (Czekoslovaquia)	Cretaceous	50N 17E	37.248	40.561
164	Boskovice (Moravia, Czekoslovaquia)	Cretaceous	49N 17E	36.249	40.625
165	Golling (Salzbourg, Austria)	Lower Cretaceous	48N 13E	35.142	37.414
166	Shaum'anowskij region (Azerbaijan)	Lower Cretaceous	40N 47E	29.748	67.06
167	Suyfun basin (Primorye, Russia)	Lower Cretaceous	43N 132E	49.07	144.262

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