AMBER

CONRAD C. LABANDEIRA

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution
Washington, D.C. 20013 USA
<labandec@si.edu>

and

Department of Entomology, University of Maryland, College Park, MD 20742 USA

ABSTRACT.—The amber fossil record provides a distinctive, 320-million-year-old taphonomic mode documenting gymnosperm, and later, angiosperm, resin-producing taxa. Resins and their subfossil (copal) and fossilized (amber) equivalents are categorized into five classes of terpenoid, phenols, and other compounds, attributed to extant family-level taxa. Copious resin accumulations commencing during the early Cretaceous are explained by two hypotheses: 1) abundant resin production as a byproduct of plant secondary metabolism, and 2) induced and constitutive host defenses for warding off insect pest and pathogen attack through profuse resin production. Forestry research and fossil wood-boring damage support a causal relationship between resin production and pest attack. Five stages characterize taphonomic conversion of resin to amber: 1) Resin flows initially caused by biotic or abiotic plant-host trauma, then resin flowage results from sap pressure, resin viscosity, solar radiation, and fluctuating temperature; 2) entrapment of live and dead organisms, resulting in 3) entombment of organisms; then 4) movement of resin clumps to 5) a deposition site. This fivefold diagenetic process of amberization results in resin→copal→amber transformation from internal biological and chemical processes and external geological forces. Four phases characterize the amber record: a late Paleozoic Phase 1 begins resin production by cordaites and medullosans. A pre-mid-Cretaceous Mesozoic Phase 2 provides increased but still sparse accumulations of gymnosperm amber. Phase 3 begins in the mid-early Cretaceous with prolific amber accumulation likely caused by biotic effects of an associated fauna of sawflies, beetles, and pathogens. Resiniferous angiosperms emerge sporadically during the late Cretaceous, but promote Phase 4 through their Cenozoic expansion. Throughout Phases 3 and 4, the amber record of trophic interactions involves parasites, parasitoids, and perhaps transmission of diseases, such as malaria. Other recorded interactions are herbivory, predation, pollination, phoresy, and mimicry. In addition to litter, amber also captures microhabitats of wood and bark, large sporocarps, dung, carrion, phytotelmata, and resin substrates. These microhabitats are differentially represented; the primary taphonomic bias is size, and then the sedentary vs. wandering life habits of organisms. Organismic abundance from lekking, ant-refuse heaps, and pest outbreaks additionally contribute to bias. Various techniques are used to image and analyze amber, allowing assessment of: 1) ancient proteins; 2) phylogenetic reconstruction; 3) macroevolutionary patterns; and 4) paleobiogeographic distributions. Three major benefits result from study of amber fossil material, in contrast to three different benefits of compression-impression fossils.

INTRODUCTION

Amber is a significant source of information about terrestrial forest and woodland ecosystems from deposits of late Pennsylvanian to Pleistocene age. Although there are hundreds of sites worldwide that provide significant accumulations of amber, only a small fraction of these sites have the greatest scientific potential for preserving the earliest biotas, including microbiotas and macroscopic inclusions. Amber first appears in the fossil record during the early Pennsylvanian (~320 Ma), but lacks any significant record of macroscopic biological inclusions until the mid-Early Cretaceous (~125 Ma), with the sole exception of very rare and isolated occurrence of late Triassic arthropods from the Dolomites Region of the Southern Alps in Italy (Schmidt et

In: *Reading and Writing of the Fossil Record: Preservational Pathways to Exceptional Fossilization. The Paleontological Society Papers, Volume 20, Marc Laflamme, James D. Schiffbauer, and Simon A. F. Darroch (eds.). The Paleontological Society Short Course, October 18, 2014.*

al., 2012). Twenty-five biotically rich or otherwise potentially important amber deposits have been identified (Table 1; <http://paleosoc.org/shortcourse2014.html>). The description of amber taxa has resulted from the considerable efforts of paleoentomologists, paleobotanists, and paleoecologists who have documented a bewildering array of specimens and taxa that includes microorganisms, plants, fungi, nematodes, arthropods, the occasional small vertebrate, and other organisms. Historically, this endeavor has accounted for discovery of many terrestrial life forms in the fossil record (Carpenter, 1992; Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005; Boucot and Poinar, 2010; Penney, 2010b). Because of these significant efforts, it is timely to provide a review spotlighting the role of taphonomy in understanding the amber fossil record.

In this contribution, eight topics concerning the amber fossil record will be addressed: 1) The natural history of resin is discussed, including its compositional variety, mode of formation, plant producers, occurrence in environments of production and deposition, and relationships with arthropods and other organisms. 2) The process of how resin flows incorporate a variety of organisms is described, including entrapment, entombment, transportation to a depositional site, and eventual conversion to copal and then to amber through the amberization process. 3) The major features of the amber fossil record are explored, including notable occurrences and their importance for understanding amber source communities in time and space. 4) An exposition of inter-organismic interactions from the amber fossil record is mentioned, with a focus on herbivory, parasitism, predation, pollination, and mimicry, as well as evidence for intraspecific relationships, such as mating behavior. 5) Biases affecting the amber fossil record is presented, with a view toward understanding how those biases affect interpretation of the fossil record. 6) A somewhat extensive section is devoted to techniques and equipment used in the imaging, analysis, and interpretation of amber. 7) A discussion of four exploratory ways that amber has provided case studies for a more complete assessment of the terrestrial fossil record. 8) A brief overview is offered regarding the benefits and liabilities of amber compared to that of the compression-impression fossil record. It is anticipated that this survey of recent developments in the role that taphonomy contributes to amber fossil record will spark new ways of investigating and understanding this vast archive of past terrestrial life.

THE NATURAL HISTORY OF RESIN

A variety of modern vascular plants produce exudates, many of which are economically important. A plant exudate is a general term that refers to a viscous liquid secreted by plants that, when released, remain sticky and hardens within days to weeks, especially when exposed to the atmosphere (Lambert et al., 2008). Typical plant exudates are gums (such as gum Arabic, myrrh, and frankincense), kino dyes, latexes (including naturally occurring rubber), mucilages, occasionally oils and waxes, and resins, the source of copal and amber (Langenheim, 1990; Vávra, 2009). With the exception of copal and amber, plant exudates have minimal preservation potential and are rarely found in the fossil record (Langenheim, 1990; Santiago-Blay et al., 2011). Gums are water-soluble polysaccharides that are the products of bacterial infection, whereas latexes and mucilage are plant products confined to internal duct tracts that ward off insect attack (Langenheim, 1990; Vávra, 2009). Resins, by contrast, are a special class of terpenoid compounds, often with phenolic components, produced in specialized secretory tissues of plant surfaces or their internal duct networks that result from plant secondary metabolism.

The definition of what amber is historically has had a murky history, and definitions are inexact. Schlee and Glöckner (1978) used a million years as the cutoff between ‘fossilized’ amber and younger, ‘unfossilized’ copal. [The name copal comes from *copulli*, the Nahuatl word for modern resin produced by a variety of plants, including the amber sources *Hymenaea* (jatobá, Fabaceae), *Protium,* and *Bursera* (copal, myrrh, Burseraceae) and *Liquidambar* (sweetgum, Hamamelidaceae).] However, hard, chemically inert, and more-or-less chemically fossilized amber occurs in sediments less than one million years (m.y.) in age. After several proposed terminological changes for the copal-to-amber time boundary, improvement was arrived at by Vávra (2009), who focused on the physical characteristics of a piece of suspect resin or copal in the fossil record, rather than its chronological age. Part of the realization for this imprecise but taphonomically more realistic definition is acknowledgement that the conversion of modern

resin or copal to recognizably fossilized amber is a highly variable diagenetic process known as 'amberization.' While inexact, copal refers to any resin that is less than 40,000 years old, whereas amber is older than 40,000 years. In addition, and without reference to geochronological age, copal consists of resin in a deposit that retains the melting point, hardness, solubility, and other physiochemical properties of modern resin (Poinar, 1992a), and is determined by the tackiness of the resin surface. While the distinction of copal versus amber remains unsatisfactory, the definition of an 'amber fossil' used by paleontologists generally refers to any trace of life occurring in the amber sedimentary record regardless of its age or preservational state.

Ambers are not true minerals because they lack a crystallographic structure, although they are treated as such informally. Most ambers consist of complex terpenoid or phenolic compounds linked by isoprene units (Langenheim, 1990). Terpenoid-based ambers contain volatile monoterpenes, sesquiterpenes, and some diterpenes mixed with nonvolatile tripterpene and other diterpenes accompanied by alcohols, aldehydes, esters, and difficult-to-characterize neutral substances (Langenheim, 1990). These compositional differences are important for segregation of ambers into chemically recognizable groups. Based on their macromolecular and structural properties, ambers are grouped into five major classes (Beck, 1999; Lambert et al., 2008). Class I ambers are based on polymers or copolymers of labanoid terpenes, and are by far the most commonly occurring type. Three subdivisions of Class I ambers—Subclass 1a, 1b and 1c ambers—are each grouped based on their molecular structure, stereochemistry, and the presence or absence of succinic acid and other constituents. Class II ambers are common, and consist of polymers of sesquiterpenoid hydrocarbons that are derived from cadienene. Class III ambers are composed of polystyrene compounds. Class IV ambers are terpenoids that lack the molecular structural organization of Class I and II ambers required for polymerization, and are based on cedranes and related compounds. Class V ambers similarly lack structural organization for polymerization, but instead contain the diterpenoids abietane, pimarane, or isopimarane, and are restricted to pinaceous taxa (Lambert et al., 2008).

The earliest amber known from the fossil record is a Class Ic amber, occurring in an early Pennsylvanian deposit (Bray and Anderson, 2009). This amber type was retained in most lineages of resin-producing plants, particularly angiosperms, and, to a much lesser extent, gymnosperms. A different distributional pattern is found in Class II ambers, which are angiosperm in origin and occur in southeastern Asia and the southern and western areas of the United States. Class III ambers are restricted to sites in Germany and the Atlantic Coastal Plain of the United States. Class IV and V ambers are friable, typically are poorly preserved, and have a sporadic fossil record.

Determination of the botanical source of an amber is fraught with difficulty. Various types of identification procedures for characterizing modern resins, such as nuclear magnetic resonance spectroscopy and pyrolysis gas chromatography-mass spectrometry analyses may reveal fossil taxa that either are closely related to, or are extinct relatives of, a modern taxon. Alternatively, fossil resins may have been diagenetically degraded so that molecular comparisons to modern taxa may not be possible (Lambert et al. 2008, 2009). Supporting anatomical determinations should buttress identifications from chemical, spectroscopic, and other determinative techniques. The botanical sources of amber include a variety of modern gymnosperms and angiosperm taxa (Langenheim, 1995; Lambert et al., 2008), and extinct seed-plant taxa (Langenheim, 1990; Alonso et al., 2000; Perrichot et al., 2010; Schmidt et al., 2012). Extinct late Carboniferous and Permian plant lineages that produced modest amounts of amber included medullosans (Kosanke and Harrison, 1957; van Bergen et al., 1995), cordaites (Jones and Murchison, 1963), and unknown seed-plant sources (Bray and Anderson, 2009). Sources of Triassic to mid-early Cretaceous amber likely included the extinct Cheirolepidaceae (Roghi et al., 2006; Schmidt et al., 2012), Araucariaceae (Litwin and Ash, 1991; Philippe et al., 2005; Azar et al., 2010), and Cupressaceae (Grimaldi, 1996). During the mid- to Late Cretaceous, amber deposits were almost entirely gymnospermous, overwhelmingly consisting of Cheirolepidiaceae, Araucariaceae, and Cupressaceae (Knight et al., 2010; Grimaldi and Nascimbene, 2010), a pattern that continued into the Paleocene, although supplemented by contributions from the Pinaceae. Angiosperm resins enter the fossil record during the mid-Late Cretaceous with the appearance of amber attributed to *Liquidambar*, and

subsequently expand during the Paleogene. Paleogene occurrences include the Combretaceae (Indian almond family), Dipterocarpaceae (dipterocarp family), Burseraceae (frankincense family), and especially the Fabaceae (legume family). Neogene *Copaifera* (copaiba), and especially *Hymenaea,* become prolific resin producers, responsible for the richest amber deposits from the Miocene to the Recent (Langenheim, 1990; Penney and Preziosi, 2010).

Modern resin producers include all of the previous taxa mentioned, but importantly, consist of taxa that are not found in the fossil amber record. Gymnosperms, while producing prolific amounts of resins, have a more limited number of resin-producing taxa than angiosperms. Extant gymnosperm resin producers include only two prominent lineages—the more southern hemispheric Araucariaceae, and the northern hemispheric Pinaceae, the latter of which encompasses the dominant resin producers of *Pinus* (pines), *Picea* (spruces), *Abies* (firs), *Larix* (larches, tamaracks), and *Pseudotsuga* (Douglas fir), which inhabit cool temperate zones. Unfortunately, the Pinaceae produce Class V resins that do not preserve well in the fossil record.

A greater diversity of angiosperm taxa are resin producers when compared to gymnosperms, and mainly occur in tropical to warm-temperate localities. On average, each angiosperm species produces significantly less amber volumetrically than the average gymnosperm producer. Lesser known angiosperm resin producers are the Clusiaceae (mangosteen family), Euphorbiaceae (spurge family), well known for producing rubber, and the Arecaceae (palm family), containing mucilage exudate and the only monocot resin producer. The better-known resin producers of Anacardiaceae (sumac family), Burseraceae, Diptercarpaceae, and Fabaceae, are overwhelmingly dominant in the Neotropical (Fabaceae), west African (Fabaceae, Burseraceae) and east Indian and Indonesian (Dipterocarpaceae) rainforests (Langenheim, 1995). These plants have evolved with plant herbivores and pollinators, resulting in interesting reciprocal adaptations involving resin as a resource. The Burseraceae contains pantropical resin-producing *Protium* and *Dacyrodes* (safou) (Cowan and Polhill, 1981), as well as xeric-adapted Old World genera, such as *Boswellia* (myrrh) and *Commiphora* (frankincense). The most copious resin producers are tropical and subtropical gymnosperms and angiosperms (Langenheim, 1995), which also are the resins that readily polymerize during amberization. Such resins have the greatest fossil persistence, in part, due to efficient transportation to nearby sites of deposition.

There are two hypotheses to explain why more resin is produced by certain arborescent taxa than others, particularly in tropical and subtropical environments (Langenheim, 1990). One hypothesis states that resin production is a consequence of a plant's secondary metabolism resulting from the availability of carbon for synthesizing complex molecules such as terpenoids. A second view holds that all environments, particularly those of the tropics, harbor a variety of arthropod herbivores, and fungal and other microbial pathogens; consequently, plants select for increasing the quality and volume of antiherbivore or antipathogen targeting of host-plant defenses. Terpenoid resin flows are a prime example of such defensive capability. Indeed, terpenoid and other resins, such as phenols, are an ideal and versatile mechanism to prevent pathogen and insect attack through constitutive and induced defenses. (Constitutive defenses are baseline mechanisms that are part of a plants' normal metabolism; induced defenses are inordinate responses that are directly triggered by pathogen or herbivore attack.) Ironically, volatilized resin components not only act as deterrents, but also serve as attractants, particularly involving certain bark- and ambrosia beetles that are enticed toward trunk surfaces (Labandeira et al., 2001).

Several lines of evidence suggest against the hypothesis that resin production is only a consequence of plant secondary metabolism. The availability of carbon for terpenoid and other similar bimolecular biosynthesis cannot explain the dazzling variability in terpenoid molecular compounds (Sturgeon, 1979), and the considerable changes in the volumes of resin produced (Tomlin et al., 2000; Klepzig et al., 2005). In addition, the broad variety of wood-attacking pathogens and arthropod herbivores—viruses, wilts, fungal endophytes, white rots, pitch-canker fungi, heartwood borers and cambium engravers—presently dominate tropical and warm-temperate ecosystems (Hillis, 1987; Pearce, 1996; Labandeira and Prevec, 2014). In these tropical ecosystems, *Hymenaea* and *Copaifera* have been examined to understand why there are large differences in resin concentration

from various organs of the plant including leaves, fruit, stems, and roots. Langenheim (1984) showed that abiotic factors such as light, soil nutrients, water availability, and climate do not materially explain resin production, whereas biotic factors, such as pathogen colonization and insect herbivory, were responsible not only for high levels of resin production, but also dramatic increases in resin levels immediately after attack (Langenheim et al., 1986). The predilection for high levels of resin production, and hence the ability for self-defense, also is contingent on the presence of particular host-plant clades that have secretory canals and the metabolic machinery to produce latexes, mucilages, gums, and resins (Fahn, 1979). In a study of plant lineages that possess secretory canals but whose sister-group lineages did not, it was found that secretory-canal-bearing lineages had a significantly greater diversity in 13 (69%) of 16 sister-group pairs examined (Farrell et al., 1991). There is a rich fossil record of damage consisting of pith borings, cambium engravings, and heartwood borings throughout the Cenozoic (Guo, 1991; Böcher, 1995; Grimaldi et al., 2000b; Labandeira et al., 2001), Mesozoic (Zhou and Zhang, 1989; Jarzembowski, 1990; Tapanila and Roberts, 2012), and late Paleozoic (Weaver et al., 1997; Labandeira and Phillips, 2002; Naugolnykh and Ponomarenko, 2010). The role of arthropods in inducing resin flow has been suggested for phytophagous mites in the production of late Triassic cheirolepidiaceous Dolomites Amber in northeastern Italy (Schmidt et al., 2012). A record of needle and leaf mining and feeding defense in resin-producing plants has been documented at the tissue (Labandeira, 2013), organ (Labandeira, 2006), and species (Labandeira, 2002; Wilf et al., 2006; Lopez-Vaamonde et al., 2006; Schachat et al., 2014) levels. In rich amber deposits, there are diverse records of wood-boring beetles such as bark and ambrosia beetles co-occurring with Baltic (Schedl, 1947; Larsson, 1978) and Dominican (Bright and Poinar, 1994) ambers.

THE AMBER PRESERVATIONAL ROUTE

The preservation of amber begins with the internal generation and movement of resin on the source plant's external surface. This is followed by the mechanisms of initial entrapment, then subsequent entombment of organic material, and eventually ending in transportation of the amber clasts to a deposit, where further modification occurs. The entire process from resin production through eventual unearthing and archiving in an amber collection continues to the present day (Fig. 1).

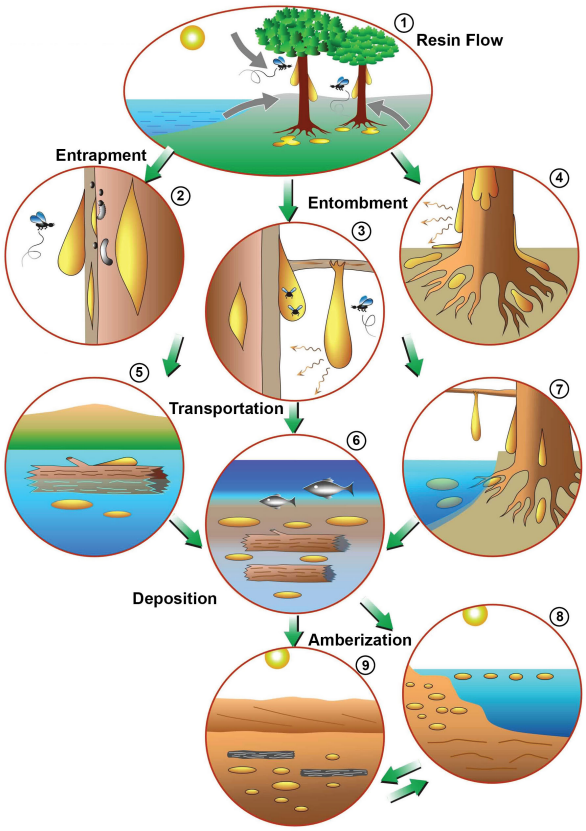


FIGURE *1*.—Amber taphonomy. 1) Resin flows can accumulate in bark fissures and cavities in the wood. 2–4) Resin engulfs and traps organisms such as insects through entrapment under subaerial conditions by: 2) drops; 3) stalactites; and 4) flows or subterranean deposits (where resins are produced by roots), eventually resulting in entombment of organisms. 5) In most cases, resins are transported to sites proximal to their source (allochthonous deposits). 6) In some cases, resins undergo transportation to sites distal to the amber source (parautochthonous deposits) through erosion. (5, 7) Resins encounter a nearby aquatic environment directly from the tree as flotsam. 8) Frequently, initial deposition of resin is associated with organic-rich sediments. Where there is significant burial, the diagenetic process of amberization begins. 9) Sometimes, these deposits can be recycled into younger deposits. Modified from Martínez-Delclòs, et al. (2004); permission for reproduction granted by Elsevier BV and image kindly provided by Enrique Peñalver.

Resin flows

Tree resin is produced in two fundamentally

different ways. One mechanism is schizogenous production, where resin is secreted by specialized parenchymatous cells that form pools in cavities within the bark, cambia, and wood, and flows to the bark surface through fissures (Fahn, 1979; Mauseth, 1988). A second mode of resin formation is lysogenous production, which secretes resin into a system of tubular canals that ramify throughout the plant (Mauseth, 1988). As resin exits the internal environment of a woody trunk or branch, or leaves and roots, it is exposed to the external environment as it begins to flow. Resin movement is dependent on internal sap pressure, resin viscosity, ambient temperature, light intensity, and the mass of the descending blob that is providing downward momentum (Martínez-Delclòs et al., 2004). As resin is exposed to the elements, particularly oxygen, radiant solar light, and elevated temperature, there is polymerization of some terpenoid compounds (Whitmore, 1977). Conditions for increased resin flow are most optimal in spring to summer in a thermally seasonal climate, but may occur during dry seasons in climates where water availability varies annually. The formation of successive resin flows may occur daily, but also may be present on a longer term, often seasonal basis, affecting especially stalactitic amber masses (Larsson, 1978). Amber stalactites have distinctive surface laminations that are rich in layered accumulations of smaller-sized insects as they become attached to ephemeral sticky surfaces between each renewed flow event (Weitschat and Wichard, 2002). The trapped insects die from asphyxia, and frequently are overwhelmed by multiple resin flows before they are sealed from the environment, occasionally undergoing predation, disarticulation, and decomposition in the process (Martínez-Delclòs et al., 2004). These daily to seasonal changes in flow determine the taxonomic composition of ambers, and typically record unique combinations of (e.g.) nocturnally versus diurnally active insects, aerial pollen maxima for particular plants, and capture of fungal spores originating from particular microhabitats, especially ephemeral events during the spring and summer (Richardson et al., 1989; Martín-Delclòs, et al., 2004; Peñalver and Grimaldi, 2006).

Saproxylic beetles consume wood but feed on fungi, and are a major cause in allowing resin to flow outward on trunk surfaces. Although wood-boring beetles have a record throughout the Triassic (Walker, 1938; Linck, 1949; Tapanila and Roberts, 2012) and back into the Late Permian (Naugolnykh and Ponomarenko, 2010), it was during the mid-early Cretaceous that there was a major volumetric expansion in resin production (Molino-Olmedo, 1999; Martínez-Delclòs et al., 2004). This event coincided with the postulated origin and earliest body- and trace-fossil occurrences of many xylophagous beetle groups, and the earliest appearance of wood-associated termite sociality (Martínez-Delclòs and Martinell, 1995). Many of these insect lineages initially were associated with the gymnospermous hosts Araucariaceae, Cheirolepidiaceae, Cupressaceae, and Pinaceae (Jarzembowski, 1990; Sequeira and Farrell, 2001; Néraudeau et al., 2002; also see Ding et al., 2013), some of which were hosted by angiosperms after the mid-Cretaceous angiosperm radiation (Labandeira, 2014). These same beetle lineages became prominent throughout the Cenozoic (Labandeira et al., 2001; Martínez-Delclòs et al., 2004), creating conditions for profuse resin production by such plants as *Hymenaea* and *Protium*. Consequently, the significantly increased production of resin was exacerbated by or even attributable to extensive tunneling activities into trunk tissues.

Entrapment

Once resin flows are present, entrapment ensues. Microorganisms, plants, fungi, arthropods, and small vertebrates are the principal organisms that are entrapped. The six fundamental factors involved in entrapment that affect arthropods the most are: 1) resin viscosity; 2) organism behavior; 3) occurrence in particular habitats; 4) various environmental conditions that promote resin production; 5) plant defenses; and 6) a variety of agents that allow accumulation of body parts, such as ant refuse heaps. The importance of resin viscosity is evident in often subtle features attending the incorporation of organisms in amber. More viscous resins possess greater surface tension, which discourages entrapment of small vertebrates, such as geckos, and larger, sturdy arthropods, such as centipedes, katydids, walkingsticks, and longhorn and scarab beetles, and also provides the ability of those same insects to struggle free when compared to considerably smaller arthropods (Henwood, 1993a). Often a struggle results in self-autopsied legs (Néraudeau et al., 2002; Weitschat and Wichard, 2002; Penney, 2005a). In analyses of various amber deposits, large insects are rare; for the Álava Amber from Spain, only 3% of insects are more than 4 mm long (Alonso et al., 2000).

Insect behavior is another factor in entrapment that favors those insects that land in or are camouflaged by bark, bore into wood or other hardened tissues, or congregate in soil-surface swarms (Koteja, 1996; Poinar and Poinar, 1999). More specific behaviors associated with particular insect taxa include resin-foraging bees (Gonçalves-Alvim, 2001) and termites that shed their wings during nuptial flights, often accumulating in great numbers (Pike, 1993). Insect pollinators, such as ginkgoalean pollinating thrips, become entrapped in amber and leave trails of pollen grains as they locomote through relatively non-viscous resin (Peñalver et al., 2012). Occasionally, aquatic insects possess behaviors that also favor disproportionate entrapment in amber. Certain aquatic beetles, such as water scavenger beetles (Hydrophilidae) and predaceous diving beetles (Dytiscidae), are disproportionately attracted to fluidized asphaltum with a water-body-like surface sheen (Horváth and Kriska, 2008), and are over-represented in brea deposits (Churcher, 1966). These same groups of insects, as well as muscid flies and wood-boring beetles, also can be attracted visually or chemically to resin pools with water-like surfaces (Agee and Patterson, 1983; Fatzinger, 1985; Horváth and Kriska, 2008). These fluid accumulations are excellent resin-pool traps (Szwedo, 2002).

Insect habitat can have a profound effect in the taxonomic composition of organisms that become trapped in amber. Five principal habitats are disproportionately represented in the fossil amber record. First are bark and wood habitats, which are perhaps the richest single source of amber inclusions (Poinar and Poinar, 1999). These cortical habitats consist overwhelmingly of beetles, including heartwood borers and cambium engravers, but also non-xylophagous animals inhabiting the nooks and crannies of bark, particularly the interface between the cambium layer and the frequently partially delaminated bark (Larsson, 1978). Bark and wood habitats are associated with patches of moss, lichens, and epiphytes nestled in bark interstices, and include tardigrades, mites, pseudoscorpions, amphipods, springtails, and a variety of minute beetles (Larsson, 1978). A second important life-mode of organisms found in amber are small, aerial insects susceptible to wind transport (Martínez-Delclòs et al., 2004), notably midge-sized nematocerous flies, but also smaller-sized insects such as thrips, parasitoid wasps, and moths. Third are folivores on upper canopy or undergrowth foliage that drop into fluidized, mobile resin flows below their habitats (Krzemińska et al., 1992). A fourth, overrepresented component of insects found in amber are large, winged insects occurring in wetland or other aquatic habitats whose immature developmental stages are aquatic, such as stoneflies (Plecoptera) and alderflies (Megaloptera), particularly in Siberian Amber (Zherikhin and Sukatcheva, 1990). For Baltic Amber, there is overrepresentation of caddisflies (Trichoptera), marsh beetles (Scirtidae), and a plethora of nematocerous flies, particularly nonbiting midges (Chironomidae) (Weitschat and Wichard, 2002), some of which originated from phytotelmata such as tank bromeliads (García-Gimeno and Peñalver, 2007). The final, perhaps nonintuitive, component of amber is underground soil fauna (Nissenbaum and Horowitz, 1992). Soil fauna houses oribatid mites, tardigrades, springtails, termites, millipedes, earwigs, root-maggot flies, ants, and small, edaphic beetles (Martínez-Delclòs et al., 2004; Nardi, 2007). The presence of in-situ underground amber produced by the roots of long-lived, resin-producing trees has been controversial (Martínez-Delclòs et al., 2004). However, evidence from modern *Hymenaea* (Henwood, 1993a) and *Agathis* (Whitmore, 1980) indicates that a significant accumulation of amber is produced autogenously by source-plant roots and litter, and is responsible for trapping underground biota (Nissenbaum and Horowitz, 1992; Perrichot, 2004).

Plant defenses (mentioned earlier in the context of terpenoids acting as an anti-xylophage mechanism to deter insect attack) also can be an attractant for insects. Resin bugs (Hemiptera: Reduviidae), resin-collecting bees (Hymenoptera: Megachilidae, Apidae), bark and ambrosia beetles, and pollinating insects of angiosperm resin-producing hosts are attracted to specific or a combination of particular volatile terpenoid molecules, and possibly phenol compounds (Armbruster, 1984; Fatzinger, 1985; Poinar, 1992b, 2010a). The ecological roles that terpenoids and associated volatile compounds play in alternatively sequestering insects for benefits such as pollination, and resisting the deleterious effects of pathogens that are vectored by bark beetles, is a fascinating aspect of the plant–insect associations of resin-producing trees (Labandeira et al., 2001; Poinar, 2010a).

The important role of environmental factors is significant for increasing resin production that

lead to increased rates of organism entrapment. Radiant solar light, temperature, and water availability are major determinants of resin production. For example, *Hymenaea courbaril* growing under conditions of greater water availability produces more resin than individuals living under water stress (Langenheim, 1967), leading to more levels of biotal entrapment. Droughts may have positive indirect effects on resin production through the fissuring of bark after major fires that induces resin production and higher volumes of flow for engulfing organisms, at least for dipterocarp forests in Indonesia (Heywood, 1993). Such a scenario also is suspected for forests of *Juniperus hypnoides* (Cupressaceae), the source plant for New Jersey Amber (Grimaldi et al., 2000b; also see Knight et al., 2010), which is associated with abundant charred remains of plants, coprolites, and insect exoskeletons (Crepet et al., 1991). A possible related environmental factor is soil type, which affects resin production through source-tree nutrition. Brazilian *Copaifera multijuga* trees growing in clayey soil produce significantly more resin than conspecifics in sandy soil (Alencar, 1982).

Another factor promoting biotal entrapment within resin involves the incorporation of arthropod fragments and other organic debris from biological processes of animals. The results of spider predation on other arthropods, for example, can result in refuse heaps of discarded sclerites and other body parts that represent a variety of prey items (Weitschat and Wichard, 2002). Other sources of biologically induced accumulations of organisms incorporated in resin include carcasses associated with spider webs (Peñalver et al., 2006; Knight et al., 2010), insect coprolites with identifiable dietary contents (Néraudeau et al., 2002), and shed exuviae from molting insects (Kutscher and Koteja, 2000).

Entombment

Entombment constitutes all of the processes immediately after entrapment and death of an organism or incorporation of an inanimate biological element as it becomes surrounded by resin, and before the resin loses contact with the external environment prior to solidification. The most consequential process of entombment is preservation of soft tissue (Stankiewicz et al., 1998). The process of modern soft-tissue preservation has been modeled in the laboratory, and deduced from compression-impression deposits for principally keratin-containing tissues, and, to a lesser extent, non-integumentary soft tissues such as eggshell membrane, muscles, digestive organs, and various cells of Mesozoic vertebrates (Schweitzer, 2011). A broader variety of organs, tissues, and cells from animals, prominently documented from penecontemporaneous mid-Eocene deposits at Geiseltal (Voigt, 1988) also occur at Messel, in central Germany (Wuttke, 1992), and offer a comparison to dipteran flight-muscle tissue in Dominican and Baltic ambers.

Probably the best-preserved documented insect flight muscle in amber is from a dance fly (Empididae) in early Miocene Dominican Amber (~17–20 Ma; Henwood, 1992a). Muscles are composed of tubular cells of muscle fibers that, in turn, consist of elongate contractile proteins, called myofibrils, which are the basic rod-shaped unit of muscle tissue. After embedding, staining, fixation, and examination under transmission electron microscopy, the specimen revealed myofibrils (Fig. 2A). Among the myofibrils, densely packed mitochondria were identified, some of which displayed cristae (Henwood, 1992a). Although the general conformation of empidid flight muscle from Dominican Amber exhibits some distortion, attributable to the entombment process of resin polymerization, it displays considerable similarity to modern dipteran flight muscle from a blow fly (Calliphoridae) (Fig. 2C). The only notable exception in this comparison is the shrinkage of fossil myofibrils to one-third the size of modern dipteran flight-muscle myofibrils, to where they approximate the size of the mitochondria. Other studies of preserved material suggest that similar preservation of muscle tissue is common (Grimaldi et al., 1994).

The flight muscle of the stingless bee *Proplebeia dominicana* (Apidae) was examined by Grimaldi et al. (1994) using scanning and transmission electron microscopy. Their results, captured in SEM images (Fig. 2D–H), are shown in a less magnified scale than that of Henwood (1992a), but provide detailed surface views of individual muscle bundles (Fig. 2D). Under transmission electron microscopy (TEM), however, longitudinal sections revealed the Z-band within the myofibrils and the M-band within each myofibril. The M-band represents the uncontracted, or relaxed myofibrillar position. Mitochondria also were preserved, seen as 'fingerprint' patterns of parallel, curvilinear

structures under TEM, and better resolved than those imaged by Henwood (1992a). Although the mitochondria were not detected in an examination of decay of modern shrimp in the laboratory, monitoring of muscle phosphatization revealed preservation of myofibrils with probable M- and Z-bands (Briggs and Kear, 1993). This suggests a similar timing for preservation of muscle during phosphatization in compression-impression fossils, analogous to early stages of carcass decay in resins.

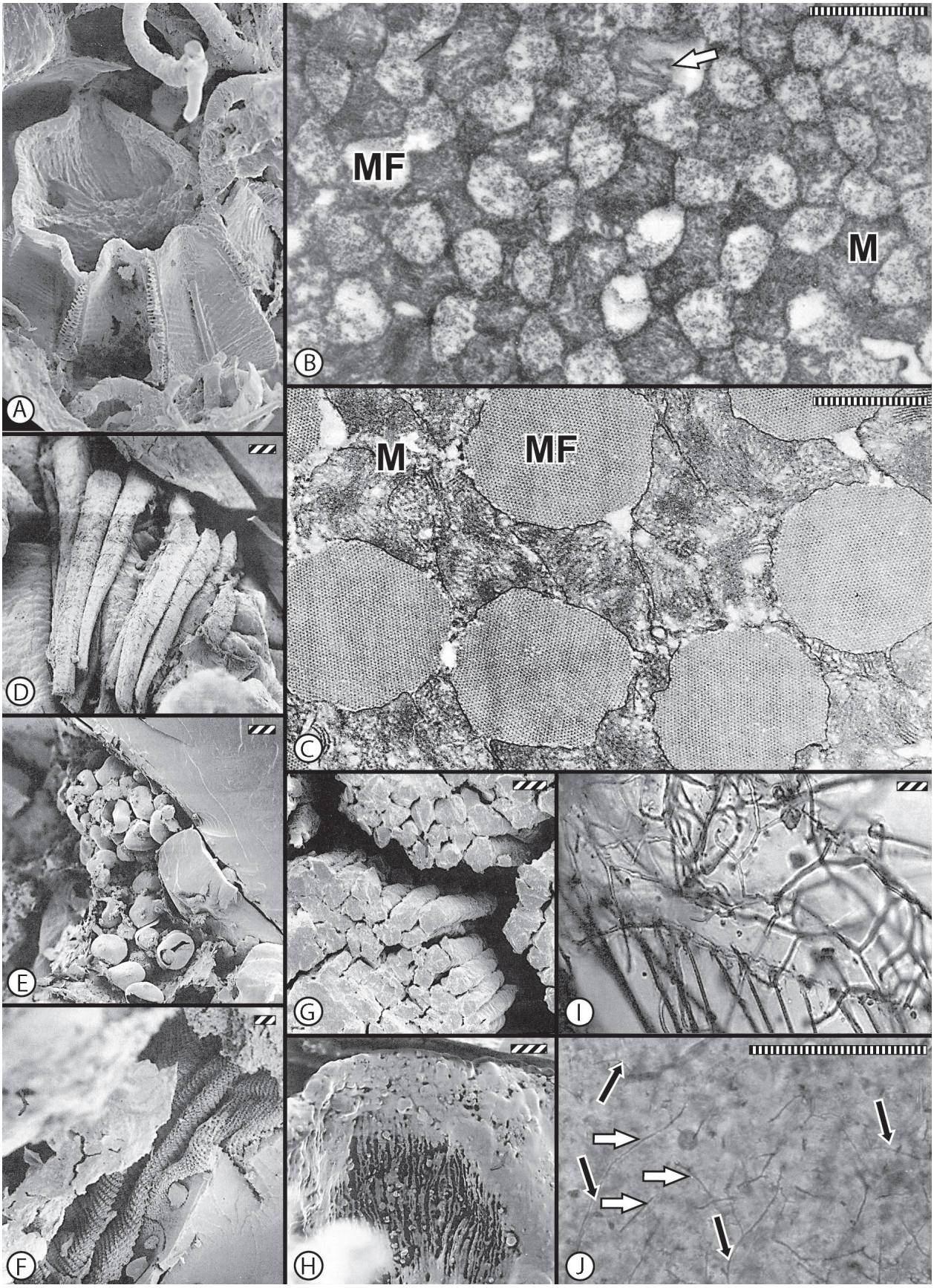
Other insect and plant structures from Dominican Amber were imaged under scanning electron microscopy (SEM). These features included pollen lodged on the abdomen of *Proplebeia dominicana* (Fig. 2E), midgut tissues of a fungus gnat *Mycetophila* sp. (Diptera: Mycetophilidae) (Fig. 2G), the pleated midgut wall of a taxonomically undetermined ambrosia beetle (Platypodidae) (Fig. 2H), and columnar cells from palisade parenchyma of a *Hymenaea protera* leaflet (Fig. 2G). Henwood (1992b) also imaged a sap beetle gut (Nitidulidae), showing the proventricular valve at the posterior end of the hindgut that acts as an ancillary triturating device for transportation of food boluses to the rectum (Fig. 2A). Penney (2005a) recorded blood tissue exiting the patellar tibial joint in an autopsied distal-leg segment during amber immersion.

Dominican Amber has been used the most for histological taphonomic studies, but a few studies have used older ambers. The foliar anatomy of a cypress twig from Baltic Amber (37–34 Ma), about twice the age of Dominican Amber, was examined by TEM and light microscopy, showing that all elements of vascular, mesophyll, and epidermal tissues, and their substructures, were nearly identical with extant Chinese swamp cypress (*Glyptostrobus pensilis*, Cupressaceae) anatomy (Koller et al., 2005). Using SEM and X-ray computer tomographic techniques, amber from the 65.5 Ma Hell Creek Formation of South Dakota revealed delicate tissues of internal organs, such as muscle fibers. Older amber (~101 Ma), from the lowermost Upper Cretaceous of Archingeay-les-Nouillers in northern France, bore exceptional preservation at the organellar level (Girard et al., 2009). In slightly older amber, of uppermost early Cretaceous age (~110 Ma) from Álava, Spain, organelles of protists were preserved as pyrite replacement, indicating 'double fossilization' resulting from an anaerobic environment in which sulfate-reducing bacteria played a major preservational role (Martín-Gonzales et al., 2009). From the same deposit, Speranza et al (2010) used bright-field light microscopy to document fungal mycelia plastered on a thrips' body, spotlighting internal details of the hyphae and associated sporangia (Fig. 2I–J). Among the oldest Mesozoic ambers known, Late Triassic Dolomites Amber (~230 Ma) from northern Italy revealed a variety of protists, fungal spores, ensheathed filamentous algae, and other microorganisms, some with preserved organellar contents (Schmidt et al., 2006).

As is the case in other types of preservation, color is very rarely preserved in amber (Martínez-Delclòs et al., 2004; Thomas et al., 2014). One exception is Dominican amber, in which certain Hemiptera, such a flat bugs (Aradidae) and leaf hoppers (Cicadellidae), reveal color patterns (Poinar, 2010a), as do butterflies (Peñalver and Grimaldi, 2006b). More commonly preserved in amber are grayscale patterns involving darker versus lighter regions, representing differential preservation of the melanin pigments in the darker, carbonized areas (Poinar, 2010a). Melanin pigments have been detected in fungi from lower Eocene amber (Beimforde et al., 2011).

Transportation and deposition

Typically, entrapment and entombment last from a few hours to a few days (Martínez-Delclòs et al., 2004), but resin masses can accumulate and remain exposed on the forest ground surface up to a few years to perhaps decades (E. Peñalver, pers. comm.) before transportation to the immediate site of deposition. Eventual deposition of the resin clasts is a much longer-term process that may take from weeks to millennia. The prelude to transportation begins with entombment, a preburial process during which inclusions are preserved amid a variety of internal chemical processes. Resin blobs assume a solid form preparatory to inclusion as clasts, such as found in Cretaceous amber of Jordan (Nissenbaum and Horowitz, 1992). The density of resin–copal–amber ranges from 1.0–1.3, depending on the degree of polymerization and density of the transporting medium, resulting in relative ease of conveyance to a nearby depositional site. With rare exceptions, such as Lower Cretaceous amber of Jordan (Nissenbaum and Horowitz, 1992), most amber-bearing deposits are allochthonous accumulations. Transportation from the amber source tree to an initial depositional area in a fluvial, deltaic, lacustrine, or even nearshore-marine environment frequently is from a few to


A
B
MF
M
C
M
MF
D
E
F
G
H
I
J

tens of kilometers; much less commonly, a few hundreds of kilometers (Martínez-Delclòs et al., 2004; Girard et al., 2008, 2009). A special exception may be lignitic strata that contain multiple amber deposits, such as some Dominican Amber (Penney, 2010a). However, it is more likely that these deposits were transported parautochthonously, close to their source area (Knight et al., 2010), or allochthonously, more distant from their source areas (Martínez-Delclòs et al., 2004). On rare occasions, amber is present within fossil wood as a result of host-plant response to beetle borings, and effectively occurs in situ (Labandeira et al., 2001). Similarly, amber may be transported long distances protected from the elements as ingested gastroliths, as in the case of an early Cretaceous bird from Lebanon that was found with amber clasts as gut contents (Dalla Veccia and Chiappe, 2002).

Often, amber is not found in deposits where it may be expected to accumulate, given the presence of source trees with abundant resin-producing capabilities and suitable nearby environments conducive for preservation. In a study of the Holocene Mobile Delta in Alabama, U.S.A., resin was not found when the plant taphonomy and sediments of a backswamp oxbow were examined (Gastaldo et al., 1987, 1989). Nor did resin occur in a crevasse splay associated with an extensive presence of resiniferous bald cypress, *Taxodium distichum* (Cupressaceae). The lack of discovery may be attributable to physical destruction of resin soon after it was produced, not far from its source. Alternatively, the fragmentary, microscopic nature of the resin as palynodebris may indicate sufficient dispersal throughout the sediment such that it did not reach levels of detection. By contrast, in a different study (Gastaldo and Hue, 1992), dipterocarpacean resins from the Mahakan River delta in Borneo were represented by rounded, large, and variously shaped cylindrical casts from resin infillings of duct-like networks associated with carbonaceous plant debris. Interestingly, the Mahakan River delta is a significantly higher-energy system than the Mobile Delta. One explanation accounting for this difference in preservation is that resin in the Bornean localities were rapidly deposited whereas at the Alabaman sites, resin underwent abrasive transport for a prolonged period of time. The Mahakan River material is analogous to the Peñacerrada II site of Spanish Álava Amber, which occurs in a coarse-grained sedimentary facies (Alonso et al., 2000; Peñalver and Delclòs, 2010).

The best-studied deposit for transportation of amber is Baltic Amber. The age of Baltic Amber is a source of considerable discussion. The oldest recorded date is middle Eocene (Lutetian Stage, 44.4 Ma; Ritzkowski, 1999), which probably represents one of the original source deposits. However, based on exacting stratigraphic studies, the vast majority of original amber comes from deposits of 37–34 Ma (Standke, 1998, 2008), and is late Eocene in age (Priabonian Stage). Nevertheless, Baltic Amber is found in younger deposits throughout northern Europe along coastlines of the Baltic Sea (Larsson, 1978; Weitschat and Wichard, 2002). The source zone of Priabonian-age Baltic Amber, the Blaue Erde

←FIGURE *2*.—Preservation potential of amber at tissue level shown from microscope sections and scanning electron micrograph (SEM) images of anatomical dissections from insect inclusions in early Miocene Dominican Amber of the Dominican Republic (A, B, D–H), and bright-field microscope images from Álava Amber, Spain (I–J). A) Proventriculus region of the foregut from a nitidulid beetle (Henwood 1992b, fig. 3, specimen SM X. 23254). B) A transmission electron micrograph in transverse section of flight muscle of a dance fly (Diptera: Empididae) (Henwood 1992a, fig. 3; MF=myofibrils; M=mitochondria; arrow=mitochondrial cristae). C) Analogous structures to (B), showing a transmission electron micrograph of modern fly flight muscle (Diptera: Cyclorrhapha) from the blow fly *Calliphora vomitoria* (Henwood 1992a, fig. 2; MF=myofibrils; M=mitochondria). D) SEM of a thoracic muscle bundle with transverse striae of the stingless bee, *Proplebeia dominicana* (Grimaldi et al., 1994; fig. 10). E) SEM of a pollen cluster retrieved from the abdomen of the stingless bee *Proplebeia dominicana* (Grimaldi et al., 1994; fig. 13). F). SEM of the opening to the proventriculus from the fungus gnat *Mycetophila* sp. (Diptera: Mycetophilidae) (Grimaldi et al., 1994; fig. 21). G). SEM showing a stack of columnar palisade cells from a leaf, probably *Hymenaea protera* (Grimaldi et al., 1994: fig. 45). H). SEM of deeply pleated microstructure lining the wall of the ventriculus of an unnamed platypodid beetle (Grimaldi et al., 1994; fig. 39). I). Fungal hyphae overgrowing an entombed thrips specimen (Speranza et al., 2010; fig. 3b). J). Fungal mycelial mat, with individual hyphae indicated by arrows (Speranza et al., 2010; fig. 6a). Figures without specimen numbers indicate that they were not provided in the original publication or were destructively analyzed. Scale bars: vertically lined=10 μm; horizontally lined=100 μm. (A–C) Reproduction courtesy of the Palaeontological Association. (D–H) Reproduction courtesy of the American Museum of Natural History. (I–J) Reproduced with permission courtesy of the Formatex Research Center.

('Blue Earth') strata, is particularly productive in the Samland Peninsula, near Kaliningrad, Russia (Kosmowska-Ceranowicz, 1996). However, older Baltic Amber was recycled in subsequent, younger deposits (Weitschat and Wichard, 2002), in which the same arthropod species of Baltic Amber occur. These younger ambers include the late Eocene Rovno Amber of Ukraine (Perkovsky et al., 2010), latest Oligocene to earliest Miocene Bitterfeld Amber (Dunlop, 2010), Pleistocene glacial deposits (Neubauer, 1994), and, during the Holocene and today, in numerous sandy and clayey littoral deposits along the Baltic Sea and its adjacent bays (Weitschat and Wichard, 2002). These Baltic Amber-bearing deposits indicate at least four cycles of sedimentary exhumation and redeposition of amber.

Amberization

The beginning of diagenesis of resin consists of two processes within a tree-resin blob as an insect becomes engulfed. The first process is short-term, and involves the effects of organisms that are embedded within the resin, which commences with entrapment (Martínez-Delclòs et al., 2004). Resin terpenoids are laden with various antiseptic and antimicrobial compounds that often protect the insect body from decomposition by saprobic microorganisms and fungi (Langenheim, 1990). In some instances, however, amber inclusions, particularly insects, display a whitish to light yellowish, cottony fungal coating, presumably a mycelial mat (Henderickx et al., 2006, 2013; Peñalver and Delclòs, 2010), that suggests a lack of effective amber fungicidal properties during late entrapment and early entombment. Such a fungal coating of the external body surface indicates that the fungus grew immediately after entrapment, sometimes into the resin itself and onto the carcass surface (E. Peñalver, pers. comm.), but before the perfusion of resin through the inner tissues of the inclusion and hardening of the resin. An alternative hypothesis is that the whitish covering is not fungi at all, but rather an emulsion of microscopic bubbles that avoided direct sunlight, which is responsible for resin clarity and elimination of the bubble cloud (Schlüter and Kühne, 1975).

Other short-term, major changes to the inclusions are dehydration and carbonization, which also begin with entrapment (Martínez-Delclòs et al., 2004). Dehydration limits the natural processes of autolysis (tissue degradation), promoted by inclusion-associated bacteria and resulting in mummification of tissue (Henwood, 1992a, 1992b). Perfusion of terpenoid compounds into the inclusion probably enhances the preservation process (Grimaldi et al., 1994). During the early phase of amberization, production of the whitish cottony covering mentioned above may be caused by the production of milky-appearing fluids, resulting in degassing of very minute bubbles. This production is especially prominent for larger invertebrates with an excess of soft tissues, such as insect larvae, making viewing very difficult. Carbonization affects structures such as cuticle, which are transformed into carbon-enriched, linear-chain hydrocarbons and aliphatic polymers (Stankiewicz et al, 1998).

Amberization also includes longer-term physical processes after amber clasts have been incorporated in a sedimentary deposit. Depending on membership of an amber clast in one of the five compositional classes of amber, and its access to the atmosphere, amber will oxidize along the periphery of the clast, particularly upon exhumation (Grimaldi et al., 2000a). This process causes a darkening in color, typically from a yellow to a darker red (Martínez-Delclòs et al., 2004), resulting in formation of a noticeable rind. In addition, exposure of amber to variable humidity, elevated temperature, and high light levels will produce surface cracking, or crazing (Bisulca et al., 2012). Older Cretaceous ambers are more susceptible to deterioration than Neogene ambers.

The role of the rock overburden is important for diagenetic processes. Extensive polymerization of amber, facilitated by considerable sediment load, causes amber clasts to become brittle and deformed. The lessening of overburden pressure often induces microscopic cracks between the inclusion and the outer margin of the enveloping amber, causing circumferential cracks and haloes surrounding the specimen. Under very high temperatures, amber may become flattened, bidirectionally deformed, and melt (Grimaldi, 1995; Zherikhin and Eskov, 1999).

Weathering is a process destructive to amber, principally through oxidation, but also by exposure to fluctuating physical variables such as the diurnal cycle of light intensity, temperature, and humidity. Weathering imparts a brittle, micro-fissured outer layer (crazing) to amber clasts that increases deterioration through time. Minerals

such as pyrite may gain entry into the amber clast and form crystalline infillings of cracks along the outer rind (Baroni-Urbani and Graeser, 1987). Penetration by pyrite may extend to the outer surfaces of inclusions from microorganisms or arthropods, representing secondary mineralization (Schlüter and Stürmer, 1982; Martín-Gonzalez et al., 2009). In very rare instances, the tissues of an entirely entombed insect may be replaced with pyrite (Schlüter, 1989).

MAJOR FEATURES OF THE AMBER RECORD

The fossil record of amber can be divided into four major phases. These four phases provide a temporal context to the 25 most significant amber deposits (Table 1, <http://paleosoc.org/shortcourse2014.html>). The 25 deposits are determined by several criteria, including: 1) abundance and diversity of inclusions; 2) strategically important biogeographic placement; 3) an occurrence that fills a major gap within the amber fossil record; and 4) the potential for capturing important, early appearing terrestrial organisms, particularly those of the late Paleozoic and earlier Mesozoic.

The characterization of the four phases of amber occurrence is associated with three major features. First is the taxonomic affinities and biology of the resin-producing plants. A second aspect of each phase is the extent and type of resin flows produced, including their chemical composition, abundance, typical clast size, and quality of preservation. The third quality is identification of the arthropod fauna of wood borers that were present, and whether the xylophagous arthropods inferred to have interacted with the host tree were important during the production of resin. (This is an important function of the host tree if there was a preventative post-attack mechanism of flushing out invasive pests). Based on these data, it seems clear that the amber fossil record generally deteriorates further back in geologic time. Nevertheless, there is great potential for understanding the evolution of the terrestrial biota by exploring some of the late Paleozoic and earlier Mesozoic occurrences that contain few described taxa, but can illuminate the early history of terrestrial habitats with woody plants. More recent amber biotas are considerably more robust, and contain hundreds of family-level lineages, such as Eocene Baltic Amber consisting of ~540 arthropod families, and Dominican Amber comprised of ~300 arthropod families. These two deposits provide the best examples in the fossil record for understanding the complexity of foodweb structure and the intricateness of inter-organismic activity.

Phase 1

The first phase involves the earliest deposits of amber in the fossil record that involves three major occurrences (Fig. 3; Table 1). The earliest appearances of amber are from early Pennsylvanian to late Permian Euramerican deposits that are attributed to extinct early seed plants—a medullosan and a cordaite. The terpenoid-based amber chemically analyzed from these paleobotanical sources apparently has no parallel in modern seed plants, and thus represents plant biomolecules that probably did not survive into the Mesozoic. The earliest occurrence of amber consists of clasts ~5 mm in average dimension, golden yellow in color (Fig. 3F), of unknown taxonomic affinities, and occurring in early Pennsylvanian coal seams (Bray and Anderson, 2009). This earliest of amber occurrences is not affiliated with any known seed plant, based on a pyrolysis-gas chromatography-mass spectrometry analysis (Bray and Anderson, 2009). The second occurrence consists of small, cylindrical resin rodlets found among Middle to late Pennsylvanian coal-ball floras (Kosanke and Harrison, 1957; Lyons et al., 1982) that have a distinctive molecular composition unlike any other vascular plant (Fig. 3A–E) (van Bergen et al., 1995). The resin rodlets are often amber in color, and frequently occur as lag accumulations in coal-ball deposits (Jones and Murchison, 1963), with the potential to trap microorganisms and minuscule arthropods. The third occurrence of amber is present in resin canals of the bark, wood, and pith of cordaites (Jones and Murchison, 1963; Lyons et al., 1982), a lineage of gymnosperm plants prominent during the Middle Pennsylvanian to early Permian. These three occurrences are found from 320–252 Ma. Arthropod colonization of woody tissues of live plants—even providing considerably more nutritious cambia—was not well established. The earliest evidence for borings is tunneled pith parenchyma of marattialean ferns and medullosan seed plants consumed by a roach-like herbivore (Labandeira and Phillips, 2002; Labandeira, 2013). Various beetle borings of the Permian occur in cordaite and conifer woods and indurated

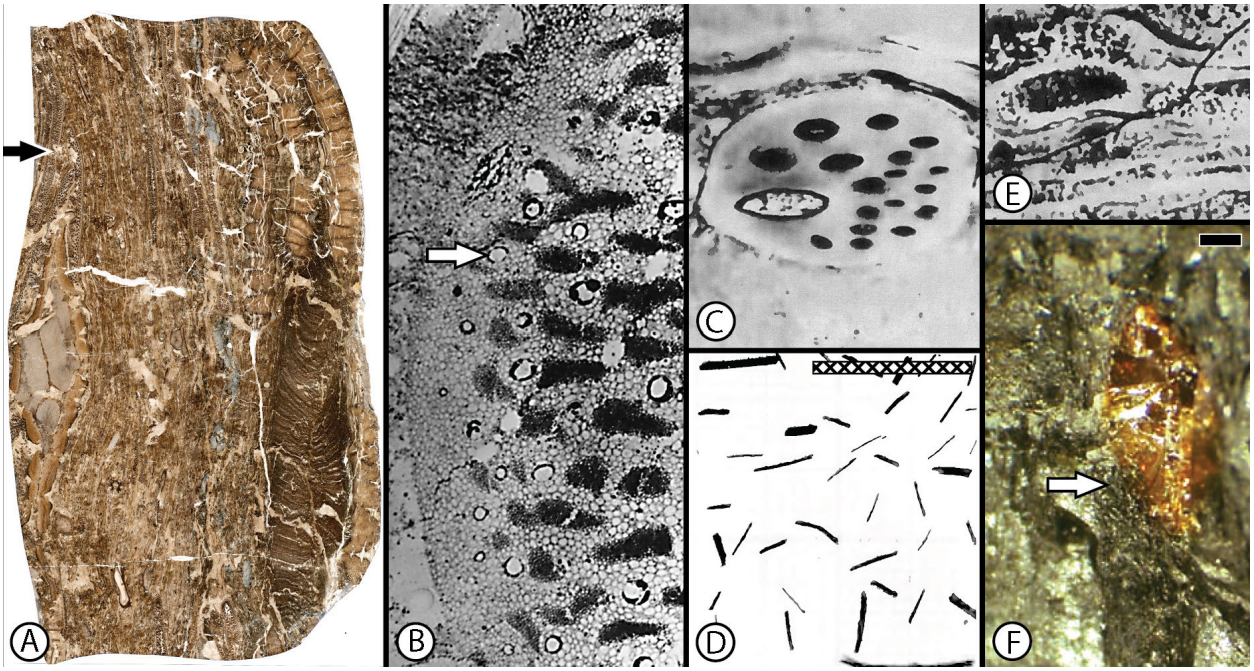


FIGURE *3*.—Paleozoic amber consists of resin rodlets in medullosan trunks (which also occurs rarely in modern conifers). A) Digital photograph of acetate peel 39875A of *Myeloxylon*, a medullosan trunk (Herrin Coal, Carbondale Formation, Middle Pennsylvanian, from the Peabody Eagle Surface Mine, Shawneetown, Illinois); black arrow indicates position of resin canals and resin rodlets within the trunk; peel is ~25 cm long (University of Illinois Urbana-Champaign Ecological Studies peel 39875A). B) Enlarged photograph of Late Pennsylvanian *Myeloxylon* trunk (Calhoun Coal, Mattoon Formation, Berryville, Illinois); transversely cut trunk ~2 cm long with darker-hued structural tissues amid smaller mucilage or resin canals, as indicated by the arrow (United States National Museum peel BV37-Gbot, microscope slide 110). C) A near-transverse section of a resin rodlet showing internal vesicles (late Pennsylvanian Danville Coal, Illinois; from Kosanke and Harrison, 1957, pl. 1, fig. 2, x900). D) Isolated, partly fusanized resin rodlets macerated from the Herrin Coal (Kosanke and Harrison, 1957; fig. 5; longest specimen is ~10 mm). E) A partly fusanized resin rodlet in oblique longitudinal section. (Kosanke and Harrison, 1957, fig. 6, x300). F). A fragment of the earliest-known amber (arrow indicates border of specimen) from a coal in the Tradewater Formation, Middle Pennsylvanian, Illinois. This specimen was determined to be amber by analysis with pyrolysis gas chromatography mass spectrometry. (Bray and Anderson, 2009, fig. 2). Figures without specimen numbers indicate that they were not provided in the original publication or possibly were destructively analyzed. Scale bars: crosshatched=10 mm; solid=1 mm. (C–E) ©1957 University of Illinois Board of Trustees, reproduced courtesy of the Illinois State Geological Survey.

tissues (Langenheim, 1990; Weaver et al., 1997; Naugolnykh and Ponomarenko, 2010), attributed to the adult and larval activities of archostematan Coleoptera, the reticulated beetles (Cupedidae) and their Permian relatives. These occurrences lack definitive body-fossil evidence associating galleries and tunnels with particular beetle taxa. However, towards the end of the Permian, various woods exhibit a significant increase in the activities of new wood-boring beetle lineages.

Phase 2

The second phase is the expansion of new, resin-producing plant clades during the late Triassic, which continued into the mid-Cretaceous. Plant taxa representative of the second expansion comes from conifers, such as *Agathoxylon* logs of the Araucariaceae (kauri, monkey-puzzle trees and wollemi pine) (Litwin and Ash, 1991), the Cheirolepidiaceae (Roghi et al., 2006; Schmidt et al., 2012), and probably the Voltziaceae (Labandeira, 2006). Amber was more copiously produced than during the late Paleozoic, and occurs as significant accumulations of teardrop-shaped clasts affiliated with the Cheirolepidiaceae, such as *Pagiophyllum* and *Brachyphyllum*, often in lignitic strata or associated lag deposits (Fig. 4A–F) (Schmidt et al., 2012). Other occurrences are associated with *Agathoxylon* logs (Litwin and Ash, 1991), or as amber replacement of the vacuities that resulted from the consumption of ovulate tissue by an

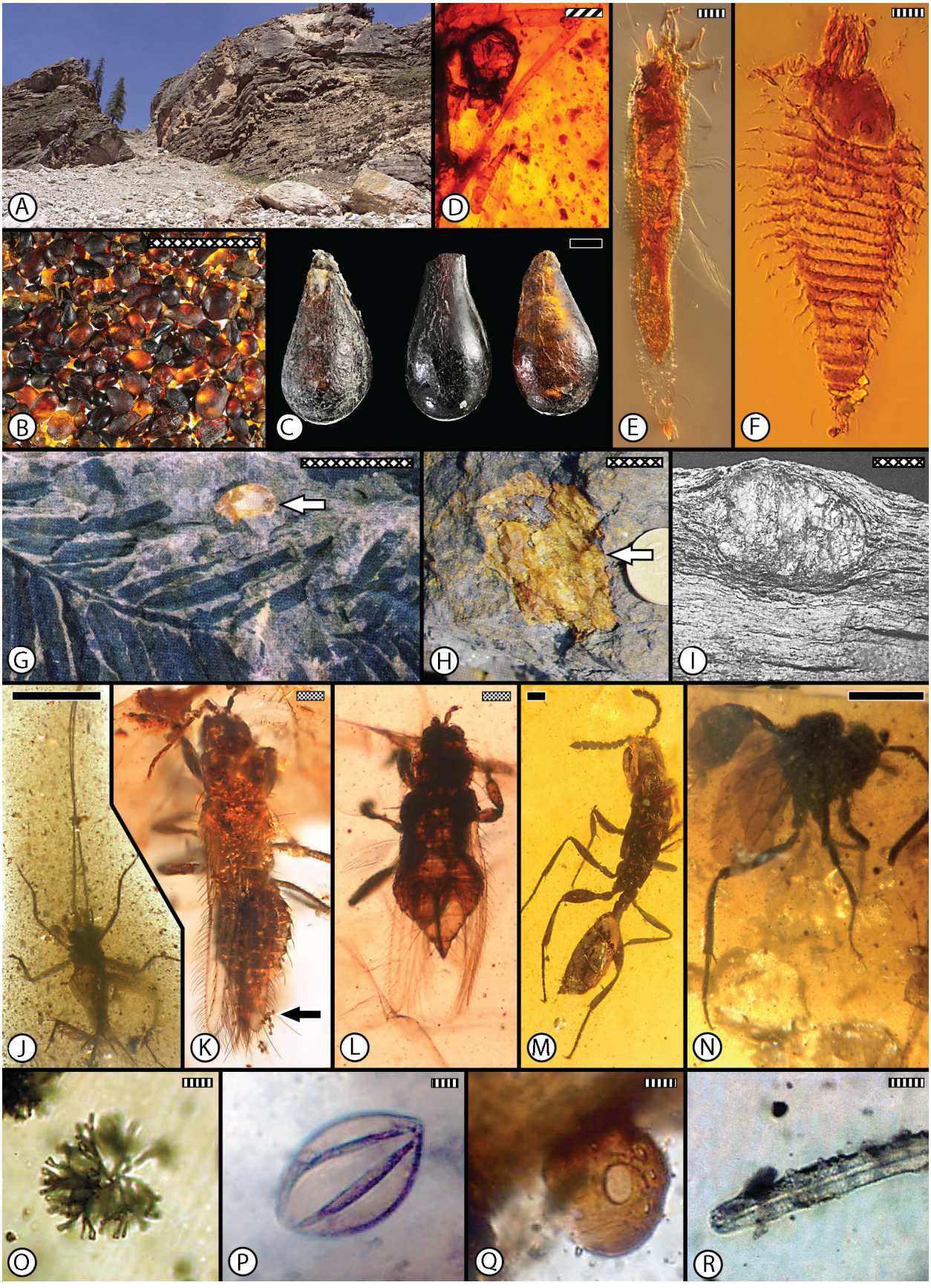
unknown seed predator (Labandeira, 2006) in woody seeds of the probable voltzialean conifer *Dordrechtites* (Anderson and Anderson, 2003). The greater prevalence of amber in a variety of mostly fine-grained deposits continued until the late Jurassic at ~145 Ma, as evidenced by several deposits with more substantial amber clasts in the range of 5 cm (Grimaldi, 1996; Philippe et al., 2005; Azar et al., 2010) (Fig. 4G–I). A likely cause for the volumetric increase in amber when compared to Paleozoic occurrences was the response of conifer trees to the activities of new wood-boring beetle lineages, including the plesiomorphic symphytan lineages of woodwasps (Xiphydriidae), horntails (Siricidae), and, later, stem sawflies (Cephidae) (Rasnitsyn, 1980; Vilhelmsen and Turrisi, 2011). The more basal and plesiomorphic archostematan beetles eventually were ecologically eclipsed by early- to mid-rank polyphagan lineages, such as the Buprestidae (metallic wood-boring beetles), Bostrichidae (powderpost beetles), Anobiidae (deathwatch beetles), and Lymexylidae (timber beetles). These hymenopteran and coleopteran lineages continue to the present day (Crowson, 1981; Solomon, 1995), even as new lineages of arborescent gymnosperms and angiosperms have largely replaced preceding phases, often associated with increased amber production.

Phase 3

The third phase of the amber fossil record began just before or during the initial angiosperm expansion. However, angiosperms do not become significant resin producers until the fourth phase, in the Cenozoic. The predominant third-phase trees are pinalean conifers, particularly the Cupressaceae (cypresses, junipers, swamp cypresses, and redwoods), and the Pinaceae (pines, spruces, firs, larches, cedars, hemlocks, and Douglas fir), although earlier resin producers such as the Araucariaceae and Cheirolepidiaceae were occasional resin producers, particularly during the Cretaceous. During the third phase, there appears to be a significant increase in the quantity of resin produced and in the chemical compositional diversity of resins. This increase is reflected in a major mid-early Cretaceous boundary of amber production, marked by the onset of Lebanese Amber, during which deposits consisted of greater amounts amber than seen in the earlier fossil record. The trend established by Lebanese Amber continues during the Cretaceous, with subsequent major deposits of Álava Amber (Albian, Spain; Fig. 4J–N), Myanmar Amber (uppermost Albian to lowermost Cenomanian, Myanmar), Charentes Amber (Albian–Cenomanian boundary, France), New Jersey Amber (Turonian, New Jersey), and Canadian Amber (Campanian, Alberta and Manitoba) (Table 1). In addition, it is during the third phase in which mid-rank Polyphaga beetle lineages originate and diversify, as evidenced by the early diversification of the Cerambycidae (longhorn beetles) and the diverse lineages of the Curculionoidea, including the Brentidae (straight-snouted weevils), Curculionidae (common weevils), Scolytinae (bark beetles), and Platypodidae (ambrosia beetles). The response of trees to beetle attack frequently involved infective, pathogenic microorganisms that were vectored by a wood-boring beetle, indicated by common tree-host signs such as extensive production of pitch and resin (Paine et al., 1997). Evidence for the presence of damage attributable to bark beetles (e.g., Solomon, 1995), other beetles with bark-beetle habits (e.g., Kuschel, 1966), or ambrosia beetles commences during the Early Cretaceous, based on beetle galleries (Jarzembowski, 1990), body fossils (Kirejtshuk et al., 2009), and the time of origin of the Scolytinae and Platypodinae (McKenna et al., 2009; Jordal et al., 2011; but see Franz and Engel, 2010). In addition, anobine beetles of the Ptiniidae are also known from Early Cretaceous ambers (Peris et al., 2014).

Phase 4

The beginning of the fourth phase of amber production occurred as a new group of angiosperms—resin-producing taxa that were inconspicuous during the late Cretaceous—became prominent during the Cenozoic. Phase four starts immediately after the K–Pg boundary, combining gymnosperm resin producers such as the Araucariaceae, Cupressaceae, and especially the Pinaceae with newly emerging, but rare woody dicot lineages. Amber deposits from angiosperms are very rare during the 35 million years of the Upper Cretaceous, perhaps a consequence of the paucity of woodiness and arborescence, or possibly because of being overshadowed by longer-lived and much earlier-appearing resin-producing gymnosperm lineages that may have been more effective in resisting insect pests. During the Paleogene, the appearance of the Dipterocarpaceae (*Shorea*, meranti), Combretaceae (*Terminalia*, Indian


A
D
E
F
B
C
G
H
I
J
K
L
M
N
O
P
Q
R

almond), and Hamamelidaceae (*Liquidambar*) were the earliest angiosperms providing amber in sufficiently large amounts to be recognized in the fossil record. However, the deposit with the greatest diversity and abundance, Baltic Amber (Fig. 5), was mainly produced by conifers, but also included angiosperm resins (Anderson and LePage, 1995; Wolfe et al., 2009; Weitschat and Wichard, 2010). By contrast, during the Neogene, amber production assumed a different character, with source plants dominantly consisting of woody shrubs and trees of the Fabaceae, particularly *Hymenaea,* as a major source of resin in deposits such as Miocene Dominican (Fig. 6) and Mexican ambers (Penney, 2010a; Solórzano Kraemer, 2010) and Pliocene to Holocene subfossil copal from Colombia, Tanzania, and Madagascar (Schlüter and Gnielinski, 1980; Penney and Preziosi, 2010). Sometime during the mid-Cretaceous to early Paleogene, but varying in time and place, there was a general supplement of Mesozoic gymnosperm lineages by angiosperms, some of which may have been caused by the transfer of life-habits of insect lineages from gymnosperms to angiosperms, paralleling a similar, earlier global host shift during the mid-Cretaceous in insect herbivores and pollinators (Labandeira, 2014). This phase was accompanied by a greater frequency of amber deposits and a volumetric increase in the amount of amber per deposit, likely attributable to a greater diversity wood-boring beetle and sawfly lineages and the addition of new dipteran and lepidopteran wood-boring clades. During the Paleogene, the wood-boring niche was invaded by the Diptera (true flies), particularly the Agromyzidae (leafmining flies) that attack tree cambium tissue, and the Panthophthalmidae (panthophthalmid flies) that bore into the trunk heartwood. The Lepidoptera represent a more extensive invasion of indurated tissues, and included the frequently large xyophagous larvae of the Sesiidae (clearwing moths), Momphidae (mompha moths), Cossidae (carpenterworm moths), Argresthidae (argresthiids), Noctuidae (owlet moths), and Pyralidae (snout moths), many of which occur in twigs and small stems of smaller woody shrubs, and to a lesser extent, the branchlets of larger trees. Individual resin production induced by shrubs and more modestly statured arborescent trees was less important in producing larger volumes of amber than were more massive gymnosperm and angiosperm trees that were much more prolific in amber production from the induction of polyphagan beetles, particularly common weevils, bark beetles, and ambrosia

← FIGURE *4*.—Mesozoic amber: Triassic (A–F), Jurassic (G–I), and Cretaceous (J–R) occurrences. A) Outcrop of Triassic (Carnian) Heiligkreuz Formation, Dolomite Mountains near Cortina, Italy, where specimens figured in B–F were collected. (Photo courtesy of Eugenio Ragazzi, University of Padova, Italy) B) Typical appearance of amber material attributed to a cheirolepidiaceous conifer (Schmidt et al., 2012; fig. S1). C) Representative amber droplets (Schmidt et al., 2012; fig. 1F, specimen DGPGP-ER-527). D) Disarticulated elements of a nematoceran fly (Schmidt et al., 2012; figs. 1G, and S2, S6; specimen MGP-31345). E) A phytophagous eriophyoid mite, *Triasacarus fedelei*, a possible galler (Schmidt et al., 2012; fig. 2C, specimen MGP-31343). F) Phytophagous eriophyoid mite *Ampezzoa triassica*, a probable external leaf feeder (Schmidt et al., 2012; fig. 3A; specimen MGP-31344). G). A rounded amber clast (arrow) of probable cupressaceous origin, Late Jurassic (Oxfordian) of Russia, surrounded by *Metasequoia* sp. foliage (Grimaldi, 1996). H) Another ovoidal shaped amber bleb (arrow) of Beit Mounzer, Caza District, northern Lebanon (Azar et al., 2010; fig. 2b). I) A parautochthonous amber clast within clayey siltstone of the Khlong Min Formation, Krabi Province, Thailand (Philippe et al., 2005; fig. 3). J–N) Álava amber (Peñacerrada I), Escucha Formation, Spain; J) Early Cretaceous (Albian) elcanid orthopteran, *Hispanelcana arilloi* (Peñalver and Grimaldi, 2010; fig. 6.3; specimen MCNA-9588); K) Ginkgophyte-pollinating thrips, *Gymnopollisthrips minor*, with black arrow showing clumps of pollen attached to specialized ring setae (Peñalver et al., 2012; fig. 1B, specimen MCNA-10731). L) An indeterminate species of thrips (Peñalver and Delclòs, 2010; fig. 18E). M) Serphitid wasp *Aposerphites angustus* (Ortega-Blanco et al., 2011: fig. 3B, specimen MCNA-8651). N) Evaniid wasp *Iberoevania roblesi*, a likely parasitoid of cockroach egg cases (Peñalver et al. 2010; fig. 11a, specimen MCNA-8759). O) A dichotomously branching actinomycete colony in amber within lignitic clay from Archingeay-Les Nouillers and Cadeuil, late Albian, France (Girard et al., 2009; fig. 1C, specimen ARC-115.22a). P) From the Cadeuil locality, a green alga very similar to *Enallax* (Girard et al., 2009: fig. 2H; specimen ARC-CDL-26c). Q-R) From the Archingeay-Les Nouillers locality. Q) a testate amoeba very similar to *Centropyxis discoides* (Girard et al., 2009; fig. 2I, specimen ARC-115.21). R) Spinose sponge spicule with a central canal (Girard et al., 2009; fig. 3E; specimen ARC-115.12c). Figures without specimen numbers indicate that they were not provided in the original publication or possibly were destructively analyzed. Scale bars: solid=1 mm; dotted=0.1 mm; vertical=10 μm; horizontal=100 μm. Permission for reproduction of B–F, K granted by the National Academy of Sciences, U.S.A.. Permission for reproduction of I–J, M granted by Elsevier B.V.

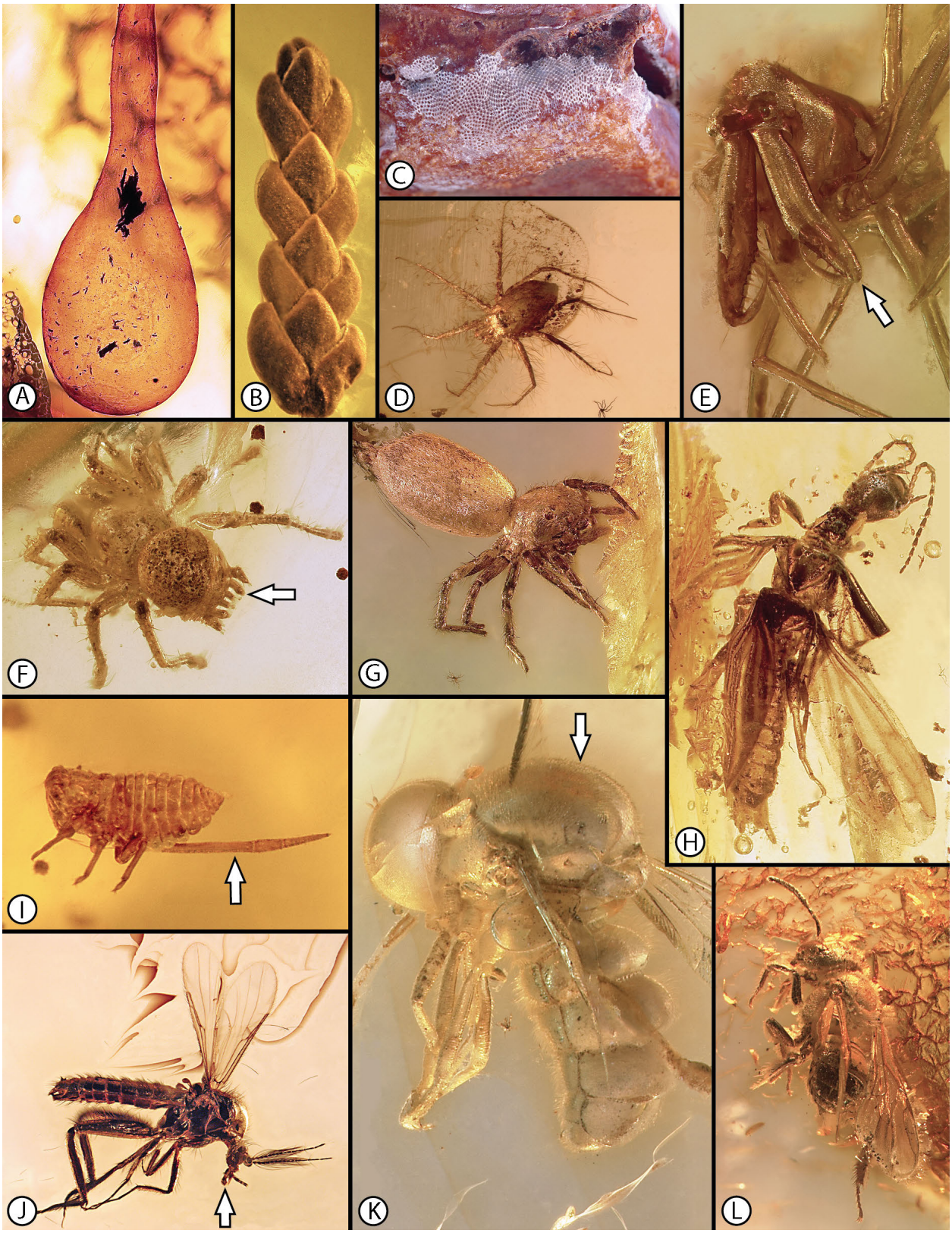


FIGURE 5.—Plants and arthropods in Paleogene Baltic amber from the early middle Eocene of northern Europe. A) Resin drop within an amber clast. B) Arborvitae branchlet (Pinales: Cupressaceae). C) Early Miocene bryozoan lattice network covering an amber clast. D) Predaceous whirligig mite (Acari: Anystidae). E) Assassin spider →

beetles. Notably, several modern sources of resin that are colonized and attacked by wood-boring insects are very rare or uncommon in the amber fossil record, including the Burseraceae, Anacardiaceae (cashew family), and Combretaceae (Langenheim, 1990).

INTER-ORGANISM INTERACTIONS

One valuable archive of the amber fossil record is the primary documentation it provides of the interactions among organisms, such as feeding, dispersal, and mimicry. Although these data have not been fully exploited, amber deposits are ideal for examining ecological structure within a diverse community. For example, the compilation of food-web data using deposits such as Dominican and Baltic Amber, could surpass that of the Messel food web (Dunne et al., 2014; Labandeira and Dunne, 2014), which is the most well-resolved so far in the fossil record. Of interest to ethologists is the information that amber deposits can provide for intraspecific interactions, such as the reproductive behaviors of mating and lekking. (Lekking is the process where males congregate during the mating season to engage in behaviors that attract conspecific females.)

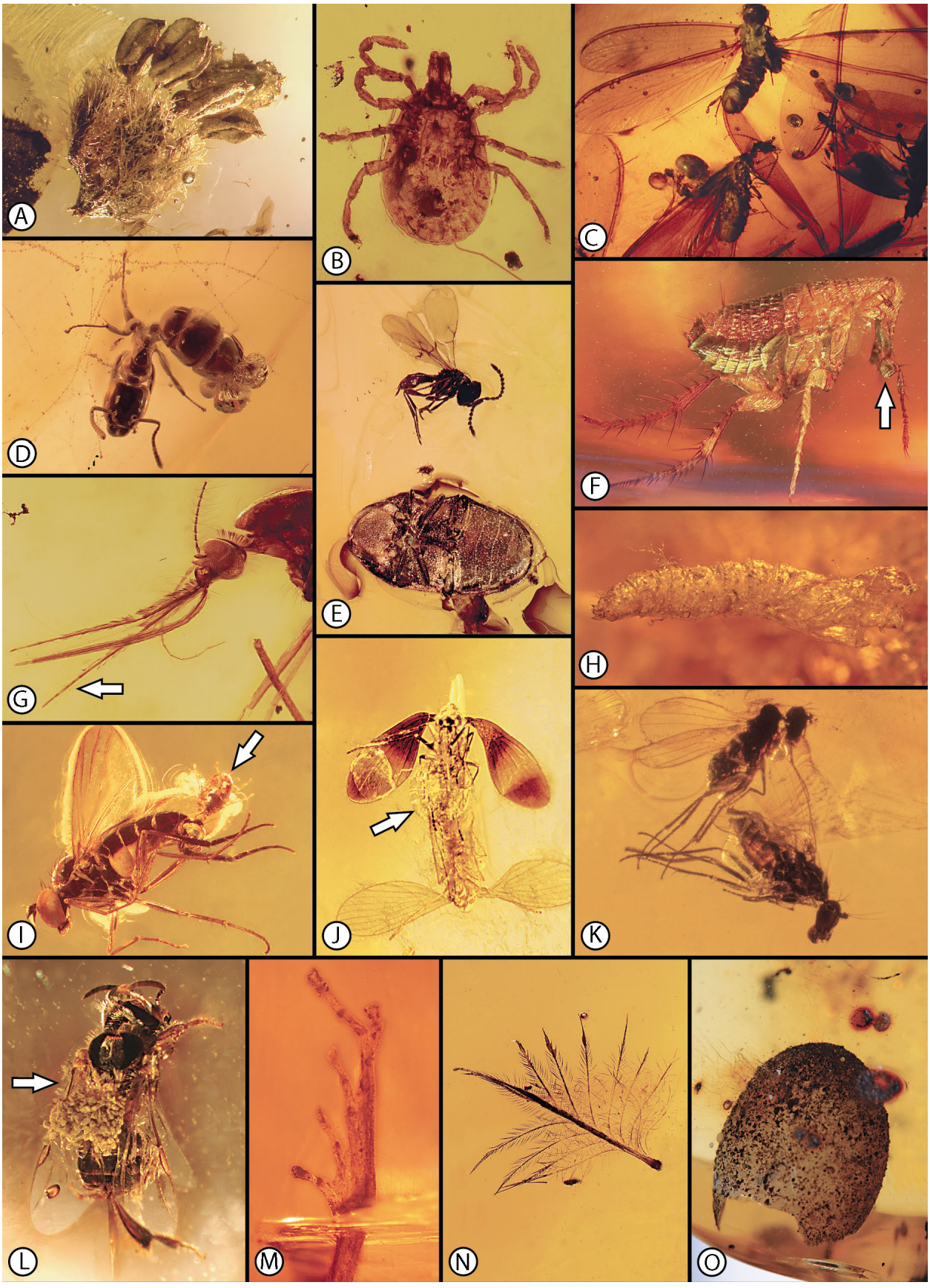
Interspecific interactions

The entire terrestrial spectrum of modern interspecific interactions is represented in the amber fossil record, characterized by antagonisms, commensalisms, and mutualisms. A broad representation of major terrestrial groups consists of a diverse menagerie of microorganisms, fungi, plants, and animals. In particular, the amber fossil record includes evidence for the presence of viruses; body fossils of bacteria; protists, especially protozoans and algae; deuteromycete, ascomycete and basidiomycete fungi; nematodes; tardigrades; onychophorans; arthropods such as crustaceans, myriapods, arachnids, and hexapods; and small vertebrates. Species from these organismic groups display particular interactions of herbivory, parasitism, pathogen-mediated disease, parasitoidism, predation, phoretic associations, pollination, and mimicry. Camouflage is another association that has a record (Pérez-de-la-Funte, 2012), but will not be discussed herein.

Amber also presents evidence for interactions that involve special, spatiotemporally ephemeral microhabitats such as bark and wood, carrion, dung, polypores and other macrofungal bodies, phytotelmata, and resin substrates. The greatest number of interactions documented in amber involve parasites and parasitoids, which differs significantly from the dominance of herbivory in the compression-impression fossil record (Labandeira, 2002). Virtually all important amber deposits have evidence that supports a variety of interspecific interactions, with Neogene Dominican Amber expressing the greatest number of documented interactions (Poinar, 2010a; Boucot and Poinar, 2010), followed by Paleogene Baltic Amber (Larsson, 1978; Weitschat and Wichard, 2002; Boucot and Poinar, 2010), then Myanmar Amber of the Lower–Upper Cretaceous boundary (Santiago-Blay et al., 2005; Boucot and Poinar, 2010; Shi et al., 2013). Levels of documentation among all amber deposits likely is a consequence of 1) the intrinsic biological richness of the deposit studied, 2) amber preservational state, 3) the availability of material to study, and 4) investigator interest.

Phytophages.—The amber record of herbivory is far exceeded by the compression-impression fossil record. Evidence for herbivory in the amber fossil record is sparse, but very rarely is there evidence of a direct interaction, such as coccids feeding on a conifer foliage (Grimaldi et al., 2000b). This sparseness is attributable to the absence of substantial expanses of two-dimensional surfaces in the permineralized record, including amber, which would be essential for statistically robust sampling of herbivory on foliage. Nevertheless, there is good evidence for some types of external foliage feeding on a very few, selected species in amber, such as leaves of

← FIGURE 5.—continued. (Araneae: Archaeidae) with extremely long raptorial chelicerae (arrow). F). Dwarf sheet spider (Araneae: Hahniidae) with six spinnerets arranged in a transverse row (arrow). G). Jumping spider (Araneae: Salticidae) with four pairs of eyes (and presumably extremely acute vision). H). Webspinner (Insecta: Embioptera) with a pair of cerci at the abdominal tip. I). *Germaraphis baltica* (Hemiptera: Aphidae), a member of an extinct lineage of aphids bearing a prominent, elongate ovipositor emerging from the ventral abdominal midsection (arrow). J) Biting midge (Diptera: Ceratopogonidae) showing piercing-and-sucking mouthparts for blood feeding (arrow). K) A small-headed fly (Diptera: Acroceridae) displaying a large, humped thorax at upper right and left (arrow). L) The social insect *Electrapis* sp. (Hymenoptera: Electrapidae), a member of a major, extinct, bee pollinator lineage. Images contributed by Patrick Craig; scale bars not provided.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O

Hymenaea protera in Dominican Amber and possibly *H. mexicana* in Chiapas Amber. Interactions such as margin feeding, hole-feeding, and skeletonization are recorded in the Dominican Amber record: occasionally interesting herbivory occurs, such as florivory on a *Hymenaea* flower petal (Solórzano Kramer, 2010; Boucot and Poinar, 2010), sometimes attributable to the special way that amber preserves leaves. Another type of herbivory evidence is recognizable in host-specific lineages of insects; in particular, taxa associated with palms such as palm beetles (Poinar, 1999a; 2005a), palm bugs (Poinar and Santiago-Blay, 1997), and other palm-associated insects found in Dominican Amber (Boucot and Poinar, 2010). Other examples of herbivory are the caterpillars of the metalmark butterfly *Vanessa* (Riodinidae), which are obligate herbivores of nettle (Urticaceae), also found in Dominican Amber (Poinar, 2010a).

Parasites and parasitoids.—A parasite is an organism that lives at the expense of another, whereas a parasitoid is major modification of parasitism whereby a larva is initially parasitic, but eventually kills its host. Parasitism and parasitoidism are the most abundant source of interspecific interactions preserved in the amber fossil record. A wealth of overwhelmingly specialized interactions occur among viral, bacterial, fungal, protistan, nematode, and arthropodan parasites and parasitoids on mostly arthropod hosts (Table 2, <http://paleosoc.org/shortcourse2014.html>; Poinar and Poinar, 2005). This proliferation of trophic activity and interactional diversity within local food webs is captured by amber flows (Poinar and Poinar, 1999). A related but under-appreciated aspect of the amber record is its record of relationships with other organisms of the dominant pathogen groups —viruses, bacteria, fungi, and nematodes (Table 2, Poinar, 2014). The amber fossil record of pathogen, vector, and host diversity is exceeded only by the record of plant-arthropod interactions from compression-impression deposits (Labandeira et al., 2007).

Pathogens.—Twenty examples of diseases recorded in amber are detailed in Table 2 (<http://paleosoc.org/shortcourse2014.html>), and involve disease pathogens that are vectored mostly by nematocerous flies, which typically target warm-blooded vertebrate hosts. The first disease considered is leishmaniasis, a disfiguring tropical disease of ulcerating cutaneous and visceral lesions caused by the protistan trypanosome, *Leishmania*, vectored by phlebotomine sand flies (Diptera: Psychodidae), and whose terminal host is a mammal, including humans (Table 2, entry 7; Poinar, 2004). The phlebotomine sand fly, *Paleomyia burmitis*, evidently housed the disease pathogen *Paleoleishmania proterus*, found in ingested reptilian red blood cells from the latest early to earliest late Cretaceous, in Myanmar Amber. Another dipteran from Myanmar Amber involves the biting midge *Protoculicoides* sp., which apparently housed the apicomplexan protist *Paleohaematoproteus burmacis*, a plasmodium parasite, in its body cavity, indicating that a form of malaria was being vectored, likely to a reptilian host (Table 2, entry 2; Poinar and Telford, 2005). (Malaria is a debilitating tropical disease caused by a protistan parasite transmitted by mosquitoes that invades the red blood cells of vertebrates.) However, these two records of disease pathogens involving leishmaniasis and malaria in Burmese

← FIGURE *6.*—Plants, arthropods, and vertebrates in Neogene Dominican amber, early Miocene, Dominican Republic. A) Catkin (male flower) of oak (Fagaceae: *Quercus*), showing five projecting anthers. B) A hard tick (Acari: Ixodidae) with a prominent, forwardly directed head process (capitulum). C) A swarm of termites (Isoptera: Termitidae) with wings still attached from a nuptial flight. D) Ant (Hymenoptera: Formicidae) trapped in a spider web; note gaseous emissions from the rectum. E) Wood-boring powderpost beetle (Coleoptera: Anobiidae) at bottom; unidentified mite at center (tiny specimen), and a parasitoid scelionid wasp (Hymenoptera: Scelionidae) at top. F). A marsupial and rodent flea (Siphonaptera: Rhopalopsyllidae) displaying piercing-and-sucking mouthparts (arrow) and spinose hindlegs and terminal claws for attaching to the pelage of its mammal host. G) Mosquito (Diptera: Culicidae) head and mouthparts, stylet assembly protruding at lower left (arrow). H) Pupal case of a wood gnat (Diptera: Anisopodidae), showing mandibles in the head section at right. I) A phoretic *Leptus* sp. mite (Acari: Erythraeidae) latched to the abdominal terminus (arrow) of a long-legged fly host (Diptera: Dolichopodidae). J) Copulating moth flies (Diptera: Psychodidae) with male and female genitalia in a locked position (arrow). K) Two long-legged flies (Diptera: Dolichopodidae) prepositioned for copulation. L) The pollinator bee *Proplebeia dominicana* (Hymenoptera: Apidae) with orchid pollinia (arrow) enveloping its body. M) The manus of a rain frog, *Eleutherodactylus* (Anura: Eleutherodactylidae), a consumer of invertebrates, particularly insects. N) Contour feather of a woodpecker (Piciformes: Picidae). O) An egg of a hummingbird (Apodiformes: Trochilidae), a nectar feeder on flowers with deep-throated corollas. Images contributed by Patrick Craig; scale bars not provided.

amber (Poinar and Telford, 2005) require considerable caution and lack convincing evidence that disease transmission was present. Of considerably more recent vintage is the Dominican Amber anopheline mosquito *Anopheles* sp. (Diptera: Culicidae), which is closely related to modern malaria-vectoring species and shares the same, distinctive anopheline egg type with float structures (Zavortink and Poinar, 2000). From the same deposit, another culicid mosquito, the culicine *Culex malariger*, possibly housed developmental stages, including oöcysts and sporozonites, of the malarial parasite, *Plasmodium dominicana*, indicating an avian host (Table 2, entry 10; Poinar, 2005b), representing a third, inconclusive study. More compelling, and with clear contextual and associational evidence, is a case from Dominican Amber wherein there is blood-feeding by five species of *Lutzomyia*, phlebotomine sand flies, one of which was associated with the hair of an unknown solenodon (Mammalia: Insectivora), and probably was involved in the transmission of *Leishmania* (Peñalver and Grimaldi, 2006b). An important aspect of excellent amber preservation is the detection of not only suspect disease vectors on their hosts, but also possible elucidation of the structure at high magnification of miniscule disease pathogens (Boucot and Poinar, 2010; Poinar, 2014), which nevertheless are very difficult to demonstrate, as are the pathological effects of viruses or fossils of bacteria, fungi, nematodes or other inconspicuous invertebrates (Labandeira and Prevec, 2014).

Predators.—Predators are well-represented in amber, some of which were trapped while pursuing partially engulfed or dangling prey. Arachnids frequently are found in the presence of prey, such as arthropods entangled in spider webs (Peñalver et al., 2006; Knight et al., 2010), a pseudoscorpion and ant in combat (Poinar, 2001), or a whipscorpion with prey clutched in its mouthparts (Grimaldi, 1996). Insect predation caught-in-the-act occasionally occurs, consisting of predators that still are grasping or otherwise associated with feeding and can be considered 'frozen behavior' (Boucot and Poinar, 2010). Examples include a dance fly with a nonbiting midge enveloped by its legs, an insect larva consuming the head of a scuttle fly, and a praying mantis attacked by ants (Grimaldi, 1996; Janzen, 2002). An atypical example of predation is the predatory fungus *Palaeoanellus dimorphus* from late Albian French amber that bears hyphal rings and specialized adhesive structures that ensnare small arthropods for eventual consumption (Schmidt et al., 2008). Amber examples of active predation appear to be less frequent than occurrences of parasitism and parasitoidism, at least in the documented record. A recurring pattern suggests that the attachment of a specialized parasite or parasitoid to their hosts is a behavior more readily captured by amber flows than weaker, more generalized interactions from predators and their prey.

Phoretic associations.—Numerous examples of phoretic associations occur in all of the major amber deposits, extending to the mid-Early Cretaceous (Boucot and Poinar, 2010). Most common are small and often inconspicuous mites, pseudoscorpions, and collembolans, which are attached to the body surfaces of much larger transporting arthropods (Fig. 6I). Phoretic erythraeid, macrochelid, and astigmatid mites provide interactions that can best be considered commensalisms, and these mites have latched onto springtails, biting midges, crane flies, pomace flies, and ambrosia beetles (Poinar, 1992a, 2010a; Dunlop et al., 2012). Small pseudoscorpions frequently are attached to the legs, wings, and other appendages of other larger arthropods, such as long-legged flies (Dolichopodidae), snipe flies (Rhagionidae), bark beetles, ambrosia beetles, braconid wasps, and harvestmen (Opiliones) (Grimaldi, 1996; Weitschat and Wichard, 2002; Boucot and Poinar, 2010). Smithurinid springtails (Collembola) also have phoretic associations with mayflies and harvestmen (Boucot and Poinar, 2010; Penney et al., 2012a), an association that has not been recorded with modern springtails, unlike those documented for modern mites and pseudoscorpions. The more common phoretic species do not appear to repeatedly target the same host species, indicating that most phoretic associations have generalist hosts.

Pollinators.—Evidence for insect pollination from compression-impression deposits considerably predates the earliest abundant amber deposits of the mid-early Cretaceous (Ren et al., 2009; Labandeira, 2010). However, there are examples of this early, mid-Mesozoic phase of pollinator history in early Cretaceous amber deposits that document mutualisms between insect-pollinated gymnosperms and more basal lineages of modern pollinator groups (Labandeira, 2010, 2014). One such example is *Libanorhinus succineus* (Kuschel and Poinar, 1993), a pine-

flower snout weevil (Coleoptera: Nemonychidae), an early member of a lineage of weevils that currently feed on pollen and other tissues from conifers, particularly Araucariaceae, Podocarpaceae, and Pinaceae (Labandeira, 2002). This weevil occurs in Lebanese Amber, at ~120 Ma, and likely fed on tissues and pollinated *Agathis* (Araucariaceae), the principal resin producer for Lebanese Amber. In the slightly younger Álava Amber of Spain (~110 Ma), another, but very different, gymnosperm-insect pollinator system involved a ginkgoalean-thrips mutualism, and revealed evidence for pollination aided by specialized ring setae occurring on the thrips wings and abdomen with adherent clumps of *Cycadopites* pollen (Fig. 4K) (Peñalver et al., 2012). In still younger Myanmar Amber (100 Ma), the earliest-known bee has several features such as branched hairs, deeply tridentate mandibles, and anterior abdominal tubercles, indicating that there was interaction with the reproductive organs of a seed plant, possibly an angiosperm. From the same deposit, mosquito-sized pseudopolycentropodid scorpionflies (Mecoptera) appear to have a similar feeding mode to that of small, modern, nematocerous dipterans, such as biting midges (Grimaldi et al., 2005b; Grimaldi and Johnston, 2014). The elongate, proboscate mouthparts in some forms appear to be siphonate for feeding on a liquid surface, most likely plant secretions (Ren et al., 2009), whereas others had stylate proboscises able to pierce skin and imbibe blood (Boucot and Poinar, 2010; Grimaldi and Johnson, 2014). In New Jersey Amber, of early late Cretaceous age (~88 Ma), there is evidence for pollinating dipterans, including dance flies and hilarimorphid flies (Hilarimorphidae) (Grimaldi et al., 2000b), that possibly made the switch from gymnosperm to angiosperm pollination.

The Cenozoic spectrum of pollinating insects becomes more modern-looking by Baltic Amber times (~34–37 Ma). For bees, pollinators consist of more recognizable electroapid bees (Fig. 5L), an early offshoot of modern bees. Baltic Amber has produced several other major bee lineages: extinct Paleomelittidae, and extant Megachilidae (leafcutting bees), Melittidae (melittid bees), Halictidae (sweat bees), and within the Apidae, the pollen-basket possessing (corbiculate) Apinae (honey bees, bumble bees, orchid bees, and stingless bees), and the acorbiculate Nomadiinae (cuckoo bees) and Xylocopinae (carpenter bees) (Engel, 2001). Both corbiculate and acorbiculate taxa are efficient pollinators. In significantly younger Dominican Amber, (~17 Ma), two associations stand out. First is the stingless bee *Proplebeia dominicana* (Fig. 6L), with one specimen covered by pollen-containing pollinaria of a *Meliorchis* orchid, indicating a considerably older relationship between Neotropical stingless bees and orchids (Ramírez et al., 2007). A second association is one of the most heavily studied and iconic of pollination mutualisms: figs (*Ficus*) and fig wasps from various taxa from the Agaonidae (Hymenoptera). The fig-fig wasp pollinator mutualism was established by the early Miocene in Hispaniola (Peñalver et al., 2006), although the relationship probably began in the Neotropics much earlier at ~34 Ma, based on molecular phylogenetic data (Compton et al., 2010).

Mimicry.—Examples of mimicry are rare in the amber fossil record. In most instances where color-based mimicry is suspected, pigmentation color is obliterated (but see Beimforde et al., 2011). In other instances, structural colors are well preserved (Weitschat and Wichard, 2002; plate 75). Perhaps the best example of mimicry involves similarities in shape, such as ant mimicry by spiders in Baltic Amber (Wunderlich, 2000).

Special microhabitats

There are a variety of ephemeral and spatially restricted habitats captured by resin flows that are represented in the amber fossil record. For amber-producing environments, the most noticeable microhabitats are: bark and wood; macrofungal fruiting bodies, dung, and carrion; phytotelmata; and resin substrates. Each of these communities is composed of a recurring spectrum of taxonomically similar species, and is trophically organized into well-contained food webs. These microhabitats are captured by resin flows ranging from open woodland to closed-canopy forests where resin-producing trees occur and often are recognizable contributors to amber biotas.

Bark and wood.—The most important and well-documented microhabitat is bark and wood (Penney, 2002), denizens of which form a significant part of all major deposits, such as Dominican Amber (Henwood, 1993a; Bright and Poinar, 1994; Grimaldi, 1996), Baltic Amber (Schedl, 1947; Larsson, 1978) and mid-Cretaceous amber from Archingeay-Les Nouilles in France (Girard et al., 2009; see also Alonso et al., 2000). This distinctive community consists of lichens; epiphytic plants; fungi, especially ascomycetes; phthiracarid and other oribatid

mites; a diverse spectrum of wood-associated insects, especially heartwood borers, bark engraver, and sap flow beetles; and cambium miners dominated by beetle taxa but also sawfly borers (Hymenoptera), pith-fleck cambium miners (Diptera), and cossid and clearwing moths (Lepidoptera). An associated predator guild consists mostly of arachnids.

Macrofungal fruiting bodies, dung, and carrion.—Another specialized microhabitat engulfed by resin flows consists of macrofungal fruiting bodies—large, often massive, sporocarps of polypore (bracket) fungi and large mushroom-like structures (Poinar, 2001; Poinar and Brown, 2003; Poinar and Buckley, 2007). These large fungal reproductive and vegetative structures have a distinctive fauna dominated by small beetles of various trophic levels, such as rove beetles (Staphylinidae), round fungus beetles (Leiodidae), sap flow beetles (Nitidulidae), minute tree-fungus beetles (Ciidae), and hairy fungus beetles (Mycetophagidae) (Larsson, 1978; Poinar and Poinar, 1999). By contrast, dung and carrion microhabitats, while also engulfed by resin flows, have a poorer amber record than either bark and wood or macrofungal bodies. Dung and carrion microhabitats have some taxa in common, mostly flies, and include termites (several families), earth-boring dung beetles (Geotrupidae), scarab beetles (Scarabaeidae), dung flies (Scatophagidae), scuttle flies (Phoridae), blow flies (Calliphoridae), and flesh flies (Sarcophagidae) (Weitschat and Wichard, 2002; Martínez-Delclòs et al., 2004).

Phytotelmata.—Phytotelmata consist of ephemeral aquatic microhabitats such as epiphytic filmy fern axils, bromeliad tank epiphytes, lianine pitcher plants, and tree holes that typically occur on bark fissures, exposed root cavities, or on trunk-branch crotches. A distinctive biota is contained within the water reservoirs of these plants, and includes particular groups of damselflies (Odonata), anopheline mosquitoes and midge species (Diptera), marsh beetles (Scirtiidae), water scavenger beetles, predaceous diving beetles, and small vertebrates such as lizards and tree frogs (Poinar, 2010b).

The special microhabitats discussed above—macrofungi, dung, carrion and phytotelmata—occasionally are captured by resin flows, providing a unique taphonomic window into biotic communities and food webs that otherwise would be a very rare part of the fossil record.

Resin substrates.—One neglected microhabitat in regions where tree resin is copiously produced are organisms that inhabit the semi-viscous to hardened resin surfaces. Resin substrates can be considered as a community of organisms that support a trophic web of microorganisms, plants, fungi, and an assortment of decomposer, fungivore, herbivore, and predatory invertebrates, principally arthropods (Henwood, 1993a). Sap and resin flows attract insects (Langenheim, 1990), notably bark and ambrosia beetles (Henwood, 1993a), but also provide an indirect food resource and access to nest-construction material for a variety of organisms. Modern resin deposits on bark surfaces house distinctive microorganisms (Cotter and Blanchard, 1982), resinicolous fungi (Campbell, 1985), sap-flow beetles, resin-collecting leafcutter and stingless bees (Johnson, 1983; Gonzalez and Griswold, 2011), their predatory apiomerine assassin bugs (Usinger, 1958), and other trophically connected organisms (Henwood, 1993a). Portions of this biota, often with indications of the particular interaction present, have been recovered from Cenozoic amber, including resinicolous fungi (Rikkinen and Poinar, 2000; Beimforde and Schmidt, 2011; Tuovila et al., 2013), apiomerine assassin bugs (Poinar, 2010a), stingless bees (Poinar, 1998), and leafcutter resin-collecting bees (Poinar, 1992b). This biota apparently occupied a special microhabitat distinct from the broader wood- and bark associated biota.

Intraspecific processes and interactions

The fossil amber record documents every major biological activity conducted by terrestrial organisms. A variety of imaging techniques have been used to record this biological activity, presented in greater detail below. At the subcellular level, reproduction by binary fission has been documented in an amoeba from Cenomanian amber from southern Germany (Poinar et al., 1993a). From mid-Cretaceous Spanish amber, a morphological series of fungal hyphae display the formation of intercellular clamp connections (Ascaso et al., 2005; Speranza et al., 2010). At a more macroscopic scale is an example of frozen behavior from Dominican Amber, which documents a lek of termites caught in a nuptial flight preparatory to mating (Fig. 6C). A pair of long-legged flies, also from Dominican Amber, is prepositioned for immediate copulation (Fig. 6K); and a pair of moth flies is shown in copulo (Fig. 6J). A common pollinator from

Dominican Amber, the fossil bee *Proplebeia dominicana*, is preserved providing resin and pollen to conspecific larval nestmates (Fig. 6L; Poinar 1992a).

BIASES OF THE AMBER FOSSIL RECORD

Several studies have investigated the differential representation of taxa in amber as compared to that of equivalent modern biotas, and concluded that there are important biases in the amber fossil record: overrepresentation, underrepresentation, and no bias. In practice, an assessment of bias can be tricky because the amber deposit must be sufficiently comparable in taxonomic diversity, specimen abundance, and ecological representation to an analogous present-day environment such that valid comparisons can be made. In addition, a comparison of biotas from ecologically analogous extinct and modern biotas presumes that collector bias, either reflected in a fossil deposit or in a recent analog, is not a factor. Given these constraints, the two most relevant deposits for understanding bias in the amber fossil record are Dominican and Baltic ambers (Penney and Langan, 2005). The Dominican Amber deposit is more relevant because the environmental conditions under which the biota was deposited were very similar to that of Hispaniola today (Penney, 2005b), with an emphasis on riparian habitats of lower elevation (Henwood, 1993b). By contrast, older Baltic Amber has its closest taxonomic parallel with southeast Asian biotas, and thus is more spatiotemporally removed than that of Dominican Amber.

Amber deposits only sample terrestrial biomes that have amber-producing trees and shrubs. Consequently, regions such as deserts, grasslands, steppe, taiga, and tundra lack representation in the amber fossil record. Within those forested and woodland biomes sampled by amber, several particular habitats are not present in the amber record, such as glacially associated habitats, and non-woody vegetation associated with large lakes (recognizing that amber originating and possessing inclusions from nearby resiniferous habitats frequently occur in lake deposits). With these caveats aside, and with the exception of highly xeric and hydric biomes, the general pattern is that amber potentially captures nearly all of Earth's terrestrial surface that has been colonized by trees and shrubs. Biomes documented by the amber fossil record range from dense tropical rainforest to cool-temperate conifer forest (Langenheim, 1990), and, when these biomes intersect shorelines of oceans, marine organisms, typically protists and small invertebrates, can be entombed in amber (Fig. 4P–R; Girard et al., 2009).

The principal bias in virtually all amber deposits is organism size. Underrepresented organisms are those larger than ~1 cm, which are rarely incorporated in amber. Small, highly mobile vertebrates such as geckos and tree frogs frequently are found incomplete (Fig. 6M), likely the consequence of predation of partially exposed tissue. Large arthropods such as scorpions, centipedes, dragonflies, katydids, scarab beetles, and digger wasps similarly are rarely encountered in amber, attributable to an ability to free themselves from resin entrapment (Poinar, 1999a; Weitschat and Wichard, 2002).

Size is not the only reason for underrepresentation of organisms in amber. One factor is sedentary versus highly mobile life habits. For Dominican Amber spiders, wandering taxa are more prone to inclusion in resin than sedentary taxa (Penney, 2002). An affiliation with particular microhabitats, such as wood and bark, macrofungal fruiting bodies, dung, carrion, phytotelmata, and resin substrates are relevant as well. Of these microhabitats, organisms inhabiting wood and bark, macrofungal fruiting bodies, and resin substrates are preferentially enriched in amber (Larsson, 1978; Poinar, 1994; Weitschat and Wichard, 2002) over those organisms occurring in dung, carrion, and phytotelmata. Insects that swarm and form leks immediately after emergence as adults occur, albeit occasionally, as massive conglomerations within amber (Poinar, 1992a). Highly fluidized resins often capture large numbers of winged termites in nuptial flights (Fig. 6C); certain mayfly and nematocerous fly taxa also swarm in lek formations, often close to the ground, and eventually can become entombed in high numbers as well (Weitschat and Wichard, 2002). Also, it would appear that pest-outbreak taxa should occasionally be overrepresented (Labandeira, 2012), but outbreak frequencies would have to be sufficiently common to be captured in resin. The reason for the high abundance of ants in certain Cenozoic ambers (Grimaldi, 1996; LaPolla et al., 2013) is difficult to discern. Elevated ant abundance may be attributable to their very high intrinsic abundance and speciosity; or, because they are mostly social insects and tend to travel in

very abundant, monospecific columns; or, as active predators of virtually all terrestrial invertebrates and vertebrates, they are overrepresented at flowing resin sites where partially engulfed prey items were exposed for consumption (Hölldobler and Wilson, 1990; Grimaldi, 1996; LaPolla et al., 2013). By contrast, winged insects involved in herbivory and pollination that occur more than a few meters above ground level are poorly represented in amber (Larsson, 1978). Insects occurring at ground level and in the uppermost soil, regardless of their feeding habits, are overrepresented in amber.

The way amber is collected in the field or archived in collections frequently induces an anthropogenic bias. Any field collecting procedure or archival sorting strategy that differentially selects for amber clasts by size, shape, appearance, preservational state, taxonomic composition of inclusions, or some other quality introduces a bias, particularly if there are few specimens per clast. One way to overcome such biases is to include clasts in collections that contain as many organism inclusions as possible, such that each clast samples a greater number of available amber specimens and species within the biota.

APPROACHES TOWARD THE STUDY OF AMBER

Each amber clast takes a long journey from the field to representation in a publication. In this section, the steps by which amber is processed for microphotography and analyses are discussed. The various types of light, epifluorescence, scanning-electron and transmission-electron microscopy for production of high-resolution images are detailed. More recent techniques that employ microtomographic methods that nondestructively assemble composite images into three-dimensional renderings, and analytic techniques that assess the composition of amber matrix and its biotic inclusions, such as various types of spectrometry, chromatography, X-ray microtomography and time-of-flight secondary ion mass spectrometry (Sutton, 2008) also are discussed.

Preparation and documentation

Historically, amber has been collected in the field by a variety of techniques. These methods include: disaggregation, sieving, and saltwater flotation of bulk sediments (McAlpine and Martin, 1969; Pike, 1993; Corral et al., 1999); large quarrying operations, such as excavations from open-pit mines, dredging of river deposits and mechanized massive shoveling with a backhoe (Corral et al., 1999; Weitschat and Wichard, 2002, 2010); or more limited collections directly from outcrops (Corral et al., 1999; Perkovsky, 2010). Collection of amber from outcrops typically involves lignite-rich strata (Grimaldi et al., 2000a), either exposed on the surface (McAlpine and Martin, 1969; Hand et al., 2010), or in underground tunnels (Penney, 2010a). Raw amber, which is visually unimpressive, requires further processing in which the pieces are sorted, then some are cut with a rock saw equipped with a thin, synthetic diamond blade to eliminate excess material that would impede viewing of the inner inclusions. Subsequent preparation involves washing in an ultrasonic cleaner, followed by grinding and polishing the pieces into very rounded specimens resembling the size and shape of gravel (Penney and Green, 2010). Sufficient optical distance between the edge of the inclusion and the amber outer surface should be allowed, such that the entombed organism is not exposed to the external environment, especially degradative oxidation of tissues from contact with air.

Amber conservation

Especially in geologically older ambers, embedding is required to rejuvenate individual specimens for viewing (Nascimbene and Silverstein, 2000). Embedding of amber includes specimens that are too small and difficult to handle, such as angular chips, and larger pieces that have deep fissures and a patchwork of surface cracks (crazing), or specimens that are otherwise too weathered and brittle and thus are unstable (Fig. 7A). Embedding requires immersion and suspension of individual amber pieces in a synthetic resin or Canada balsam of the same hardness and refractive index as the amber (Fig. 7B; Santiago-Blay, pers. comm., 2011). The amber is placed in cube- or rectangular-shaped plastic molds, the walls of which are composed of a plastic that should not chemically react with the synthetic resin. Typical embedding media are the resins Epotek® 301 (Peñalver and Delclòs, 2010) and Buehler Epoxicure® (Schmidt, et al., 2012). The molds are filled to three-fourths capacity with synthetic polyester resin and hardener (Fig. 7C), placed in a vacuum chamber, and then

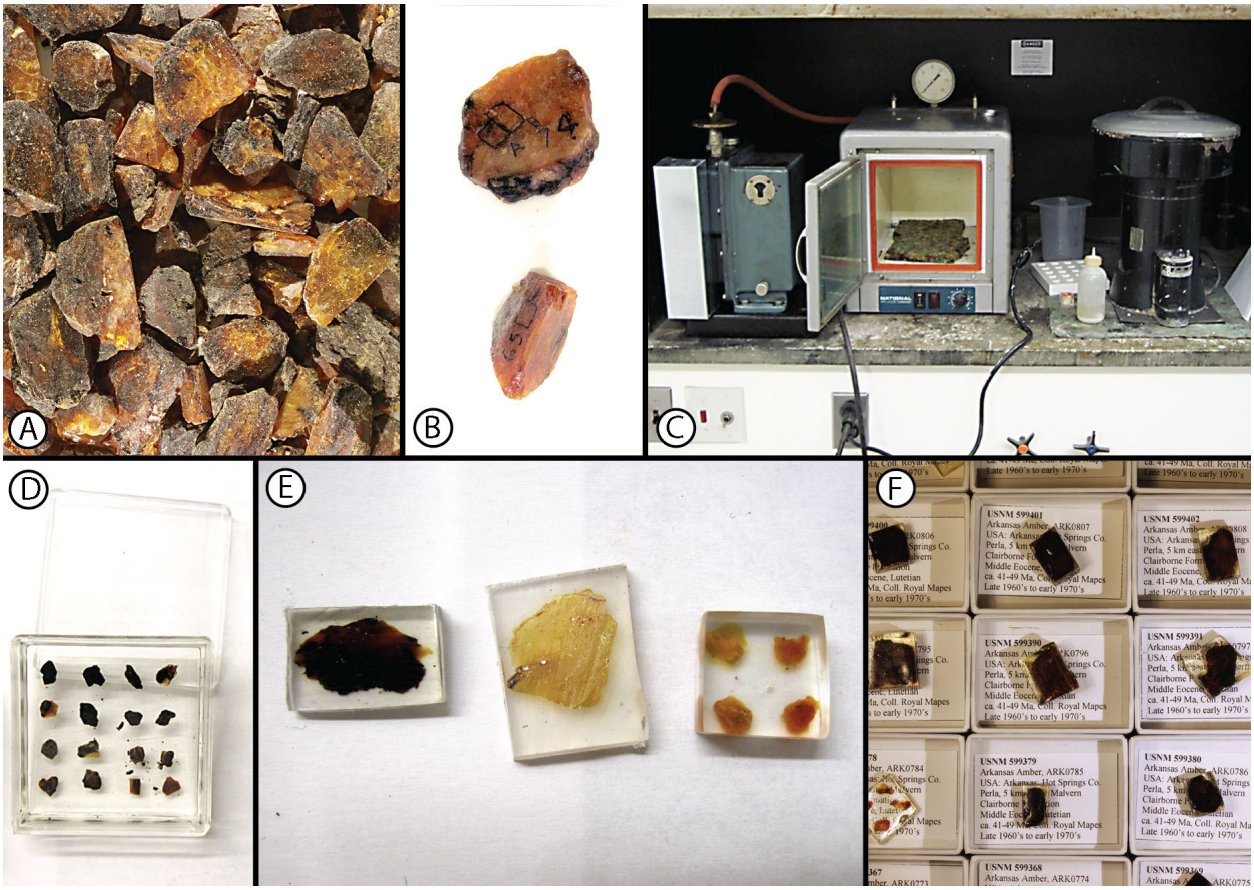


FIGURE 7.—Steps in the transformation of raw, unprocessed amber of probable dipterocarpacean origin into a high-value collection. This material is Arkansas Amber, from lower middle Eocene strata, central Arkansas Coastal Plain near Malvern, Arkansas (Saunders et al., 1974). A) Unprocessed amber chips and angular to rounded clasts ranging in size from ~2 mm to ~2 cm long. B) Two clasts of washed amber. C) Workstation including a vacuum pump (left), vacuum chamber (center) and polishing wheel (right). D) Amber that has been embedded but not extracted from their plastic containers. E) Amber pieces from (D) at left that have been sawn, trimmed, polished, and surface-coated with nail hardener. F) The finished archival collection.

immediately followed by immersion of the amber pieces such that they are suspended in synthetic resin without touching the mold walls (Corral, 1999; Hoffeins, 2001). Each of the transparent plastic molds can hold a single, large piece or several, smaller pieces of amber (Fig. 7D). Care should be taken that bubbles are eliminated, particularly at the amber–resin interface (Corral, 1999; Penney and Green 2010). After the plastic container-resin-amber block has hardened (Fig. 7E), a circular diamond saw with a very thin diamond blade can be used to saw off extraneous thicknesses of the sides of the block, followed by the standard amber techniques of grinding and polishing.

Each side of the solid amber-containing block is coated with a lacquer, such as clear fingernail polish, that hardens and smooths any surface imperfections or occluding micro-particles. This should be done in a dust-free environment if possible. The amber blocks then are placed in appropriately sized archival trays with paper identification and provenance data (Fig. 7F). This general process is used for the conservation of amber, and is particularly important for older ambers, such as those of Cretaceous and Paleogene age. Older ambers often are fragile, highly fractured, and have discolored, denatured rinds that have undergone crazing, oxidation, surface discoloration, a general increase in opacity, and other chemically degradative processes (Williams, 1990; Bisulca et al. 2012). The use of paper archival materials is urged for permanence of the collection, such as middle Eocene Arkansas Amber (Saunders et al., 1974) in the Department of Paleobiology at the National

Museum of Natural History (Fig. 7). At this point, specimens are ready for micro- and macrophotography (Crichton and Carrió, 2007).

One modification of the amber-embedding technique involves fixing cover slips onto the two exposed surfaces of a thinly sawed and polished amber wafer (Perrichot, 2005). Alternatively, a small specimen can be emplaced on a microscope slide with a hemispheroidal well, followed by flooding the specimen with Canada balsam, and placement of a cover slip on the upper surface of the slide for viewing (Penney and Green, 2010). An alternative technique avoids the embedding process altogether and dissolves out biological inclusions from the amber matrix using a solvent such as chloroform (Azar, 1997; Penney et al., 2013b). However, this technique is destructive and risks major loss of biological information.

Imaging, processing, and analyses

Light microscopy.—Light microscopy is the standard, traditional method for examining inclusions in amber. Amber pieces require significant processing to allow ideal viewing conditions under a stereo- or compound microscope. For stereomicroscope observation, each piece needs to be manipulated in three-dimensional space below the focal plane such that the best image can be generated from a combination of incident light from above and illumination from the sides and bottom. Embedding may be used to stabilize the amber pieces and improve clarity of the amber for viewing by eliminating surface boundaries of different refractive indices associated with deeper fissures, pits, and surface crazing. Various viscous oils of appropriate refractive index, such as an adjusted paraffin oil-alkylaromate mixture (Schmidt et al., 2004), have been used, but this also degrades the amber, so caution must be exercised. The most common and preferred embedding medium is Canada balsam (Girard et al., 2009). Various optical immersion oils have been used (Girard et al., 2011), but they irreversibly change the optical qualities of surrounding amber.

Alternatively, visual observation can be made by mounting a thin slice of amber with inclusion material and adding distilled or, preferably, sugar-saturated water, which evaporates much less quickly, on a microscope coverslip placed over the amber slice. Optical oil can slowly dissolve the amber, and its use is not suggested. Contact between the amber and oil medium should be avoided, as the amber surface may be destroyed (Schönborn et al., 1999; Schmidt et al., 2012). The specimen then can be viewed under high magnification with transmitted light microscopy (Girard et al., 2009). Standard high-resolution light microscopy allows nondestructive observation of amber whether organisms are situated partly exposed in fissures or completely entombed (Beimforde and Schmidt, 2011; Ragazzi and Schmidt, 2011). Otherwise, viewing preferably is done under two other techniques—bright-field and/or differential interference microscopy. Bright-field microscopy consists of a illuminating a sample by white light, typically under a compound microscope (Fig. 2I-J). In differential interference microscopy, also known as Nomarski microscopy, a polarized light source fitted with condensers and variable polarizing filters is used to improve contrast and clarity of observed specimens. Both bright-field and differential interference microscopy have been used extensively in amber studies (Schmidt et al., 2004; Girard et al., 2008) and often are the default viewing modes when other methods are unavailable.

Recent improvement in image clarity, and the addition of three-dimensionality to specimens, have benefited by various techniques such as tiling. Tiling consists of computer-assisted software that uses input from microscope images to achieve a three-dimensional rendering of two-dimensional images. Tiling involves stitching together multiple images in the generation of a single, composite, two-dimensional image within a focal plane. Tiling also requires stacking, or the integration of a vertical series of successive focal-plane images, for rendering into a single, composite, three-dimensional image. The production of a three-dimensionally rendered image from a series of two-dimensional microscope images allows greater clarity, detail, and understanding of biological microstructure (Schmidt et al., 2010).

Epifluorescence microscopy.—Epifluorescence microscopy is a method of viewing small specimens using a high-energy light source that emits a broad, intense spectrum of light ranging from visible through ultraviolet wavelengths. Most epifluorescence microscopes use incident illumination above the specimen from a light source that collects and condenses light into a beam, typically a bright blue color. A desired wavelength of light appropriate to the specimen is the excitation level, which is selected by three sets

of filters (termed the fluorescent cube), responsible for filtering and varying the light wavelength. Particular organic molecules, such as melanin pigments, spider chitin, and even the materials in ambient lint, absorb epifluorescent light, the re-radiation of which creates the effect of fluorescence.

Several studies have published results from epifluorescence of amber inclusions. In a study of a Baltic Amber cypress twig with preserved tissues, Koller et al. (2005) showed strong fluorescence of cuticle and resin canals within internal foliar tissues. Another example from the Álava Amber of Spain, fluorescence occurred within protist (Ascaso et al., 2005) and fungal (Speranza et al., 2010) microorganisms. Other studies of epifluorescence indicate that pollen strongly fluoresces (Ren et al., 2009), suggesting applicability to amber material.

Transmission electron microscopy.—Transmission electron microscopy (TEM) is a technique that is used mostly for tissues and other biomedical materials that are ultrathin, are relatively translucent, and can be seen under a microscope with transmitted light. For TEM, an image results when electrons are transmitted through the specimen, wherein areas of greater or lesser density provide the contrast in intensity, translated into grayscale hues. This image is projected or focused onto a fluorescent screen and often recorded through a camera as a digital image. Based on the physics involving the very narrow wavelength of electrons, TEM can produce images thousands of times more highly magnified than any light microscope. Whereas higher-magnification images typically reveal accurate structures in a sample, the varied interactions of waves in TEM can introduce artifacts that require further scrutiny by a skilled TEM operator for correct interpretation of images. The problem of artificial generation of spurious structures also afflicts scanning electron microscopy (SEM).

In a limited number of instances, TEM has been used successfully for imaging very thin to ultrathin slices of amber. Unfortunately, such slices are thinner than the bodies of most entombed amber specimens, making TEM of amber a destructive procedure. However, for microorganisms such as protists, bacteria, fungal spores, and pollen, TEM is a viable method of analysis. Alternatively, TEM has been used to examine the ultrastructure of tissues within amber inclusions, particularly from Dominican Amber. One TEM-based study examined cross-sections of dance fly flight muscle in comparison to the same tissue types from modern, equivalent tissue from a blow fly (Fig. 2B–C; Henwood, 1992b). In a separate study (Grimaldi et al., 1994), flight muscle tissue, connective tissue attached to flight muscle, and brain tissue of the stingless bee *Proplebeia dominicana*, also from Dominican Amber, were examined under TEM and deemed comparable in preservation to that of modern insect taxa. Similarly, a TEM study of a sectioned, stained juniper leaf revealed all major foliar tissues were well preserved, including cuticle, epidermis, parenchyma, and phloem and xylem of vascular tissue, as well as the specialized structures of resin canals, tracheid-like cells, and stomatal pores (Koller et al., 2005). A very high level of specimen preservation is required to effectively delineate histological, cellular and subcellular structure under TEM.

Confocal laser-scanning microscopy.—Confocal laser-scanning microscopy (CLSM) is a microscope-based method for generating focused optical images of specimens at selected depths. This process, termed serial optical sectioning, uses a scanning laser beam that produces an electronic image similar to a scanning electron micrograph. This procedure allows for imaging along one focal plane at a time, with subtractions of the original laser beam not emanating at the focal plane, to achieve complete visualization of an object's inner structure. These images then are imported into a computer-based three-dimensional or four-dimensional rendering program (in the case of a CLSM with time-lapse capability). This procedure involves the stacking and stitching together of serial images for a highly focused, three-dimensional rendered image. In the case of amber and other non-opaque objects where illumination can reveal density boundaries, other CLSM procedures can be applied. One variation is fluorescence emission, whereby objects at focal microscope planes emit a quality of light that otherwise would not produce an observable image, similar to that of epifluorescence microscopy.

For applications involving amber materials, CLSM has been used mostly for microorganisms in European Cretaceous ambers. Spanish amber from Álava in particular was examined by CLSM techniques, revealing amoeba-like, parameciumlike, and other protists that contained subcellular structures such as pseudopodia, anterior and recurrent flagellae, oral grooves, and vacuoles

(Ascaso et al., 2003). The vacuoles were preserved as 'molds' seemingly adpressed against the cell walls (Ascaso et al., 2003, 2005). From the same deposit, septate and aseptate hyphae that displayed germinal bud development, perhaps preliminary to spore development, were found, as well as the encompassing cellular membranes and internal organellar structures of algae (Ascaso et al., 2003, 2005; Speranza et al., 2010) were found. Filamentous structures reminiscent of bacteria also were preserved (Ascaso et al., 2003). CLSM is a powerful technique for examining microorganisms and their organellar and cell-wall substructure, but requires exceptional, pristine preservation to be useful in examining amber inclusions.

Scanning electron microscopy.—Scanning electron microscopy (SEM) has had a distinguished history of an exploratory technique for documenting microscopic to ultramicroscopic structures in scientific and industrial research. SEM operates by producing a directed electron beam from an electron gun that discharges a high-energy electron beam onto a surface-clean specimen. This discharge occurs under an elevated vacuum at the bottom of a vertical cylindrical chamber to produce a focused image. The image is achieved by the electron beam scanning across the surface of the examined specimen, which interacts with surface atoms. The impact of the electron beam produces a variety of secondary subatomic forms of energy, including secondary electrons, backscattered electrons, cathode-luminescent light, x-rays, electromagnetic current, and the original transmitted electrons. A detector then captures secondary forms of energy as electrons or other types of particulate- or wave-based energy that originate from the sample surface. The emission spectrum detector is attached to an interface that includes imaging controls and processing software that provides a black-and-white image of the specimen on a video monitor. The images are produced at a wide variety of magnifications that reveal detail from ~1 nm to a few mm in length that, at low magnifications, overlaps with light microscopy.

Although there are several types of emitted electrons and other types of radiation, typically SEMs have a signal detector that retrieves only one type of radiation. The most widely used and standard type of detector captures secondary electrons. One special application of SEM is a detector that images backscattered electrons, which produce data that can be used for assessing the relative distribution of atomic elements based on their atomic number. By contrast, cathode luminescence (CL) involves a detector that captures excited, high-energy electrons as light. Energy-dispersive X-ray spectroscopy (EDS) is a special technique that is applicable to modern and fossil resins, and will be discussed later.

Examination of essentially mummified tissues within inclusions is one of the practical uses of SEM that has documented the high preservation potential of amber (De Palma et al., 2010). In an extensive study (Grimaldi et al., 1994), the tissues of five Dominican Amber insects and a *Hymenaea protera* leaflet were scrutinized. In the same study, two indeterminate long-legged flies and two fungus gnats were examined. Tissues from all major internal regions of the insect's bodies were scanned, revealing highly detailed structure of the bee's glossate mouthparts, protocerebral portion of the brain, head, sucking pump, esophagus, thoracic musculature, and clumps of pollen on the body exoskeletal surface (Grimaldi et al., 1994). Under higher resolution and magnification, micromorphological detail was revealed for a scuttle fly, including antennal sensillae and brain tissue. Mycangial cavities with fungal spores, ventricular (Fig. 2H–I) and pyloric portions of the intestinal tract, and malpighian tubules were examined in an ambrosia beetle (Grimaldi et al., 1994). The internal foliar structure of the *H. protera* leaflet also was exposed (Fig. 2G). Using SEM, Henwood (1992b) examined the internal anatomy of an undetermined sap-flow beetle and a soldier beetle, showing the complex structure of the proventricular valve within the intestinal tract (Fig. 2A), as well as the structure of the compound eyes and thoracic respiratory and muscle structures. In a more targeted study (Briggs and Kear, 1993), SEM images were produced of muscle sarcolemma, fibrils, and the Z and M fibrillar bands of the recent shrimp *Palaemon*, resembling the results of Grimaldi et al. (1994) in many details.

One particular use of SEM for study of amber inclusions is in the backscattered electron mode (SEM-BSE), which provides images of specimens that employ contrast based on the atomic number of the target. In one study of lower Cretaceous Álava Amber from Spain (Martín-Gonzales et al., 2008), the inner organellar structure of the protists *Euglena*, *Phacus*, *Chlamydomonas*, and others were examined. The authors concluded that there was evolutionary stasis from 100 Ma to the

present. In a parallel study (Martínez-Gonzalez et al., 2009), SEM-BSE provided evidence for how amber-entombed protists were penecontemporaneously pyritized, a process the authors called 'double fossilization.'

Energy dispersive X-ray spectroscopy.—Energy-dispersive X-ray spectroscopy (EDS) is a technique for element analysis, such as the spatial distribution of elements on a sample of interest within a SEM vacuum chamber. EDS provides a frequency-distribution spectrum of elements based on their characteristic excitation states for each of their distinct atomic nuclei. Distinctive excitation states for each atomic nucleus are determined by the specific amount of energy, measured in the amount of kilo-electron volts (KeV) required for electrons of a particular unknown isotope at an unexcited ground state to be ejected at an excited state to the superjacent electron shell bound to the atom's nucleus. The resulting electron 'hole' is replaced by an electron from the subjacent shell. The difference in energy between the subjacent lower-energy shell and the superjacent higher-energy shell is released as an X-ray. The amount of this emitted energy, together with knowledge of the atomic structure of the relevant atomic nucleus, provides for identification, measurement of abundance, and spatial distribution of the emitting element. Often, the accuracy of chemical determinations varies, and can be compromised by different elements registering the same or undifferentiable peaks. In such cases, the detector fails to capture all of the individual X-rays emitted by the sample atomic nuclei, resulting in poor segregation of the characteristic signatures of each element.

Analyses of amber by EDS in several studies have resulted in determination of the amber (matrix) composition surrounding the inclusions. In one study of a Baltic Amber leafhopper (Kowalewska and Szwedo, 2009), EDS analyses of distinctive amber matrices surrounding insect carcasses pieced together the sequence of short-term events leading to the initial onset of amberization, or diagenesis, within the amber. These transformations included early reducing conditions and pyrite formation. In another study involving Spanish Álava Amber, quantitative EDS analyses demonstrated that mineralization of fungal hyphae under anoxic conditions probably occurred soon before amberization (Speranza et al., 2010). For a third use of EDS data (Ascaso et al., 2005), fossil microalgae were found to be differentially mineralized, with elevated Si occurring in the pyrenoid body, high Fe at the chloroplast cell wall and in general cytoplasm, and the rest of the cell exhibiting enriched Al, K, and Fe.

Pyrolysis gas chromatography-mass spectrometry.—Pyrolysis gas chromatography-mass spectrometry (Py-GC-MS) is a type of chemical analysis that uses a sample heated to the point of molecular decomposition in order to characterize the resulting production of smaller biomolecules. In Py-GC-MS the thermal destructuring of materials, or pyrolysis, occurs in a vacuum where a variety of heating techniques are used, although commonly the sample contacts a conducting element such as a platinum filament, and is heated to 600–1000°C. The molecular fragments that have been thermally cleaved are then analyzed by standard gas chromatography techniques; the segregated molecular fragments are indicated by a gas chromatogram output. Because of the variety of degraded molecular species produced from pyrolysis, gas chromatograms are difficult to interpret. Nevertheless, with experience in technique, knowledge of fossil material with complex organic signatures such as amber, specific 'fingerprints' can be developed and recognized for bulk identification of chemically stereotyped varieties of amber. The use of Py-GC-MS typically involves qualitative identification, particularly the polymeric resins that constitute (to greater or less degree) all ambers. In summary, Py-GC-MS is generally poor for producing useful quantitative data.

An interesting application of Py-GC-MS for understanding amber chemistry is determining the provenance of ambers whose botanical source remains contentious. Romanian Amber, of early Oligocene age and known as 'rumanite,' was considered very similar to Baltic Amber and thought to share the same botanical source (Stout et al., 2000). Examinations of the botanical affinity of Romanian Amber after its discovery in the 1930s suggested a confusing array of potential sources, including cupressaceous, pinaceous (both *Abies* and *Pinus*), and an angiosperm origin in the Fabaceae. From an extensive analysis of 13 representative samples of Romanian Amber, it was concluded that the botanical source was, indeed, the same as Baltic Amber, but there were subtle compositional differences attributable to varying degrees of elevated thermal maturation (Stout, 2000).

A similar analysis of latest early Cretaceous

Álava Amber using gas chromatography indicated an araucarian origin (Alonso et al., 2000). A later, more robust study using chemical fingerprinting techniques of Py-GC-MS supported an araucarian origin as well, but with an interesting development in that the identification was done on the chemically transformed compounds and not the original primary resin terpenoids, as is the case with much younger Baltic Amber (Chaler and Grimalt, 2005). In late Triassic Dolomites Amber, Py-GC-MS analyses identified amber samples to a Class II resin (Lambert et al., 2008), indicating that the source plant was a member of the Cheirolepidiaceae, consistent with associated botanical context of the deposit (Roghi et al., 2006)

Nuclear magnetic resonance spectroscopy.—Nuclear magnetic resonance spectroscopy (NMR spectroscopy) is an exploratory and confirmatory technique for determining the chemical and physical properties of atoms within objects by taking advantage of the magnetic properties in certain atomic nuclei. Detailed data on the structure, electromagnetic state, and chemical context of molecules are provided by characterization of their nuclear magnetic resonance and changes in their resonance frequency. NMR spectroscopy uses atomic nuclei that are placed in an electromagnetic field and records the frequency absorption of electromagnetic radiation that is distinctive for each particular isotope. This resonant frequency of absorption is proportional to the isotope's magnetic field, and involves the difference in energy between the two spin states—one in conformity to the magnetic field and the other in opposition. Through a complicated process of assessing each local, unique energy-absorption frequency of a particular molecule species relative to the reference frequency resulting from the externally applied magnetic field strength, a distinctive 'chemical shift' is produced for each molecular species. This chemical shift provides data on the structure of molecular species, usually at levels of ppm.

Any sample that possesses atomic nuclei with electromagnetic spin can be characterized by NMR spectroscopy, although the most appropriate samples tend to be organic molecules, including those that occur in plant exudates such as gums and resins. These samples can be examined using three-or four-dimensional techniques, usually in relatively large quantities of 2–50 mg, preferably dissolved in a solvent. However, analyses of solids, such as anisotropic amber with molecules not in motion, can be accomplished by the variant technique of solid-state nuclear magnetic resonance spectroscopy. One limitation of solid-state NMR spectroscopy is the dependence on sample orientation to visualization of the molecular structure, requiring multiple iterations of sample position to achieve better molecular characterization. A second hindrance is the lessening of isotopic nuclear magnetic interactions when the sample is spun, a consequence that can be remediated by certain corrective actions.

There have been few applications of NMR spectroscopy to the examination of amber composition in the fossil record. Most of the application of NMR spectroscopy has been devoted to general characterization of modern exudates, such as resins, gums, kinos, and latexes (Lambert et al., 2008). More specific applications involve examination of the evolution of exudate types within major clades of the Fabaceae (Lambert et al., 2009). One example from the earliest amber record is the physiochemical characterization of late Triassic Dolomites amber, using NMR spectroscopy (Roghi et al., 2006). From a ^{13}C-NMR-spectroscopy analysis, the results indicated a complex pattern of thermal maturation for the Triassic amber, consistent with Py-GC-MS analyses.

X-ray computed tomography.—X-ray computed tomography (X-ray CT) is a procedure by which two-dimensional virtual tomographic slices are produced by digital geometric processing of a scanned object without the laborious process of actual physical sectioning. This procedure allows a viewer to nondestructively 'penetrate' into an object to obtain a three-dimensional rendering of an inner structure from a series of integrated, radiographic, two-dimensional slices about an axis of rotation. X-ray CT allows three-dimensional renderings to be manipulated remotely by computer, such as object rotation along preselected axes of rotation, or to traverse across a series of slices to examine the virtual appearance and disappearance of objects of interest, or for a closer inspection of microstructure. X-ray CT results are effective because the incident X-ray beams take advantage of density differences along interfaces of the examined object, allowing accentuation of surfaces. A synonym for X-ray CT is computed axial tomography (CAT scan), often used for medical applications. Special applications of X-

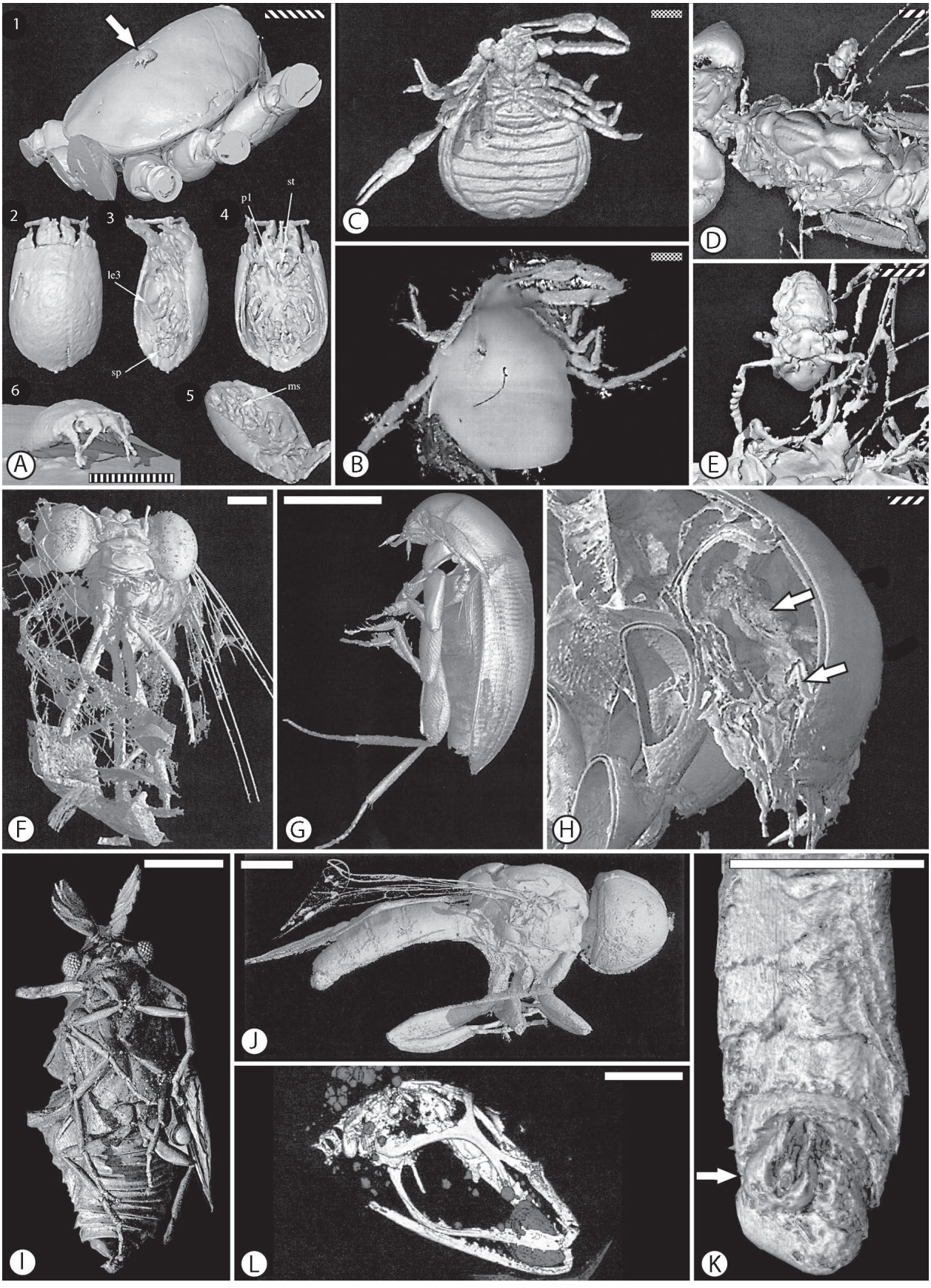
ray CT are positron emission tomography (PET) and single-photon emission computed tomography (SPECT), defined principally by differences in the energy source.

Beginning in the early 2000s (e.g., Polcyn et al., 2002), X-ray CT offered an entirely new mode for visualizing the amber fossil record with the benefits of a nondestructive technique. Although almost all of the samples examined were from the Cenozoic, this technique was extended to Mesozoic ambers (De Palma et al., 2010); by contrast, X-ray CT also was used to characterize inclusions in very recent copal and resin. In one study, Bosselaers et al. (2010), described a modern liocranid spider, and compared it to a conspecific specimen from few-hundred-year-old Madagascaran copal—a comparison made possible by X-ray CT imaging of the male pedipalp, without which a species-level determination would not have been possible. In Neogene Dominican Amber, an example of springtail phoresis on a mayfly was established (Fig. 8D–E), documenting a unique paired association for the first time either in the fossil or modern record of this group (Penney et al., 2012a). Also imaged from Dominican Amber was an anole skull (Fig. 8L), whose species-group membership indicated establishment of a broader clade of Caribbean anoles on Hispaniola sometime during the mid-Oligocene (Polcyn et al., 2002).

Amber from older deposits, such as Baltic and similar ambers represent the greatest application of X-ray CT analyses. Some legacy Baltic Amber collections are historically old, dating to more than 160 years since first collected, and have deteriorated as the amber has oxidized, resulting in specimens correspondingly being difficult to recognize. X-ray CT has rescued some of these specimens by imaging: for example, a huntsman spider from the Berendt Collection in Berlin was assigned to a modern pantropical genus representing a major time and range extension for the family (Dunlop et al, 2011). Another specimen, a pseudoscorpion, had an opaque outer surface because of a layer of milky, clouded amber covering almost the entire body (Fig. 8B). The specimen was rendered visible by X-ray CT (Fig. 8C), allowing confident attribution of the species to an extant genus (Henderickx et al., 2006), an assignment that otherwise would have been impossible. An additional species assignment was made for a minute spider of early Eocene amber from the Paris Basin, made possible by very-high-resolution X-ray CT of the male pedipalpal surface (Penney et al., 2007). A different structure required for systematic assignment was provided by a Baltic Amber specimen of a big-headed fly (Pipunculidae) (Fig. 8J), in which details of the male genitalia, in particular the phallic guide complex and related gonopods (Fig. 8K), allowed placement of the specimen into a new species of an extant genus (Kehlmaier et al., 2014). A similar basis for assignment was available for a new Baltic Amber strepsipteran genus, *Eocenoxenos*, whose antennae was examined using X-ray CT (Fig. 8I), a result of which was a considerably earlier time-of-origin of the related strepsipteran lineage Corioxenidae (Henderickx et al., 2013). Last, a minuscule Baltic Amber astigmatid mite was found attached, apparently in-situ, to the dorsal carapace of a dysderid spider (Dunlop et al., 2012). The imaging of the 176-µm long phoretic mite (Fig. 8A) indicates the limits of X-ray CT resolution, although X-ray synchrotron microtomography, discussed next, can render even smaller specimens.

X-ray synchrotron microtomography.—Synchrotron radiation-based computed microtomography (SRµCT) is a technique that examines a volumetric structure and renders volume within objects by the two-dimensional projection of volumes (Tafforeau et al., 2006). The volume is produced by a scanner along increments of microns-thick slices within a fixed volumetric grid. With an ultrafine spatial resolution on a micron scale, SRµCT can measure the attenuation via varying electromagnetic fields of accelerator-produced high-energy electrons in three-dimensional samples. This attenuation results in emission of powerful electromagnetic waves, termed synchrotron radiation. Synchrotron radiation can allow for quantitative measurement that is not compromised by X-ray beam hardening of the examined material. One variant of SRµCT is phase-contrast imaging, in which the difference between the refractive index of an object of interest and its surroundings can cause a phase-shift, or interference pattern. The resulting interference pattern augments contrast, and often reveals exquisite three-dimensional detail.

SRµCT has had a dramatic impact on imaging of inclusions in amber, particularly for manipulation of insects to reveal minute ultrastructural detail. Although not supplanting X-ray CT, SRµCT has supplemented the earlier technique of X-ray CT by penetrating specimen


1
2
3
4
st
p1
le3
sp
6
5
ms
A
B
C
D
E
F
G
H
I
J
L
K

microstructure at even higher levels of magnification. However, access at a synchrotron facility may be limited, and only a few major facilities are available in scheduling beam time for specimen microimaging, such as Argonne (U.S.A.) and Grenoble (France). The advantages of SRμCT, other than revealing extraordinary micromorphological detail, include more efficient penetration of visually opaque amber specimens than X-ray CT, and, in conjunction with X-ray fluorescence, the production of elemental maps, including trace-element mapping, revealing the presence of molecules such as melanin (McNamara, 2013), analogous to EDS analyses.

Although used in compression-impression deposits for three-dimensional rendering (e.g., seeds) (Smith et al., 2009), Cenozoic ambers show heightened practical possibilities for SRμCT (Soriano et al., 2010). In a study of the taxonomic placement of a Chiapas Amber centipede, the micromorphological detail of the character-rich head and forcipules (poison organ) allowed a clearer establishment of the phylogeny and past paleogeography of its larger, encompassing clade (Edgecombe et al., 2012). Another study (Heethoff et al., 2009) explored the degree to which resolution of very fine-grained micromorphological detail can be resolved for an oribatid mite only 1200 μm long, including minute cuticular sculpturing. In an examination of a Baltic Amber leiodid beetle (Fig. 8G), and using a phase-contrast modification of SRμCT, Perreau and Tafforeau (2011) explored a virtual, three-dimensional dissection of brain tissue (Fig. 8H), and the three-dimensional rendering of internal and external male genitalic structure.

There has been an emphasis on the examination of Cretaceous European ambers using SRμCT. One exception was the anatomy of the Baltic Amber strepsipteran *Mengea tertiaria* that was analyzed, including impressive imaging of the internal organs, allowing placement of this specimen within the Strepsiptera, the twisted-wing parasites (Pohl et al., 2010). In another study of a moth fly (Psychodidae) from Cenomanian Amber of France (Lak et al., 2008b), the

← FIGURE *8*.—Examples of X-ray computed tomography (X-ray CT) and X-ray synchrotron microtomography (SRμCT) techniques for three-dimensional imaging of amber. A) X-ray CT visualization of a minuscule phoretic mite deuteronymph (white arrow) on the dorsal carapace of a middle Eocene Baltic amber dysderid spider at top in (1), with scale bar indicated; (2-5) are various rotational views of the mite, including a collective scale bar and an enlarged image of the attached mite in (6); ms=movable suckers; p1=apodemes; st=sternum; sucker plate=sp; third pair of legs=le3; from Dunlop et al., 2012; fig. 1, specimen SMNG-07/36290. B) Pseudoscorpion *Pseudogarypus pangaea*, from Baltic Amber shown under visible light microscopy; note near-complete obscuring of opisthosomal dorsal detail (Henderickx et al., 2006; fig. 1, specimen MRAC-219415). C) The same specimen as (B) shown as a visualization under X-ray CT; note detail of opisthosomal segments. D) X-ray CT of early Miocene mayfly *Borinquena parva* from Dominican amber displaying a miniscule phoretic collembolan (springtail) at the base of the right forewing (Penney et al., 2012a; fig. 1D; specimen PRC-DRA-Eph-002). E) A 4x enlargement of the right forewing and attached phoretic collembolan in (D) above (Penney et al., 2012, fig. 1E). F) Phase contrast SRμCT of the head, mouthparts, and wings of *Electrohemiphlebia barucheli* from Early Cretaceous (Albian) French amber, validating the appearance of the Hemiphlebiidae during the Jurassic (Lak et al., 2009; fig. 3; ARC-372.1). G). Phase contrast SRμCT of a middle Eocene Baltic amber rove beetle *Nemadus microtomographicus*, the source of microtomographic dissection in (H) at right (Perreau and Tafforeau, 2011; fig. 1c; specimen BB-1445-K). H) Transverse section of the head in (G) showing the transparency effect of microtomography for the internal expression of the epistomal suture (lower arrow), and brain structure (upper arrow). I). X-ray computed microtomography of the middle Eocene Baltic amber twisted-wing parasitoid *Eocenoxenos palintropos*, in ventral view revealing distinctive antennomere features that place this taxon as basal member of the Corioxenidae (Henderickx et al., 2013; fig. 2; specimen IG.32.287). J) X-ray computed microtomography in right-lateral view of the Baltic amber big-headed fly, *Metanephrocerus hoffeinsorum*, in which details in the male genitalia of a related species allowed identification of several congeneric species (Kehlmaier et al., 2014; fig. 11; specimen DB1537-4). K) X-ray computed microtomography of the ventral male abdomen of a related species, *M. groehni*, showing sternites (e.g., st3), and the genital capsule (arrow) that display the crucial structures of cerci, epandria, and phallic guide complex for species assignment (Kehlmaier et al., 2014; fig. 28; specimen DB1895). L) X-ray computed tomography of a skull of an early Miocene Dominican amber anole lizard, *Anolis* sp., showing a morphology indicating extreme deep-time longevity of this species complex (Polcyn et al., 2002; fig. 7: SMU-74976). Scale bars: solid=1 mm; dotted=0.1 mm; diagonally lined=1 μm; vertically lined=10 μm; horizontally lined=100 μm. (A, F) Permission for use granted by Wiley-Blackwell. Permission for reproduction of figures 1c and 2a in Perreau and Tafforeau (2011), herein as G and H, is granted by Blackwell Publishing. (J) Permission for reproduction kindly granted by the Palaeontological Association. (L) Permission for use granted by the Society of Vertebrate Paleontology.

rendering of the external body surface and female genitalia allowed a better temporally constrained hypothesis for the origin of the larger subsuming clade. In a different study. Lak et al. (2009) documented phoretic behavior between a hitchhiking collembolan (Fig. 8E) and its mayfly host (Fig. 8D). Although reporting fossil interspecies mutualisms rarely involve computer-based microtome and imaging techniques, one study of Spanish Álava Amber (Peñalver et al., 2012) provided intricate detail of a pollinator interaction. In this mutualism, two species of the merothripid *Gymnopollisthrips* (Thysanoptera) bore specialized pollen-attracting structures that included ring setae with affixed clumps of *Cycadopites* pollen, preserved in amber within strata that contain its likely pollinated seed-plant, the ginkgoalean *Nehvizdyella*.

Time of flight–secondary ion mass spectrometry.—Time-of-flight-secondary ion mass spectrometry (ToF-SIMS) consists of a pulsed ion beam shot from a particle-emitting gun within a vertical chamber, at the bottom of which is a secured sample of interest. When the ion beam contacts the outermost surface of the sample, molecules are removed (the secondary ions), and are propelled into the vertical chamber, or flight tube, that records the molecular emission from the sample. The masses of these molecules are recorded by a particle detector that measures the exact time for each molecule to reach the detector, known as 'time of flight.' The exact time of flight, measured in nanoseconds, is directly proportional to the molecular masses of the compounds that are spalled off the sample impact site. ToF-SIMS operates under several regimes, including surface spectroscopy surface imaging and profiling at depth. Detection of negatively or positively charged inorganic or organic ions and molecular compounds is highly discrete, and molecular masses can be exact, in the range of 1 to 10^5 atomic mass units, with trace-level detection levels in the range of parts per million. The capabilities of ToF-SIMS include producing output of instantaneous or retrospective spectra of frequency-molecular mass data.

For detection of organic molecules, such as polymerized resins in amber, the ToF-SIMS static mode is used, which employs a lower ion beam current that teases out ions, molecules, and molecular aggregates for special qualitative analyses, as compared to the dynamic mode, which uses much more beam current to produce data for semiquantitative analyses of organic compounds. Organic compounds such as those present in amber are essentially destroyed under the dynamic mode. However, under the static mode, and when connected to a system that compares a molecule suspected to occur in the sample with a provided standard containing the same or similar molecules, ToF-SIMS can reassemble fossilized molecular fragments into the complete molecule from which they originated. These reconstructed molecules can be identified and interpreted by an organic geochemist. One example of the uses of ToF-SIMS in compression material was detection of hemoglobin in the abdomen of a middle Eocene mosquito, using a swine blood standard (Greenwalt et al., 2013).

ToF-SIMS is the most recent analytical method for determining the chemical composition of ambers. ToF-SIMS is a powerful technique, particularly when provided a chemical standard for calibration in assembling chemical compounds, and when coupled with computer-interfacing software for identifying and assembling organic molecular structures. One of the first examinations of amber composition using ToF-SIMS (Sodhi et al., 2013) was characterization of Paleogene Baltic and Bitterfeld ambers, which were compared to previous determinations from techniques such as gas chromatography. ToF-SIMS analysis confirmed the organic molecular constituents of particular ambers elucidated in earlier analyses, and additionally detected slight differences across samples. These subtle distinctions, made by ToF-SIMS determination of variation in amber composition, highlighted the differences in the provenance, taphonomic history, and age of the two ambers. Importantly, it indicated that Baltic and Bitterfeld ambers were, indeed, distinct deposits and not geographic versions of each other (Sodhi et al., 2013), contrary to earlier predictions. In a similar study by Sodhi et al. (2014), twelve diterpenoid resin standards were provided to ToF-SIMS, which was tasked to differentiate among larger set of fossil resins with known chemical compositions. In that study, ToF-SIMS successfully differentiated the resin compositions, with few complications.

DISCUSSION: ROLE OF AMBER IN UNDERSTANDING THE FOSSIL RECORD

The exceptional taphonomic window provided by amber deposits allows a discussion of four themes

that provide a better understanding of the terrestrial fossil record. These are: 1) the biomolecular characterization of amber-entombed organisms; 2) phylogenetic reconstruction of organisms found in amber; 3) the macroevolutionary patterns of amber taxa; and 4) paleobiogeographic inferences resulting from the distribution of amber taxa. For each theme, there are particularly noteworthy examples that illustrate the importance of amber in illustrating the fossil history of terrestrial life.

Biomolecular characterization

Amber-entombed tissues of arthropods in Dominican and Baltic ambers display a remarkable state of preservation. Microorganisms from older, mid-Cretaceous ambers of Spain and France similarly exhibit exceptional retention of subcellular organellar detail. Because of this exceptional preservation, it was once thought that the retention of biological structure could extend to lower levels of biological organization to include not only cells and organelles, but also biomolecules such as proteins and DNA. At about the same time that histological microstructure was being fleshed out (e.g., Henwood, 1992a, b), there were published studies that claimed that DNA isolated from amber organisms was sequenced and characterized (Poinar, 1994). Specifically, the claim was DNA was sequenced from a nemonychid weevil *Libanorhinus succineus* from Lebanese Amber (Cano et al., 1993), and two species from Dominican Amber, the termite *Mastotermes electrodominicanus* (DeSalle et al., 1992, 1993) and the bee *Proplebeia dominicana* (Cano et al., 1992). In addition, the Dominican Amber resin-producing source plant, *Hymenaea protera*, presumably also had characterizable DNA (Poinar et al., 1993c, 1994). A bacterium comparable to modern *Bacillus sphaericus*, was revived and cultured, and sequenced, after presumably surviving a ~17 Ma interval in a piece of Dominican Amber (Cano and Borucki, 1995; also see Yousten and Rippere, 1997; Greenblatt et al., 2004).

In 1997 and 1998, several studies could not confirm the results of DNA sequences retrieved from multimillion-year-old amber insects (Austin et al., 1997a, b; Smith and Austin, 1997; Walden and Robertson, 1997; Gutiérrez and Marín, 1998). These follow-up reports detected a variety of issues in the original studies, including insufficient internal laboratory checks of results, other studies indicating that extensive degradation of DNA in resins is common, and lack of reproducibility of the resulting data (Penney et al., 2013a). While this episode involving the idiosyncrasies of amber preservation was disappointing to some, these events do point to the taphonomic limitations of amber. The degrees of amber preservation are based on the biological level of organization: what is preserved at the organ level may not be preserved at the tissue level; and excellent preservation at the tissue level does not ensure that constituent cellular and organellar levels are preserved; and perhaps most disappointing of all, evidently biomolecules such as proteins, lipids, carbohydrates, and DNA are probably not preserved intact in deep time, at least older than ~ 1 Ma (Rogers et al., 2000; Hebsgaard et al., 2005). Nevertheless, there are heartening signs that, in limited instances, sufficient, original molecular structure is retained for subsequent reassembly of molecular fragments with ToF-SIMS technology, or other techniques (Allentoft et al., 2009). Evidently, 44-million-year-old degraded hemoglobin fragments can be reconstructed into a viable biomolecule (Greenwalt et al., 2013), and carotenoid pigment structure can be retrieved from preserved feathers in younger Dominican Amber (Thomas et al., 2014).

Phylogenetic reconstruction

Several examples have been presented where detailed resolution of important micromorphological structures, particularly involving genitalic characters, were crucial for taxonomic assignment to a modern clade (e.g., Polcyn et al., 2002; Penney et al., 2007; Henderickx et al., 2013; Kehlmaier et al., 2014). These revised assignments almost always had three effects. First was resolution of species phylogenetic relationships within the large clade containing the fossils. Second was downward temporal extension of the modern clade containing the newly described fossil, indicating an earlier time of origin. Third was the extension of the broader encompassing clade that includes the fossil and sister clades to an even earlier time of origin, often to the Mesozoic for many Cenozoic forms. The overall effect of preservation of exquisite micromorphological detail in amber is to more adequately resolve systematic relationships among taxa. This produces a more error-free tree of life, at least for those organisms that entered the taphonomic window of an exceptional amber deposit.

Macroevolutionary patterns

There are three patterns that the amber fossil record contributes to understanding the broader sweep of macroevolutionary processes. The first involves mid-Mesozoic protists that presumably show an amazing amount of evolutionary stasis, assuming that any potential organellar, integumentary or other intracellular differences are recognizable. Examples of microorganismic stasis was indicated for ~110 Ma mid-Cretaceous Spanish amber (Martín-Gonzalez et al., 2008; Peñalver and Delclòs, 2010), that affected a variety of protistan taxa at the generic level. However, as in the studies of disease transmission in Myanmar amber, the presence of evolutionary stasis has not been convincing, and some of the structures described may be artifacts (Girard et al., 2011). A more compelling case are several studies demonstrating evolutionary stasis in protists from mid-Cretaceous (Cenomanian) Schiersee Amber of the southern Alps, slightly younger than the age of Spanish Amber, although erroneously reported earlier to be of Triassic age (Schmidt et al., 2001). Schiersee Amber microorganisms include cyanobacteria, amoebae, protists, and fungal spores (Poinar et al., 1993a, b; Schönborn et al., 1999; Schmidt et al., 2004, 2006). While mid-Cretaceous German and Spanish ambers display considerable evolutionary stasis for microorganisms, the co-occurring arthropods provide evidence for evolutionary turnover. One interesting study of a considerably more recent example of stasis involves a spirochete symbiont in the termite *Mastotermes electrodominicus* from Dominican Amber (Wier et al., 2002).

The second pattern documents changes in the composition of insect faunas during the early to mid-Cretaceous. An intriguing aspect of amber deposits during this time interval involves insect taxa occurring in principally Lebanese Amber (Azar et al., 2010), Álava Amber (Peñalver and Delclòs, 2010) and Myanmar Amber (Ross et al., 2010), collectively ranging from ~120–100 Ma. These deposits capture a mix of species that represent the two major evolutionary biotas of the terrestrial Mesozoic. Represented from earlier biotas are gymnosperm lineages (which peaked in the Jurassic), such as cycads, cheirolepidiaceous and araucariaceous conifers, corystosperms, bennettitaleans, and a range of ginkgophytes, often as pollen or smaller foliage elements. These deposits also contain many extinct or currently relict insect lineages phylogenetically basal to modern clades, many of which consist of herbivores that interacted with gymnosperms (Labandeira, 2014). Included among these earlier insect lineages are the Protopsyllidiidae, Burmacoccidae, Albicocociidae and Schizopteridae (all Hemiptera), Caloblattinidae (Blattodea), Elcanidae (Orthoptera), Lophioneuridae (Thysanoptera), Nemonychidae and Belidae (Coleoptera), Pseudopolycentropodidae and Mesopsychidae (Mecoptera), and Serphitidae and Stigmaphronidae (Hymenoptera) (Kuschel and Poinar, 1993; Grimaldi et al, 2002, 2005b; Grimaldi, 2003; Grimaldi and Ross, 2004; Koteja, 2004; Nel et al., 2007; Ren et al., 2009; Peñalver and Grimaldi, 2010; Ortega-Blanco et al., 2011a, b; Labandeira, 2010, 2014). Overlapping with these older plant and insect lineages in these deposits are modern 'paleoherb' grade and other early lineages of angiosperms, centered in the late Cretaceous and Paleogene, many of which were interacting with insect lineages that became dominant during the late Cretaceous and Cenozoic. More derived, modern lineages of insects occurring in these same deposits include the Tettigoniidae and Tetigridae (katydids and pigmy grasshoppers, Orthoptera), Thripidae (common thrips, Thysanoptera), Curculionidae and Chrysomelidae (common weevils and leaf beetles, Coleoptera), Melittosphecidae, Formicidae and the Scolebythidae (the earliest bee, the earliest ants, and scolebythid wasps, Hymenoptera), the Cecidomyiidae, Empididae, and Therevidae (gall midges, dance flies, and stiletto flies, Diptera), and the Gracillariidae (leaf-blotch miner moths, Lepidoptera) (Kuschel and Poinar, 1993; Labandeira et al, 1994; Poinar and Danforth, 2006; LaPolla et al., 2013; Labandeira, 2010, 2014).

These three amber deposits sample the last occurrences of insects that either became extinct or underwent substantially reduced diversities from a greater presence in a formerly gymnosperm-dominated world. At the same time, the three amber deposits also record the earliest appearing insect lineages that became dominant in the more recent, angiosperm-dominated world. Although never rigorously studied, perhaps because of inadequate sample size at the family or genus levels, three outcomes of this transitional interval of time would have been elevated extinction rates, elevated origination rates, and an overall decrease in insect diversity during the shift from gymnosperm- to angiosperm-dominated

biotas (Labandeira and Sepkoski, 1993; Labandeira, 2014).

A third pattern is attributable to the preservation of evidence for disease transmission, evident especially in Dominican, Baltic, and Myanmar ambers (Table 2, <http://paleosoc.org/shortcourse2014.html>; also see Labandeira and Prevec, 2014). Were it not for the robust amber documentation of parasitic vectors, mostly nematodes, fleas, and especially flies, and the identification of the effects of viruses and the disease-pathogens of bacteria, fungi, and nematodes in their host bodies, very little would be known about the past history of disease transmission (Kohring, 1995; Lewis and Grimaldi, 1997). Some of the diseases known from the amber fossil record, with varying degrees of evidence, are yersiniosis (also known as plague), Chagas disease, leishmaniasis, trypansomiasis, malaria, and filariasis (Table 2). These diseases evidently had a long, often-circuitous history involving transmission of similar, highly stereotypical pathogens by vectors on hosts as those of today. The key to recognition of disease in the amber fossil record is, with appropriate caution, identification by high-resolution microscopy or other methods of detection, such as external signs of disease syndromes (Labandeira and Prevec, 2014), indicating the effects of viruses, bacteria, trypanosomes, plasomodia, fungal bodies, or mermithid parasites on their hosts, or alternatively, direct detection of the disease pathogen.

Paleobiogeographic inference

Cenozoic amber deposits record considerable biogeographic data in the form of taxa that possess current and past biogeographical distributions. Taxa from major amber deposits are often compared to where their descendant taxa currently occur. The two richest and abundant amber deposits are early Miocene (~17 Ma) Dominican Amber and middle Eocene (~44.4 Ma) Baltic Amber, which are taphonomically similar deposits, but have very different biogeographical affinities. Whereas the most similar biogeographical analog for Dominican Amber is the immediate area of the island Hispaniola (Penney, 2005b, 2010b), Baltic Amber shares the greatest biogeographical affinity with Southeast Asia (Grimaldi and Engel, 2005; Hughes et al., 2011). Reasons for the disparate biogeographical affinities of these two amber deposits may involve differences in an insular versus a continental setting, or that the age of Baltic Amber is about twice that of Dominican Amber, thus allowing greater time for biogeographical divergence; or perhaps the effects of Pliocene–Pleistocene cooling and related glaciation that was more pronounced in Northern Europe than the Caribbean.

A second, older biogeographical issue involves the recent discovery of a biota preserved in early Eocene (~52–Ma) Cambay Amber from Gujarat State, in central-eastern India (Alimohammadian et al., 2005; Rust et al., 2010). India was a continental fragment that rafted northward after the breakup of Gondwana during the Late Jurassic ~160 Ma (Rowley, 1996), so it appears reasonable to infer that India's initial, pre-breakup Gondwanan biota should have been preserved during its ~110 Ma interval of isolation. However, an analysis of the dipterocarpaceous amber assemblage, enriched in arthropod taxa did not reveal a Gondwanan biota during the early Eocene, but instead possessed biogeographical affinities elsewhere (Rust et al., 2010). The affinities of Cambay Amber are: 1) the Eocene of Northern Europe; 2) Holocene Australasia; and 3) the Miocene of the tropical Americas. This incongruous result is most parsimoniously explained by assuming that India had already docked with the southern margin of Eurasia when the Cambay Amber was formed (Rowley, 1996), and thus already was overrun by Eurasian and New World taxa. Such an account would necessitate a search for even older amber in India that would represent a pre-contact Gondwanan biota.

OVERVIEW: AMBER AND COMPRESSION-IMPRESSION DEPOSITS COMPARED

There are advantages and disadvantages when comparing the amber and the compression-impression fossil records. Three major advantages and disadvantages of amber versus compression-impression deposits have an important role in differentiating these two different modes of preservation. Although this list is not exhaustive, it represents the major benefits and liabilities of each deposit type.

Advantages of amber deposits

Preservation.—The amber fossil record provides exceptional preservation of the whole

organism in micromorphological detail. Nevertheless, some compression-impression deposits are almost as well-preserved as amber deposits, such as the late Miocene Calico Mountains hot-spring deposit of southern California (Palmer, 1957; Park and Downing, 2001) and the middle Eocene Kishenehn biota from western Montana (Greenwalt and Labandeira 2013; Greenwalt et al., 2013).

Trophic data.—The amber fossil record preserves splendid inter-organismic trophic data. These data could best be put to use by an exhaustive study of the trophic relationships of one spatiotemporally constrained abundant and diverse amber deposit using the food-web techniques used for the Messel food web (Dunne et al., 2014; Labandeira and Dunne, 2014).

Parasites, pathogens, and disease.—The amber fossil record is very good for documenting parasite, pathogen, and disease relationships among animals (Poinar, 2014). The compression-impression fossil record is much better, by contrast, for recording plant diseases, including their pathogens, vectors, and hosts (Labandeira and Prevec, 2014)

Advantages of compression-impression deposits

Greater temporal completeness.—The compression-impression record of megascopic fossils is more complete, and replaces, with minor exceptions, the amber fossil record from the Paleozoic to mid-early Cretaceous, before the onset of Lebanese Amber (Labandeira, 1999). The mid-Cretaceous fossil record does have rare biological inclusions, but they are overwhelmingly microorganisms (Schmidt et al. 2006) or very rare arthropods (Schmidt et al., 2012).

An expanse of two-dimensional surfaces.—The compression-impression fossil record allows for two-dimensional examination and analysis of herbivory (Wilf and Labandeira, 1999; Labandeira et al., 2007), which requires fossils in layered beds that display an extensive amount of foliar surface area. The type of research involving quantification plant-insect interactional data is not possible by examining amber material.

Range of environments.—The compression-impression record samples a broader range of environments, some of which are essentially absent in the amber fossil record. Environments not sampled by the amber fossil record are where resin-producing trees are absent, and include grassland, desert, tundra, taiga, steppe, glacial, and aquatic habitats such as lakes. Although amber sometimes is deposited in lacustrine or shallow-marine nearshore environments, the source material almost always originated from wooded or forested habitats.

ACKNOWLEDGMENTS

Thanks go to Finnegan Marsh for rendering Figures 2-8. I am grateful to Xavier Delclòs of the University of Barcelona for granting permission to reproduce Figure 1. Tom Phillips of the University of Illinois at Urbana-Champaign provided the acetate-peel image for Figure 3A. Figure 4A is courtesy of Stefano Castelli of the University of Padova; Figure 4B, courtesy of Guido Roghi of the University of Padova, Italy; and Figures 4D–G courtesy of Alexander Schmidt of the University of Göttingen, Germany. Enrique Peñalver of the Institute of Geology and Mines in Madrid, Spain, provided images for Figures 4J–N. I am also grateful for Patrick Craig for supplying images for Figures 5 and 6. This contribution benefitted significantly form discussions with Jorge Santiago-Blay and two anonymous reviewers. This is contribution 298 of the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History, in Washington, D.C.

REFERENCES

AGEE, H. R., AND R. S. PATTERSON. 1983. Spectral sensitivity of stable, face, and horn flies and flies and behavioral responses of stable flies to visual traps (Diptera: Muscidae). Environmental Entomology, 12:1823–1828.

ALENCAR, J. C. 1982. Estudos silviculturais de uma população natural de *Copaifera multijuga* Hayne —Leguminosae, na Amazonia Central. 2. Produção de óleoresina. Acta Amazonica, 12:75–89.

ALIMOHAMMADIAN, H., A. SAHNI, R. PUTNAIK, R. S. RANA, AND H. SINGH. 2005. First record of an exceptionally diverse and well-preserved amber-embedded biota from Lower Eocene (~52 Ma) lignites, Vastan, Gujarat. Current Science, 89: 1328–1330.

ALLENTOFT, M. E., S. C. SCHLEUSTER, R. N. HOLDAWAY, M. L. HALE, E. MCLAY, C. OSKAM, M. T. P. GILBERT, P. SPENCER, E. WILLERSLEV, AND M. BUNCE. 2009. Identification of microsatellites from an ancient moa species using high-throughput (454) sequence data.

BioTechniques, 46:195–200

ALONSO, J., A. ARILLO, E. BARRÓN, J. C. CORRAL, J. GRIMALT, J. F. LÓPEZ, X. MARTÍNEZ-DELCLÒS, V. ORTUÑO, E. PEÑALVER, AND P. R. TRINCAO. 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (Northern Spain, Basque-Cantabrian Basin). Journal of Paleontology, 74:1158–1178.

ANDERSON, J. M., AND H. M. ANDERSON. 2003. Heyday of the Gymnosperms: Systematics and Biodiversity of the Late Triassic Molteno Fructifications. Strelitzia 15. National Botanical Institute, Pretoria, South Africa.

ANDERSON, K. B., AND B. LEPAGE. 1995. Analysis of fossil resins from Axel Heiberg Island, Canadian Arctic, p. 170–192. *In* K. B. Anderson and J. C. Crelling (eds.), Amber, Resinite, and Fossil Resins. American Chemical Society Symposium Series 617. American Chemical Society, Washington, D. C.

ANTOINE, P. O., D. DE FRANCHESCHI, J. J. FLYNN, A. NEL, P. BABY, M. BENAMMI, Y. CALDERÓN, N. ESPURT, A. GOSWAMI, AND R. SALAS-GISMONDI. 2006. Amber from western Amazonia reveals Neotropical diversity during the middle Miocene. Proceedings of the National Academy of Sciences of the United States of America, 103:13595–13600.

ARMBRUSTER, W. S. 1984. The role of resin in angiosperm pollination: ecological and chemical considerations. American Journal of Botany, 71:1149–1160.

ASCASO, C., J. WIERZCHOS, J. C. CORRAL, R. LÓPEZ, AND J. ALONSO. 2003. New applications of light and electron microscopic techniques for the study of microbiological inclusions in amber. Journal of Paleontology, 77:1182–1192.

ASCASO, C., J. WIERZCHOS, M. SPERANZA, J. C. GUTIÉRREZ, A. M. GONZÁLEZ, A. DE LOS RIOS, AND J. ALONSO. 2005. Fossil protists and fungi in amber and rock substrates. Micropaleontology, 51:59–72.

ASH, S. R., AND R. A. SAVIDGE. 2004. The bark of the Late Triassic *Araucarioxylon arizonicum* tree from Petrified Forest National Park, Arizona. International Association of Wood Anatomists Journal, 25:349–368.

AUSTIN, J. J., A. J. ROSS, A. B. SMITH, R. A. FORTEY, AND R. H. THOMAS. 1997a. Problems of reproducibility—does geologically ancient DNA survive in amber-preserved insects? Proceedings of the Royal Society of London B-Biological Sciences, 264:467–474.

AUSTIN, J. J., A. B. SMITH, AND R. H. THOMAS. 1997b. Palaeontology in a molecular world: the search for authentic ancient DNA. Trends in Ecology and Evolution, 12:303–306.

AZAR, D. 1997. A new method for extracting plant and insect fossils from Lebanese amber. Palaeontology, 40:1027–1029.

AZAR, D., R. GÈZE, A. EL-SAMRANI, J. MAALOULY, AND A. NEL. 2010. Jurassic amber in Lebanon. Acta Geologica Sinica, 84:977–983.

BARONI-URBANI, C., AND S. GRAESER. 1987. REM-Analysen an einer pyritisierten Ameise aus Baltischen Bernstein. Stuttgarter Beitrage zur Naturkunde B, 133:1–16.

BECK, C. W. 1999. The chemistry of amber. Estudios de Museo Ciencias Naturales del Álava, 14:33–48.

BEIMFORDE, C., N. SCHÄFER, H. DÖRFELT, P. C. NASCIMBENE, H. SINGH, J. HEINRICHS, J. REITNER, R. S. RANA, AND A. R. SCHMIDT. 2011. Ectomycorrhizas from a Lower Eocene angiosperm forest. New Phytologist, 192:988–996.

BEIMFORDE, C., AND A. R. SCHMIDT. 2011. Microbes in resinous habitats: a compilation from modern and fossil resins, p. 391–407. *In* J. Reitner, N.-V. Quéric, and G. Arp (eds.), Advances in Stromatolite Biology. Lecture Notes in Earth Sciences, 131. Springer.

BICKEL, D. J. 2009. The first species described from Cape York amber, Australia: *Chaetogonopteron bethnorrisae* n. sp. (Diptera: Dolichopodidae). Denisia, 26:35–39.

BISULCA, C., P. C. NASCIMBENE, L. ELKIN, AND D. GRIMALDI. 2012. Variation in the deterioration of fossil resins and implications for the conservation of fossils in amber. American Museum Novitates, 3734:1–19.

BÖCHER, J. 1995. Palaeoentomology of the Kap København Formation, a Plio-Pleistocene sequence in Peary Land, North Greenland. Meddelelser om Grønland, Geoscience, 33:1–82.

BORKENT, A. 1995. Biting Midges in the Cretaceous Amber of North America (Diptera: Ceratopogonidae). Backhuys, Leiden, Netherlands.

BORKENT, A. 2000. Further biting midges (Diptera: Ceratopogonidae) from Upper Cretaceous New Jersey amber, p. 453–472. *In* D. Grimaldi (ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys, Leiden, Netherlands.

BOSSELAERS, J., M. DIERICK, V. CNUDDE, B. MASSCHAELE, L. VAN HOOREBEKE, AND P. JACOBS. 2010. High-resolution X-ray computed tomography of an extant new *Donuea* (Araneae: Liocranidae) species in Madagascaran copal. Zootaxa, 2427:25–35.

BOUCOT, A. J., AND G. O. POINAR, JR. 2010. Fossil Behavior Compendium. CRC Press, Boca Raton, Florida.

BRASERO, N., A. NEL, AND D. MICHEZ. 2009. Insects from the early Eocene amber of Oise (France): diversity and palaeontological significance. Denisia, 26:41–52.

BRAY, P. S., AND K. B. ANDERSON. 2009. Identification of Carboniferous (320 million years old) Class 1c amber. Science, 326:132–134.

BRIGGS, D. E. G., AND A. J. KEAR. 1993. Fossilization of soft tissues in the laboratory. Science, 259:1439–1442.

BRIGHT, D. E., AND G. O. POINAR, JR. 1994. Scolytidae and Platypodidae (Coleoptera) from Dominican Republic amber. Annals of the Entomological Society of America, 87:170–194.

CAMPBELL, R. 1985. Plant Microbiology. Arnold, London.

CANO, R. J., AND M. K. BORUKI. 1995. Revival and identification of bacterial spores in 25 to 40 million year old Dominican amber. Science, 268:1060–1064.

CANO, R. J., H. N. POINAR, N. J. PIENIAZEK, A. ACRA, AND G. O. POINAR, JR. 1993. Amplification and sequencing of DNA from a 125–135-million-year-old weevil. Nature, 363:536–538.

CANO, R. J., H. N. POINAR, D. W. ROUBIK, AND G. O. POINAR, JR. 1992. Enzymatic amplification and nucleotide sequencing of portions of the 18S rRNA gene of the bee *Proplebeia dominicana* (Apidae: Hymenoptera) isolated from 25–40 million year old Dominican amber. Medical Science Research, 20:619–622.

CARPENTER, F. M. 1992. Superclass Hexapoda. *In* R. C. Moore, R. L. Kaesler, E. Brosius, J. Keim, and J. Priesner (eds.), Treatise on Invertebrate Paleontology, Part 4 (Arthropoda 4), volumes 3 and 4. Geological Society of America and The University of Kansas, Boulder, CO, and Lawrence, KS.

CARPENTER, F. M., J. W. FOLSOM, E. O. ESSIG, A. C. KINSEY, C. T. BRUES, M. W. BOESEL, AND H. E. EWING. 1937. Insects and arachnids from Canadian amber. University of Toronto Studies in Geology Series, 40:7–62.

CHALER, R., AND J. O. GRIMALT. 2004. Fingerprinting of Cretaceous higher plant resins by infrared spectroscopy and gas chromatography coupled to mass spectrometry. Phytochemical Analysis, 16:446–450.

CHURCHER, C. S. 1966. The insect fauna from the Talara tar seeps, Peru. Canadian Journal of Zoology, 44:985–993.

COMPTON, S. G., A. D. BALL, M. E. COLLINSON, P. HAYES, A. P. RASNITSYN, AND A. J. ROSS. 2010. Ancient fig wasps indicate at least 34 Myr of stasis in their mutualism with fig trees. Biology Letters, 6:838–842.

CORRAL, J. C. 1999. La conservación del ámbar. Revisión de los principals agentes de deterioro y soluciones publicados. Estudios del Museo Ciencias Naturales de Álava, 14:23–32.

CORRAL, J. C., R. LÓPEZ, AND J. ALONSO. 1999. El ámbar Cretácico de Álava (Cuenca Basco-Cantabrica, norte de España). Su colecta y preparación. Estudios del Museo Ciencias Naturales de Álava, 14:7–21.

COTTER, H. VAN, AND R. O. BLANCHARD. 1982. Beech bark flora. Mycologia, 74:836–843.

COWAN, R. A., AND R. M. POLHILL. 1981. Detarieae, p. 117–134. *In* R. M. Polhill and P. R. Raven (eds.), Advances in Legume Systematics, Part 1. Royal Botanic Gardens, Kew, U.K.

CREPET, W. L., K. C. NIXON, E. M. FRIIS, AND J. V. FREUDENSTEIN. 1991. Oldest fossil flowers of hamamelidaceous affinity, from the Late Cretaceous of New Jersey. Proceedings of the National Academy of Sciences of the United States of America, 89:8986–8989.

CRICHTON, W. R. B., AND V. CARRIÓ. 2007. Photography of amber inclusions in the collections of the National Museums of Scotland. Scottish Journal of Geology, 43:89–96.

CROWSON, R. A. 1981. The Biology of the Coleoptera. Academic Press, London.

DALLA VECCIA, F. M., AND L. M. CHIAPPE. 2002. First avian skeleton from the Mesozoic of Northern Gondwana. Journal of Vertebrate Paleontology, 22:856–860.

DE PALMA, R., F. CICHOCKI, M. DIERICK, AND R. FEENEY. 2010. Preliminary notes on the first recorded amber insects from the Hell Creek Formation. Journal of the Paleontological Sciences, PS.C.10.0001. www.aaps-journal.org/pdf/JPS-C-10-0001.pdf

DESALLE, R., M. BARCIA, AND C. WRAY. 1993. PCR jumping in clones of 30 million-year-old DNA fragments from amber preserved termites (*Mastotermes electrodominicus*). Experientia, 49:906–909.

DESALLE, R., J. GATESY, W. WHEELER AND D. GRIMALDI. 1992. DNA sequences from a fossil termite in Oligo-Miocene amber and their phylogenetic implications. Science, 257:1933–1936.

DING, Q., C. C. LABANDEIRA, AND D. REN. 2013. Herbivore persistence and change on broad-leaved conifers between the Middle Jurassic and Early Cretaceous of northeastern China. Geological Society of America Abstracts with Programs, 45(7):699.

DUNLOP, J. A. 2010. Bitterfeld amber, p. 57–67. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

DUNLOP, J. A., D. PENNEY, N. DALÜGE, P. JÄGER, A. MCNEIL, R. S. BRADLEY, P. J. WITHERS, AND R. F. PREZIOSI. 2011. Computed tomography recovers data from historical amber: an example from huntsman spiders. Naturwissenschaften, 98:519–527.

DUNLOP, J. A., S. WIRTH, D. PENNEY, A. MCNEIL, R.

S. BRADLEY, P. J. WITHERS, AND R. F. PREZIOSI. 2012. A minute fossil phoretic mite recovered by phase-contrast X-ray microtomography. Biology Letters, 8:457–460.

DUNNE, J. A., C. C. LABANDEIRA, AND R. J. WILLIAMS. 2014. Highly resolved middle Eocene food webs show early development of modern trophic structure after the end-Cretaceous extinction. Proceedings of the Royal Society of London B-Biological Sciences, 281(1782): 20133280. doi: 10.1098/rspb.2013.3280

DURHAM, J. W., AND P. D. HURD. 1957. Fossiliferous amber of Chiapas, Mexico. Bulletin of the Geological Society of America, 68:18–24.

EDGECOMBE, G. D., V. VAHTERA, S. R. STOCK, A. KALLONEN, X. XIAO, A. RACK, AND G. GIRIBET. 2012. A scolopocryptoid centipede (Chilopoda: Scolopendromorpha) from Mexican amber: synchrotron microtomography and phylogenic placement using a combined morphological and molecular data set. Zoological Journal of the Linnean Society, 166:768–786.

ENGEL, M. S. 2001. A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). Bulletin of the American Museum of Natural History, 259:1–192.

FAHN, A. 1979. Secretory Tissues in Plants. Academic Press, London.

FARRELL, B. D., D. E. DUSSOURD, AND C. MITTER. 1991. Escalation of plant defense: Do latex and resin canals spur plant diversification? American Naturalist, 138:881–900.

FATZINGER, C. W. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-based traps. Environmental Entomology, 14:768–775.

FRANZ, N. M., AND M. S. ENGEL. 2010. Can higher-level phylogenies of weevils explain their evolutionary success? A critical review. Systematic Entomology, 35:597–606.

GARCÍA-GIMENO, V., AND E. PEÑALVER. 2007. Faunal populations in tank bromeliads in the Miocene and description of a new form of limoniid flies of the subgenus *Trentepohlia* (*Paramongoma*) in Dominican amber. Abstract Book, Fossils X3, International Amber Congress, Vitoria-Gastiez, Spain, p. 214.

GASTALDO, R. A., S. BEARCE, C. W. DEGGES, R. J. HUNT, M. W. PEEBLES, AND D. L. VIOLETTE. 1989. Biostratinomy of a Holocene oxbow lake: A backswamp to mid-channel transect. Review of Palaeobotany and Palynology, 58:47–59.

GASTALDO, R. A., D. P. DOUGLASS, AND S. M. MCCARROLL. 1987. Origin, characteristics, and provenance of plant macrodetritus in a Holocene crevasse splay, Mobile Delta, Alabama. PALAIOS, 2:229–240.

GASTALDO, R. A., AND A. Y. HUC. 1992. Sediment facies, depositional environments, and distribution of phytoclasts in the Recent Mahakam River Delta, Kalimantan, Indonesia. PALAIOS, 7:574–591.

GIRARD, V., D. NÉRAUDEAU, S. M. ADL, AND G. BRETON. 2011. Protist-like inclusions in amber, as evidenced by Charentes amber. European Journal of Protistology, 47:59–66.

GIRARD, V., A. R. SCHMIDT, S. SAINT MARTIN, S. STRUWE, V. PERRICHOT, J.-P. SAINT MARTIN, D. GROSHENY, G. BRETON, AND D. NÉRAUDEAU. 2008. Evidence for marine microfossils from amber. Proceedings of the National Academy of Sciences of the United States of America, 105:17426–17429.

GIRARD, V., A. R. SCHMIDT, S. STRUWE, V. PERRICHOT, G. BRETON, AND D. NÉRAUDEAU. 2009. Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. Geodiversitas, 31:153–162.

GONÇALVES-ALVIM, S. D. 2001. Resin-collecting bees (Apidae) on *Clusia palmicida* (Clusiaceae) in a riparian forest in Brazil. Journal of Tropical Ecology, 17:149–153.

GONZALEZ, V. H., AND T. L. GRISWOLD. 2011. Taxonomic notes on the small resin bee *Hyphantridioides* subgenus *Michanthidium* (Hymenoptera, Megachilidae). Zookeys, 117:51–58.

GREENBLATT, C. L., J. BAUM, B. Y. KLEIN, S. NACHSHON, V. KOLTUNOV, AND R. J. CANO. 2004. *Micrococcus luteus*—survival in amber. Microbial Ecology, 48:120–127.

GREENWALT, D., Y. S. GOREVA, S. M. SIJLSTRÖM, T. ROSE, AND R. E. HARBACH. 2013. Hemoglobin-derived porphyrins preserved in a Middle Eocene blood-engorged mosquito. Proceedings of the National Academy of Sciences of the United States of America, 110:18496–18500.

GREENWALT, D., AND C. C. LABANDEIRA. 2013. The amazing fossil insects of the Eocene Kishenehn Formation in northwestern Montana. Rocks & Minerals, 88:434–439.

GRIMALDI, D. A. 1995. The age of Dominican amber, p. 203–217. *In* K. G. Anderson, and J. C. Crelling (eds.), Amber, Resinite and Fossil Resins. American Chemical Society Symposium Series, 617. American Chemical Society, Washington, D.C.

GRIMALDI, D. A. 1996. Amber: Window to the Past. Abrams, New York.

GRIMALDI, D. A. 2003. First amber fossils of the extinct family Protopsyllidiidae, and their phylogenetic significance among Hemiptera. Insect Systematics and Evolution, 34:329–344.

GRIMALDI, D. A., E. BONWICH, M. DELANNOY, AND S. DOBERSTEIN. 1994. Electron microscopic studies of mummified tissues in amber fossils. American

Museum Novitates, 3097:1–31.

GRIMALDI, D. A., AND M. S. ENGEL. 2005. Evolution of the Insects. Cambridge University Press, New York.

GRIMALDI, D. A., M. S. ENGEL, AND P. C. NASCIMBENE. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates, 3361:1–71.

GRIMALDI, D., AND A. JOHNSON. 2014. The long-tongued Cretaceous scorpionfly *Parapolycentropus* Grimaldi and Rasnitsyn (Mecoptera: Pseudopolycentropodidae): new data and interpretations. American Museum Novitates, 3973:1–23.

GRIMALDI, D., J. KATHIRITHAMBY, AND V. SCHAWAROCH. 2005a. Strepsiptera and triungula in Cretaceous amber. Insect Systematics and Evolution, 36:1–20.

GRIMALDI, D. A., AND P. C. NASCIMBENE. 2010. Raritan (New Jersey) amber, p. 167–191. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

GRIMALDI, D., T. NGUYEN, AND R. KETCHAM. 2000a. Ultra-High-Resolution X-Ray Computed Tomography (UHR CT) and the study of fossils in amber, p. 77–91. *In* D. Grimaldi (ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys, Leiden, Netherlands.

GRIMALDI, D. A., AND A. J. ROSS. 2004. *Raphidiomimula*, an enigmatic new cockroach in Cretaceous amber from Myanmar (Burma) (Insecta: Blattodea: Raphidiomimidae). Journal of Systematic Palaeontology, 2:101–104.

GRIMALDI, D. A., A. SHEDRINSKY, AND T. P. WAMPLER. 2000b. A remarkable deposit of fossiliferous amber from the Upper Cretaceous (Turonian) of New Jersey, p. 1–76. *In* D. Grimaldi (ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys, Leiden, Netherlands.

GRIMALDI, D., J. ZHANG, N. C. FRASER, AND A. RASNITSYN. 2005b. Revision of the bizarre Mesozoic scorpionflies in the Pseudopolycentropodidae (Mecopteroidea). Insect Systematics and Evolution, 36:443–458.

GUO, S. 1991. A Miocene trace fossil of an insect from Shanwang Formation in Linqu, Shandong. Acta Palaeontologica Sinica, 30:739–742.

GUTIÉRREZ, G., AND A. MARÍN. 1998. The most ancient DNA recovered from amber-preserved specimen may not be as ancient as it seems. Molecular Biology & Evolution, 15:926–929.

HAND, W., M. ARCHER, D. BICKEL, P. CREASER, M. DETTMANN, H. GODTHELP, A. JONES, B. NORRIS, AND D. WICKS. 2010. Australian Cape York amber, p. 69–79. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

HEBSGAARD, M. B., M. J. PHILLIPS, AND E. WILLERSLEV. 2005. Geologically ancient DNA: fact or artefact? Trends in Microbiology, 13:212–220.

HEETHOFF, M., L. HELFEN, AND R. A. NORTON. 2009. Description of *Neoliodes dominicus* n. sp. (Acari, Oribatida) from Dominican amber, aided by synchrotron X-ray microtomography. Journal of Paleontology, 83:153–159.

HENDERICKX, H., J. BOSSELAERS, E. PAUWELLS, L. VAN HOOREBEKE, AND M. BOONE. 2013. X-ray micro-CT reconstruction reveals eight antennomeres in a new fossil taxon that constitutes a sister clade to *Dundoxenos* and *Triozera* (Strepsiptera: Corioxenidae). Paleontologia Electronica, 16(3):29A. palaeo-electronica.org/content/2013/552-a-new-strepsiptera-genus

HENDERICKX, H., V. CNUDDE, B. MASSCHAELE, M. DIERICK, J. VLASSENBROECK, AND L. VAN HOOREBEKE. 2006. Description of a new fossil *Pseudogarypus* (Pseudoscorpiones: Pseudogarypidae) with the use of X-ray micro-CT to penetrate opaque amber. Zootaxa, 1305:41–50.

HENWOOD, A. 1992a. Soft-part preservation of beetles in Tertiary amber from the Dominican Republic. Palaeontology, 35:901–912.

HENWOOD, A. 1992b. Exceptional preservation of dipteran flight muscle and the taphonomy of insects in amber. PALAIOS, 7:203–212.

HENWOOD, A. 1993a. Recent plant resins and the taphonomy of organisms in amber: a review. Modern Geology, 19:35–59.

HENWOOD, A. 1993b. Ecology and taphonomy of Dominican Republic amber and its inclusions. Lethaia, 26:237–245.

HEYWOOD, V. H. 1993. Flowering Plants of the World. Oxford University Press, New York.

HILLIS, W. E. 1987. Heartwood and Tree Exudates. Springer-Verlag, Berlin.

HOFFEINS, H. W. 2001. On the preparation and conservation of amber inclusions in artificial resin. Polish Journal of Entomology, 70:215–219.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The Ants. Harvard University Press, Cambridge, Massachusetts.

HONG, Y. 2002. Amber Insects of China. Beijing Science and Technology Press, Beijing, China.

HORVÁTH, G., AND G. KRISKA. 2008. Polarization vision in aquatic insects and ecological traps for polaro-tactic insects, p. 204–229. *In* J. Lancaster and P. A. Briers (eds.), Aquatic Insects: Challenges to Populations. C.A.B. International, Wallingford, U.K.

HUEBER, F. M., AND J. LANGENHEIM. 1986. Dominican amber tree had African ancestors. Geotimes, 31:8–

10.

HUGHES, D., T. WAPPLER, AND C. C. LABANDEIRA 2011. Life after death: Ancient death-grip leaf scars reveal ant–fungal parasitism. Biology Letters, 7:67–70.

JANZEN, J.-W. 2002. Arthropods in Baltic Amber. Ampyx-Verlag, Halle, Germany.

JARZEMBOWSKI, E. A. 1990. A boring beetle from the Wealden of the Weald, p. 373–377. *In* A. J. Boucot (ed.), Evolutionary Paleobiology of Behavior and Coevolution. Elsevier, Amsterdam.

JOHNSON, L. K. 1983. *Trigona fulviventris* (abeja atarrá, abeja jicore, culo de vaca, trigona, stingless bee), p. 684–687. *In* D. A. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois.

JONES, J. M., AND D. G. MURCHISON. 1963. The occurrence of resinite in bituminous coals. Economic Geology, 58:263–273.

JORDAL, B. H., A. S. SEQUEIRA, AND A. I. COGNATO. 2011. The age and phylogeny of wood boring weevils and the origin of subsociality. Molecular Phylogenetics and Evolution, 59:708–724.

KEHLMAIER, C., M. DIERICK, AND J. H. SKEVINGTON. 2014. Micro-CT studies of inclusions reveal internal genitalic features of big-headed flies, enabling a systematic placement of *Metanephrocerus* Aczél, 1948 (Insecta: Diptera: Pipunculidae). Arthropod Systematics & Phylogeny, 72:23–36.

KIREJTSHUK, A. G., D. AZAR, R. A. BEAVER, M. Y. MANDELSHTAM, AND A. NEL. 2009. The most ancient bark beetle known: a new tribe, genus and species from Lebanese amber (Coleoptera, Curculionidae, Scolytinae). Systematic Entomology, 34:101–112.

KLEPZIG, K. D., D. J. ROBISON, G. FOWLER, P. R. MINCHIN, F. P. HAIN, AND H. L. ALLEN. 2005. Effects of mass inoculation on induced oleoresin response in intensively managed loblolly pine. Tree Physiology, 25:681–688.

KNIGHT, T. K., P. S. BINGHAM, D. A. GRIMALDI, K. ANDERSON, R. D. LEWIS, AND C. E. SAVRDA. 2010. A new Upper Cretaceous (Santonian) amber deposit from the Eutaw Formation of eastern Alabama, U.S.A. Cretaceous Research, 31: 85–93.

KOHRING, R. 1995. Fossile Bakterien und Pilzsporen aus den Baltischen Bernstein. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte 1995(6):321–335.

KOLLER, B., J. M. SCHMITT, AND G. TISCHENDORF. 2005. Cellular fine structures and histochemical reactions in the tissue of a cypress twig preserved in Baltic amber. Proceedings of the Royal Society of London B-Biological Sciences, 272:121–126.

KOSANKE, R. M., AND J. A. HARRISON. 1957. Microscopy of the resin rodlets of Illinois coal. Illinois Geological Survey Circular, 234:1–14.

KOSMOWSKA-CERANOWICZ, B. 1996. Die tertiären und quartiären Bernsteinvorkommen in Polen, p. 299–310. *In* M. Ganzelewski, and R. Slotta (eds.), Bernstein: Tränen der Götter. Deutsches Bergbau-Museum, Bochum.

KOTEJA, J. 1996. Syninclusions. Inclusion-Wrostek, 22:10–12.

KOTEJA, J. 2004. Scale insects (Hemiptera: Coccinea) from Cretaceous Myanmar (Burmese) amber. Journal of Systematic Palaeontology, 2:109–114.

KOTEJA, J., AND D. AZAR. 2008. Scale insects from Lower Cretaceous amber of Lebanon (Hemiptera: Sternorrhyncha: Coccinea). Alavesia, 2:133–167.

KOWALEWSKA, M., AND J. SZWEDO. 2009. Examination of the Baltic amber inclusion surface using SEM techniques and X-ray microanalysis. Palaeogeography, Palaeoclimatology, Palaeoecology, 271:287–291.

KRZEMIŃSKA, E., E. KRZEMIŃSKI, J.-P. HAENNI, AND C. DUFOUR. 1992. Les Fantomes de l'Ambre. Musée d'Histoire Naturelle de Neuchâtel, Neuchâtel, Switzerland.

KUSCHEL, G. 1966. A cossonine genus with bark-beetle habits with remarks on relationships and biogeography (Coleoptera, Curculionidae). New Zealand Journal of Science, 9:3–29.

KUSCHEL, G., AND G. O. POINAR, JR. 1993. *Libanorhinus succinus* gen. and sp. n. (Coleoptera: Nemonychidae) from Lebanese amber. Entomological Scandinavica, 24:143–146.

KUTSCHER, M., AND J. KOTEJA. 2000. Coccids and aphids (Hemiptera: Coccinea, Aphidinea) prey of ants (Hymenoptera: Formicidae): evidence from Bitterfeld amber. Polskie Pismo Entomologiczne, 69:179–185.

LABANDEIRA, C. C. 1999. Insects and other hexapods, p. 603–624. In R. Singer (ed.), Encyclopedia of Paleontology. Fitzroy Dearborn, Chicago.

LABANDEIRA, C. C. 2002. The history of associations between plants and animals, p. 26–74 (appendix 248–261). In C. Herrera and O. Pellmyr (eds.), Plant–Animal Interactions: An Evolutionary Approach. Blackwell Science, Oxford, U.K.

LABANDEIRA, C. C. 2006. The four phases of plant–arthropod associations in deep time. Geologica Acta, 4:409–438.

LABANDEIRA, C. C. 2010. The pollination of mid Mesozoic seed plants and the early history of long-proboscid insects. Annals of the Missouri Garden, 97:469–513.

LABANDEIRA, C. C. 2012. Evidence for outbreaks from the fossil record of insect herbivory, p. 269–290. In P. Barbosa, D. K. Letourneau, and A. A. Agrawal (eds.), Insect Outbreaks Revisited. Wiley-Blackwell, Chichester, U.K.

LABANDEIRA, C. C. 2013. Deep-time patterns of tissue consumption by terrestrial arthropod herbivores. Naturwissenschaften, 100:355–363.

LABANDEIRA, C. C. 2014. Why did terrestrial insect diversity not increase during the angiosperm radiation? Plant-associated insect lineages harbor some clues, p. 261–299. *In* P. Pontarotti (ed.), Evolutionary Biology: Genome, Evolution, Speciation, Coevolution and Origin of Life. Springer, Berlin. doi: 10.1007/978-3-319.

LABANDEIRA, C. C., D. L. DILCHER, D. R. DAVIS, AND D. L. WAGNER. 1994. Ninety-seven million years of angiosperm–insect association: paleobiological insights into the meaning of coevolution. Proceedings of the National Academy of Sciences of the United States of America, 91:12278–12282.

LABANDEIRA, C. C., AND J. A. DUNNE. 2014. Data sets for "Highly resolved early Eocene food webs show development of modern trophic structure after the end-Cretaceous extinction" DRYAD Digital Repository. doi: 10.5061/dryad.ps0f0

LABANDEIRA, C. C., B. A. LEPAGE, AND A. H. JOHNSON. 2001. A *Dendroctonus* bark engraving (Coleoptera: Scolytidae) from a middle Eocene *Larix* (Coniferales: Pinaceae): Early or delayed colonization? American Journal of Botany, 88:2026–2039.

LABANDEIRA, C. C., AND T. L. PHILLIPS. 2002. Stem borings and petiole galls from Pennsylvanian tree ferns of Illinois, USA: Implications for the origin of the borer and galling functional-feeding-groups and holometabolous insects. Palaeontographica (A), 264:1–84.

LABANDEIRA, C. C., AND R. PREVEC. 2014. Plant paleopathology and the roles of pathogens and insects. International Journal of Paleopathology, 4:1–16.

LABANDEIRA, C. C., AND J. J. SEPKOSKI, JR. 1993. Insect diversity in the fossil record. Science, 261:310–315.

LABANDEIRA, C. C., P. WILF, K. R. JOHNSON, AND F. MARSH. 2007. Guide to Insect (and Other) Damage Types on Compressed Plant Fossils. Smithsonian Institution, Version 3.0. http://paleobiology.si.edu/pdfs/InsectDamageGuide3.01.pdf

LAK, M., D. AZAR, A. NEL, D. NÉRAUDEAU, AND P. TAFFOREAU. 2008a. The oldest representative of the Trichomyiinae (Diptera: Psychodidae) from the lower Cenomanian French amber studied with phase-contrast synchrotron X-ray imaging. Invertebrate Systematics, 22:471–478.

LAK, M., G. FLECK, D. AZAR, M. S. ENGEL, H. F. KADDUMI, D. NÉRAUDEAU, P. TAFFOREAU, AND A. NEL. 2009. Phase contast X-ray synchrotron microtomography and the oldest damselflies in amber (Odonata: Zygoptera: Hemiphlebiidae). Zoological Journal of the Linnean Society, 156:913–923.

LAK, M., D. NÉRAUDEAU, A. NEL, P. CLOETENS, V. PERRICHOT, AND P. TAFFOREAU. 2008b. Phase contrast X-ray synchrotron imaging: opening access to fossil inclusions in opaque amber studied with phase-contrast synchrotron X-ray imaging. Microscopy and Microanalysis, 14:251–259.

LAMBERT, J. B., E. A. HECKENBACH, A. E. HURTLEY, Y. WU, AND J. A. SANTIAGO-BLAY. 2009. Nuclear magnetic resonance spectroscopic characterization of legume exudates. Journal of Natural Products, 72:1028–1035.

LAMBERT, L. H., J. A. SANTIAGO-BLAY, AND K. B. ANDERSON. 2008. Chemical signatures of fossilized resins and recent plant exudates. Angewandte Chemie, 47: 9608–9616.

LANGENHEIM, J. H. 1967. Preliminary investigations of *Hymenaea coubaril* as a resin producer. Journal of the Arnold Arboretum, 48:203–230.

LANGENHEIM, J. H. 1984. The roles of plant secondary chemicals in wet tropical ecosystems, p. 189–208. *In* E. Medina, H. A. Mooney, and C. Vázquez-Yánes (eds.), Physiological Ecology of Plants of the Wet Tropics. Junk, The Hague.

LANGENHEIM, J. H. 1990. Plant resins. American Scientist, 78:16–24.

LANGENHEIM, J. H. 1995. Biology of amber-producing trees: focus on case studies of *Hymenaea* and *Agathis*, p. 1–31. *In* K. B. Anderson and J. C. Crelling (eds.), Amber, Resinite, and Fossil Resins. American Chemical Society Symposium Series 617. American Chemical Society, Washington, D. C.

LANGENHEIM, J. H., C. L. CONVIS, C. A. MACEDO, AND W. H STUBBLEBINE. 1986. *Hymenaea* and *Copaifera* leaf sesquiterpenes in relation to lepidopteran herbivory in southeastern Brazil. Biochemical Systematics and Ecology, 14:41–49.

LAPOLLA, J. S., G. M. DLUSSKY, AND V. PERRICHOT. 2013. Ants and the fossil record. Annual Review of Entomology, 58:609–630.

LARSSON, S. G. 1978. Baltic Amber—A Palaeobiological Study. Entomonograph, 1:1–192.

LEWIS, R. E., AND D. A. GRIMALDI. 1997. A pulicid flea in Miocene amber from the Dominican Republic (Insecta: Siphonaptera: Pulicidae). American Museum Novitates, 3205:1–9.

LINCK, O. 1949. Fossile Bohrgänge an einem Keuperholz. Neues Jahrbuch für Geologie und Paläontologie Monatschefte, 1949:180–185.

LITWIN, R. J., AND S. R. ASH. 1991. First early Mesozoic amber in the Western Hemisphere. Geology, 19:173–276.

LOPEZ-VAAMONDE, C., N. WIKSTRÖM, C. C. LABANDEIRA, S. GOODMAN, H. C. J. GODFRAY, AND J. M. COOK. 2006. Fossil-calibrated molecular phylogenies reveal that leaf-mining moths radiated millions of years after their host plants. Journal of Evolutionary Biology, 19:1314–1326.

LYONS, P., R. FINKELMAN, C. THOMPSON, F. BROWN,

AND P. HATCHER. 1982. Properties, origin and nomenclature of rodlets of the inertinite maceral group in coals of the central Appalachian basin, U.S.A. International Journal of Coal Geology, 1:313–346.

MARTÍNEZ-DELCLÒS, X., D. E. G. BRIGGS, AND E. PEÑALVER. 2004. Taphonomy of insects in carbonate and amber. Palaeogeography, Palaeoclimatology, Palaeoecology, 203:19–64.

MARTÍNEZ-DELCLÒS, X., AND J. MARTINELL. 1995. The oldest known record of social insects. Journal of Paleontology, 69:594–599.

MARTÍN-GONZÁLEZ, A., J. WIERZCHOS, J.-C. GUTIÉRREZ, J. ALONSO, AND C. ACASO. 2009. Double fossilization in eukaryotic microorganisms from Lower Cretaceous amber. BMC Biology, 7:9. doi: 10.1186/1741.7007-7-9

MARTÍN-GONZÁLEZ, A., J. WIERZCHOS, J. C. GUTIÉRREZ, J. ALONSO, AND C. ACASIO. 2008. Morphological stasis of protists in Lower Cretaceous amber. Protist, 159:251–257.

MAUSETH, J. D. 1988. Plant Anatomy. Benjamin Cummings Co., Menlo Park, California.

MCALPINE, J. F., AND J. E. H. MARTIN. 1969. Canadian amber—a paleontological treasure-chest. Canadian Entomologist, 101:819–838.

MCKELLAR, R. C., AND A. P. WOLFE. 2010. Canadian amber, p. 149–165. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

MCKENNA, D. D., A. S. SEQUEIRA, A. E. MARVALDI, AND B. D. FARRELL. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences of the United States of America, 106: 7083–7088.

MCNAMARA, M. E. 2013. The taphonomy of colour in fossil insects and feathers. Palaeontology, 56:557–575.

MOLINO-OLMEDO, F. 1999. Importancia del ámbar en el registro fósil de coleópteros saproxilicos. Estudios Museo Ciencias Naturales de Álava, 14(special number 2):211–215.

NARDI, J. B. 2007. Life in the Soil. University of Chicago Press, Chicago, Illinois.

NASCIMBENE, P., AND H. SILVERSTEIN. 2000. The preparation of fragile Cretaceous ambers for conservation and study of organismal inclusions, p. 93–102. *In* D. A. Grimaldi (ed.), Studies on Fossils in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys, Leiden, Netherlands.

NAUGOLNYKH, S. V., AND A. G. PONOMARENKO. 2010. Possible traces of feeding traces by beetles in coniferophyte wood from the Kazanian of the Kama River Basin. Paleontological Journal, 44:468–474.

NEL, A., AND N. BRASERO. 2010. Oise amber, p. 137–148. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

NEL, P., E. PEÑALVER, AND A. NEL. 2007. A new 'primitive' family of thrips from Early Cretaceous Lebanese amber (Insecta, Thysanoptera). Cretaceous Research, 28:1033–1038.

NÉRAUDEAU, D., V. PERRICHOT, J. DEJAS, E. MASURE, A. NEL, M. PHILIPPE, P. MOREAU, F. GUILLOCHEAU, AND T. GUYOT. 2002. Un noveau gisement à amber insectifère et à végétaux (Albien terminal probable): Archingeay (Charente-Maritime, France). Geobios, 35:233–240.

NEUBAUER, M. 1994. Die Bernsteinverbreitung in glazialen Ablagerungen inbesondere von Nordwestdeutschland Unveröffl. Report of the University of Bremen.

NISSENBAUM, A., AND A. HOROWITZ. 1992. The Levantine amber belt. Journal of African Earth Science, 14:295–300.

ORTEGA-BLANCO, J., X. DELCLÒS, E. PEÑALVER, AND M. S. ENGEL. 2011a. Serphitid wasps in Early Cretaceous amber from Spain (Hymenoptera: Serphitidae). Cretaceous Research, 32:143–154.

ORTEGA-BLANCO, J., X. DELCLÒS, AND M. S. ENGEL. 2011b. Diverse stigmaphronid wasps in Early Cretaceous amber from Spain (Hymenoptera: Ceraphronoidea: Stigmaphronidae). Cretaceous Research, 32:762–773.

PAINE, T. D., K. F. RAFFA, AND T. C. HARRINGTON. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annual Review of Entomology, 42:179–206.

PALMER, A. R. 1957. Miocene arthropods from the Mojave Desert, California. United States Geological Survey Professional Paper 294-G, United States Printing Office, Washington, D. C.

PARK, L. E., AND K. F. DOWNING. 2001. Paleoecology of an exceptionally preserved arthropod fauna from lake deposits of the Miocene Barstow Formation, Southern California, U.S.A. PALAIOS, 16:175–184.

PEARCE, R. B. 1996. Antimicrobial defences in the wood of living trees. New Phytologist, 132:203–233.

PEÑALVER, E., AND X. DELCLÒS. 2010. Spanish amber, p. 236–270. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PEÑALVER, E., M. S. ENGEL, AND D. A. GRIMALDI. 2006. Fig wasps in Dominican amber (Hymenoptera: Agaonidae). American Museum Novitates, 3541:1–16.

PEÑALVER, E., AND D. A. GRIMALDI. 2006a. Assemblages of mammalian hair and blood-feeding midges (Insecta: Diptera: Psychodidae: Phlebotominae) in Miocene amber. Transactions

of the Royal Society of Edinburgh-Earth Sciences, 96:177–195.

PEÑALVER, E., AND D. A. GRIMALDI. 2006b. New data on Miocene amber butterflies in Dominican amber (Lepidoptera: Riodinidae and Nymphalidae) with the description of a new nymphalid. American Museum Novitates, 3519:1–17.

PEÑALVER, E., AND D. A. GRIMALDI. 2010. Latest occurrence of the family Elcanidae (Insecta: Orthoptera) in Cretaceous amber from Myanmar and Spain. Annales de la Société Entomologique de France, 46:88–99.

PEÑALVER, E., D. A. GRIMALDI, AND X. DELCLÒS. 2006. Early Cretaceous spider web with its prey. Science, 312:176.

PEÑALVER, E., C. C. LABANDEIRA, E. BARRÓN, X. DELCLÒS, P. NEL, A. NEL, P. TAFFOREAU, AND C. SORIANO. 2012. Thrips pollination of Mesozoic gymnosperms. Proceedings of the National Academy of Sciences of the United States of America, 109:8623–8628.

PEÑALVER, E., J. ORTEGA-BLANCO, A. NEL, AND X. DELCLÒS. 2010. Mesozoic Evaniidae (Insecta: Hymenoptera) in Spanish amber: reanalysis of the phylogeny of the Evanioidea. Acta Geological Sinica, 84:809–827.

PENNEY, D. 2002. Paleoecology of Dominican amber preservation—spider (Araneae) inclusions demonstrate a bias for active, trunk-dwelling faunas. Paleobiology, 28:389–398.

PENNEY, D. 2005a. Fossil blood droplets in Miocene Dominican amber yield clues to speed and direction of resin secretion. Palaeontology, 48: 935–928.

PENNEY, D. 2005b. Importance of Dominican Republic amber for determining taxonomic bias of fossil resin preservation—A case study of spiders. Palaeogeography, Palaeoclimatology, Palaeoecology, 223:1–8.

PENNEY, D. (ed). 2010a. Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PENNEY, D. 2010b. Dominican amber, p. 22–41. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PENNEY, D., M. DIERICK, V. CNUDDE, B. MASSCHAELE, J. VLASSENBROECK, L. VAN HOOREBEKE, AND P. JACOBS. 2007. First fossil Micropholcommatidae (Araneae), imaged in Eocene Paris amber using X-ray computed tomography. Zootaxa, 1623:47–53.

PENNEY, D., AND D. I. GREEN. 2010. Introduction, preparation, study and conservation of amber inclusions, p. 5–21. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PENNEY, D., AND A. M. LANGAN. 2006. Comparing amber fossils across the Cenozoic. Biology Letters, 2:266–270.

PENNEY, D., A. MCNEIL, D. I. GREEN, R. S. BRADLEY, J. E. JEPSON, P. J. WITHERS, AND R. F. PREZIOSI. 2012a. Ancient Ephemeroptera–Collembola symbiosis fossilized in amber predicts contemporary phoretic associations. PLoS ONE, 7(10), e47651. doi: 10.1371/journal.pone.0047651

PENNEY, D., A. MCNEIL, D. I. GREEN, R. BRADLEY, P. J. WITHERS, AND R. F. PREZIOSI. 2012b. The oldest fossil pirate spider (Araneae: Mimetidae), in uppermost Eocene Indian amber, imaged using X-ray computed tomography. Arachnology, 15:299–302.

PENNEY, D. A., AND R. F. PREZIOSI. 2010. On inclusions in subfossil resins (copal), p. 299–303. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PENNEY, D., C. WADSWORTH, G. FOX, S. L. KENNEDY, R. F. PREZIOSI, AND T. A. BROWN. 2013a. Absence of ancient DNA in sub-fossil insect inclusions preserved in 'Anthropocene' Colombian copal. PLoS ONE, 8(9): e73150. doi: 10.1371/journal.pone.0073150

PENNEY, D., C. WADSWORTH, D. I. GREEN, S. L. KENNEDY, R. F. PREZIOSI, AND T. A. BROWN. 2013b. Extraction of inclusions from (sub)fossil resins, with description of a new species of stingless bee (Hymenoptera: Apidae: Meliponini) in Quaternary Colombian copal. Paleontological Contributions of the University of Kansas Paleontological Institute, 7:1–6.

PÉREZ-DE-LA-FUENTE, R., X. DECLÒS, E. PEÑALVER, M. SPERANZA, J. WIERCHOS, C. ACASO, AND M. S. ENGEL. 2012. Early evolution and ecology of camouflage in insects. Proceedings of the National Academy of Sciences of the United States of America, 190:21414–21419.

PERIS, D., T. PHILIPS, AND X. DELCLÒS. 2014. Ptinid beetles from the Cretaceous gymnosperm-dominated forests. Cretaceous Research, 54. doi.ort/10.1016/j.cretres.2014.02.009

PERKOVSKY, E. E., V. Y. ZOSIMOVICH, AND A. P. VLASKIN. 2010. Rovno amber, p. 116–137. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PERREAU, M., AND P. TAFFOREAU. 2011. Virtual dissection using phase-contrast X-ray synchrotron microtomography: reducing the gap between fossils and extant species. Systematic Entomology, 36:573–580.

PERRICHOT, V. 2004. Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna. Geologica Acta, 2:9–22.

PERRICHOT, V. 2005. Environnements paraliques à

amber et à végétaux du Crétacé Nord-Aquitain (Charentes, Sud-Ouest de la France). Mémoires Géosciences Rennes, 118:1–213.

PERRICHOT, V., D. NÉRAUDEAU, AND P. TAFFOREAU. 2010. Charentese Amber, p. 192–207. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

PHILIPPE, M., G. CUNY, V. SUTEEHORN, N. TEERARUNGSIGUL, G. BARALE, F. THÉVENARD, J. LE LOEUFF, E. BUFFETAUT, T. GAONA, A. KOŠIR, AND H. TONG. 2005. A Jurassic amber deposit in Southern Thailand. Historical Biology, 17:1–6.

PIKE, E. M. 1993. Amber taphonomy and collecting biases. PALAIOS, 8:411–419.

PIKE, E. M. 1994. Historical changes in insect community structure as indicated by hexapods of Upper Cretaceous Alberta (Grassy Lake) amber. Canadian Entomologist, 126:695–702.

POHL, H., B. WIPFLER, D. GRIMALDI, F. BECKMANN, AND R. G. BEUTEL. 2010. Reconstructing the anatomy of the 42 million-year-old fossil †*Mengea tertiara* (Insecta, Strepsiptera). Naturwissenschaften, 97:855–859.

POINAR, G. O., JR. 1992a. Life in Amber. Stanford University Press, Redwood City, California.

POINAR, G. O., JR. 1992b. Fossil evidence of resin utilization by insects. Biotropica, 24:466–468.

POINAR, G. O., JR. 1994. The range of life in amber: significance and implications in DNA studies. Experientia, 50:536–542.

POINAR, G. O., JR. 1998. Fossils explained 22: palaeontology of amber. Geology Today, 14:154–160.

POINAR, G. O., JR. 1999a. A fossil palm bruchid, *Coryobruchus domincanus*, sp. n. (Pachymerini: Bruchidae) in Dominican amber. Entomologica Scandinavica, 30:219–224.

POINAR, G. O., JR. 1999b. *Paleochordodes protus* n. g., n. sp. (Nematomorpha: Chorodidae), parasites of a fossil cockroach, with a critical examination of other fossil hairworms and helminthes of extant cockroaches (Insecta: Blattaria). Invertebrate Biology, 188:109–115.

POINAR, G. O., JR. 2001. Dominican amber, p. 362–364. *In* D. E. G. Briggs and P. Crowther (eds.), Palaeobiology II. Blackwell Scientific, Oxford, U.K.

POINAR, G. O., JR. 2003. Coelomycetes in Dominican and Mexican amber. Mycological Research, 197:117–122.

POINAR, G. O., JR. 2004. *Palaeomyia burmitis* (Diptera: Phlebotomidae), a new genus and species of Cretaceous sand flies with evidence of blood-sucking habits. Proceedings of the Entomological Society of Washington, 106:598–605.

POINAR, G. O., JR. 2005a. A Cretaceous palm bruchid, *Mesopachymerus antiqua*, n. gen., n. sp. (Coleoptera: Bruchidae: Pachymerini) and biogeographical implications. Proceedings of the Entomological Society of Washington, 107:392–397.

POINAR, G. O., JR. 2005b. *Culex malariager*, n. sp. (Diptera: Culicidae) from Dominican amber: the first fossil mosquito vector of plasmodium. Proceedings of the Entomological Society of Washington, 107:548–553.

POINAR, G. O., JR. 2005c. *Triatoma dominicana* sp. n. (Hemiptera: Reduviidae: Triatominae) and *Trypanosoma antiquus* sp. n. (Stercoraria: Trypanosomatidae), the first fossil evidence of a triatomine-trypanosomatid vector association. Vector-Borne and Zoonotic Diseases, 5:72–81.

POINAR, G. O., JR. 2008a. *Leptoconops nosopheris* sp. n. (Diptera: Ceratopogonidae) and *Paleotrypanosoma burmanicus* gen. n., sp. n. (Kinetoplastida: Trypanosomatidae), a biting midge-trypanosome vector association from the Early Cretaceous. Memorias do Instituto Oswaldo Cruz, 103:468–471.

POINAR, G. O., JR. 2008b. *Lutzomyia adiketis* sp. n. (Diptera: Phlebotomidae), a vector of *Paleoleishmania neotropicum* sp. n. (Kinetoplastida: Trypanosomatidae) in Dominican amber. Parasites & Vectors, 1:22. doi: 10.1186/1756-3305-1-22

POINAR, G. O., JR. 2010a. Palaeoecological perspectives in Dominican amber. Annals de la Société Entomologique du France, 46:23–52.

POINAR, G. O., JR. 2010b. Cases of camouflage in amber, p. 188–191. *In* A. J. Boucot and G. O. Poinar Jr. (eds.), Fossil Behavior Compendium. CRC Press, Boca Raton, Florida.

POINAR, G. O., JR. 2011a. The Evolutionary History of Nematodes. Brill, Leiden, Netherlands.

POINAR, G. O., JR. 2011b. *Vetufebrus ovatus* n. gen., n. sp. (Haemosporoida: Plasmodiidae) vectored by a streblid bat fly (Diptera: Streblidae) in Dominican amber. Parasites & Vectors, 4:229. http://www.parasitesandvectors.com/content/4/229

POINAR, G. O., JR. 2012. Fossil gregarines in Dominican and Burmese amber: examples of accelerated development? Palaeodiversity, 5:1–6.

POINAR, G. O., JR. 2014. Evolutionary history of terrestrial pathogens and endoparasites as revealed in fossils and subfossils. Advances in Biology, article 18135. http://dx.doi.ort/10.1155/2014/181353

POINAR, G. O., JR., AND A. E. BROWN. 2003. A non-gilled hymenomycete in Cretaceous amber. Mycological Research, 107:763–768.

POINAR, G. O., JR., AND A. E. BROWN. 2012. The first fossil streblid bat fly, *Enischonomyia stegosoma* n. g., n. sp. (Diptera: Hippoboscoidea: Streblidae). Systematic Parasitology, 81:79–86.

POINAR, G. O., JR., AND R. BUCKLEY. 2006. Nematode (Nematoda: Mermithidae and hairworm (Nematomorpha: Chorodidae) parasites in Early Cretaceous amber. Journal of Invertebrate Pathology, 93: 36–41.

POINAR, G. O., JR., AND R. BUCKLEY. 2007. Evidence of mycoparasitism and hypermycoparasitism in Early Cretaceous amber. Mycological Research, 111:503–506.

POINAR, G. O., JR., AND B. N. DANFORTH. 2006. A fossil bee from Early Cretaceous Burmese amber. Science, 314:614.

POINAR, G. O., JR., R. HESS, AND L. E. CALTAGIRONE. 1976. Virus-like particles in the calyx of *Phaneratoma flavitestacea* (Hymenoptera: Braconidae) and their transfer into host tissues. Acta Zoologica, 57:161–165.

POINAR, G. O., JR., J.-P. LACHAUD, A. CASTILLO, AND F. INFANTE. 2006. Recent and fossil nematode parasites (Nematoda: Mermithidae) of Neotropical ants. Journal of Invertebrate Pathology, 91:19–26.

POINAR, G. O., JR., AND POINAR, R. 1999. The Amber Forest: A Reconstruction of a Vanished World. Princeton University Press, Princeton, New Jersey.

POINAR, G. O., JR., AND R. POINAR. 2004a. *Paleoleishmania proterus* n. gen., n. sp. (Trypanosomatidae: Kinetoplastida) from Cretaceous Burmese amber. Protist, 155:305–310.

POINAR, G. O., JR., AND R. POINAR. 2004b. Evidence of vector-borne disease of Early Cretaceous reptiles. Vector-Borne and Zoonotic Diseases, 4:281–284.

POINAR, G. O., JR., AND R. POINAR. 2005. Fossil evidence of insect pathogens. Journal of Invertebrate Pathology, 89:243–250.

POINAR, G. O., JR., AND J. A. SANTIAGO-BLAY. 1997. *Paleodoris lattini* gen. n. sp. n., a fossil palm bug (Hemiptera: Thaumastocoridae, Xylastodorinae) in Dominican amber, with habits discernible by comparative functional morphology. Entomologica Scandinavica, 28:307–310.

POINAR, G. O., JR., AND R. SINGER. 1990. Upper Eocene gilled mushroom from the Dominican Republic. Science, 248:1099–1101.

POINAR, G. O., JR., AND S. R. TELFORD, JR. 2005. *Paleohaemoproteus burmacis* gen. no., sp. n. (Haemosporida: Plasmodiidae) from an Early Cretaceous biting midge (Diptera: Ceratopogonidae). Parasitology, 131:79–84.

POINAR, G. O., JR., B. M. WAGGONER, AND U.-C. BAUER. 1993a. Terrestrial and soft-bodied protists and other microorganisms in Triassic amber. Science, 259:222–224.

POINAR, G. O., JR., B. M. WAGGONER, AND U.-C. BAUER. 1993b. Description and paleoecology of a Triassic amoeba. Naturwissenschaften, 80:566–568.

POINAR, T., JR., R. J. CANO, AND G. O. POINAR, JR. 1993c. DNA from an extinct plant. Nature, 363:677.

POLCYN, M. J., J. V. ROGERS, Y. KOBAYASHI, AND L. L. JACOBS. 2002. Computed tomography of an *Anolis* lizard in Dominican amber: systematic, taphonomic, biogeographic and evolutionary implications. Palaeontologia Electronica, 5(1), http://palaeo-electronica.org/2002_1/amber/issue1_02.htm

RAGAZZI, E., AND A. R. SCHMIDT. 2011. Amber, p. 24–36. *In* J. Reitner, and V. Thiel, (eds.) Encyclopedia of Geobiology. Springer, Dordrecht, The Netherlands.

RAMÍREZ, S. R., B. GRAVENDEEL, R. B. SINGER, C. R. MARSHALL, AND N. E. PIERCE. 2007. Dating the origin of the Orchidaceae from a fossil orchid with its pollinator. Nature, 448:1042–1045.

RASNITSYN, A. P. 1980. Origin and evolution of the Hymenoptera. Transactions of the Paleontological Institute, 174:1–192 [in Russian; English translation, 1984, Biosystematics Research Centre, Ottawa, Canada].

RASNITSYN, A. P., AND D. L. J. QUICKE (eds.). 2002. History of Insects. Kluwer Academic Publishers, Dordrecht, Netherlands.

REN, D., C. C. LABANDEIRA, J. A. SANTIAGO-BLAY, A. RASNITSYN, C. SHIH, A. BASHKUEV, M. A. V. LOGAN, C. L. HOTTON, AND D. DILCHER. 2009. A probable pollination mode before angiosperms: Eurasian, long-proboscid scorpionflies. Science, 326:840–847.

RICHARDSON, D. P., A. C. S. MESSER, H. H. GREENBERG, P. HAGEDORN, AND P. MEINWOLD. 1989. Defensive sesquiterpenoids from a dipterocarp (*Dipterocarpus kerri*). Journal of Chemical Ecology, 15:731–747.

RIKKINEN, J., AND G. POINAR, JR. 2000. A new species of resinicolous *Chaenothecopsis* (Mycocaliciaceae, Ascomycota) from 20 million year old Bitterfeld amber, with remarks on the biology of resinicolous amber. Mycological Research, 104:7–15.

RITZKOWSKI, S. 1999. K-Ar-Altersbestimmungen der bernsteinfuehrenden Sedimente des Samlandes (Palaeogen), Bezirk Kaliningrad. Metalla, 66:19–23.

ROGERS, S. O., K. LANGENEGGER, AND O. HOLDENRIEDER. 2000. DNA changes in tissues entrapped in plant resins (the precursors of amber). Naturwissenschaften, 87:70–75.

ROGHI, G., E. RAGAZZI, AND P. GIANOLLA. 2006. Triassic amber of the Southern Alps (Italy). PALAIOS, 21:143–154.

ROSS, A., C. MELLISH, P. YORK, AND B. CRIGHTON. 2010. Burmese Amber, p. 208–235. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

ROWLEY, D. A. 1996. Age of initiation of collision between India and Asia: a review of stratigraphic data. Earth and Planetary Science Letters, 145:1–13.

RUST, J., H. SINGH, R. S. RANA, T. MCCANN, L. SINGH, K. ANDERSON, N. SARKAR, P. C. NASCIMBENE, F. STEBNER, J. C. THOMAS, M. SOLÓRZANO KRAEMER, J. C. WILLIAMS, M. S. ENGEL, A. SAHNI, AND D. GRIMALDI. 2010. Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. Proceedings of the National Academy of Sciences of the United States of America, 107:18360–18365.

SANTIAGO-BLAY, J. A., S. R. ANDERSON, AND R. T. BUCKLEY. 2005. Possible implications of two new angiosperm flowers from Burmese amber (Lower Cretaceous) for well-established and diversified insect–plant associations. Entomologica News, 116:341–346.

SANTIAGO-BLAY, J. A., LAMBERT, J. B., AND P. P. CREASMAN. 2011. Expanded application of dendrochronology collections: collect and save exudates. Tree-Ring Research, 67:67–68.

SANTIAGO-BLAY, J. A., AND G. O. POINAR, JR. 1993. First scorpion (Buthidae: *Centuroides*) from Mexican amber (Lower Miocene to Upper Oligocene). Journal of Arachnology, 21:147–151.

SAUNDERS, W. B., R. H. MAPES, F. M. CARPENTER, AND W. C. ELSIK. 1974. Fossiliferous amber from the Eocene (Claiborne) of the Gulf Coastal Plain. Geological Society of America Bulletin, 85:979–984.

SCHACHAT, S. C. C. LABANDEIRA, J. GORDON, D. S. CHANEY, S. LEVI, M. HALTHORE, AND J. ALVAREZ. 2012. Extensive and varied herbivory for the Lower Permian Colwell Creek Pond site of north-central Texas, USA. Geological Society of America Abstracts with Programs, 44(7):289–290.

SCHEDL, K. E. 1947. Die Borkenkäfer des baltischen Bernsteins. Zentralblatt für Gesamtgebiet der Entomologie, 2:12–45.

SCHLEE, D., AND H. G. DIETRICH. 1970. Insectenfuhrender Bernstein aus der Unterkreide des Libanon. Neues Jahrbuch für Geologie und Paläontologie Monatschefte, 1970:40–50.

SCHLEE, D., AND W. GLÖCKNER. 1978. Bernstein—Bernsteine und Bernsteinfossilien. Stuttgarter Beiträge zur Naturkunde, Serie C, 8:1–72.

SCHLÜTER, T. 1989. Neue Daten über harzenconservierte Arthropoden aus dem Cenomanium NW-Frankreichs. Documenta Naturae, 56:59–70.

SCHLÜTER, T., AND F. VON GNIELINSKI. 1980. The East African copal: Its geology, stratigraphy, palaeontological significance and comparison with other fossil resins of similar age. Occasional Papers of the National Museum of Tanzania, 8:1–32.

SCHLÜTER, T., AND KÜHNE, W. G. 1975. Die einseitige Trübung von Harzinklusen—ein Indiz gleicher Bildungsumstände. Entomologia Germanica, 2:308–315.

SCHLÜTER, T., AND W. STÜRMER. 1982. X-ray examination of fossil insects in Cretaceous amber of N.W. France. Annales de la Société Entomologique de France, 18:527–529.

SCHMIDT, A. R., H. DÖRFELT, AND V. PERRICHOT. 2008. *Palaeoanellus dimorphus* gen. et sp. nov. (Deuteromycotina): a Cretaceous predatory fungus. American Journal of Botany, 95:1328–1334.

SCHMIDT, A. R., S. JANCKE, E. E. LINDQUIST, E. RAGAZZI, G. ROGHI, P. C. NASCIMBENE, K. SCHMIDT, T. WAPPLER, AND D. A. GRIMALDI. 2012. Arthropods in amber from the Triassic Period. Proceedings of the National Academy of Sciences of the United States of America, 109:14796–14801.

SCHMIDT, A. R., V. PERRICHOT, M. SVOJTKA, K. B. ANDERSON, K. H. BELETE, R. BUSSERT, H. DÖRFELT, S. JANCKE, B. MOHR, E. MOHRMANN, P. C. NASCIMBENE, A. NEL, P. NEL, E. RAGAZZI, G. ROGHI, E. E. SAUPE, K. SCHMIDT, H. SCHNEIDER, P. A. SELDEN, AND N. VÁVRA. 2010. Cretaceous African life captured in amber. Proceedings of the National Academy of Sciences of the United States of America, 107:7329–7334.

SCHMIDT, A. R., E. RAGAZZI, O. COPPELLOTTI, AND G. ROGHI. 2006. A microworld in Triassic amber. Nature, 444:835.

SCHMIDT, A. R., W. SCHÖNBORN, AND U. SCHÄFER. 2004. Diverse fossil amoebae in German Mesozoic amber. Palaeontology, 47:185–197.

SCHMIDT, A. R., H. VON EYNATTEN, AND M. WAGREICH. 2001. The Mesozoic amber of Schliersee (southern Germany) is Cretaceous in age. Cretaceous Research, 22:423–428.

SCHÖNBORN, W., H. DÖRFELT, W. FOISSNER, L. KRIENITZ, AND U. SCHÄFER. 1999. A fossilized microcoenosis in Triassic amber. Journal of Eukaryotic Microbiology, 46:571–584.

SCHWEITZER, M. H. 2011. Soft tissue preservation in terrestrial Mesozoic vertebrates. Annual Review of Earth and Planetary Sciences, 39:187–216.

SEQUEIRA, A. S., AND B. D. FARRELL. 2001. Evolutionary origins of Gondwanan interactions: How old are *Araucaria* beetle herbivores? Biological Journal of the Linnaean Society, 74:459–474.

SHI, G., D. A. GRIMALDI, G. E. HARLOW, J. WANG, J. WANG, M. YANG, W. LEI, Q. LI, AND X. LI. 2013. Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research, 37:155–163.

SMITH, A. B., AND J. J. AUSTIN. 1997. Can

geologically ancient DNA be recovered from the fossil record? Geoscientist, 7:58–61.

SMITH, S. Y., M. E. COLLINSON, P. J. RUDALL, D. A. SIMPSON, F. MARONE, AND M. STAMPANONI. 2009. Virtual taphonomy using synchrotron tomographic microscopy reveals cryptic features and internal structure of modern and fossil plants. Proceedings of the National Academy of Sciences of the United States of America, 106:12013–12018.

SODHI, R. N. S., C. A. MIMS, R. E. GOACHER, B. MCKAGUE, AND A. P. WOLFE. 2013. Preliminary characterization of Palaeogene European ambers using ToF-SIMS. Surface and Interface Analysis, 45:557–560.

SODHI, R. N. S., C. A. MIMS, R. E. GOACHER, B. MCKAGUE, AND A. P. WOLFE. 2014. Differentiating diterpene resin acids using ToF-SIMS and principal compound analysis new tools for assessing the geochemistry of amber. Surface and Interface Analysis, 46(4). doi: 10.1002/sia.5416

SOLOMON, J. D. 1995. Guide to insect borers in North American broadleaf trees and shrubs. U. S. Forest Service Agriculture Handbook AH-706, United States Department of Agriculture, Washington, D.C.

SOLÓRZANO KRAEMER, M. M. 2010. Mexican amber, p. 42–56. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

SORIANO, C., M. ARCHER, D. AZAR, P. CREASER, X. DELCLÒS, H. GODTHELP, S. HAND, A. JONES, A. NEL, D. NÉRAUDEAU, J. ORTEGA-BLANCO, J. PÉREZ-DE-LA-FUENTE, V. PERRICHOT, E. SAUPE, M. Y. SOLÓRZANO-KRAEMER, AND P. TAFFOREAU. 2010. Synchrotron X-ray imaging of inclusions in amber. Comptes Rendus Paleovol, 9:361–368.

SPERANZA, M., J. WIERZCHOS, J. ALONSO, L. BETTUCCI, A. MARTÍN-GONZÁLEZ, AND C. ACASO. 2010. Traditional and new microscopy techniques applied to the study of microscopic fungi included in amber, p. 1135–1145. *In* A. Méndez-Vilas and J. Díaz (eds.), Microscopy: Science, Technology, Applications and Education. Formatex Research Center, Badajoz, Spain.

STANDKE, G. 1998. Die Tertiärprofile der Samländischen Bernsteinküste bei Rauschen. Schriftenreihe für Geowissenschaften, 7:93–133.

STANDKE, G. 2008. Bitterfelder Bernstein gleich Baltischer Bernstein? Eine geologische Raum-Zeit-Betrachtung und genetische Schlußfolgerungen, p. 11–33. *In* J. Rascher, R. Wimmer, G. Krumbiegel, S. Schmiedel (eds), Bitterfelder Bernstein versus Baltischer Bernstein —Hypothesen, Fakten, Fragen. Exkursionsführer und Veröffentlichungen der Deutschen Gesellschaft für Geowissenschaften 236.

STANKIEWICZ, B. A., H. N. POINAR, D. E. G. BRIGGS, R. P. EVERSHED, AND G. O. POINAR, JR. 1998. Chemical preservation of plants and insects in natural resins. Proceedings of the Royal Society of London B-Biological Sciences, 265:641–647.

STOUT, E. C., C. W. BECK, AND K. B. ANDERSON. 2000. Identification of rumanite (Romanian amber) as thermally altered succinite (Baltic amber). Physics and Chemistry of Minerals, 27:665–678.

STURGEON, K. B. 1979. Monoterpene variation in ponderosa pine xylem resin related to western pine beetle predation. Evolution, 33:803–814.

SUNG, G.-H., G. O. POINAR, JR., AND J. W. SPATAFORA. 2008. The oldest fossil evidence of animal parasitism by fungi supports a Cretaceous diversification of fungal–arthropod symbioses. Molecular Phylogenetics and Evolution, 49:495–502.

SUTTON, M. P. 2008. Tomographic techniques for the study of exceptionally preserved fossils. Proceedings of the Royal Society of London B-Biological Sciences, 275:1587–1593.

SZWEDO, J. 2002. Amber and amber inclusions of planthoppers, leafhoppers and their relatives (Hemiptera, Archaeorrhyncha et Clypaeorrhyncha), p. 37–56. *In* W. E. Holzinger (ed.), Zikaden—Leafhoppers, Planthoppers and Cicadas (Insecta: Hemiptera: Auchenorrhyncha). Biologiezentrum Oberösterreichisches Landesmuseum, Linz.

TAFFOREAU, P., R. BOISTEL, E. BOLLER, A. BRAVIN, M. BRUNET, Y. CHAIMANEE, P. CLOETENS, M. FEIST, J. HOSZOWSKA, J. J. HAEGER, R. F. KAY, V. LAZZARI, L. MRIVAUX, A. NEL, C. NEMOZ, X. THIBAULT, P. VIGNAUD, AND S. ZABLER. 2006. Applications of X-ray synchrotron microtomography for non-destructive 3D studies of paleontological specimens. Applied Physics A (Materials Science & Processing), 83:195–202.

TAPANILA, L., AND E. M. ROBERTS. 2012. The earliest evidence of holometabolan insect pupation in conifer wood. PLoS ONE, 7(2):e31668.

THOMAS, D. B., P. C. NASCIMBENE, C. J. DOVE, D. A. GRIMALDI, AND H. F. JAMES. 2014. Seeking carotenoid pigments in amber-preserved fossil feathers. Scientific Reports, 4(5226):1–6 doi: 10.1038/srep05226

TOMLIN, E. S., E. ANTONEJEVIC, R. I. ALFARO, AND J. H. BORDEN. 2000. Changes in volatile terpene and diterpene resin acid composition of resistant and susceptible white spruce leaders exposed to simulated white pine weevil damage. Tree Physiology, 20:1087–1095.

TUOVILA, H., A. R. SCHMIDT, C. BEIMFORDE, H. DÖRFELT, H. GRABENHORST, AND J. RIKKINEN. 2013. Stuck in time—a new *Chaenothecopsis* species with proliferating ascomata from

Cunninghamia resin and its fossil ancestors in European amber. Fungal Diversity, 58:199-213.

USINGER, R. L. 1958. Harzwanzen or "resin bugs" in Thailand. Pan-Pacific Entomologist, 34:52.

VAN BERGEN, P. F., M. E. COLLINSON, A. C. SCOTT, AND J. W. DE LEEUW. 1995. Unusual resin chemistry from Upper Carboniferous pteridosperm resin rodlets, p. 149–169. *In* K. B. Anderson and J. C. Crelling (eds.), Amber, Resinite, and Fossil Resins. American Chemical Society Symposium Series 617. American Chemical Society, Washington, D. C.

VÁVRA, N. 2009. Amber, fossil resins and copal—contributions to the terminology of fossil plant resins. Denisia, 26:213–222.

VOIGT, E. 1988. Preservation of soft tissues in the Eocene lignite of Geiseltal near Halle (Saale). Courier Forschungs Institut Senckenberg, 107:325–343.

VILHELMSEN, L., AND G. F. TURRISI. 2011. Per arborem ad astra: Morphological adaptations to exploiting the woody habitat in the early evolution of Hymenoptera. Arthropod Structure & Development, 40:2–20.

WALDEN, K. K. O., AND H. M. ROBERTSON. 1997. Ancient DNA from amber fossil bees? Molecular Biology and Evolution, 14:1075–1077.

WALKER, M. V. 1938. Evidence of Triassic insects in the Petrified Forest National Monument, Arizona. Proceedings of the United States National Museum, 85:137–141.

WANG, B., H. ZHANG, AND D. AZAR. 2011. The first Psychodidae (Insecta: Diptera) from the lower Eocene Fushun amber of China. Journal of Paleontology, 85:1154–1159.

WANG, Q., D. K. FERGUSON, G.-P FENG, A. G. ABLAEV, Y.-F. WANG, J. YANG, Y.-L. LI, AND C. S. LI. 2010. Climatic change during the Palaeocene to Eocene based on fossil plants from Fushun, China. Palaeogeography, Palaeoclimatology, Palaeoecology, 295:323–331.

WEAVER, L., S. MCLOUGHLIN, A. N. DRINNAN. 1997. Fossil woods from the Upper Permian Bainmedart Coal Measures, northern Prince Charles Mountains, East Antarctica. Journal of Australian Geology & Geophysics, 16:655–676.

WEITSCHAT, W., AND WICHARD, W. 2002. Atlas of Plants and Animals in Baltic Amber. Fredrich Pfeil, Munich.

WEITSCHAT, W., AND WICHARD, W. 2010. Baltic amber, p. 80–115. *In* D. Penney (ed.), Biodiversity of Fossils in Amber from the Major World Deposits. Siri Scientific Press, Manchester, U.K.

WHITMORE, T. C. 1977. A first look at *Agathis*. Tropical Forest Papers, 11:1–66.

WHITMORE, T. C. 1980. Utilization, potential and conservation of *Agathis*, a genus of tropical Asian conifers. Economic Botany, 34:1–12.

WIER, A., M. DOLAN, D. GRIMALDI, R. GUERRERO, J. WAGENSBERG, AND L. MARGULIS. 2002. Spirochaete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber. Proceedings of the National Academy of Sciences of the United States of America, 99:1410–1413.

WILF, P., AND C. C. LABANDEIRA. 1999. Response of plant–insect associations to Paleocene–Eocene warming. Science, 284:2153–2156.

WILF, P., C. C. LABANDEIRA, K. R. JOHNSON, AND B. ELLIS. 2006. Decoupled plant and insect diversity after the end-Cretaceous extinction. Science, 313:1112–1115.

WILLIAMS, S. R. 1990. Infrared spectroscopic analysis of Central and South American amber exposed to air pollutants, biocides, light and moisture. Public Collections Forum, 6:1–14.

WOLFE, A. P., R. TAPPERT, K. MUEHLENBACHS, M. BOUDREAU, R. C. MCKELLAR, R, J. F. BASINGER, AND A. GARRETT. 2009. A new proposal concerning the botanical origin of Baltic amber. Proceedings of the Royal Society of London B-Biological Sciences, 276:3403–3412.

WUNDERLICH, J. 2000. Ant mimicry by spiders and spider-mite interactions preserved in Baltic amber (Arachnida: Acari, Araneae), p. 355–358. *In* S. Toft and N. Scharff (eds.), European Arachnology 2000. Proceedings of the Nineteenth European Colloquium of Arachnology, Århus, Denmark, 17–22 July 2000.

WUTTKE, M. 1992. Conservation–dissolution–transformation. On the behaviour of biogenic materials during fossilization, p. 263–275. *In* S. Schaal and W. Ziegler (eds.), Messel: An Insight Into The History of Life and of The Earth. Oxford University Press, Oxford, U.K.

YOUSTEN, A.A., AND K. E. RIPPERE. 1997. DNA similarity of a putative ancient bacterial isolate obtained from amber. FEMS Microbiology Letters, 152:345–347.

ZAVORTINK, T. J., AND G. O. POINAR, JR. 2000. *Anopheles* (*Nyssorhynchus*) *dominicanus* sp. n. (Diptera: Culicidae) from Dominican amber. Annals of the Entomological Society of America, 93:1230–1235.

ZHANG, G., AND Y. HONG. 1999. A new family Drepanochaitophoridae (Homoptera: Aphidoidea) from Eocene Fuschun amber of Liaoning Province, China. Insect Science, 6:127–134.

ZHERIKHIN, V. V., AND K. Y. ESKOV. 1999. Mesozoic and Lower Tertiary resins in former USSR. Estudios del Museo de Ciencias Naturales de Álava, 14 (special number 2):119–131.

ZHERIKHIN, V. V., AND N. D. SUKATCHEVA. 1990. The regularities of burial of insects in present-day and fossil resins. Prace Muzeum Ziemi, 41:163.

ZHOU, Z., AND B. ZHANG. 1989. A sideritic

Protocupressinoxylon with insect borings and frass from the Middle Jurassic, Henan, China. Review of Palaeobotany and Palynology, 59:133–143.