

Biological Inclusions in Amber from the Paleogene Chickaloon Formation of Alaska

Authors: Grimaldi, David A., Sunderlin, David, Aaroe, Georgene A., Dempsky, Michelle R., Parker, Nancy E., et al.

Source: American Museum Novitates, 2018(3908) : 1-37

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/3908.1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Biological Inclusions in Amber from the Paleogene Chickaloon Formation of Alaska

DAVID A. GRIMALDI,¹ DAVID SUNDERLIN,² GEORGENE A. AAROE,²
MICHELLE R. DEMPSKY,² NANCY E. PARKER,² GEORGE Q. TILLERY,²
JACLYN G. WHITE,² PHILLIP BARDEN,³ PAUL C. NASCIMBENE,¹
AND CHRISTOPHER J. WILLIAMS⁴

ABSTRACT

The Chickaloon Formation in south-central Alaska contains rich coal deposits dated very close to the Paleocene-Eocene boundary, immediately beneath which occur dispersed nodules of amber along with abundant remains of *Metasequoia*, dicots, and monocots. The nodules are small (less than 10 mm in length), nearly 10,000 of which were screened, yielding several inclusions of fungi and plant fragments, but mostly terrestrial arthropods: 29 specimens in 10 orders and 13 families. The fungi include resinicolous hyphae and a dark, multiseptate hyphomycete. Plants include wood/bark fragments and fibers, and the microphylls of a bryophyte (probably a moss, Musci). Among the arthropods are arachnids: mites (Acari: Oribatida), Pseudoscorpionida, and the bodies and a silken cocoon of spiders (Araneae). Insecta include Blattodea, Thysanoptera, Hemiptera (Heteroptera and Aphidoidea), Coleoptera (Dermestidae: Megatominae), Trichoptera, Diptera (Chironomidae: Tanypodinae), and Hymenoptera (Formicidae: Formicinae). Nymphal aphids predominate (65% of the arthropod individuals), which were probably feeding on the source tree, likely *Metasequoia*. There is a bias in preservation toward small arthropods (mean body length 0.75 mm) that are surface-dwelling (nonwinged) stages and taxa. Chickaloon amber contains the most northerly fossil records of pseudoscorpions, thrips, Dermestidae, and Cenozoic ants and mites, so the deposit is contributing unique data on high-latitude paleodiversity of the Paleogene hothouse earth.

¹ Division of Invertebrate Zoology, American Museum of Natural History, New York.

² Department of Geology & Environmental Geosciences, Lafayette College, Easton, Pennsylvania.

³ Department of Biology, New Jersey Institute of Technology, Newark.

⁴ Department of Earth & Environment, Franklin & Marshall College, Lancaster, Pennsylvania.

INTRODUCTION

The late Paleocene through early Eocene is biotically one of the most significant periods of the Cenozoic. The earth was in a hothouse climate phase with ice-free poles, having an equitable global climate with a shallow latitudinal temperature gradient evidenced by the mean annual temperature (MAT) of $\sim 5^{\circ}$ C. Earth's temperature gradually rose through the Paleocene, then spiked at the Paleocene-Eocene Thermal Maximum (PETM) (Bains et al., 1999; Katz et al., 1999), an event lasting some 200,000 years around 55 Ma, with global temperatures rising by some 5° – 8° C. Approximately half the species of benthic foraminiferans became extinct during this event, and there was profound turnover of Paleocene mammal faunas into the radiation of modern orders in the Early Eocene (Gingerich, 2003; McInerney and Wing, 2011). This brief episode is correlated with a massive infusion of isotopically negative carbon into the biosphere, called the Carbon Isotope Event (CIE). Its cause is debated: volcanism (e.g., North Atlantic Volcanic Province); release of huge stores of methane from slumping of continental shelves (Bains et al., 1999); and possibly even cometary impact. After the PETM subsided, temperatures gradually rose to another Cenozoic peak at the Early Eocene Climatic Optimum.

One of the most compelling examples of the global hothouse climate derives from the Early to middle Eocene Eureka Sound Group of Ellesmere and Axel Heiberg Islands in the Canadian arctic (Eberle and Greenwood, 2012). At approximately 75° N paleolatitude (just a few degrees south of the current latitude), there existed lush forests of ferns, conifers, birches, oaks, and ginkgo, inhabited by lizards, turtles, alligators, early tapirs, and plagiomenid mammals similar to flying lemurs, among many others. Seasonal ranges are estimated from 2° – 3° C to 20° C and an annual precipitation of 120 cm/yr (Eberle and Greenwood, 2012). Similar conditions, including mangrove swamps, were circumpolar at approximately the same paleolatitudes in present-day Siberia (Suan et al., 2017). Not only did the polar warmth facilitate dispersal and spread of Laurasian biotas, but, given the direct and well-established relationship between area and species diversity (MacArthur and Wilson, 1963; Lomolino, 2000), the expansion of earth's habitable landmass must have vastly increased the diversification of all life, not just mammals.

Another biotic event of substantial biological significance around the Paleocene-Eocene transition, and well into the Eocene, was the deposition of massive quantities of tree resin, which fossilized into amber. Perhaps stimulated by the warm overall paleoclimate, the Eocene is arguably the most prolific geological period for amber, resulting in huge deposits, for example, on the southern Baltic (Larsson, 1978; Weitschat and Wichard, 2010), in India (Rust et al., 2010), and elsewhere. The effects on ecosystems were not inconsequential (large quantities of unrecycled carbon are locked in these amber deposits), but the really important consequence of all this amber is paleontological, providing an archive of delicate, highly diverse ancient life preserved with unmatched microscopic fidelity. Here we report biological inclusions in the most northerly deposit of fossiliferous amber from the Cenozoic, a finding with implications for biogeography and paleoclimatology.

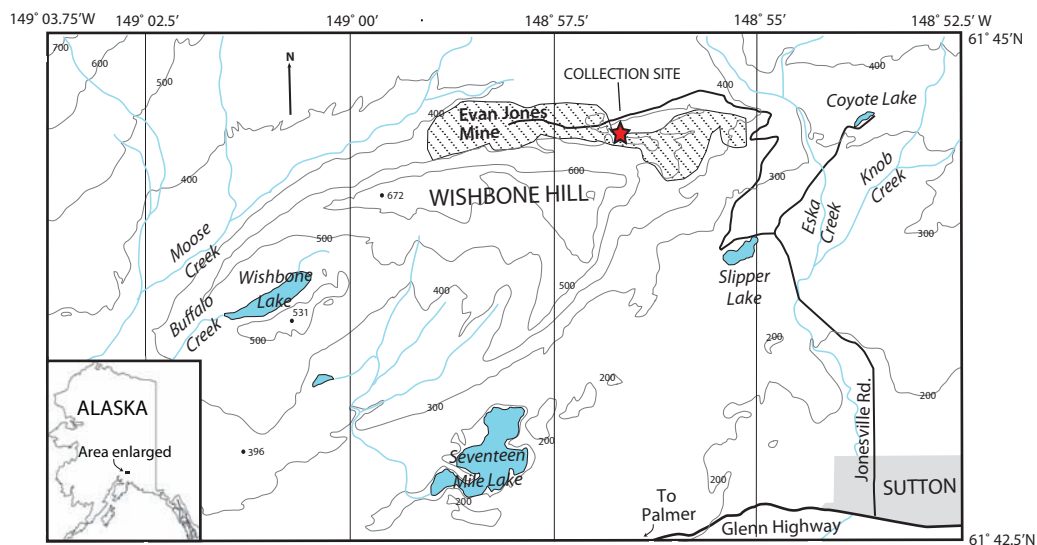


FIG. 1. Chickaloon amber collection site in the reclaimed Evan Jones Mine. Contour intervals in meters.

GEOLOGIC AND PALEOENVIRONMENTAL SETTING

The field collections of dispersed amber in this study were recovered from an exposure of the upper Chickaloon Formation in the reclaimed Evan Jones Mine on the north slope of Wishbone Hill near Sutton, Alaska ($61^{\circ}44.5'N/148^{\circ}56.4'W$) (fig. 1). The Chickaloon Formation is exposed there and elsewhere throughout the east-west trending Matanuska Valley in south-central Alaska and overall comprises a ~1500 m thick sequence predominantly made up of sandstones, mudrocks, and coals of Late Paleocene/Early Eocene age (Flores and Stricker, 1993; Trop et al., 2003; Neff et al., 2011). Zircon fission track and K/Ar dates on ash partings in the upper Chickaloon Formation at the collection site provide age constraint, placing the Paleocene-Eocene boundary within the Chickaloon's Premier Coal Zone (Triplehorn et al., 1984; Flores and Stricker, 1993) (fig. 2). The overlying Early Eocene Jonesville coal zone in the Chickaloon is in conformable contact with Eocene-age Wishbone Formation conglomerates exposed at the top of Wishbone Hill (Trop et al., 2003; Neff et al., 2011). The ammonoid-bearing, Late Cretaceous Matanuska Formation unconformably underlies the Chickaloon Formation and represents marine conditions before regional regression and basin fill.

Trop et al. (2003) provided a depositional model of the Matanuska Valley/Talkeetna Mountains forearc basin, indicating progressive basin fill during which Chickaloon sediments were deposited in floodplain fluvio-lacustrine conditions that gave way to estuarine depositional settings along the basin axis to the southwest. Based on geological and paleomagnetic data, the Chickaloon was likely deposited near its present latitude ($\sim 62^{\circ}N$) (see Sunderlin et al., 2011). Site-specific studies at the Evan Jones Mine by Flores and Stricker (1993) and Neff et al. (2011) described facies associations interpreted as meander-channel, crevasse-splay, and floodplain-mire depositional environments. The dispersed amber described in this study was recovered

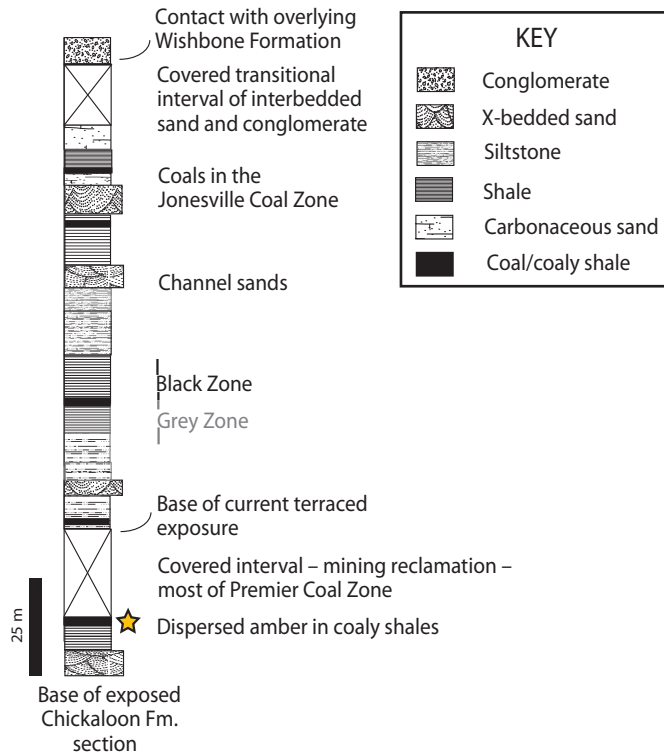


FIG. 2. Generalized stratigraphy of the upper Chickaloon Formation at the reclaimed Evan Jones Mine (modified from Neff et al., 2011). Amber collections were made from coaly shales near the base of the accessible succession.

from a single horizon (fig. 2) of coaly mudrock lithofacies in close proximity—but not attached to—permineralized cupressaceous (*Metasequoia*) wood (Williams et al., 2010).

Other paleofloral remains in carbonate-cemented mudrocks and fine sandstones of the upper Chickaloon Formation include abundant *Metasequoia* shoots and cones, leaves of dip-terid ferns and the monocot *Haemanthophyllum*, *Equisetites* axes, rare fragments of putative palm fronds, numerous types of reproductive bodies with affinities to those of the modern *Platanus* and *Acer* (among others), and a diverse magnoliid and eudicot foliar assemblage preserved as compressions/impressions (Wolfe et al., 1966; Sunderlin et al., 2011). Faunal remains in the formation include a freshwater gastropod fauna (Viviparidae) (Walker et al., 2009) and a chelydrid turtle carapace (Hutchison and Pasch, 2004).

Leaf physiognomy-based methods for estimating paleoclimatic parameters suggest that the Chickaloon flood basin was temperate, with MAT (11–14.6° C) and mean annual precipitation (MAP; 120–180 cm/yr) estimates much higher than the present-day climate of southern Alaska (Sunderlin et al., 2011). Dicot-leaf herbivory in the forms of margin feeding, hole-feeding, and skeletonization was documented by Sunderlin et al. (2011) and Brannick et al. (2012) and is believed to have been caused by insect cohabitants. Foliar damage frequency (proportion of leaves damaged) and intensity (area damaged on each leaf) is low in comparison with other floras of similar age, paleoenvironment, and paleoclimate (Sunderlin et al., 2011, 2014).

MATERIALS AND METHODS

A field collection of 9677 dispersed amber pieces was hand picked (“picking” method) from the surface of the study horizon and examined in the lab under stereomicroscopy (7×–45× magnification) for included faunal and floral remains. When necessary, pieces were ground on a lapidary wheel with discs of P800–P2500 grit to provide clear views into the pieces.

Amber pieces with inclusions were embedded in EpoTek 301-2 synthetic resin, for stabilization of the brittle amber during preparation. Embedded pieces were trimmed with a water-fed diamond-edge trim saw, and carefully ground and polished using 600, 800, 1200, and 2400 grit emery papers (Buehler, Inc.) on a water-fed lapidary wheel. Final preparations commonly were 1–2 mm thick, to optimize observation of inclusion details at high magnifications. Inclusions were observed by applying the amber piece to a glass microscope slide using a drop of glycerin or water, and covering with a glass cover slip. General observations up to 150× were made using several stereoscopes (Wild, Nikon, Leitz), as well as a Wild compound scope at 100× and 200×; the latter was also used for measurements and illustrations (with an attached drawing tube). For observation at high magnification (400×), a Nikon Eclipse E600 compound scope was used with a Nikon Plan Fluor ELWD (extended-length working distance) 40×/0.60 objective. The Nikon Eclipse and a Nikon SMZ1500 stereoscope were used for photomicrography, along with NIS Elements software for z-stacking and scales.

To further evaluate preservation of an ant inclusion, specimen AMNH WH-1 was examined using X-rays, examined under multiple parameters with a Bruker (Kontich, Belgium) Skyscan 1275 Micro-CT system at the New Jersey Institute of Technology. The specimen was assessed under live imaging with X-ray energies ranging from 20–70 kV, as well as detector settings ranging from ~100–750 msec. While the amber itself exhibited differential X-ray attenuation and penetration relative to the surrounding air, under no permutation of X-ray energies or detector exposure settings did the inclusion itself resolve, revealing no detectable density differential between the cuticle/body cavity of the ant inclusion and the amber matrix.

RESULTS AND DISCUSSION

AMBER COLLECTIONS

Each examined piece of amber was categorized by morphology and size (table 1). Amber nodules that appear to originally have been formed internally in wood or under bark (“blisters” in Pike, 1993) comprise ~58% of the collection, while pieces exhibiting drip or “flow” (Pike, 1993) morphologies (i.e., runnels) and those that could not be categorized are less represented (~28% and ~14%, respectively). Large pieces (>10 mm in long axis, ~>0.25 g) comprise less than 1% of the collection, while medium (5–10 mm) and small (<5 mm, ~<0.03 g) pieces make up most of the material (~12% and 87%, respectively).

Pike (1993), in his study of Late Cretaceous amber from southwestern Canada, emphasized the need to examine small amber pieces for inclusions, noting this size fraction’s disproportionate likelihood (by weight) to contain inclusions. Even though a sampling strategy of “picking”

Table 1. Chickaloon Formation amber collection by morphological and size categories.

| | Blister | Flow | Uncategorized | Total |
|------------------|---------|------|---------------|-------|
| Small (<5 mm) | 4632 | 2500 | 1259 | 8391 |
| Medium (5-10 mm) | 936 | 250 | 66 | 1252 |
| Large (>10 mm) | 30 | 2 | 2 | 34 |
| TOTAL | 5598 | 2752 | 1327 | 9677 |

may lead to underrepresentation of small amber pieces (as compared to “floating”) (Pike, 1993), we made a pointed effort to collect across the size spectrum in the Chickaloon study horizon, including small nodules <0.2 g. Thus, we feel that our amber collection is minimally biased against sampling inclusions in the ways against which Pike (1993) cautioned.

AMBER INCLUSIONS

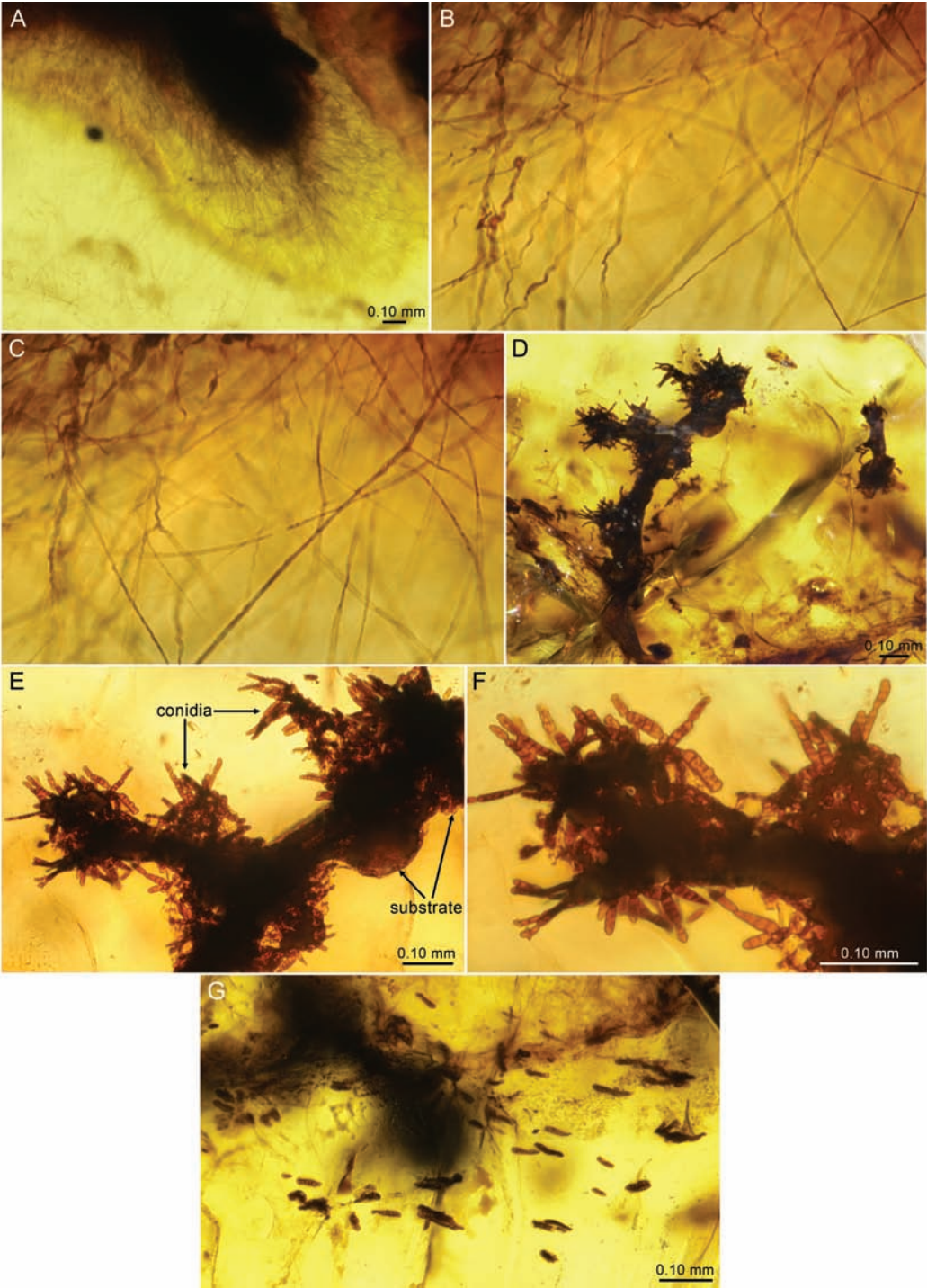
FUNGI

Figures 3, 10A

AMNH LC-D4: A small piece containing very fine, filamentous hyphae with a very uniform thickness ca. 2–3 μm (fig. 3A–C). Most hyphal strands are sinuous and straight, some squiggly. The hyphae are very webby and possibly interconnecting (their density makes it difficult to tell), but they definitely branch. The hyphae grew on a dark mass of substrate that is partially preserved near the surface of the amber piece, with a dark reddish “halo” over the surface of the substrate and most hyphae (indicating some pyritization and/or oxidation). This substrate may be bark, since there are fragments of discernable bark fibers nearby (fig. 4A–C). Interestingly, the hyphae appear to have been growing into the fresher, lighter-yellow resin, since the fine, delicate filaments are perfectly arranged and undisturbed by any flow.

The filaments do not appear to be sheathed bacteria, since their cores do not appear to have cell chains. Sheathed bacteria are reported to occur in amber (Schmidt and Schäfer, 2005; Girard et al., 2009), although various lines of other data led Speranza et al. (2015) to conclude that these reports are instead of fungal hyphae. Saint Martin and Saint Martin (2017) disputed the interpretation of hyphae, even though Speranza et al. (2015) used confocal laser microscopy to detect the diagnostic presence of chitin polysaccharides, which occur in fungi but not bacteria. The filaments in Chickaloon amber are very similar to the webby hyphae of certain resinicolous ascomycetes that thrive on conifers, Mycocaliciales, which are known from the present through the Cenozoic (Tuovila et al., 2013). The genus *Chaeontheopsis*, for example,

FIG. 3. Fungal inclusions. A–C (AMNH LC-D4): Hyphae of apparent resinicolous fungus (?Mycocaliciales), penetrating into core of amber. A. Most of hyphal mass. B, C. Different focal planes of same area, at higher magnification. D–G. Clumps of a hyphomycete with multiseptate phragmaconidia growing on substrate (AMNH GC-A8), possibly of a sooty mold (Capnodiales), or closely related to the enigmatic Eocene hyphomycete *Casparytorula*. D. Entire mass. E. Portion of fungal mass at higher (200 \times) magnification. F. Detail, 400 \times . G. Dispersed phragmaconidia adjacent to the sessile masses.



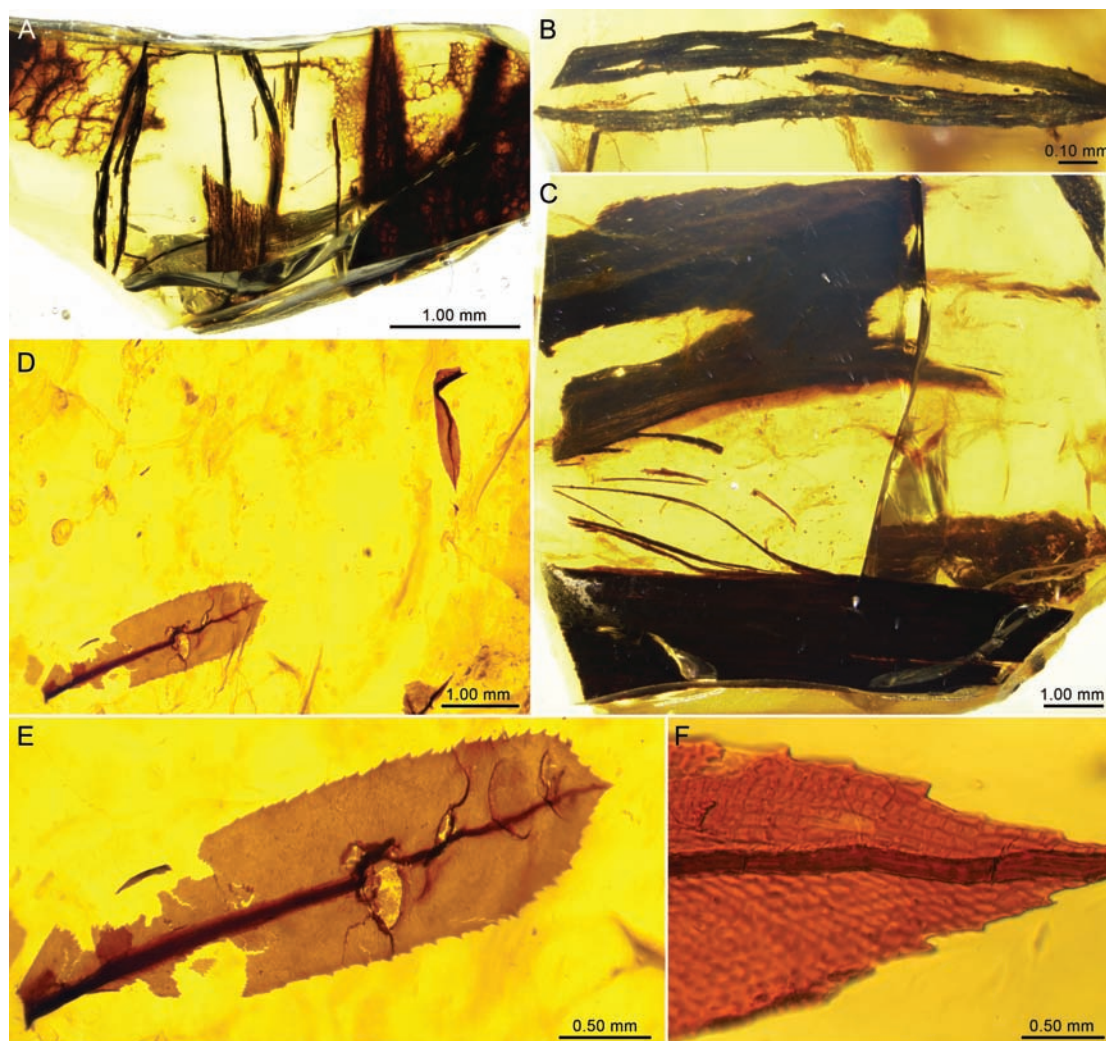


FIG. 4. Plant remains. A–C. Bark or wood fibers, AMNH WH-13. D–F, Microphylls of a moss (AMNH WH-2). D. Entire specimen. E. Larger microphyll at higher magnification. F. Tip of smaller microphyll, 200 \times .

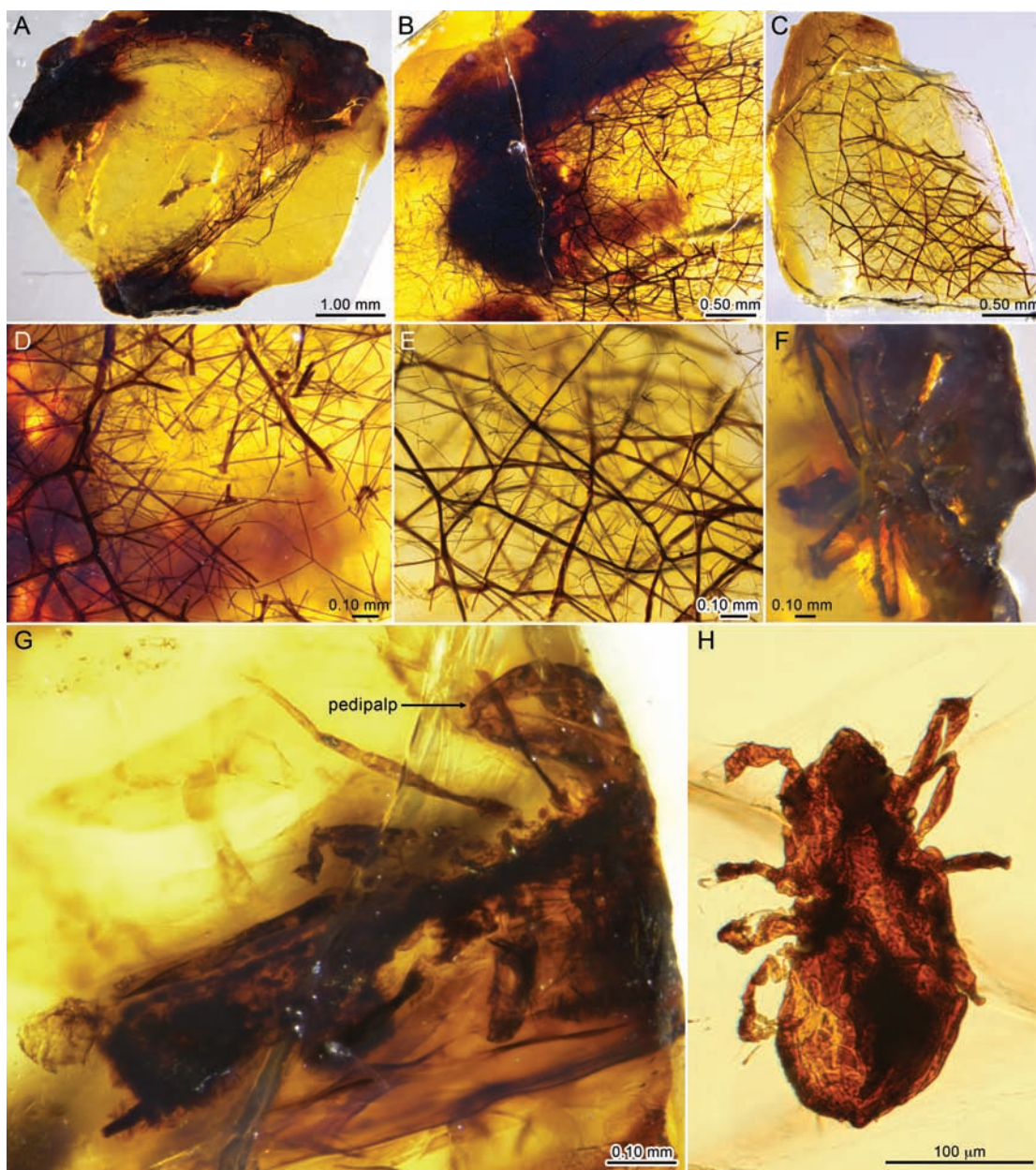


FIG. 5. Arachnids. **A–E**. Two fragments of the same piece containing portion of a spider egg sac, shown in different views and magnifications (AMNH LC-B3a, b). **D, E**. Highest magnification, showing how silk strands are cabled and woven. **F**. Spider (unidentified), ventral view (AMNH LC-D7). **G**. Pseudoscorpion, family indet. AMNH GC-A8b. **H**. Mite, Acari: Oribatida (family indet.), ventral view (AMNH LC-D1). See figure 7D for another spider inclusion.

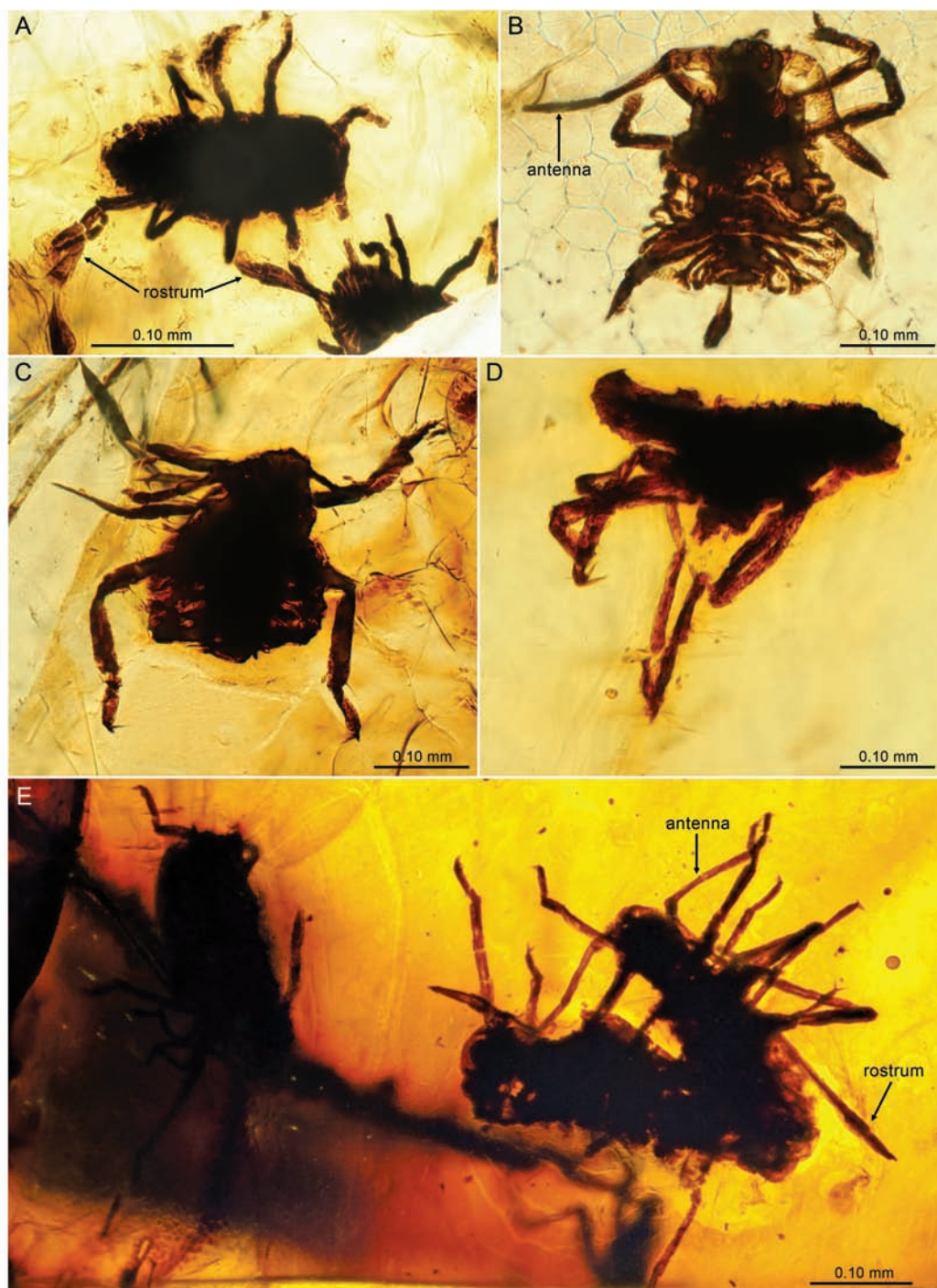


FIG. 6. Aphid apterae/nymphs (Hemiptera: Aphidoidea). A. One complete and one partial aphid. B. Complete aphid, dorsal view (AMNH LC-A2). C. Complete aphid, dorsal view (AMNH LC-D3). D. Complete aphid, lateral view (AMNH WH-9). E. AMNH WH-5, showing remains of four aphids.

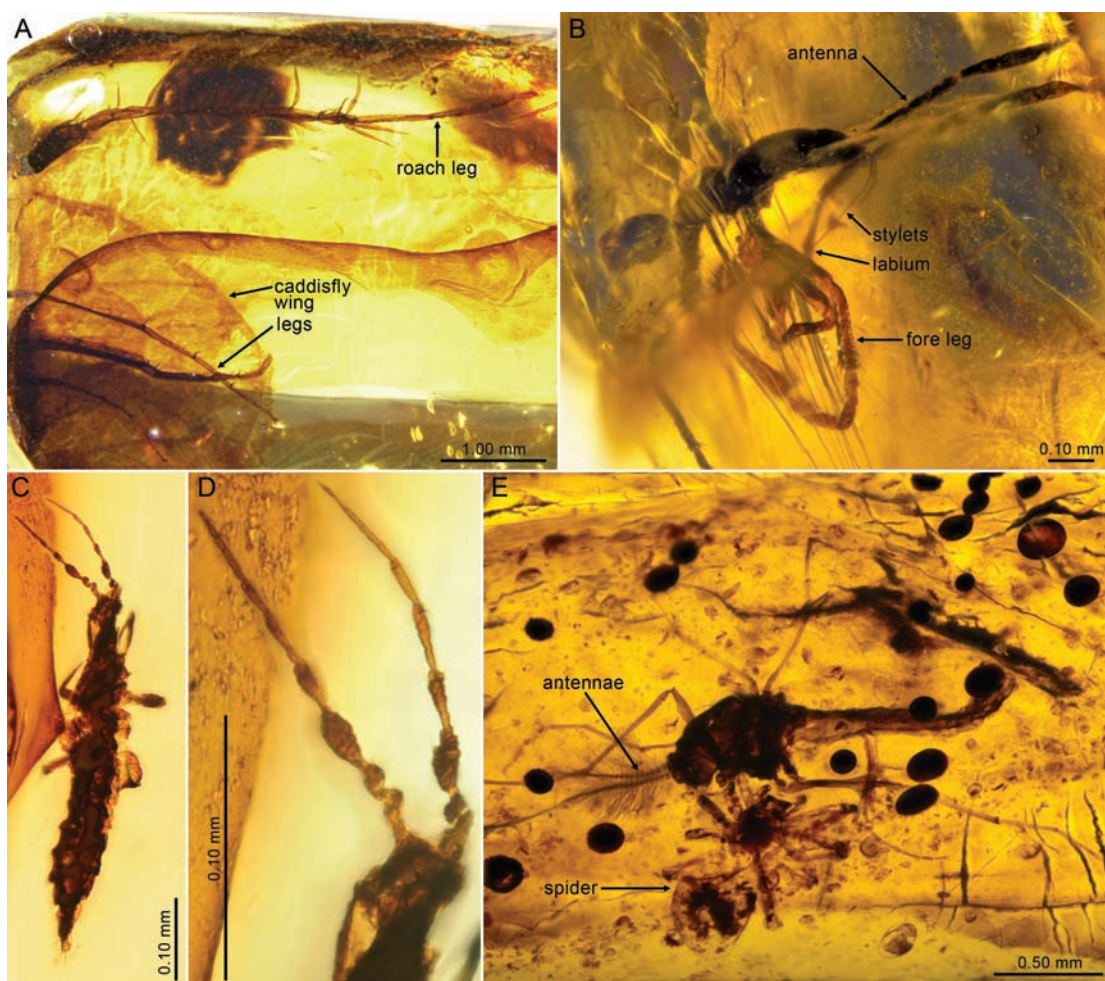


FIG. 7. Various insect inclusions. **A.** AMNH WH-12, with legs from a roach (Blattodea), and the legs and distal portions of two wings from a caddisfly (Trichoptera). **B.** AMNH LC-A4, nymph of Heteroptera (Hemiptera). **C, D.** AMNH LC-B6, nymphal thrips (Thysanoptera), habitus (C) and detail of antennae (D). **E.** AMNH WH-3, with inclusion of entire male Chironomidae: Tanypodinae, and juvenile spider.

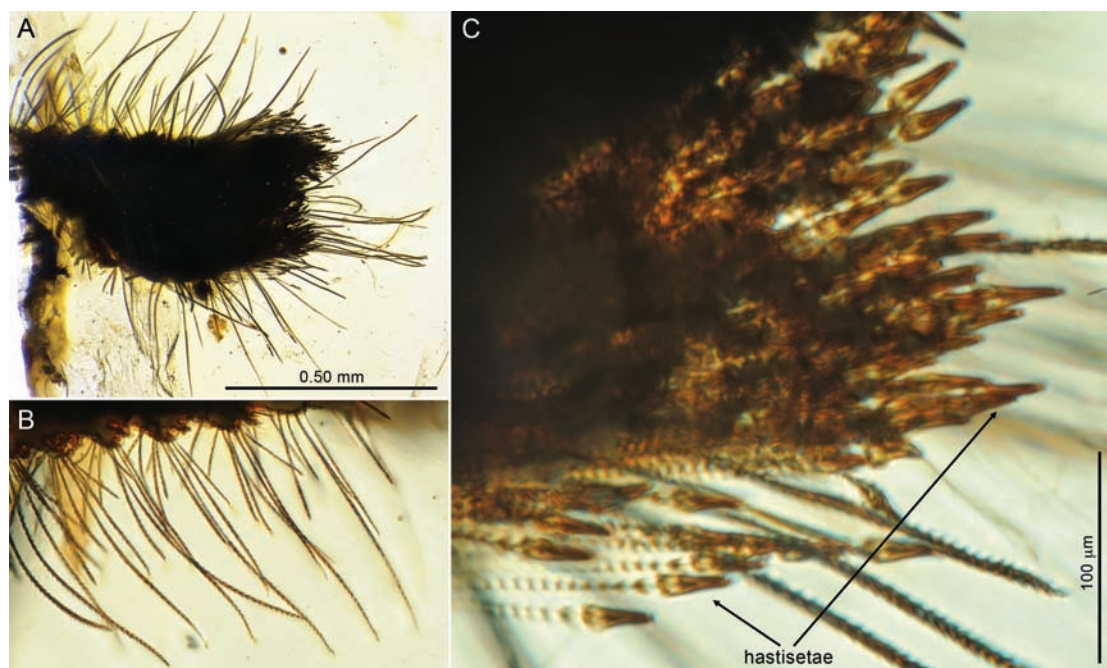


FIG. 8. Abdomen of a larval beetle (Coleoptera), family Dermestidae subfamily Megatominae (AMNH LC-II-B4). **A.** Entire specimen. **B.** Detail of plumose setae. **C.** Detail of posterior tufts of specialized, entangling hastisetae.

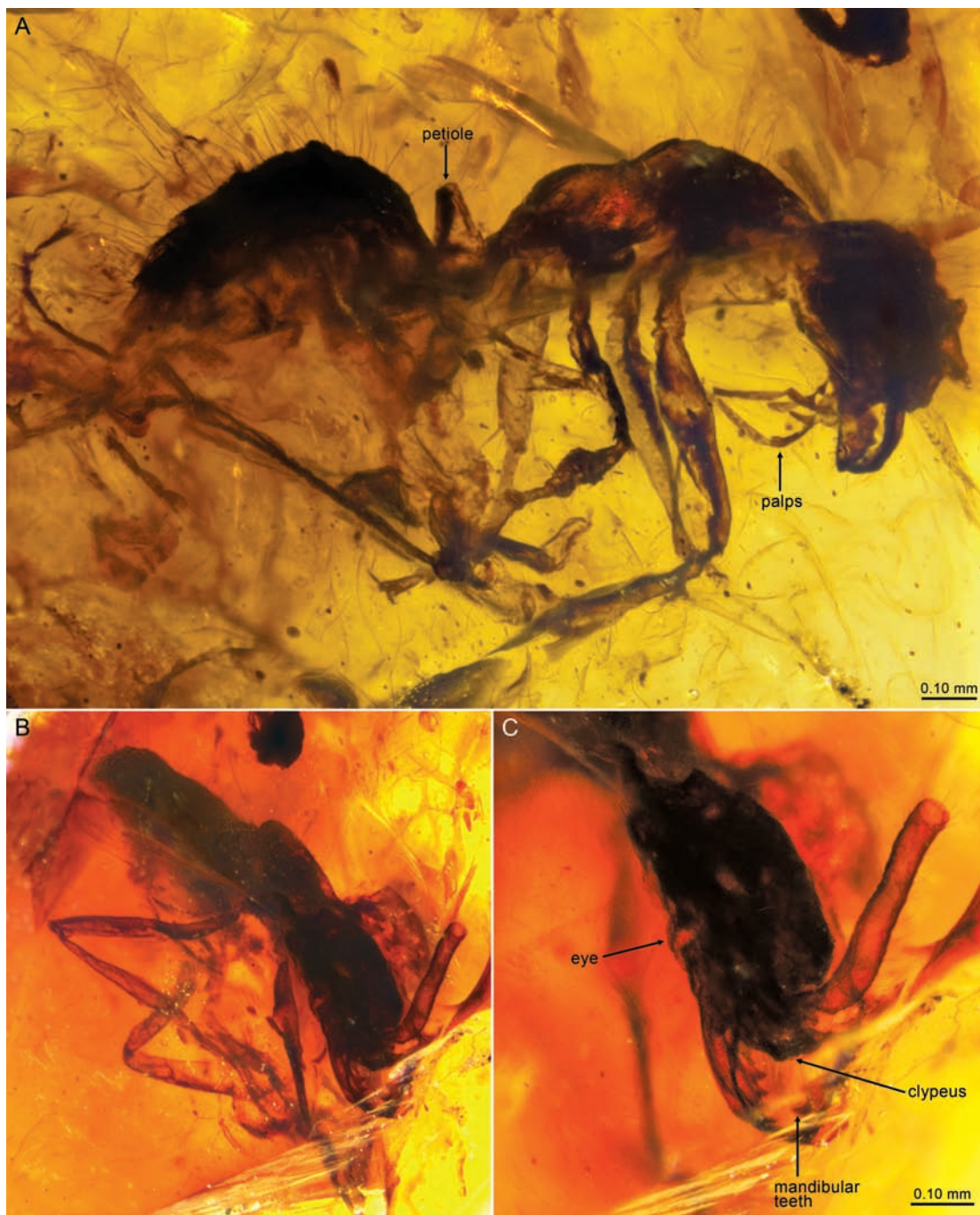


FIG. 9. Worker of ant (Formicidae: Formicinae), AMNH WH-1. **A.** Lateral habitus. **B.** Oblique frontal habitus. **C.** Oblique frontal view of head, showing mandibles and dentition.

is known from the Eocene (Baltic amber), the Oligocene (Bitterfeld amber), to the Recent; even the diagnostic capitulum and long stipe of the fossil ascomata are preserved in some of the fossils (Tuovila et al., 2013). No ascomata parts are preserved in the Chickaloon amber.

AMNH GC-A8: The specimen consists of roughly five clusters of fungal filaments attached to a dark, dense substrate that is probably a portion of a twig or other plant fragment (figs. 3D–G; 10A). Each filament is heavily melanized, multiseptate, linear, with 12 or fewer cells, approximately 10–15 μm thick and less than 100 μm in length. Tips are slightly narrower than the bases, and in longer strands there is a well-developed constriction between the apical and penultimate, or the penultimate and antepenultimate, cells; the apical or penultimate cells are enlarged in most conidia. Otherwise, there is little constriction between other cells. Some isolated conidia are floating free in the amber next to the clusters attached to substrate. We are grateful to Elina Kettunen (University of Helsinki) and Alexander Schmidt (University of Göttingen), who inform us that the fungus is a dematiaceous hyphomycete with multiseptate phragmaconidia. Though it bears some resemblance to sooty molds (Capnodiales), AMNH GC-A8 does not appear to belong to this group. One extant family of sooty mold, Metacapnodiaceae, comprises most of the fossil record of the group, which occur as fossils exclusively in amber from the upper part of the Early Cretaceous to the Miocene (Schmidt et al., 2014). Sooty molds are epiphytic ascomycetes with dark, flocculent hyphae (hence the name); they grow abundantly on sugar-rich secretions such as plant saps and honeydew excreted by sternorhynchans (scale insects and aphids), the latter of which are abundant in the Chickaloon amber. AMNH GC-A8 differs from sooty molds by lacking moniliform (beadlike) conidia, but instead more closely resembles conidia of *Casparytora* spp., a hyphomycete known from Eocene Baltic and Oligocene Bitterfeld ambers (Kettunen et al., 2015) (A. Schmidt, personal commun. to D.A.G., February 2018).

PLANTS

Figures 4, 10B–D

AMNH WH-2: Bryophyta: Musci (mosses). A piece containing two small microphyll “leaves” and clumps of spores, some of the latter within or bursting from membranous sacs (figs. 4D–F). Both microphylls have a thick midrib but lack veins; the epidermis appears to be one cell thick, the midrib is composed of several cell layers. The largest microphyll is 620 μm at its widest point, the midrib width 80 μm (microphyll length is unknown since the bases of both are not preserved). Apex of the larger microphyll is much less tapered, its margins with somewhat irregular serrations ca. 30–40 μm long, alternating with much smaller serrations (fig. 10C, D). Serrations of the smaller microphyll are more uniform and less dentate. Damage at the base of the larger microphyll does not appear to be feeding damage, such as from an insect, since the margins of the breaks correspond to the cell walls, as if the microphyll dried and fragmented.

The spores are generally associated with very thin, transparent, membranous, ovoid sacs, which are not cellular at 400 \times magnification; the sacs appear to occur in two size classes: the

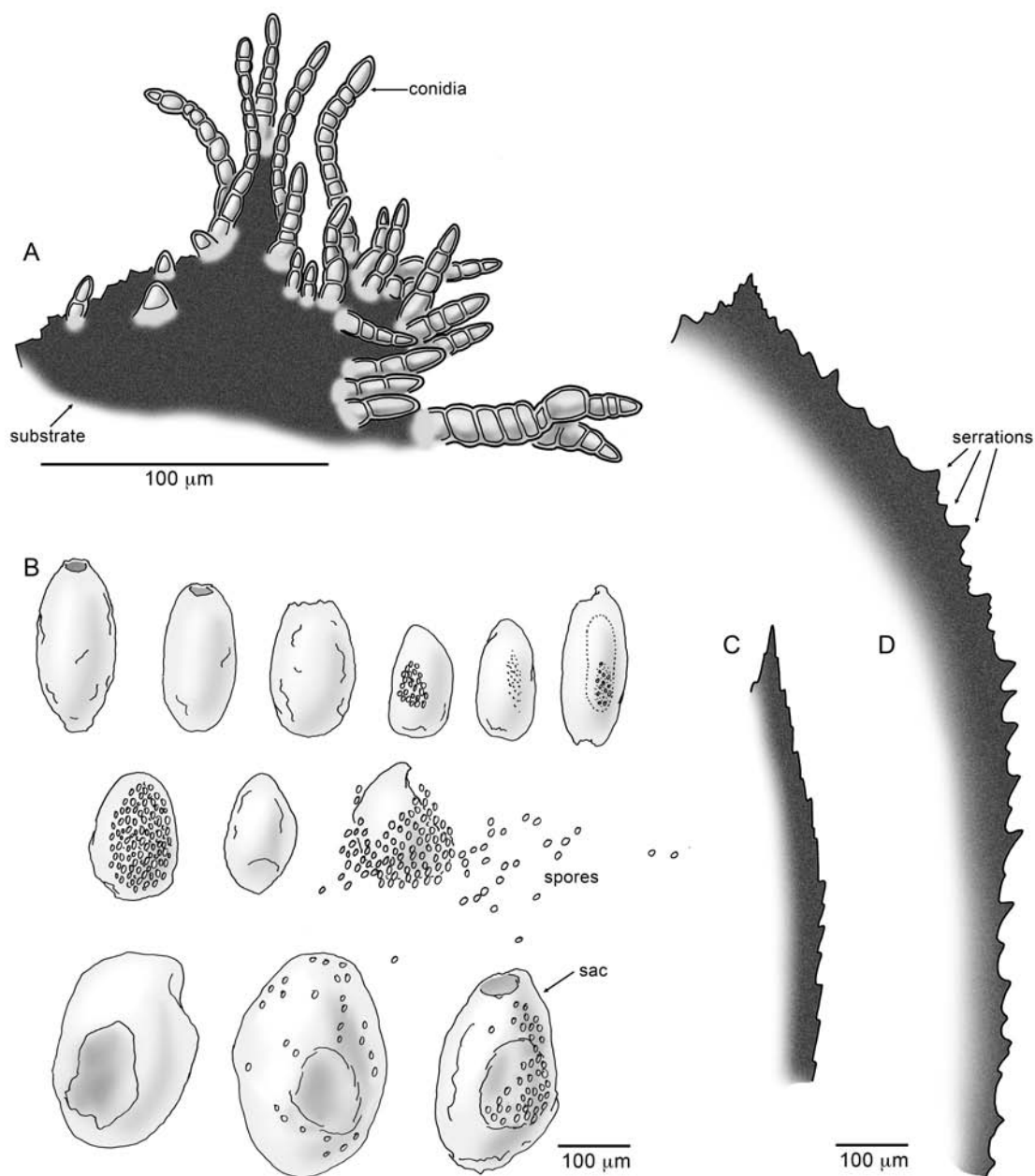


FIG. 10. Details of fungal (A) and plant (B–D) inclusions. **A.** AMNH GC-A8, Hyphomycota, showing clump of phragmaconidia on substrate. **B–D.** AMNH WH-2, Bryophyta: ?Musci: **B.** Various membranous sacs, some with spores, dispersed between bryophyte microphylls. **C, D.** Margins of small (C) and larger (D) microphylls.

smaller class ranging from $150 \times 90 \mu\text{m}$ to $220 \times 110 \mu\text{m}$ (among the ones that were measured), and the larger ones $280 \times 160 \mu\text{m}$ to $320 \times 220 \mu\text{m}$. Smaller sacs that are empty have a small hole at one or both ends; the larger sacs have a large hole in the middle (fig. 10B). Some sacs are completely empty; some have a small amount of unidentifiable granular material (probably degraded spores); others are replete with obvious spores. Spores are ovoid, size appearing the same between the two sizes of sacs, all spores ca. $5 \mu\text{m}$ in length and $3 \mu\text{m}$ width, with a longitudinal sulcus partially down the middle of some of the better-preserved and observable ones, like a coffee bean. Some clumps of spores are not associated with a sac, which presumably degraded. For two discrete clumps that were examined there were 98 and 120 spores. The spores are very small for bryophytes; this and the distinctive, membranous sacs suggest that they originated from another plant (or possibly a fungus), and their preservation with microphylls is coincidental.

Mosses have a fossil record that extend to the Carboniferous (Hübers and Kerp, 2012), and by the Cretaceous many modern families had appeared, including many taxa in Cretaceous amber (Bell and York, 2007; Katagiri et al., 2013; Hedenäs et al., 2014; Ignatov et al., 2016) and in Eocene Baltic and Miocene Dominican amber (e.g., ; Frahm and Newton, 2005; Heinrichs et al., 2014 many apparently belonging to epiphytic taxa. The microphyll structure resembles that of the living moss genus *Thamnobrym* (N. Cleavitt, personal commun. to C.J.W., March 2018).

ARTHROPODA

ARACHNIDA

ACARI (MITES)

Figures 5H, 11A

AMNH WH-6: A small piece containing most of the remains of an oribatid mite, similar in overall structure to the family Damaeidae (fig. 11A), which consists of fewer than 100 living species in 14 genera, primarily as mycophagous and algophagous inhabitants of leaf litter and subcortical microhabitats of temperate and boreal forests. Damaeidae occur in Eocene amber from the Baltic region and Rovno, Ukraine (Weitschat and Wichard, 2010; Perkovsky et al., 2010). The mite is near the corner of the amber piece, with the appendages of one side lost or completely obscured; the piece also contains dark layers from various resin flows as well as particulate plant matter. Body length (without appendages) is approximately $400 \mu\text{m}$, with a slight constriction between the prodorsum and notogaster; legs are long and slender, length of the longest is $550 \mu\text{m}$. The mite is dark and opaque, generally obscuring many of the setae, sensilla, and cuticular details except those visible at margins. Anterior-most appendage (pedipalps) (only one of a pair observable), with three short, stout podites, apical one pointed, with two long, fine solenidia. A pair of long, stiff solenidia occurs at the anterior end of the prodorsum. Structure of the legs is very distinctive and quite similar to that of the living family Damaeidae, in particular the “moniliform” legs (although this habitus also occurs in oribatid

superfamilies closely related to Damaeioidea). Leg I has bulbous portions of the femur, genu, tibia, and at the base of the tibia + basitarsus. The only bulbous portion of leg II is on what is either the genu or tibia (boundaries between podites are barely visible). The apices of tibiae in legs II and III each have a long, stiff solenidium that is nearly equal in length to that of its respective podite. Pretarsal claws are long, slender, and sickle shaped.

AMNH LC-D1: A piece of amber containing a complete mite (~280 μm body length), which is moderately well preserved (fig. 5H). Cuticle of the notogaster and prodorsum is cracked and slightly disintegrated, precluding observation of most of the chaetotaxy, glands, and sensilla, though a pair of thick, plumose trichobothria/bothridial setae is visible, one at each posterolateral corner of the prodorsum. While identification of the mite in the Oribatida is certain, a more detailed identification will be challenging. The mite is rather generalized in structure, lacking specialized (e.g., plumose) setae and obvious cuticular microstructure (e.g., reticulations). The gnathosoma is well integrated and conical, laterally with a pair of projecting solenidia; legs are relatively short, pair I with an elongate solenidium dorsoapically on what appears to be the genu; all pretarsal claws are long, slender, and hooked.

The Oribatida is a highly diverse, speciose group of mites comprised of some 9000 living species in 172 families, largely inhabitants of soils, leaf litter, and moss (Norton and Behan-Pelletier, 2009). The fossil record of the group is ancient and diverse, beginning with unambiguous cuticular remains from the Devonian that are preserved in microscopic detail (Norton et al., 1988). Oribatids have even been implicated in the processing of plant detritus from Carboniferous swamps (Labandeira et al., 1997). Their fossil record in amber from the Cretaceous and Cenozoic is excellent (Dunlop et al., 2018). This is due partly to the improved techniques in preparation and high-magnification (400–1000 \times) microscopy (Sidorchuk, 2013), and the discovery of major new amber deposits. Taxa described more than a century ago in Eocene Baltic amber are being redescribed in great detail (e.g., Norton, 2000; Sidorchuk and Norton, 2010, 2011), which establish a new standard for study.

PSEUDOSCORPIONIDA (PSEUDOSCORPIONS)

Figures 5G, 11B

AMNH GC-A8: An amber piece containing most of a small (~0.90 mm long) pseudoscorpion. The specimen is rather poorly preserved, the anterior portion lost at one surface of the amber, and most of the appendages on the left side are either lost or obscured among cracks in the amber. The body contents and cuticle are black and opaque, obscuring trichobothria, which are critical to identification of pseudoscorpions; eyes are not observable. The right pedipalp is mostly preserved, revealing a relatively long femur and short tibia (typical of pseudoscorpions), and most of the chela. Leg I is very slender (possibly preservational); leg II is best preserved, showing that the patella, tibia, and metatarsus are nearly equal in length; tarsus of leg IV is relatively stout. More distinctive is the long, slender body shape, which may be partly preservational but not entirely. Six opisthosoma segments are visible (of the typical 12); in many pseudoscorpions the opisthosoma is half this length or even less.

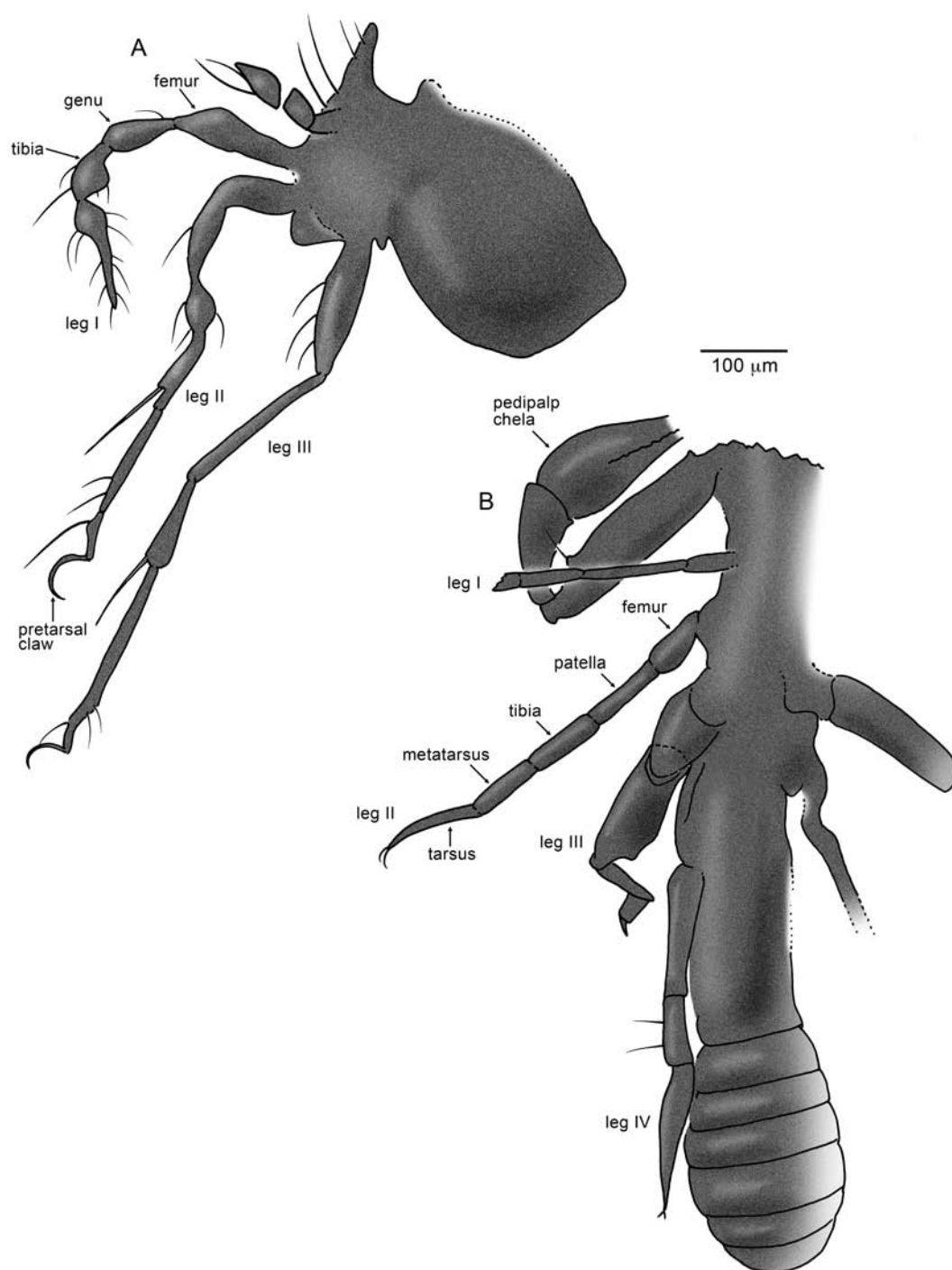


FIG. 11. Details of two arachnid inclusions, to same scale. **A.** Partially preserved oribatid mite (AMNH LC-D1), ventral view, showing long legs with swollen podites and large claws, similar to those in *Damaeioidea*. **B.** Partial pseudoscorpion, ventral view (AMNH GC-A8b).

Like mites and spiders, Pseudoscorpionida is an ancient group that extends to at least the Middle Devonian (Schawaller et al., 1991). Their fossil record is not nearly as extensive as that of spiders and mites, however, owing to their lesser abundance and preferences for concealed microhabitats (e.g., subcortical, under stones, in leaf litter). The fossil record consists of 46 species in 16 families (primarily in Cenozoic and Cretaceous amber), reviewed by Harms and Dunlop (2017), who report a bias in the fossilization of families that live under bark. Interestingly, no extinct families are known from the Cretaceous, which may just reflect antiquity of the group. Eocene Baltic amber is the most diverse source of described pseudoscorpions, some of which show Mediterranean and African connections, even Gondwanan distributions (e.g., Feaellidae). Prior to discovery of the Chickaloon amber specimen the most northerly records of fossil pseudoscorpions were in Baltic amber and Late Cretaceous amber from Grassy Lake, southern Alberta, Canada. The specimen reported here extends the northernmost fossil occurrence by approximately 10° N paleolatitude.

ARANEAE (SPIDERS)

Figures 5A–F, 7E

Three pieces contain the remains of spiders, none of which could be identified to family level. AMNH WH-3B is a small (0.80 mm body length), complete juvenile lying next to a male chironomid, the cuticle of which is mostly cleared but with some decayed internal tissue visible (fig. 7D). AMNH LC-D7 (0.84 mm) is a different taxon, having considerably longer legs, which are folded and cover the ventral surface of the cephalothorax (fig. 5F). The entire dorsum and a portion of the anterior end of the spider are obscured by a dark mass; the opisthosoma is shriveled. AMNH LC-B3a, b is in two sections (A, B), both from the same piece, each containing a distinctive mesh of fibers that form a rounded structure some 5 mm in diameter (figs. 5A–E). The individual, fine strands are uniform in thickness, many of them woven and cabled into thick fibers, all interconnected into a mesh lying in several concentric layers. The interior of the rounded structure is empty. This is clearly the silken cocoon of a terrestrial arthropod, probably that of a spider. Many spiders form spherical cocoons around their egg masses (which they may carry or suspend from a web), or hemispherical ones (woven to a substrate), and the structure of the fossil silk strands conforms to that of spiders. No remains of eggs or spiderlings occur in the cocoon. Fossilized spider egg sacs are exceptionally rare, even in amber from prolific deposits.

The fossil record of spiders extends to the Devonian and has been reviewed several times (e.g., Selden et al., 2009; Selden and Penney, 2010; Dunlop et al., 2018). Spiders are abundant and very diverse in the major amber deposits of the world, from the Early Cretaceous to the Miocene, allowing conclusions that many (most?) modern families are Cretaceous in origin, and that spiders were hardly affected by the end-Cretaceous extinctions, at least at higher-taxon (e.g., family) levels (Penney et al., 2003).

INSECTA

BLATTODEA (COCKROACHES)

Figure 7A

Two pieces of amber, AMNH WH-12 and AMNH WH-11, contain fragmentary remains of small roaches, probably nymphs. WH-12 contains a portion of one leg: apical portion of the femur and the entire tibia and tarsus. The tibia has 18 spinelike setae (including a pair of apical tibial spurs), in roughly four longitudinal rows. WH-11 contains portions of three legs and an antenna, all very dark and surrounded by a dark reddish “halo” of pyritization/oxidation. One leg is preserved as a portion of a femur; the tarsi and portions of the tibia are preserved for the other two legs. Approximately 30 filiform flagellomeres are preserved; the basal ones short (lengths about twice the width), gradually increasing in length distad to about five times the width. Leg segments of WH-11 are shorter than in WH-12, and tarsomere four has a long ventral lobe. Thus, there appears to be two taxa of roaches. Though these specimens cannot be identified to family or superfamily, they are clearly Blattodea based on the antennal structure and the tibial spines, which further have minute serrations on the ventral margin.

The fossil record and natural history of roaches are reviewed by Grimaldi and Engel (2005). The natural distribution of Blattodea worldwide is almost entirely tropical to warm temperate; pest species reach higher latitudes in association with human habitations. Of the 69 species of roaches in North America, 24 are introduced from other regions, and only three native species (*Parcoblatta pensylvanica*, *P. uhleriana*, and *P. virginica*) have distributions that extend into southernmost Ontario and Québec (Vickery and McKevan, 1985; Atkinson et al., 1991). The roaches are the most obvious example in Chickaloon amber of a taxon that has retreated from high northern latitudes.

THYSANOPTERA (THRIPS)

Figures 7C, D; 12A, B

AMNH LC-B6: A piece of amber containing a complete but minute (0.60 mm body length), wingless thrips, presumably a nymph (fig. 7C, D). The body is slightly compressed and distorted, the opaque body contents preventing observation of cuticular microsculpture, chaetotaxy, and sutures. The head is not well preserved, being partially collapsed, but the postocular region does not appear long (as in Phlaeothripidae); mouthparts are not visible. Antennae are preserved well enough to reveal segment proportions, cuticular microstructure, and sensilla (fig. 12B), their total lengths 440–460 μm . There are seven antennomeres, plus a minute terminal stylus, with relative lengths: $7 > 5 = 3 > 4 > 6 = 1 > 2$. Most antennomeres have very fine transverse wrinkles and minute setigerous pimples; article 3 is the broadest and bears sensorial plaques, several of which also appear to occur on article 2; sensory cones appear to be absent, as do any thickened, blunt, setiform sensilla (fig. 12B). Femora are moderately thick (approximately twice the thickness of the tibiae); tarsi appear to be 1-segmented (best seen ventrally on

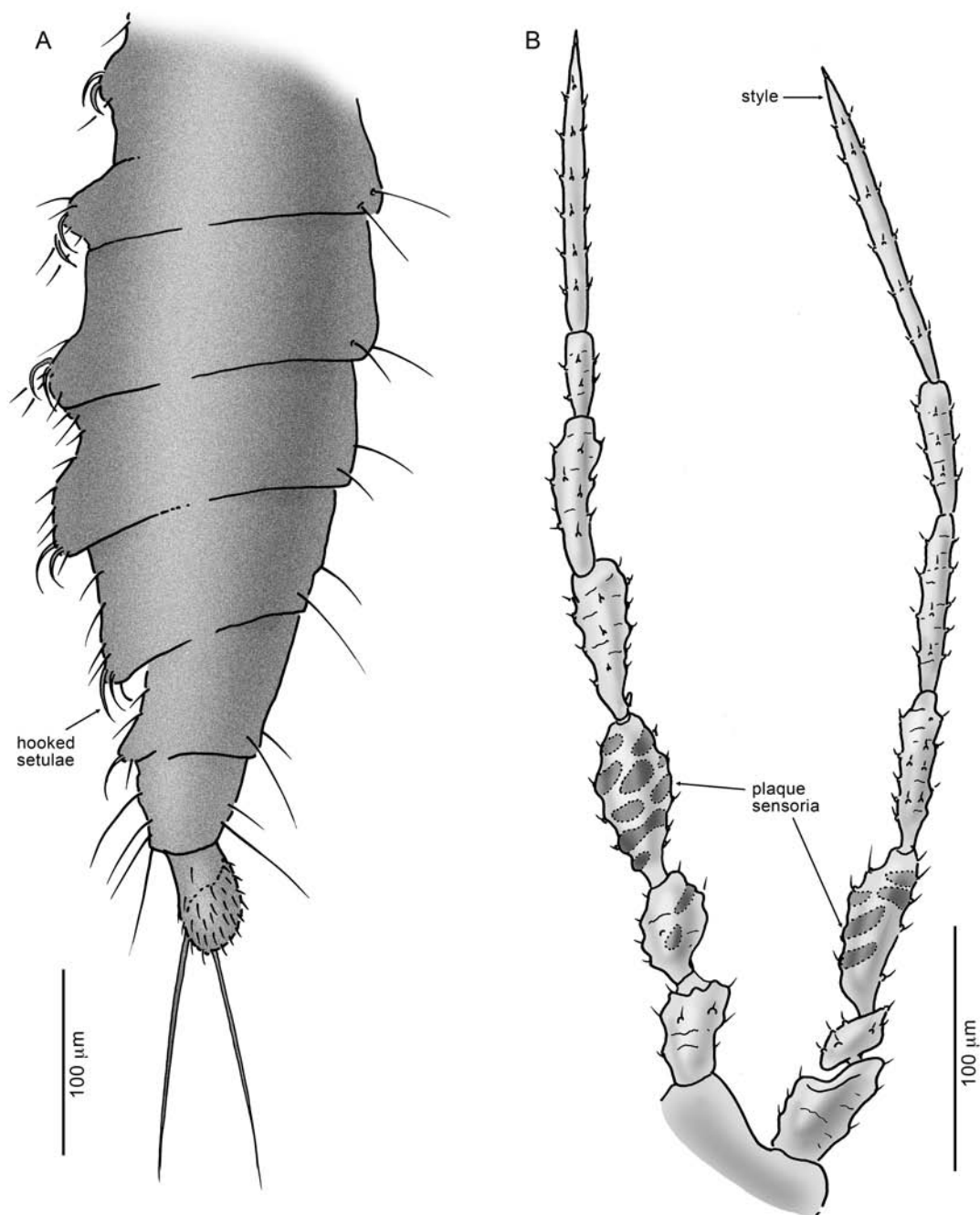


FIG. 12. Details of a nymphal thrips (Thysanoptera) (AMNH LC-B6). **A.** Abdomen, dorsolateral view. Note pairs of recurved setae on lateral lobes. **B.** Antennae.

the midlegs). Abdomen is somewhat fusiform in shape, with a small lateral lobe on most tergites (6 are visible) bearing a pair of recurved setae (fig. 12A). Presumably there is a pair of these lobes on each of the segments. Apex of the abdomen appears laterally compressed, the tip rounded and bearing a pair of long setae.

In lieu of wings and other structures it is difficult to definitively place the thrips to family, though the antennal structure provides good information. Seven antennomeres are found in the Uzelothripidae and in most Thripidae and Phlaeothripidae (which also have 1-segmented tarsi); thrips plesiomorphically have nine antennomeres. Uzelothripidae is highly doubtful, since the fossil does not have antennomeres 3 + 4 fused or an annulate apical segment (also, the family is monotypic in the Recent fauna, and has just one fossil species, in Early Eocene Oise amber from France [Nel et al., 2011]). Phlaeothripidae further have sensoria on segments three and four, but given that the postocular region of the head in LC-B6 does not appear long (perhaps preservational), and the terminal abdominal segment is not tubular, placement of the fossil in this family is uncertain. Phlaeothripidae and Thripidae comprise some 85% of the approximately 6000 living species of thrips, and they have diverse diets, which include phytophagy, pollenivory, and mycophagy. The oldest Thysanoptera are Late Triassic (Grimaldi et al., 2004); the oldest Thripidae and Phlaeothripidae occur in Early Cretaceous amber and are diverse in Cenozoic ambers (Nel et al., 2010). This is the northernmost fossil occurrence of Thysanoptera.

HEMIPTERA

HETEROPTERA (TRUE BUGS)

Figure 7B

AMNH LC-A4: Amber piece contains most of a nymphal heteropteran (0.56 mm body length). Very little can be said about this specimen since it is fragmentary and portions of it are obscured (lying under a cracked and chipped corner of the amber); it is also very small, probably an early instar. It is clearly identifiable as a heteropteran, though, based on a proboscis that is curved anteroventrally, with a thick labium at the base and with fine stylets separated and exposed from the dorsal groove of the labium. Also, there are 2–3 short tarsomeres and the antenna is comprised of four thick flagellomeres that are held forward. Heteroptera are generally uncommon to rare in Cretaceous and Cenozoic amber, often comprising less than 1% of the individual arthropods. The fossil history of Heteroptera is reviewed by Grimaldi and Engel (2005).

HEMIPTERA

STERNORRHYNCHA: APHIDOIDEA (APHIDS)

Figures 6A–E; 13A–E

Eleven pieces of amber contain the partial or complete remains of 21 wingless aphids (nymphs and/or apterae), as follows: **AMNH LC-A2**, 1 individual; **LC-C4**, partial aphid?;

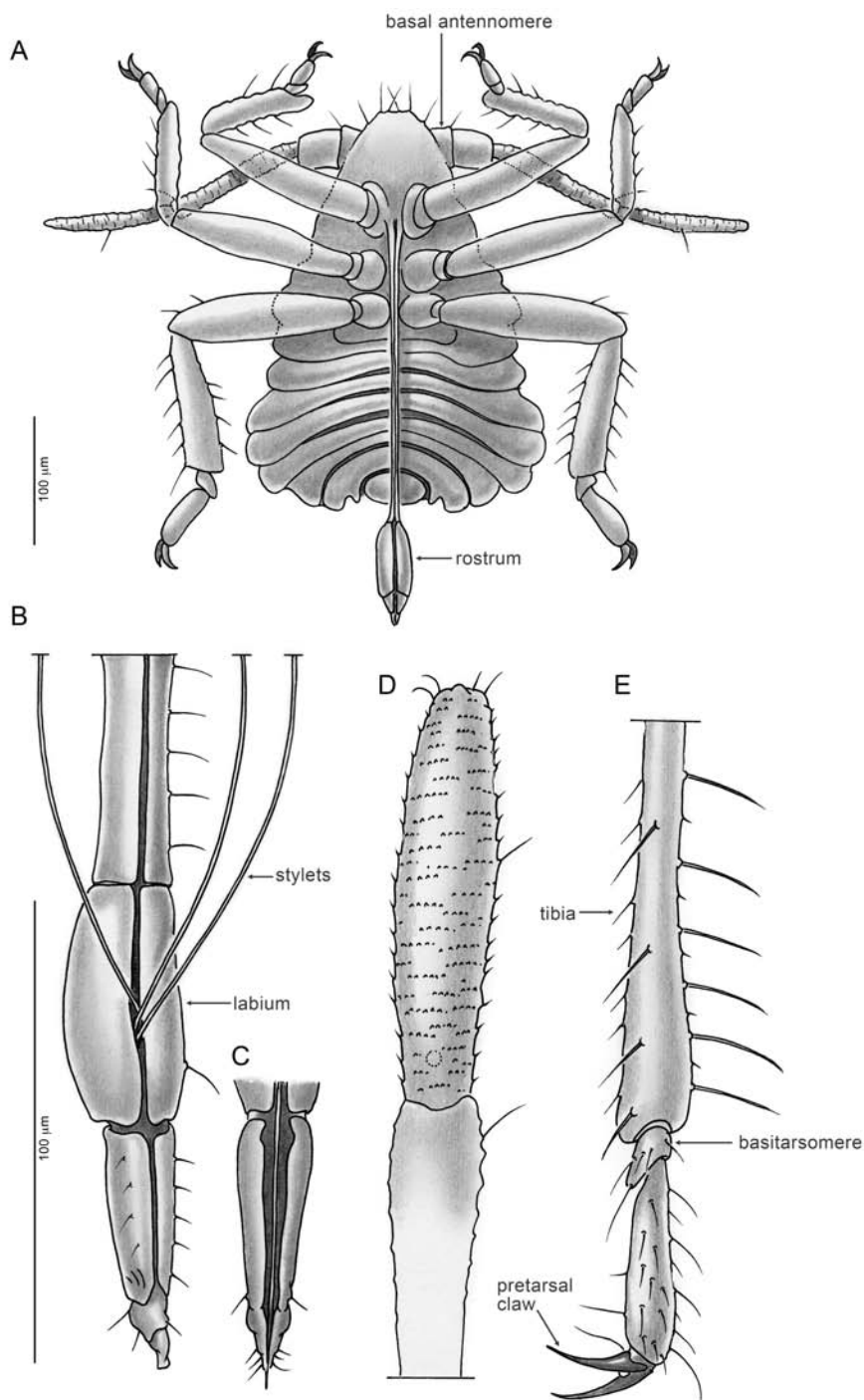


FIG. 13. Aphidoidea (aphids) in Chickaloon amber. **A.** Reconstructed habitus in ventral view, derived from specimens AMNH LC-A2 and LC-D3. **B, C.** Rostrum: **B.** Oblique dorsal view, specimens AMNH WH-5a. **C.** Dorsal view of apex, specimen AMNH WH-5b. **D.** Apical flagellomeres, AMNH WH-5e. **E.** Metatibia and metatarsus, AMNH WH-5e.

LC-D3, 1 individual; **LC-II-A4**, 2 aphids; **LC-II-A6**, 1 complete, 1 partial; **LC-II-C2**, 1.5 aphids, very small (early instar?); **WH-4**, 1 individual; **WH-5**, 4.5 aphids, same species and all approximately same size; **WH-7**, 2 partial aphids; **WH-8**, 3 very small (early instar?) individuals; **WH-9**, 1 individual. Many are incomplete, heavily pyritized, or too poorly preserved for detailed study, but four pieces contain specimens amenable to detailed study at 100×–400× magnification. Among these four, AMNH LC-A2 and LC-D3 clearly belong to the same species (species A); the specimens in WH-5 belong to a different species (sp. B), since they have longer legs, the abdomen is not as short and broad, and distal segments of the rostrum are distinctly different. AMNH LC-II-C2 contains one partial and one complete aphid, both very small (probably early instar nymphs), but which appear to have shorter, more compact flagellomeres. Body lengths range from 0.40 mm (WH-8) to 1.66 mm (WH-4).

Both species, A and B, clearly belong to the same family and genus, sharing the following features (fig. 13): Rostrum very long (slightly longer than body), 3-segmented, apex extending beyond apex of abdomen, apical two segments of rostrum distinctly swollen. Eyes small, inconspicuous; antenna 4-segmented, basal 2 antennomeres short, apical two articles approximately equal in length, apical articles apparently without rhinaria (or these are few, small, and obscure); head and notal sclerites possibly fused into shield (difficult to observe); tarsi 2-segmented, with small, oblique basitarsomere, pretarsal claws large and stout; abdominal tergites apparently without wax plates; siphunculi absent (presence/absence of siphuncular pores not observable); cauda apparently absent, or so small as to not be observable; body lacking enlarged or other specialized setae. The antennal segmentation, long rostrum, and structure of the abdominal apex indicate these species are in the Mesozoicaphididae according to the diagnosis by Heie and Pike (1992, 1996).

The Chickaloon aphids are clearly a very important group for understanding the paleoecology and biogeography of the Chickaloon amber. A long siphon and stout pretarsal claws are found in aphids that feed in the fissures of bark; this and the abundance of apterous forms in the amber indicate that the aphids were feeding on the tree that produced the amber. Modern Aphidoidea that feed on conifers include many Adelgidae, which seem to be a specialized offshoot of certain Cretaceous aphids. The Mesozoicaphididae, to which the Chickaloon aphids appear to belong, were placed in the Phylloxeroidea by Heie and Pike (1992), a family that until now was known only from Late Cretaceous (Campanian-aged) amber of western Canada (Heie and Pike, 1992).

Canadian Cretaceous amber contains abundant and diverse aphids, some 16 species in 10 genera and several families (Essig, 1938; Richards, 1966; Heie and Pike, 1992, 1996; Kania and Wegierek, 2005), although the taxonomy and classification needs to be reexamined. In amber from Medicine Hat, Alberta (Foremost Formation, or Foremost Member of the Judith River Formation [Campanian]), aphids comprise some 35%–40% of all individual arthropod inclusions (Heie and Pike, 1992). The tree that is the best candidate for the production of the Canadian Cretaceous amber is also in the Cupressaceae, specifically *Parataxodium* (an extinct genus closely related to *Taxodium* and *Glyptostrobus*) (McKellar and Wolfe, 2010). Aphids are also abundant in Late Cretaceous Siberian amber from the

Taimyr Peninsula (Zherikhin and Sukatsheva, 1973); in Late Eocene Baltic amber aphids comprise some 2% of arthropod inclusions (Larsson, 1978). Early Eocene amber from Hat Creek, British Columbia, is also preserved in strata that contain abundant *Metasequoia* remains, as well as *Glyptostrobus* (Read, 1990; Legun, 1996); Hemiptera are reported in that amber (Poinar et al., 1999), but there is no mention of aphids. Aphids are rare in amber from the Miocene of the Dominican Republic and Mexico, Eocene of Ukraine, and the Cretaceous of Lebanon, Myanmar, New Jersey, and Spain; they are absent in amber from the Eocene and Cretaceous of France (see contributions in Penney, 2010). Thus, like the Recent, aphids have been primarily higher latitude insects since the Cretaceous, though they did not become abundant until the Cenozoic.

COLEOPTERA

DERMESTIDAE (CARPET BEETLES)

Figures 8A–C; 14F

AMNH LC-II-B4: A partial larva that is missing the head and legs, but has seven abdominal segments largely to entirely preserved (portions of the anterior segments are lost at the amber surface on the right side) (fig. 8A). The dorsum of the abdomen is covered with a dense vestiture of long setae having short, thick plumosity; presence/absence of bare patches on tergites is not observable. The apical abdominal segments have tufts of peculiar spear-shaped setae, which are very well preserved. These specialized setae have a bullet-shaped head that is hollow, with an asymmetrical, sharp basal rim; the setal shaft has evenly spaced nodes, each node with a crenulated collar of small spines or tubercles (fig. 14F). Such setae, called hastisetæ, allowed identification of the partial larva to the Dermestidae, and in fact hastisetæ of this structure are confined to the subfamily Megatominae (Kiselyova and McHugh, 2006), most similar to the genus *Cryptorhopalum*. The hastisetæ in extant dermestids are defensive, being dehiscent and snagging together when the larva is attacked, entangling the attacker (Nutting and Spangler, 1969). There are 1300 living species of Dermestidae in 53 genera, well-known for their larval diet of dried animal remains (including carrion, and shed feathers, hairs, and skin in nests). The genus *Anthrenus* (also a megatomine) is the notorious museum pest that decimates unprotected collections of skins and pinned insects. The oldest putative dermestid is in Jurassic shale (Deng et al., 2017), with definitive larvae and adults in Early Cretaceous amber from Lebanon (Kirejtshuk et al., 2009), and the oldest Attageninae from the mid-Cretaceous of Myanmar (Cai et al., 2017) and Late Cretaceous of New Jersey (Peris and Háva, 2016). Hastisetæ of megatomine dermestids are preserved in Upper Albian-aged amber from Spain, snagged in the legs and body of ticks (Peñalver et al., 2017). The ticks most likely acquired the hastisetæ in the arboreal nest of a vertebrate host (Peñalver et al., 2017). Diverse modern genera of dermestids occur in Eocene Baltic amber (e.g., Háva et al., 2008) and Miocene Dominican amber. The Chickaloon amber specimen is the most northerly fossil record of the Dermestidae, the prior ones being in Baltic amber.

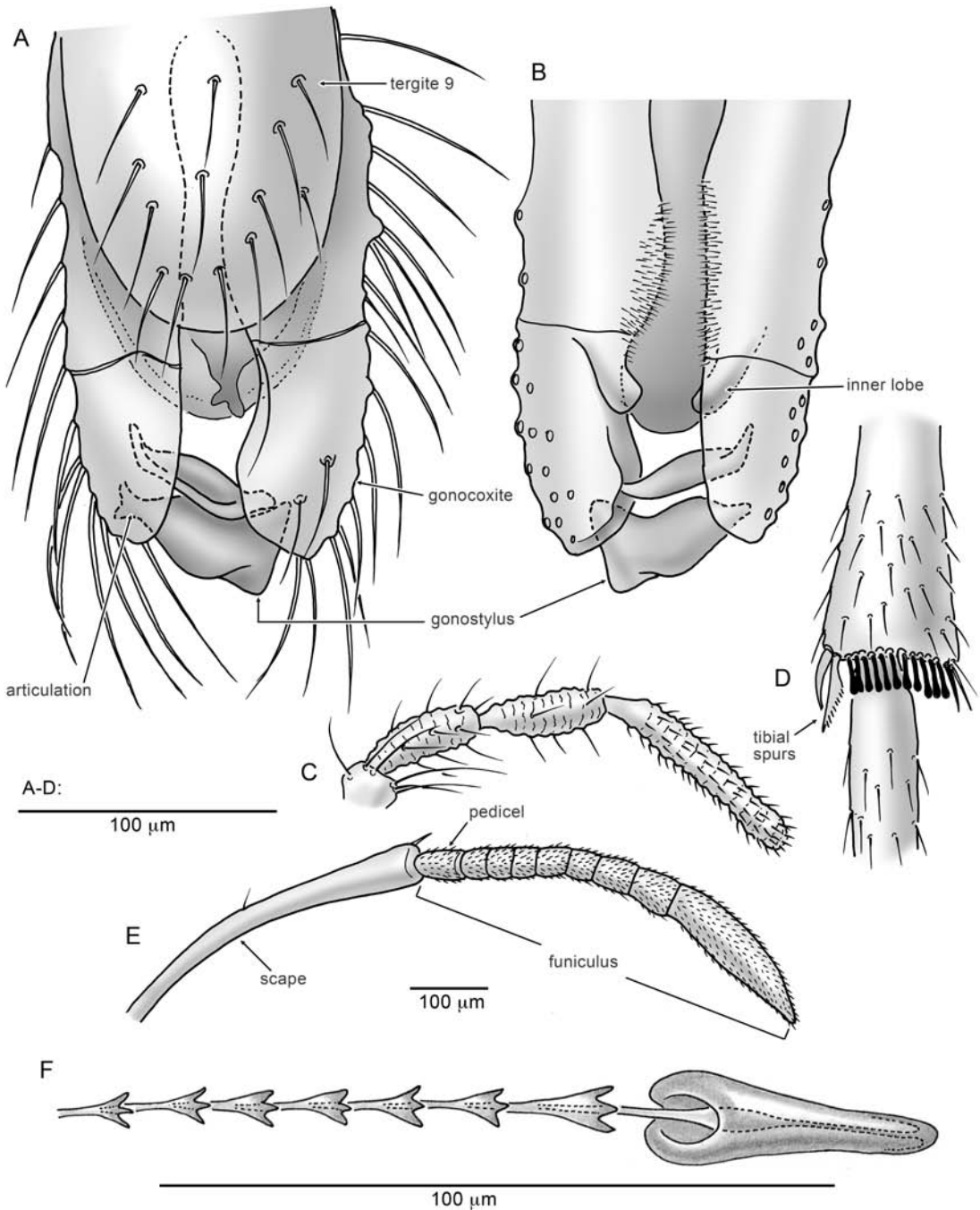


FIG. 14. Details of various holometabolous insect inclusions. **A–D**, Male midge (Diptera: Chironomidae: Tanypodinae) (AMNH WH-3): **A**, **B**. Male terminalia, dorsal (**A**) and ventral (**B**) views. **C**. Maxillary palp. **D**. Mesotibial apex (mesal surface). **E**. Isolated antenna of ant (Hymenoptera: Formicidae) (AMNH GC-A4). **F**. Detail of highly specialized, entangling hastisetula from larval beetle (Dermestidae: Megatominae) (AMNH LC-II-B4).

TRICHOPTERA (CADDISFLIES)

Figure 7A

AMNH WH-12: The amber piece contains the apical third or so of two partially overlapping wings and the distal portions of three legs. Preserved leg portions include portions of the tibiae and entire tarsi. There are five rather long tarsomeres, the basitarsomere significantly the longest. The pretarsal claws are well developed and the empodium is pulvilliform. These remains are identifiable as Trichoptera based on the dense vestiture of long, fine setae on the wing veins and membrane; and legs with short, slender, spinelike setae, especially circlets of these at the apices of leg podites. No diagnostic features are preserved that allow identification to family or even superfamily/subordinal level. Larval Trichoptera inhabit freshwater (rarely are semiterrestrial), and are well-known for their construction of cases, sometimes elaborate ones. Definitive Trichoptera first appeared in the Jurassic; the fossil record is reviewed by Grimaldi and Engel (2005). Baltic amber is the most abundant and diverse source of fossil Trichoptera, which otherwise are uncommon in amber. AMNH WH-12 is the largest arthropod preserved in the Chickaloon amber (albeit partial), with an estimated body length of 6 mm.

DIPTERA

CHIRONOMIDAE (MIDGES)

Figures 7E, 14A–D

AMNH WH-3: A complete male nonbiting midge (Chironomidae) (body length 1.60 mm), preserved adjacent to a small juvenile spider (fig. 7E). Eyes are bare; pedicel large, subspherical; antenna with long plumosity, apparently having 11 flagellar articles, apical article longest; maxillary palp with four palpomeres, lengths $4 > 2 = 3 > 1$ (fig. 14C). Legs: mesotibia having two bladelike apical spurs (one with fine pectination), apical comb of 11–12 thick, sclerotized, slightly clavate setae (fig. 14D); pretarsal claws simple (untoothed), pulvilli either minute or lost. Wings are very faint, obscuring the venation; no macrotrichia occur on the wing membrane. Male genitalia well preserved: tergite 9 (epandrium) large, shieldlike; gonocoxite large; gonostylus articulating with (not fused to) gonocoxite, bare, flattened and hatchetlike, without discernable apical peg/tooth; pair of inner lobes present, bare; anal point absent (fig. 14A, B).

Chironomidae have a rich fossil record, partly because the larvae are aquatic and semi-aquatic and both adults and larvae are readily fossilized in lacustrine sediments. The oldest Chironomidae are Triassic, and they are frequently among the most abundant and diverse winged insects in many deposits of amber, such as Eocene Baltic amber and Late Cretaceous ambers from western Canada, New Jersey, and Siberia. The fossil record has been reviewed by Evenhuis (1994). Critical study relies on various microscopic features, and most of the described fossils, done decades to a century ago, require re-description based on modern standards. The male genitalia of the Chickaloon fossil appear most similar to those in the large, widespread subfamily Tanypodinae.

HYMENOPTERA
FORMICIDAE (ANTS)

Figures 9A–C

AMNH WH-1: A single worker ant specimen, approximately 1.7 mm total body length (excluding antennae), attributable to the subfamily Formicinae. The acidopore, a primary diagnostic feature of formicine ants, appears faintly visible as a circular opening at the terminus of the abdomen. The petiole—a waistlike segment separating the trunk and gaster—is conspicuously scale shaped, with its dorsal margin reaching the same approximate height as the propodeum, a syndrome found in multiple extant and fossil formicine genera. Specimen WH-1 is heavily desiccated and partially disarticulated, making precise placement difficult. Nevertheless, the specimen clearly does not fit into any currently described genus of formicine, in particular due to its widely spaced mandibular dentition and shortened antennal scape (figs. 9B, C). The isolated antenna of another ant specimen, in piece GC-A4 (fig. 14E), has different segmental proportions than the formicine above, indicating the existence of another ant species in this amber. Very little can be determined taxonomically on the basis of an antenna.

The subfamily Formicinae is presently distributed worldwide, and fossils are similarly cosmopolitan. In total, 196 fossil formicine species are described, comprising 43 genera from 44 localities across North America, Europe, Asia, and New Zealand (Barden, 2017). Potentially a result of high sampling bias (nearly 13,000 ant inclusions were utilized in a recent analysis of ant species richness [Penney and Preziosi, 2014]), nearly 40 formicine species are described from Baltic amber, the greatest of any deposit. The Chickaloon amber species has not yet been formally described, however, it may represent a stem relative of the primarily Palearctic and Nearctic tribe Formicini or the cosmopolitan tribe Lasiini, based on current understanding of relationships (e.g., Lapolla et al., 2010; Ward et al., 2016)—both represented in the fossil record, including in Baltic amber. This preliminary diagnosis is based on the large circular propodeal spiracle, gradually sloping mesonotum, 5:4 palpomere formula, and mandibular shape. Interestingly, this new specimen is contemporaneous with formicine ants described from Fushun amber (Hong, 2002), making it, along with its counterparts in Asia, the oldest formicines known following *Kyromyrma neffi* in Turonian-aged New Jersey amber (Grimaldi and Agosti, 2000). This is a valuable window into ant evolution as the Fushun amber holotypes have since been lost. Slightly younger ants (Dolichoderinae, Myrmecinae, Formicinae, and Myrmeciinae) are reported in mid to Late Eocene shales and Hat Creek amber from British Columbia (Archibald et al., 2018). It should be noted that the identification of *Technomyrmex* (Dolichoderinae) in Poinar et al. (1999) was changed to Formicinae incertae sedis in Archibald et al. (2018).

CONCLUSIONS

LATE PALEOCENE–EARLY EOCENE AMBER RECORD

The Late Paleocene Chickaloon amber fauna reported here joins only a handful of others from near the Paleocene/Eocene (P/E) boundary (table 2). While Late Paleocene amber from

Table 2. Late Paleocene and Early Eocene amber records (see fig. 15).

| Locality | Age | Inclusions? | Selected References |
|----------------------|-----------------|-------------|------------------------|
| Le Quesnoy, France | Paleo/Eocene | Y | Nel et al., 2004 |
| Douzens, France | Early Eocene | N | Breton et al., 1999 |
| Cambay Shale, India | Early Eocene | Y | Rust et al., 2010 |
| Lissini Mts, Italy | Early Eocene | N | Trevisani et al., 2005 |
| Fushun, China | Early Eocene(?) | Y | Wang et al., 2014 |
| Hat Creek BC, Canada | Early Eocene | Y | Poinar et al., 1999 |
| Hanna Basin, Wyoming | Paleocene | N | Grimaldi et al., 2000 |

Ellesmere Island has been reported (Anderson and LePage, 1995; Grimaldi, 1996), it is highly oxidized, opaque and friable, thus no inclusions are known from this amber (D.A.G., personal obs.). The Chickaloon is the only such Paleogene deposit yet known that has yielded biological remains from high northern latitudes (fig. 15).

It will be very interesting eventually to compare Chickaloon taxa with taxa in slightly younger amber from Hat Creek, British Columbia (Poinar et al., 1999; Archibald et al., 2018), particularly groups like ants, where extant distributions are well sampled and relationships well studied. Hat Creek amber is one of eight deposits in the Paleogene Okanagan Highlands series, all other deposits consisting of lacustrine shales between 49° and 55° N in British Columbia and Washington state (Archibald et al., 2018). Some of the lacustrine deposits have been dated as Early Eocene (Ypresian). Hat Creek amber lies above a thick fluvio-lacustrine sequence of the Eocene Kamploops Group (Legun, 1996), the latter placed as Late Eocene by Read (1990) based on palynology, although Poinar et al. (1999) indicate Early Eocene, without explanation. Interestingly, a dominant plant of the Hat Creek coal is also *Metasequoia* (Goodarzi and Gentzis, 1987), as it is for the Chickaloon amber outcrops. Poinar et al. (1999) attributed the source tree of Hat Creek amber as Araucariaceae near *Agathis*, based on unpublished NMR spectra, despite the fact that definitive araucarian fossils do not occur in the northern hemisphere. Like the Chickaloon amber, Hat Creek amber also contains remains of roaches, thrips, beetle larvae, bryophytes, and ants (Poinar et al., 1999; Archibald et al., 2018).

Other amber deposits from the Pacific coast of North America that are approximately contemporaneous with the Hat Creek amber are from the Tiger Mountain Formation in Washington state, and amber near Coalmont, British Columbia (Mustoe, 1985). Both are dated paleobotanically to approximately the mid-Eocene, and the infrared spectrum of at least the Tiger Mountain amber corresponds to *Metasequoia* (Mustoe, 1985). Neither the Tiger Mountain nor the Coalmont amber deposits have yielded insects, however. Tiger Mountain amber is dark red, very brittle, and highly fractured (physical characteristics often termed “highly mature” by organic geochemists), and occurs in small blebs of a centimeter or less in diameter (D.A.G., personal obs.). The primary significance of these amber deposits is that it implicates *Metasequoia* as a likely source tree for amber along much of the northwestern coast of North America during the Paleogene. This needs to be rigorously tested, ideally using molecular comparisons between amber samples dispersed in sediments and in situ within fossil wood that can be anatomically identified.

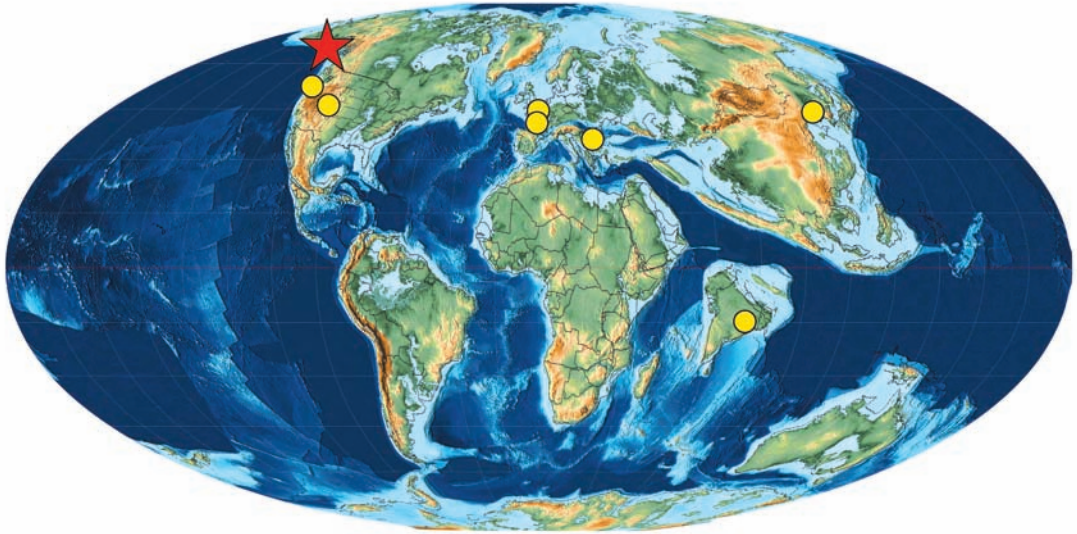


FIG. 15. Paleocene (Danian and Thanetian; 55.8 Ma) global paleogeography (Scotese, 2014) with Late Paleocene and Early Eocene amber localities (yellow dots; see table 2). Chickaloon amber at red star.

TAPHONOMIC BIAS

The most striking pattern of the Chickaloon amber arthropods is the small body size of completely encapsulated specimens, a mean of 0.75 mm body length, ranging from 0.28 to 1.66 mm (the spread of appendages was not measured, nor were fragmentary specimens) ($N = 14$ specimens). There are several explanations for this. One relates to the fact that the Chickaloon amber was formed around the time of the PETM. Mammals (Gingerich, 2003) and arthropod burrows (Smith et al., 2009) from the Paleocene-Eocene (P-E) boundary in the Bighorn Basin of eastern Wyoming have excellent stratigraphic resolution and radiometric age constraints, and both show rather dramatic dwarfing at the PETM. In the case of mammals, there is an approximate average 40% reduction in body size at this time interval, followed by extensive and sustained faunal turnover of taxa (Gingerich, 2003). Hot, dry conditions presumably greatly reduced plant productivity, and thus forage. However, this was a transient situation, of approximately 86,000 years duration for mammals (Gingerich, 2003), and this level of time control for Chickaloon amber has not been established, nor is there likely to be a stratigraphic sequence of the amber that straddles the PETM, which is necessary for statistically establishing a pattern.

A more parsimonious explanation for the small size of Chickaloon amber arthropods is taphonomy. Less than 1% of the amber by mass was formed in blebs of a centimeter or more in diameter. This greatly constrains the size of inclusions that become entrapped. In fact, there is a striking bias toward taxa that do not have wings (i.e., arachnids: mites, pseudoscorpions, spiders) and developmental stages or castes that have not developed wings (nymphal thrips, Heteroptera, aphids, roaches, larval dermestid beetle, worker ant). The only winged adults are a partial caddisfly (Trichoptera) and a complete male midge (Chironomidae). This strongly

indicates capture of a surface-dwelling fauna. The abundance of lenticular, blisterlike pieces indicates that much of the amber was formed subcortically. Perhaps small arthropods that could maneuver within or under tight spaces of the bark were particularly susceptible to entrapment. It is interesting to note that of the four families/family groups of Hymenoptera identified from Hat Creek amber (Archibald et al., 2018) (ants being one of the families), species in three of the groups are commonly very small, ≤ 1.5 mm body length (i.e., Megaspilidae, Mymarommatidae, and Chalcidoidea). This suggests that preservation in Hat Creek amber is likewise biased toward small species of arthropods.

BIOGEOGRAPHY

Some insect taxa from the more southerly Eocene deposits of the Okanagan Highlands in British Columbia preserve evidence of geographic extinctions. Perhaps the most dramatic examples include *Eomerope* scorpionflies (Mecoptera: Eomeropidae), which presently exist only in Chile; they also occur in Eocene shales from Russia and Florissant, Colorado (Archibald and Rasnitsyn, 2018). Myrmecine (bulldog) ants presently occur only in Australia, but their remains are found in Eocene shales from British Columbia (Archibald et al., 2006), as well as Denmark (Rust and Andersen, 1999) and eastern Russia (Dlussky et al., 2015). Likewise, there are many insect taxa in Eocene Baltic amber whose closest living relatives are in the southern hemisphere (e.g., Ander, 1942; Hennig, 1964; Engel and Grimaldi, 2004). For the Chickaloon amber the most obvious such example involves the roaches (Blattodea), which today naturally occur no farther north than southernmost Canada, ca. 50° N (Vickery and McKevan, 1985; Atkinson et al., 1991). The remaining Chickaloon amber arthropods are either nymphs or poorly preserved specimens, which preclude identification to taxonomic levels most meaningful for biogeography. The formicine ant specimen, which possibly can yield further character information, holds the most promise.

The results presented here indicate that intensive excavation of the Chickaloon amber is likely to yield further inclusions that will be informative about high-latitude life during one of the most fascinating time periods of the Cenozoic.

ACKNOWLEDGMENTS

D.S. and C.J.W. are grateful for generous funding through the Keck Geology Consortium (NSF-REU 0648782 and NSF-REU1062720), and the National Geographic Society Committee for Research and Exploration Grant #9109-12, Lafayette College and Franklin & Marshall College. Field and laboratory assistance at Lafayette College was provided by G.R. Loope, B.J. Walker, J. Neff, T. Schuetz, L. Curtin, B. O'Connell, A. Brannick, J. Lerback, L. Westley, K. Trostle, A. LeComte, and M. Reynolds. Ann Pasch (University of Alaska, Anchorage) collected some of the initial amber specimens now at the AMNH (labelled WH specimens). We are grateful for expert feedback from Cheryl Hiyashi (AMNH), on the structure of the silk webbing, and to Alexander Schmidt (University of Goettingen), Elina Kettunen (University of

Helsinki), and Natalie Cleavitt (Cornell University), regarding the plant and fungal inclusions. Reviews by Michael S. Engel (University of Kansas) and Enrique Peñalver (Museo Geominero, Madrid) substantially improved the manuscript.

REFERENCES

- Ander, K. 1942. Die Insektenfauna des baltischen Bernsteins nebst damit verknüpften zoogeographischen Problem. Lunds Universitets Årsskrift 38: 3–82.
- Anderson, K.B., and B.A. LePage. 1995. Analysis of fossil resins from Axel Heiburg Island, Canadian Arctic. In K.B. Anderson and J.C. Crelling (editors), *Amber, resinite, and fossil resins*: 170–192. Washington D.C.: American Chemical Society Symposium Series 617.
- Archibald, S.B., and A.P. Rasnitsyn. 2018. Two new species of fossil *Eomerope* (Mecoptera: Eomeropidae) from the Ypresian Okanagan Highlands, far-western North America, and Eocene Holarctic dispersal of the genus. *Canadian Entomologist* 150 (3): 393–403.
- Archibald, S.B., S.D. Cover, and C.S. Moreau. 2006. Bulldog ants of the Eocene Okanagan Highlands (British Columbia, Canada and Washington State, USA). *Canadian Journal of Earth Sciences* 42: 119–136.
- Archibald, S.B., A.P. Rasnitsyn, D.J. Brothers, and R.W. Mathewes. 2018. Modernisation of the Hymenoptera: ants, bees, wasps, and sawflies of the early Eocene Okanagan Highlands of western North America. *Canadian Entomologist* 150 (2): 205–257.
- Atkinson, T.H., P.G. Koehler, and R.S. Patterson. 1991. Catalog and atlas of the cockroaches (Dictyoptera) of North America north of Mexico. *Miscellaneous Publications of the Entomological Society of America* 78: 1–86.
- Bains, S.R., M. Corfield, and R.D. Norris. 1999. Mechanisms of climate warming at the end of the Paleocene. *Science* 285: 724–727.
- Barden, P. 2017. Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. *Myrmecological News* 24: 1–30.
- Bell, N.E., and P.V. York. 2007. *Vetioplanaxis pyrrhobryoides*, a new fossil moss genus and species from Middle Cretaceous Burmese amber. *Bryologist* 110: 514–520.
- Brannick, A., D. Sunderlin, C.J. Williams, and J. Lerback. 2012. Leaf damage intensity and diversity in the Paleogene Chickaloon and Arkose Ridge formations, south-central Alaska. *Geological Society of America Abstracts with Programs* 44 (2): 64.
- Breton, G., C. Gauthier, and D. Vizcaino. 1999. Land and freshwater microflora in a Sparnacian amber from the Corbières (South France): first observations. *Estudios del Museo de Ciencias Naturales de Alava* 14 (2): 161–166.
- Cai, C., J. Háva, and D. Huang. 2017. The earliest *Attagenus* species (Coleoptera: Dermestidae: Attageninae) from Upper Cretaceous Burmese amber. *Cretaceous Research* 72: 95–99.
- Deng, C., A. Ślipiński, D. Ren, and H. Pang. 2017. The oldest dermestid beetle from the Middle Jurassic of China (Coleoptera: Dermestidae). *Annales Zoologici* 67: 109–112.
- Dlussky, G.M., A.P. Rasnitsyn, and K.S. Perfilieva. 2015. The ants (Hymenoptera: Formicidae) of Bol'shaya Svetlovodnaya (Late Eocene of Sikhotealin, Russian Far East). *Caucasian Entomological Bulletin* 11: 131–152.
- Dunlop, J.A., D. Penney, and D. Jekel. 2018. A summary list of fossil spiders and their relatives. The world spider catalog. Natural History Museum Bern. Online resource (<http://wsc.nmbe.ch>), version 19.0, accessed on 10 March 2018. [doi: 10.24436/2]

- Eberle, J.J., and D.R. Greenwood. 2012. Life at the top of the greenhouse Eocene world – a review of the Eocene flora and vertebrate fauna from Canada's High Arctic. *Bulletin of the Geological Society of America* 124: 3–23.
- Engel, M.S., and D.A. Grimaldi. 2004. A new rock crawler in Baltic amber, with comments on the order (Mantophasmatodea: Mantophasmatidae). *American Museum Novitates* 3431: 1–11.
- Essig, E.O. 1938. Family Aphididae. In F.M. Carpenter et al. (editors), *Insects and arachnids from Canadian amber*: 7–62. University of Toronto Studies, Geological Series 40 (1937).
- Evenhuis, N.L. 1994. *Catalogue of the fossil flies of the world (Insecta: Diptera)*. Leiden: Backhuys Publishers.
- Flores, R.M., and G.D. Stricker. 1993. Early Cenozoic depositional systems, Wishbone Hill District, Matanuska Coal Field, Alaska. *Geologic Studies in Alaska by the U.S. Geological Survey: U.S. Geological Survey Bulletin* 2068: 101–117.
- Frahm, J.P., and A.E. Newton. 2005. A new contribution to the moss flora of Dominican amber. *Bryologist* 108: 526–536.
- Gingerich, P.D. 2003. Mammalian responses to climate change at the Paleocene-Eocene boundary: Polecat Bench record in the northern Bighorn Basin, Wyoming. *Geological Society of America Special Paper* 369: 463–478.
- Girard, V., et al. 2009. Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from southwestern France. *Geodiversitas* 31: 153–162.
- Goodarzi, F., and T. Gentzis. 1987. Depositional setting determined by organic petrography of the Middle Eocene Hat Creek No. 2 Coal Deposit, British Columbia, Canada. *Bulletin of Canadian Petroleum Geologists* 35: 197–211.
- Grimaldi, D.A. 1996. *Amber: window to the past*. New York: Abrams/American Museum of Natural History.
- Grimaldi, D., and D. Agosti. 2000. A formicine in New Jersey Cretaceous amber (Hymenoptera: Formicidae) and early evolution of the ants. *Proceedings of the National Academy of Sciences of the United States of America* 97: 13678–13683.
- Grimaldi, D.A., and M.S. Engel. 2005. *Evolution of the insects*. New York: Cambridge University Press.
- Grimaldi, D. A., J.A. Lillegraven, T.W. Wampler, D. Bookwalter, and A. Shedrinsky. 2000. Amber from Upper Cretaceous through Paleocene strata of the Hanna Basin, Wyoming, with evidence for source and taphonomy of fossil resins. *Rocky Mountain Geology* 35 (2): 163–204.
- Grimaldi, D., A. Shmakov, and N. Fraser. 2004. Mesozoic thrips and early evolution of the order Thysanoptera (Insecta). *Journal of Paleontology* 78: 941–952.
- Harms, D., and J.A. Dunlop. 2017. The fossil history of pseudoscorpions (Arachnida: Pseudoscorpiones). *Mitteilungen aus dem Museum für Naturkunde in Berlin. Fossil Record* 20: 215–238.
- Háva, J., J. Prokop, and A. Herrmann. 2008. New fossil dermestid beetles (Coleoptera: Dermestidae) from the Baltic amber–III. *Acta Societatis Zoologicae Bohemicae* 17 (2007): 151–157.
- Hedenäs, L., J. Heinrichs, and A.R. Schmidt. 2014. Bryophytes of the Burmese amber forest: amending and expanding the circumscription of the Cretaceous moss genus *Vetiplanaxis*. *Review of Palaeobotany and Palynology* 209: 1–10.
- Heie, O.E., and E.M. Pike. 1992. New aphids in Cretaceous amber from Alberta (Insecta, Homoptera). *Canadian Entomologist* 124: 1027–1053.
- Heinrichs, J., L. Hedenäs, A. Schäfer-Verwimp, K. Feldberg, and A.R. Schmidt. 2014a. An in situ preserved moss community in Eocene Baltic amber. *Review of Palaeobotany and Palynology* 210: 113–118.

- Hennig, W. 1964. Die Dipteren-Familie Sciadoceridae im baltischen Bernstein (Diptera: Cyclorrhapha Aschiza). *Stuttgarter Beiträge zur Naturkunde* 127: 1–10.
- Hong, Y. 2002. *Amber insects of China*. Beijing: Beijing Scientific and Technological Publishing House.
- Hübers, M., and H. Kerp. 2012. Oldest known mosses discovered in Mississippian (late Visean) strata of Germany. *Geology* 40: 755–758.
- Hutchison, J.H., and A.D. Pasch. 2004. First record of a turtle (*Protochelydra*, Chelydridae, Testudines) from the Cenozoic of Alaska (Chickaloon Formation, Paleocene-Eocene). *PaleoBios* 24: 1–5.
- Ignatov, M.S., J. Heinrichs, A. Schäfer-Verwimp, and E.E. Perkovsky. 2016. The first record of a bryophyte in Upper Cretaceous amber from Taimyr, northern Siberia: *Taimyrobryum martynoviorum* gen. et sp. nov. (Bryopsida). *Cretaceous Research* 65: 25–31.
- Kania, I., and P. Wegierek. 2005. Two new species of alate aphids (Hemiptera: Aphidoidea) from Upper Cretaceous Canadian amber. *Polski Pismo Entomologiczne* 74: 277–286.
- Katz, M.E., D.K. Pak, G.R. Dickens, and K.G. Miller. 1999. The source and fate of massive carbon input during the latest Paleocene Thermal Maximum. *Science* 286: 1531–1533.
- Kettunen, E., et al. 2015. The enigmatic hyphomycete *Torula* sensu Caspary revisited. *Review of Palaeobotany and Palynology* 219: 183–193.
- Kirejtshuk, A.G., D. Azar, P. Tafforeau, R. Boistel, and V. Fernandez. 2009. New beetles of Polyphaga (Coleoptera, Polyphaga) from Lower Cretaceous Lebanese amber. *Denisia* 26: 119–130.
- Kiselyova, T., and J.V. McHugh. 2006. A phylogenetic study of Dermestidae (Coleoptera) based on larval morphology. *Systematic Entomology* 31: 469–507.
- Krivolutsky, D.A., and A.Y. Druk. 1986. Fossil oribatid mites. *Annual Review of Entomology* 31: 533–545.
- Labandeira, C.C., T.L. Phillips, and R.A. Norton. 1997. Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. *Palaios* 12: 319–353.
- Lapolla, J.S., S.G. Brady, and S.O. Shattuck. 2010. Phylogeny and taxonomy of the *Prenolepis* genus-group of ants (Hymenoptera: Formicidae). *Systematic Entomology* 35: 118–131.
- Larsson, S.G. 1978. Baltic amber – a paleobiological study. *Entomonograph* 1: 1–192.
- Legun, A. 1996. Amber in British Columbia. *British Columbia Geological Survey, Geological Fieldwork* 1996, Paper 1997-1: 333–338.
- Lomolino, M.V. 2000. Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* 27: 17–26.
- MacArthur, R.H., and E.O. Wilson. 1963. An equilibrium theory of insular biogeography. *Evolution* 17: 428–442.
- McInerney, F.A., and S.L. Wing. 2011. The Paleocene-Eocene Thermal Maximum: A perturbation of carbon cycle, climate, and biosphere with implications for the future. *Annual Review of Earth and Planetary Sciences* 39: 489–516.
- McKellar, R.C., and A.P. Wolfe. 2010. Canadian amber. Chapter 9. *In* D. Penney (editor), *Biodiversity of fossils in amber from the major world deposits*: 149–167. Manchester: Siri Scientific Press.
- Mustoe, G.E. 1985. Eocene amber from the Pacific coast of North America. *Bulletin of the Geological Society of America* 96: 1530–1536.
- Neff, J., J. Hagadorn, D. Sunderlin, and C.J. Williams. 2011. Sedimentology, paleoenvironment and paleoecology of a Late Paleocene high-latitude facies of the Cook Inlet region, Alaska. *United States Geological Survey Professional Paper* 389-A: A1–A29.
- Nel, A., G. De Ploëg, J. Milliet, J.J. Menier, and A. Waller. 2004. The French ambers: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin. *Geologica Acta* 2 (1): 3.

- Nel, P., E. Peñalver, D. Azar, G. Hodebert, and A. Nel. 2010. Modern thrips families Thripidae and Phlaeothripidae in Early Cretaceous amber (Insecta: Thysanoptera). *Annales de la Société Entomologique de France* 46: 154–163.
- Nel, P., A. R. Schmidt, C. Bässler, and A. Nel. 2011. Fossil thrips of the family Uzelothripidae suggest 53 million years of morphological and ecological stability. *Acta Palaeontologica Polonica* 58 (3): 609–614.
- Norton, R.A. 2000. First record of *Collohmanna* (*C. schusteri* n. sp.) and *Hermannia* (*H. sellnicki* n. sp.) from Baltic amber, with notes on Sellnick's genera of fossil oribatid mites (Acari: Oribatida). *Acarologia* 46 (1–2), 111–125.
- Norton, R.A., and V.M. Behan-Pelletier. 2009. Suborder Oribatida. In G.W. Krantz and D.E. Walter, A manual of acarology, 3rd ed.: 430–564. Lubbock, TX: Texas Tech University Press.
- Norton, R.A., P.M. Bonamo, J.D. Grierson, and W.A. Shear. 1988. Oribatid mite fossils from a terrestrial Devonian deposit near Gilboa, New York. *Journal of Paleontology* 62: 259–269.
- Nutting, W.L., and H.G. Spangler. 1969. The hastate setae of certain dermestid larvae: an entangling defense mechanism. *Annals of the Entomological Society of America* 62: 763–769.
- Peñalver, E., et al. 2017. Ticks parasitised feathered dinosaurs as revealed by Cretaceous amber assemblages. *Nature Communications* 8: 1924. [doi: 10.1038/s41467-017-01550]
- Penney, D. (editor). 2010. Biodiversity of fossils in amber from the major world deposits. Manchester: Siri Scientific Press.
- Penney, D., and R.F. Preziosi. 2014. Estimating fossil ant species richness in Eocene Baltic amber. *Acta Palaeontologica Polonica* 59: 927–929.
- Penney, D., C.P. Wheeler, and P.A. Selden. 2003. Resistance of spiders to Cretaceous–Tertiary extinction events. *Evolution* 57: 2599–2607.
- Peris, D., and J. Háva. 2016. New species from Late Cretaceous New Jersey amber and stasis in subfamily Attageninae (Insecta: Coleoptera: Dermestidae). *Journal of Paleontology* 90: 491–498.
- Perkovsky, E.E., V. Yu. Zosimovich, A.P. Vlaskin. 2010. Rovno amber. Chapter 7. In D. Penney (editor), Biodiversity of fossils in amber from the major world deposits: 116–136. Manchester: Siri Scientific Press.
- Pike, E.M. 1993. Amber taphonomy and collecting biases. *Palaos* 8: 411–419.
- Poinar, G., B. Archibald, and A. Brown. 1999. New amber deposit provides evidence of early Paleogene extinctions, paleoclimates, and past distributions. *Canadian Entomologist* 131: 171–177.
- Read, P.B. 1990. Cretaceous and Tertiary stratigraphy and industrial minerals, Hat Creek, Southern British Columbia. Ministry of Energy, Mines and Petroleum Resources, BCMEMPR Open File 1990–23. Online resource (<http://www.empr.gov.bc.ca/Mining/Geoscience/PublicationsCatalogue/Open-Files/1990/Pages/1990-23.aspx>).
- Richards, W.R. 1966. Systematics of fossil aphids from Canadian amber (Homoptera: Aphididae). *Canadian Entomologist* 98: 746–760.
- Rust, J., and N.M. Andersen. 1999. Giants ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae). *Zoological Journal of the Linnean Society* 125: 331–348.
- Rust, J., et al. 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.
- Saint Martin, J.-P., and S. Saint Martin. 2018. Exquisite preservation of a widespread filamentous microorganism in French Cretaceous ambers: Crucial for revising a controversial fossil. *Comptes Rendus Palevol* 17: 417–434.

- Schawaller, W., W.A. Shear, and P.M. Bonamo. 1991. The first Paleozoic pseudoscorpions (Arachnida, Pseudoscorpionida). *American Museum Novitates* 3009: 1–17.
- Schmidt, A.R., and U. Schäfer. 2005. *Leptotrichites resinatus* new genus and species: a fossil sheathed bacterium in alpine Cretaceous amber. *Journal of Paleontology* 79: 175–184.
- Schmidt, A.R., et al. 2014. Amber fossils of sooty moulds. *Review of Palaeobotany and Palynology* 200: 53–64.
- Scotese, C. 2014. Atlas of Paleogene paleogeographic maps (Mollweide projection), maps 8–15, vol. 1, The Cenozoic. Evanston, IL: PALEOMAP Project Atlas for ArcGIS.
- Selden, P.A., and D. Penney. 2010. Fossil spiders. *Biological Reviews* 85: 171–206.
- Selden, P.A., H.M. Anderson, and J.M. Anderson. 2009. A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from the Triassic Molteno Formation of South Africa. *African Invertebrates* 50: 105–116.
- Sidorchuk, E.A. 2013. A new technique for the preparation of small-sized amber samples with application to mites. *In* *Insect Evolution in an amberiferous and stone alphabet. Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber: 189–201*. Leiden: E.J. Brill.
- Sidorchuk, E.A., and R.A. Norton. 2010. Redescription of the fossil oribatid mite *Scutoribates perornatus*, with implications for systematics of Unduloribatidae (Acari: Oribatida). *Zootaxa* 2666: 45–67.
- Sidorchuk, E.A., and R.A. Norton. 2011. The fossil mite family Archaeorchestidae (Acari, Oribatida) II: redescription of *Plategeocranus sulcatus* and family-group relationships. *Zootaxa* 3051: 14–40.
- Smith, J.J., S.T. Hasiotis, M.J. Kraus, and D.T. Woody. 2009. Transient dwarfism of soil fauna during the Paleocene-Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences of the United States of America* 106: 17655–17660.
- Speranza, M., C. Ascaso, X. Delclòs, and E. Peñalver. 2015. Cretaceous mycelia preserving fungal polysaccharides: taphonomic and paleoecological potential of microorganisms preserved in fossil resins. *Geologica Acta* 13 (4): 363–385.
- Suan, G., et al. 2017. Subtropical climate conditions and mangrove growth in Arctic Siberia during the Early Eocene. *Geology* 45: 539–542.
- Sunderlin, D., G. Loope, N.E. Parker, and C.J. Williams. 2011. Paleoclimatic and paleoecological implications of a Paleocene-Eocene fossil leaf assemblage, Chickaloon Formation, Alaska. *Palaaios* 26: 335–345.
- Sunderlin, D., et al. 2014. Paleoenvironment and paleoecology of a late Paleocene high-latitude terrestrial succession, Arkose Ridge Formation at Box Canyon, southern Talkeetna Mountains, Alaska. *Palaeogeography, Palaeoclimatology, Palaeoecology* 401: 57–80.
- Trevisani, E., C.A. Papazzoni, E. Ragazzi, and G. Roghi. 2005. Early Eocene amber from the “Pesciara di Bolca” (Lessini Mountains, Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 223 (3–4): 260–274.
- Triplehorn, D.M., D.L. Turner, and C.W. Naeser. 1984. Radiometric age of the Chickaloon Formation of south-central Alaska: Location of the Paleocene-Eocene boundary. *Geological Society of America Bulletin* 95: 740–742.
- Trop, J.M., K.D. Ridgway, and T.L. Spell. 2003. Synorogenic sedimentation and forearc basin development along a transpressional plate boundary, Matanuska Valley–Talkeetna Mountains, southern Alaska. *In* V.B. Sisson, S. Roeske, and T.L. Pavlis (editors), *Geology of a transpressional orogen developed during ridge-trench interaction along the north Pacific margin*. Geological Society of America Special Paper 371: 89–118.

- Tuovila, H., et al. 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.
- Vickery, V.R., and D.K. McE. McKevan. 1985. The insects and arachnids of Canada, part 14. The grasshoppers, crickets and related insects of Canada and adjacent regions. Ulonata: Dermaptera, Cheleutoptera, Notoptera, Dictuoptera, Grylloptera, and Orthoptera. Agriculture Canada, Research Branch Publication 1777.
- Walker, B.J. 2009. Gastropod assemblages from the Tertiary Chickaloon Formation in southern Alaska. In A.P. deWet, S. Mertzman, K. Erb, and D. Kadyk (editors), *Proceedings of the 22nd Annual Keck Research Symposium in Geology* (Franklin & Marshall College, April 2009): 101–105. Lancaster, Pennsylvania: Consortium Colleges and the National Science Foundation.
- Wang, B., J. Rust, M.S. Engel, J. Szwedo, S. Dutta, A. Nel, Y. Fan, F. Meng, G. Shi, E. A. Jarzembowski, and T. Wappler. 2014. A diverse paleobiota in Early Eocene Fushun amber from China. *Current Biology* 24 (14): 1606–1610.
- Ward, P.S., B.B. Blaimer, and B.B. and B.L. Fisher. 2016. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex*. *Zootaxa* 4072: 343–357.
- Weitschat, W., and W. Wichard. 2010. Baltic amber. Chapter 6. In D. Penney (editor), *Biodiversity of fossils in amber from the major world deposits*: 80–115. Manchester: Siri Scientific Press.
- Williams, C.J., K.D. Trostle, and D. Sunderlin. 2010. Fossil wood in coal-forming environments of the late Paleocene-early Eocene Chickaloon Formation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295: 363–375.
- Wolfe, J.A., D. Hopkins, and E.B. Leopold. 1966. Tertiary stratigraphy and paleobotany of the Cook Inlet Region, Alaska. U.S. Geological Survey Professional Paper 398-A: 1–29.
- Zherikhin, V.V., and I.D. Sukatsheva. 1973. On the Cretaceous insect-bearing “ambers” (retinites) from North Siberia. In E.P. Narchuk (editor), *Problems in insect palaeontology, XXIV annual lectures in memory of N.A. Kholodkovskogo* 1–2 April 1971: 3–48. Leningrad: Nauka Press.

All issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from:

<http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

Ⓒ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).